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# Restoration of shortleaf pine (*Pinus echinata*)-hardwood ecosystems severely impacted by the southern pine beetle (*Dendroctonus frontalis*)

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ABSTRACT

In the Southern Appalachian Mountains of eastern USA, pine-hardwood ecosystems have been severely impacted by the interactions of past land use, fire exclusion, drought, and southern pine beetle (SPB, *Dendroctonus frontalis*). We examined the effects of restoration treatments: burn only (BURN); cut + burn on dry sites (DC + B); cut + burn on sub-mesic sites (MC + B); and reference sites (REF; no cutting or burning) on shortleaf pine-hardwood forests. We also evaluated the effectiveness of seeding native bluestem grasses. Structural (down wood, live and dead standing trees, shrubs, herbaceous layer) and functional (forest floor mass, C, and N; soil C, N, P, and cations; and soil solution N and P) attributes were measured before and the first and second growing seasons after treatment. We used path analysis to test our conceptual model that restoration treatments will have direct and indirect effects on these ecosystems. Total aboveground mass loss ranged from 24.33 Mg ha$^{-1}$ on the BURN to 74.44 Mg ha$^{-1}$ on the DC + B treatment; whereas, REF gained 13.68 Mg ha$^{-1}$ between pre-burn and post-burn. Only DC + B sites had increased soil $NO_3$–N, $NH_4$–N Ca, Mg, and $PO_4$–P and soil solution $NO_3$–N, $NH_4$–N, O–$PO_4$ for several months.

We found a significant increase in the density of oak species (*Quercus alba*, *Q. coccinea*, *Q. montana*, *Q. rubra*, and *Q. velutina*) on all burn treatments. However, oaks accounted for a smaller proportion of the total stem density than red maple, other tree species, and shrubs. The high densities of woody species other than oaks, coupled with the fast growth rates of some of these species, suggests that oaks will continue to be at a competitive disadvantage in these pine-hardwood communities through time, without further intervention. Pine regeneration was not improved on any of our burned sites with little to no recruitment of pines into the understory after two years and the pine saplings that were present before the burns were killed by fire on all sites. We found an increase in herbaceous layer cover and richness on all fire treatments. DC + B had higher bluestem grass cover than the other treatments, and it was the only treatment with increased bluestem grass cover between the first (2.96%, SE = 0.29) and second (6.88%, SE = 0.70) growing seasons. Our path model showed that fire severity explained a large proportion of the variation in overstory response; and fire severity and overstory response partially explained soil $NO_3$–N. These variables, directly and indirectly, explained 64% of the variation in soil solution $NO_3$–N at 30 cm soil depth (within the rooting zone for most plants). We found a good-fit path model for herbaceous layer response in the second growing season, where fire severity had direct effects on overstory and herbaceous layer responses and indirect effects on herbaceous layer response mediated through overstory response. Our path model explained 46% and 42% of the variation in herbaceous layer cover and species richness, respectively.

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## 1. Introduction

In the Southern Appalachian Mountains of eastern USA, pine-hardwood ecosystems were historically maintained in open pine-hardwood-grass savannas with frequent fire (DeVivo, 1991; Fesenmyer and Christensen, 2010). Interactions of past land use, fire exclusion, drought, and southern pine beetle [SPB; *Dendroctonus frontalis* Zimmerman (Coleoptera: Scolytidae)] have significantly impacted the structure and function of pine-hardwood ecosystems in this region (Brose et al., 2001). Over the past century, these ecosystems have been on a trajectory of increased pine overstory mortality, a lack of regeneration of all overstory species, loss of herbaceous layer herbs and grasses, and expansion of the evergreen shrub, mountain laurel (*Kalmia latifolia* L.), in the midstory layer (Elliott et al., 1999; Clinton and Vose, 2007). The most recent SPB outbreak (1999–2001) resulted in extensive pine mortality, more than 400,000 ha (an estimated economic loss of 1.0 billion USA

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dollars) were impacted (Nowak et al., 2008). The impacted area encompassed the southern Appalachians and Cumberland Plateau (North Carolina, South Carolina, Georgia, Kentucky, and Tennessee). While rainfall is usually abundant in this region, dry years, such as occurred from 1998 to 2002, are increasingly common (Coweeta Hydrologic Laboratory, http://www.coweeta.uga.edu). The co-occurrence of an increased fuel load, dry conditions, and increased densities of mountain homes in close proximity to federal land creates hazardous conditions that could result in catastrophic fires. Land managers need information on treatment options that will reduce heavy fuel accumulation from fallen and dying trees, particularly in the wildland–urban interface; restore forests impacted by SPB; and prevent the development of future stand conditions that attract SPB, promote heavy fuel accumulation, and increase fire risk.

Much of the mixed pine-hardwood forests in this region included some component of shortleaf pine (*Pinus echinata* Mill.) in the overstory. The shortleaf pine and shortleaf pine-hardwood forest types currently occupy about $3 \times 10^6$ ha in the central and eastern US (Moser et al., 2007). Many of the shortleaf pine-bluestem grass woodlands and savannas were historically maintained by surface fires resulting from anthropogenic ignitions about every 3–4 years (Guyette et al., 2002), or mixed severity fires, resulting in small stand-replacement fires about every 20 years (Guyette et al., 2006). These fire maintained ecosystems are characterized by a shortleaf pine-dominated overstory of large, well spaced trees with <20 $m^2\ ha^{-1}$ basal area and a herbaceous layer that includes native bluestem grasses, such as big bluestem (*Androgogon gerardii* Vitman) and little bluestem (*Schizachyrium scoparium* (Michx.) Nash) (Kabrick et al., 2007).

Previous research in pine-hardwood forests has shown that fire can be an effective and relatively inexpensive management tool for fuel load reduction and restoration of degraded ecosystems (Vose et al., 1999; Elliott and Vose, 2010). However, the combination of chronic stand degradation and acute conditions resulting from SPB infestation may require a new suite of treatments to restore the structural and functional attributes of shortleaf pine-bluestem grass communities. For example, prescribed fire alone may be insufficient to reduce the heavy fuel loads created by SPB mortality and provide the conditions necessary for successful re-establishment of shortleaf pine, and a diverse herbaceous layer that includes native bluestem grasses. One goal of restoration treatments on SPB-killed pine-hardwood stands is to establish forests that are more resistant to future SPB outbreaks (see Coulson and Klepzig (2011)). Forest restoration prescriptions must be designed to create ecosystem structures consistent with those that may have developed under a more frequent burning regime (Guyette et al., 2002, 2006) and, consequently, create stands that are more resistant to SPB. More open shortleaf pine stands will allow for more vigorous pine growth, larger crowns, and greater synthesis of oleoresins increasing resistance to pine beetle attack (Lorio and Hodges, 1985; Stroma et al., 2002; Duehl et al., 2011).

Restoration treatments that include cutting and burning will also affect pools and fluxes of water, carbon (C), and nutrients, characteristics referred to collectively as ecosystem function. Burning may increase plant available nutrients (Elliott et al., 2004; Knoepp et al., 2009), whereas, nutrient pools in forest floor and soil organic matter may be lost through volatilization and oxidation of C and nitrogen (N), leaching of N and exchangeable cations [i.e., calcium (Ca), magnesium (Mg), and potassium (K)], and erosion (Debano et al., 1998; Certini, 2005; Knoepp et al., 2005). However, changes in aboveground mass, C, and N (Vose and Swank, 1993; Wan et al., 2001) and soil C, N, and exchangeable cations (Tomkins et al., 1991; Wan et al., 2001; Knoepp et al., 2005; Nobles et al., 2009) following burning are variable and often temporary; and the magnitude of the response depends on fire severity (Wan et al., 2001; Knoepp et al., 2005; Hatten and Zabowski, 2009). Numerous studies have evaluated functional attributes of fire maintained ecosystems, including longleaf pine (*Pinus palustris* Mill) (see Jose et al. (2006), chaparral (e.g., Vourlitis and Pasquini, 2008), pitch pine (*Pinus rigida* L.)-hardwoods (e.g., Vose et al., 1999; Knoepp et al., 2004), oak savannas (e.g., Peterson et al., 2007; Hernández and Hobbie, 2008), and ponderosa pine (*Pinus ponderosa* L.) (e.g., Kaye et al., 2005; Selmants et al., 2008; Hatten and Zabowski, 2009; Sorensen et al., 2010), but only a few studies have evaluated functional attributes of shortleaf pine-bluestem ecosystems (Liechty et al., 2005; Ponder et al., 2009). One example, in the Missouri Ozarks, compared closed canopy shortleaf pine-hardwood stands (control) and shortleaf pine-bluestem restoration stands (Liechty et al., 2005), where the restoration treatment included an initial overstory and midstory felling, followed by prescribed fire at 3–4 year intervals for at least 17 years. The restoration treatment maintained an open canopy forest with overstory basal area of 14–16 $m^2\ ha^{-1}$. They found that N-mineralization, total N, C, Ca, and pH of the surface soil were higher in the restored stands than in the stands without restoration activities (Liechty et al., 2005).

We examined the effects of restoration methods (cutting SPB killed pines and thinning fire-intolerant hardwoods followed by prescribed fire (cut + burn); prescribed fire only (burn); and no treatment) on ecosystem structure and function in degraded shortleaf pine-hardwood forests heavily impacted by SPB induced tree mortality. We also evaluated the effectiveness of seeding bluestem grasses on these treatment sites as a means to accelerate ecosystem recovery. We hypothesized that these restoration treatments would: (1) result in differing fire severities, consequently producing a gradient in ecosystem responses with the highest severity on cut + burn treatments; and (2) restore these ecosystems to a shortleaf pine-bluestem grass community (i.e., more open savannas that are less susceptible to future SPB outbreaks and have lower wildfire risk). To answer these questions, we measured numerous structural attributes (down wood, live and dead standing trees, shrubs and tree saplings, herbaceous layer cover, as well as, species composition and diversity of all vegetative layers i.e., overstory, understory, and herbaceous layer) and functional attributes (forest floor mass, C, and N, soil C, N, phosphorus (P), and cations, and soil solution inorganic N and P) before and after the restoration treatments.

To address the complex ecological interactions and multiple controlling factors in our study, we constructed a conceptual model (Fig. 1) and tested it using path analysis, a form of structural

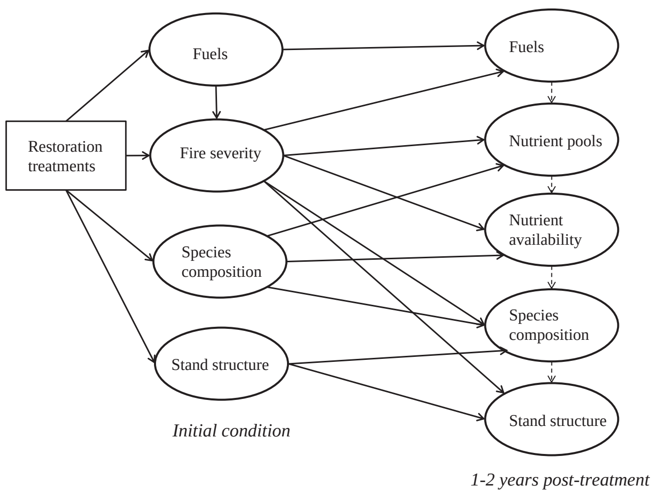


**Fig. 1.** Conceptual path model.

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equation modeling (Grace et al., 2010). Structural equation modeling (SEM) is an advanced multivariate statistical process used to construct theoretical concepts, test hypotheses, account for measurement errors, and consider both direct and indirect effects of variables on one another (Malaeb et al., 2000; Kline, 2005). We proposed that restoration treatments, such as cutting and burning, will have direct and indirect effects on ecosystem structure and function. Specifically, we hypothesized that restoration treatments will have direct effects on fuels, fire severity, species composition, and stand structure; fire severity will have direct and indirect effects on residual fuels, nutrient pools and availability, species composition and stand structure; and initial species composition will have direct effects on nutrient pools and availability, and residual species composition and structure (Fig. 1).

## 2. Methods

### 2.1. Site description

Our study encompassed a 60 $km^2$ area north and south of the Ocoee River (35°05′ to 35°09′N latitude, 84°37′ to 84°34′W longitude) within the Ocoee Ranger District, Cherokee National Forest in eastern, Tennessee, USA. Mixed stands with varying abundances of five pine species, Virginia (*Pinus virginiana* Mill.), shortleaf, pitch (*P. rigida* Mill.), table mountain (*Pinus pungens* Lamb.), and white (*Pinus strobus* L.), were severely impacted by the SPB outbreak in 1999–2001. Some of the dead pines were standing (snags), while many others had already fallen by 2005. We selected eight study sites, 5–6 ha in size, that were pine-hardwood ecosystems where SPB caused tree mortality was abundant and prescribed fire was a management alternative (http://www.fs.fed.us/r8/cherokee; Forest Management Plan, Cherokee National Forest). Six of the eight sites were dry with southerly to westerly aspects while the other two sites were sub-mesic (Table 1). Soils on dry sites were mapped as fine-loamy mesic Typic Hapludults. These soils are described as having A horizons ranging from 8 to 15 cm deep and a Bt layer at depths ranging from 130 to 200 cm. Soils on the sub-mesic sites were mapped as fine-loamy mesic Typic Hapludults or fine-loamy mesic Humic Dystrudepts. These soils are described as having an A horizon depth of 28 cm and a Bt or Bw layer at 50–100 cm (Newton and Moffitt, 2001). As expected, soil moisture was consistently higher on the sub-mesic sites than the dry sites over the course of this study (Table 1).

### 2.2. Experimental design and treatment descriptions

We used a Before–After/Control–Impact experimental design (BACI) (van Mantgem et al., 2001). Within the BACI design, we had two replicate sites for each of four stand restoration treatment categories: (1) burn only (BURN), (2) cut + burn on dry sites (DC + B), (3) cut + burn on sub-mesic sites (MC + B), and (4) reference sites (REF; areas with SPB tree mortality, but no cutting or burning) for a total of eight sites. In each site, we established four 20- × 20-m plots for a total of 32 plots. In the cut + burn treatments, all SPB killed pine trees, midstory saplings 5–15 cm DBH (diameter at breast height, 1.37 m height) of some hardwoods [red maple (*Acer rubrum* L.), blackgum (*Nyssa sylvatica* Marsh.), sourwood (*Oxydendrum arboretum* (L.) De Candolle), sweetgum (*Liquidambar styraciflua* L.)], and pines (Virginia and white pine) ⩽25 cm DBH were cut in August 2005 and left on site. The prescribed fires were conducted in March 2006 for all cut + burn and burn only treatment sites. The fire technique on all six sites was a backfire along the upper ridge, and then ignition of a headfire at the bottom of the slope. The prescribed burning occurred within conditions specified in the Prescribed Burning Plan for USDA Forest Service, Region 8 (http://www.fs.fed.us/r8/cherokee).

In May 2006, the first spring following the prescribed fires, native bluestem grasses were seeded on one site per treatment, including one REF site, to accelerate the establishment of these grasses. A 50/50 mix of little bluestem and big bluestem seeds was broadcast spread at 7.4 kg $ha^{-1}$ of each species, a total of 14.8 kg $ha^{-1}$ of pure live seeds (Sharp Brothers Seed, Clinton, MO).

### 2.3. Fire characterization

Fire intensity and fire severity were quantified on all plots. Air temperature (°C) at 30 cm aboveground was recorded every 1.5 s using high temperature stainless steel Type-K thermocouple probes connected to data loggers (Onset Computer Corp., Pocasset, MA). Three thermocouple probes were placed in each plot for a total of 12 probes per site. Temperature response was noted as the initial incline on the heat pulse curve from fire ignition to residual smoldering. Duration of the temperature response was calculated as the time between the start of the incline on the response curve to the point where temperatures fell below 45 °C. Based on analyses of the heat pulse curves, 45 °C was the average sustained temperature during the smoldering stage. We calculated an index of

**Table 1**
Site descriptions[a] for the eight treatment areas within the Ocoee Ranger District, Cherokee National Forest, eastern Tennessee.

| Site code | Treatment | Treatment code | Area (ha) | Latitude Longitude | Mid-slope elevation (m) | Average slope (%) | Aspect | Mean soil moisture[b] (%) | Previous burn |
|---|---|---|---|---|---|---|---|---|---|
| REF | None (reference) | REF | 3.2 | 35°5′2″ 84°39′2″ | 290 | 19 | S | 28.05 bc (0.62) | None |
| 525 | None (reference) | REF | 2.9 | 35°5′3″ 84°35′18″ | 335 | 16 | W | 29.78 bc (2.25) | None |
| 407 | Burn only | BURN | 4.6 | 35°9′13″ 84°36′32″ | 625 | 25 | W | 35.96 b (1.78) | Spring – 2001 |
| 526 | Burn only | BURN | 3.7 | 35°5′24″ 84°35′1″ | 310 | 37 | SW | 28.57 bc (2.82) | Spring – 2001 |
| 527 | Dry, cut + burn | DC + B | 4.9 | 35°5′41″ 84°35′1″ | 360 | 43 | W | 29.33 bc (0.94) | Spring – 2001 |
| 529 | Dry, cut + burn | DC + B | 4.1 | 35°5′42″ 84°35′4″ | 358 | 57 | Knoll | 25.82 c (1.60) | Spring – 2001 |
| 584 | Sub-mesic, cut + burn | MC + B | 2.7 | 35°7′1″ 84°33′22″ | 365 | 9 | Flat | 42.52 a (1.46) | Spring – 2000 |
| 585 | Sub-mesic, cut + burn | MC + B | 2.0 | 35°6′59″ 84°33′34″ | 370 | 22 | S | 45.21 a (1.09) | Spring – 2000 |

[a] All sites were delineated around patches of high pine mortality due to the SPB outbreak from 2001 to 2002.
[b] Mean soil moisture was based on measurements taken 2–3 times per year on each plot, then the four plots were averaged for a site mean, standard errors are in parentheses. Values followed by different letters are significantly different ($P < 0.05$) based on Ryan–Einot–Gabriel–Welsch multiple range test (PROC GLM, SAS, 2002-2003).

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fire severity using time integrated temperatures, the area under the temperature response curve was calculated by a simple summation (Kennard et al., 2005; Bova and Dickinson, 2008). Specifically, the cumulative heat pulse was summed at 1.5 s intervals over the period of time between initial response (rising limb) and 45 °C (falling limb) expressed in degree-hrs using the following equation:

$$\sum_{i=1}^{n}\left(\frac{1.5t_i}{3600}\right) \quad (1)$$

where, $t_i$ is the air temperature at time $i$ (initial response), and $n$ is the number of 1.5 s intervals along the curve from the initial response to the 45 °C threshold on the falling limb of the curve.

### 2.4. Aboveground woody biomass

All down and standing dead wood, as well as aboveground live biomass was measured before and after the burn treatments to estimate woody biomass response to restoration treatments. Biomass was estimated using measured diameter (see *Vegetation measurements* below) and allometric equations developed for woody species in the southern Appalachians (Boring and Swank, 1986; Martin et al., 1998; Elliott et al., 2002).

Small and large down wood were measured before (January 2006) and after the burn treatments (April–May 2006). Small down wood (<7.6 cm diameter) mass was estimated using the line transect method (Brown, 1974). We measured the diameter of all woody material <7.6 cm diameter that intercepted a 40 m line transect that crossed each 20- × 20-m plot. Large down wood (⩾7.6 cm diameter) was measured in a 4- × 20-m belt that transected each 20- × 20-m plot. Large down wood volume was estimated by measuring total length and circumference at 1.0 m intervals or at the plot edge if the log extended beyond the plot boundary. All down woody material was assigned a decay class of I–V (Vanderwel et al., 2006) and volume was converted to mass using specific gravity estimates by species and decay class for similar ecosystems in the southern Appalachians (see Hubbard et al. (2004)). We used the same procedures for sampling small and large down wood post-burn.

### 2.5. Forest floor biomass and nutrients

Forest floor was sampled in February 2006, before the burn treatments, and within two weeks after the burn treatments (March–April 2006). Procedures for estimating forest floor mass followed Vose and Swank (1993). Forest floor was sampled using a 0.3 × 0.3 m wooden frame. Five samples were collected within each 20- × 20-m plot, one in the center and one at each corner. Material was separated into two components: litter (Oi) and a combined fermentation and humus component (Oe + Oa). The post-burn forest floor quadrats, located immediately adjacent to the pre-burn quadrats, were sampled using the same procedures. Forest floor samples were dried at 60 °C, to a constant weight, and weighed to the nearest 0.1 g. All samples were ground to <1 mm, mixed thoroughly, and analyzed for total C and total N concentrations using a Perkin-Elmer 2400 CHN Elemental Analyzer (Norwalk, CT, USA). Lost-on-ignition (Nelson and Sommers, 1996) was used to determine the ash-free weight of the Oe + Oa layer. This procedure consisted of incinerating a 0.5 g sample of forest floor for 12 h in a muffle furnace at 450 °C and then calculating by weight difference the organic and mineral fractions of the sample. Estimates of N and C pools for each forest floor layer were made by multiplying N or C concentration by mass. We did not re-measure the REF treatment sites post-burn for forest floor mass; we assumed that forest floor mass would not have changed within the two week sampling period between pre-burn to post-burn collections on the burned sites.

### 2.6. Soil nutrients

We measured soil N transformations (N mineralization and nitrification) before (July and December 2005), and after burning in March and April (spring), July (summer) and November (winter) of 2006, and April (spring) of 2007. For each sample period, N-mineralization was determined in the surface 0–10 cm using the closed-core *in situ* incubation method (Knoepp and Swank, 1993). We randomly selected sample locations on 4 transects dissecting each 20- × 20-m plot. At each location two PVC cores (4.3 cm internal diameter) were driven 10 cm into the mineral soil, one core was removed to determine $NO_3$ and $NH_4$ concentrations at the time of collection ($t = 0$) and one core was left in place for a 28 day incubation period ($t = 1$). Within 1 h of collection, soils were mixed thoroughly and a subsample (approximately 10 g) of soil was added to a pre-weighed 125 ml polyethylene bottles containing 50 ml 2 M KCl. The bottles plus soil were kept cool until returning to the laboratory and then stored at 4 °C. Bottles plus soil were weighed to determine the actual weight of soil extracted. Soil plus KCl samples were shaken and allowed to settle overnight (refrigerated); 15 ml of the clear KCl was pipetted into a sample tube and the supernatant was analyzed for $NO_3$–N and $NH_4$–N on an Alpkem model 3590 autoanalyzer (Alpkem Corporation, College Station, TX) using alkaline phenol (USEPA, 1983a) and cadmium reduction (USEPA, 1983b) techniques, respectively. Remaining soil samples were moist sieved to <6 mm and a subsample (~20 g) was dried at 105 °C for >12 h to obtain oven-dry weight. All soil N data are reported on an oven dry weight basis. We used the gravimetric soil moisture content of the $t = 0$ soil samples to verify the difference between the dry sites and sub-mesic sites (Table 1).

Soil samples collected during the $t = 0$ N transformation sampling were air dried and used for chemical analyses. We conducted chemical analyses on soils collected before prescribed burning (December 2005), the first collection after burning (April 2006) and one year after burning (April 2007). Analyses included total C and total N, ortho-phosphate-phosphorus ($PO_4$–P), and exchangeable K, Ca, and Mg. Total C and N were determined by combustion as described above. Exchangeable cations (Ca, Mg, and K) were determined using 1 M $NH_4Cl$ extraction on a mechanical vacuum extractor, followed by analysis on a JY Ultima Inductively Coupled Plasma Spectrophotometer (Horiba Inc., Edison, NJ). Following the initial 12-h extraction excess $NH_4Cl$ was removed from the soil interstitial spaces with 95% EtOH. $NH_4$–N on the soil exchange sites was then extracted with 2 M KCl as a measure of effective soil cation exchange capacity (ECEC). We determined dilute double acid extractable $PO_4$ colorimetrically using ascorbic acid on a Perstorp Enviroflow 3500 ion chromatograph (Alpkem Corp., Wilsonville, OR) (Deal et al., 1996).

Falling-tension porous cup lysimeters were placed in the mineral soil (30 cm soil depth) to collect soil solution as an index of plant available nutrients. Additional lysimeters were placed in the lower B horizon (60 cm soil depth) as an index of nutrients leaving the plot. We collected soil solution samples bi-weekly beginning in January 2006 (three months prior to burn treatments) through April 2007 (one year following treatments). Two sets of lysimeters were installed in each 20- × 20-m plot of the eight sites. Each set included one lysimeter at 30 cm and one at 60 cm soil depth (a total of 128 lysimeters). Lysimeters were allowed to stabilize for approximately three months before water samples were collected for chemical analyses. During the stabilization period, lysimeter solutions were collected bi-weekly and analyzed for $NO_3$–N to insure a consistent pre-treatment concentration following installation before sample collection began. Samples were analyzed for $NO_3$–N, $NH_4$–N, and $PO_4$–P as described above.

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### 2.7. Vegetation measurements

All vascular plants were measured in each permanent plot using a nested plot design (overstory 400 $m^2$, understory 25 $m^2$, and herbaceous layer 4.0 $m^2$) following methods described in Elliott et al. (1999). All plots were sampled at the time of plot establishment (July 2005) before the cutting and burning treatments, and in July 2006 and 2007, the first and second growing seasons after treatments. Vegetation was measured by layer: the overstory layer included all trees $\geqslant$ 5.0 cm diameter at breast height (DBH, 1.37 m above ground) in the 20- × 20-m plot; the understory layer included all woody stems <5.0 cm DBH and $\geqslant$0.5 m height in the 5.0- × 5.0-m subplot; the herbaceous layer included a percent cover estimate for woody stems <0.5 m height and all herbaceous species in 4–1.0 $m^2$ quadrats per plot. In addition, woody stems <0.5 m height were counted in each 1.0- × 1.0-m quadrat. Trees with <0.5 m height were counted as seedlings regardless of the mode of reproduction (i.e., seedling or sprout origin).

Diameter of all live and dead overstory trees was measured to the nearest 0.1 cm and recorded by species in every plot. Live trees were tagged before the cutting so that mortality could be calculated after treatment. In the understory layer, basal diameter of trees and shrubs was measured to the nearest 0.1 cm and recorded by species in a 5.0- × 5.0-m subplot located in the northeast corner of each 20- × 20-m plot. Percent cover of herbaceous layer species was visually estimated using a scale that emphasizes intermediate accuracy (Gauch, 1982): 1% intervals from 1–5%, 5% intervals from 5–20%, and 10% intervals above 20%.

Grasses were inventoried in the first (August 2006) and second (August 2007) growing seasons after the seeding of bluestem grasses (*A. gerardii* and *S. scoparium*) in spring (May 2006). Belt transects (1.0- × 20-m) were used to estimate cover of seeded bluestem grasses and total graminoids (i.e., native grasses, sedges, and seeded bluestem grasses). Two transects were placed in each 20- × 20-m plot; transects were parallel to each other with 6 meters between transects. In every 1.0- × 1.0-m segment of a belt transect ($n$ = 20 segments per belt), percent cover was visually estimated using the same scale as the herbaceous layer. Grass transects were placed only in sites that were seeded with bluestem grasses.

### 2.8. Statistical analyses

We used one-way analysis of variance (PROC GLM, SAS, 2002–2003) to identify significant differences among sites in thermocouple temperature and fire characteristics. When significant differences were found, the Ryan–Einot–Gabriel–Welsch multiple range test was used to identify differences among sites and to control for Type I experiment-wise error.

Species diversity (alpha diversity) of the herbaceous layer was evaluated using species richness ($S$) and Shannon–Wiener's index of diversity ($H'$). Shannon–Wiener's index incorporates both species richness and the evenness of species abundance (Magurran, 2004). $H'$ was calculated at the plot level based on herbaceous layer percent cover ($H'_{cover}$). $S$ was calculated as the total number of species per plot (0.04 ha).

To analyze the data for the BACI experimental design, we used a mixed linear model with repeated measures (PROC MIXED, SAS, 2002–2003) to identify significant treatment-to-treatment differences in aboveground biomass, soil and soil solution chemistry, and vegetation. Separate statistical analyses were performed for each vegetative layer (i.e., overstory, understory, and herbaceous layer) and grass cover. In the repeated statement, the experimental unit ('subject') was the plot within each site ∗ treatment. We used the unstructured covariance option in the repeated statement because it produced the largest value for the Akaike's Information Criterion (AIC) and Schwarz' Bayesian Criterion (SBC) (Little et al., 1996). We evaluated the main effects of year and treatment and year ∗ treatment interactions. If overall $F$-tests were significant ($P \leqslant 0.05$) then least squares means (LS-means, Tukey–Kramer adjusted $t$-statistic) tests were used to evaluate significance among year (pre-burn 2005, post-burn 2006 and 2007) or date (multiple samples per year) and treatment (BURN, DC + B, MC + B, and REF) interactions.

We used path analysis, a form structural equation modeling (SEM), to evaluate the a priori conceptual model (Fig. 1). Our purpose in using path analysis was to gain insight into the relative importance of various processes that may influence restoration of structural and functional attributes by partitioning covariance among variables along pathways. Our analyses were exploratory in nature since the direct and indirect effects of fire on structural and functional attributes have not been examined in this way for southern Appalachian forests. Thus, we used path analysis with manifest (observed) variables to test the theoretical model presented in Fig. 1. Path models are most effective when the variable structure is parsimonious using a small number of correlated predictor variables that have notable effects on each response variable (Kline, 2005). Using numerous variables that are highly correlated with each other complicates the analysis and masks the influence of predictors on response variables. In path analysis, correlation produces a matrix that is the foundation for the regression equations in the path model. Thus, we used Pearson correlation coefficients (PROC CORR, SAS, 2002–2003) to estimate the strength and direction of the linear relationships between the potential predictors and the response variables. Response was calculated by simple subtraction, i.e., pre-treatment value minus post-treatment value for the attribute of interest and denoted with the change symbol $\Delta$ (Appendices B and C). The variables in the path diagrams were chosen based on their significant correlation with soil and soil solution nutrients, herbaceous layer response variables, and each other. All analyses were performed on the variance covariance matrix using PROC CALIS (SAS, 2002–2003). Indices of goodness of fit were used to select the models that best fit the data. The chi-square statistic provides a test of the null hypothesis that the covariance matrix has the specified model structure. A large $P$-value means that you cannot reject the null hypothesis of a good model fit (Hatcher, 1994; Kline, 2005). The comparative fit index (CFI), normed fit index (NFI), and non-normed fit index (NNFI) provide additional goodness of fit tests. The CFI and NNFI are variations on the NFI that have been shown to be less biased with small sample numbers (Bentler, 1989). Values on the CFI, NFI, and NNFI over 0.9 indicate an acceptable fit between model and data (Hatcher, 1994). We also examined the normalized residual matrix for all models, and selected the model as a good fit if all values in the matrix were less than 1 (Hatcher, 1994).

## 3. Results

### 3.1. Fire characteristics

All prescribed fire treatments resulted in moderate to high intensity burns (Table 2). All thermocouples recorded a rapid rise to the maximum temperature achieved that dropped off quickly and was followed by a prolonged slow cooling as fuels smoldered. Average maximum thermocouple temperatures at 30 cm aboveground ranged from 132 to 788 °C. Both DC + B sites had significantly higher average maximum temperatures than the other sites (Table 2). Duration of the temperature response was nearly twice as long on DC + B, lasting for more than 30 min. Temperature responses on the other sites lasted less than 20 min. Fire severity, measured as degree-hr, the integration of flame temperature and duration, was also twice as high on the DC + B sites compared to other sites (Table 2).

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**Table 2**
Fire characteristics for each of the six prescribed burn sites, all sites were burned in March, 2006. The three burn treatments were: burn only (BURN); dry, cut + burn (DC + B); and sub-mesic, cut + burn (MC + B). The fire prescription was site preparation burns with high intensity and moderate severity to reduce fuel loads. Values presented are site means or ranges with standard errors in parentheses.

| Treatment | Site | Average maximum temperature (°C) @ 30 cm aboveground | Duration[a] (minutes) | Degree-hr[b] | Peak temperature[c] range (°C) |
|---|---|---|---|---|---|
| BURN | 407 | 270.2 (43.6) c | 10.02 (1.91) b | 18.72 (5.51) c | 136–678 |
| | 526 | 558.5 (81.1) b | 18.08 (2.59) ab | 36.35 (3.56) b | 323–747 |
| DC + B | 527 | 771.9 (80.6) a | 32.83 (4.57) a | 67.59 (10.38) a | 530–880 |
| | 529 | 477.3 (107.4) ab | 27.26 (6.35) ab | 47.48 (10.92) ab | 294–890 |
| MC + B | 584 | 153.7 (43.9) c | 14.97 (6.34) ab | 13.87 (5.92) c | 27–432 |
| | 585 | 132.0 (42.6) c | 9.41 (2.89) b | 9.00 (4.03) c | 32–230 |

Values followed by different letters are significantly different ($P < 0.05$) based on Ryan–Einot–Gabriel–Welsch multiple range test (PROC GLM, SAS 2002–2003).
[a] Duration of the temperature response was calculated as the difference in time between the start of the incline on response curve to the end where curve fell below 45 °C.
[b] Degree-hr was calculated from integrating area below the temperature response curve.
[c] Average of the peak temperature recorded for each sensor per site ($n = 6$). Range in the maximum temperatures recorded for the six sensors per site.

### 3.2. Aboveground biomass and forest floor mass, carbon, and nutrients

All prescribed burn treatments resulted in the loss of a significant amount of total and component aboveground mass (Tables 3 and 4). Total aboveground mass loss ranged from 24.33 Mg ha$^{-1}$ on the BURN to 74.44 Mg ha$^{-1}$ on the DC + B treatment; whereas, the REF sites gained 13.68 Mg ha$^{-1}$ between 2005 and 2006 (Table 4). DC + B had significantly less live tree biomass, than the other treatments ($t_{1,14} = -2.94$, adjusted $P = 0.032$ for BURN; $t_{1,14} = -4.24$, adjusted $P = 0.001$ for MC + B, and $t_{1,14} = -5.71$, adjusted $P < 0.0001$ for REF). BURN and MC + B did not differ significantly ($t_{1,14} = -1.41$, adjusted $P = 0.506$).

Burning resulted in a large loss of forest floor mass (Tables 3 and 4); 94–100% of the Oi layer and 18–39% of the Oe + Oa layer (Table 4). Although Oi mass was significantly reduced on all burn treatments (BURN, $t_{1,14} = 12.24$, adjusted $P < 0.0001$; DC + B, $t_{1,14} = 12.69$, adjusted $P < 0.0001$; and MC + B, $t_{1,14} = 14.09$, adjusted $P < 0.0001$), post-burn Oi mass loss did not differ among burn treatments (Table 4). Oe + Oa mass was significantly reduced on BURN ($t_{1,14} = 3.62$, adjusted $P = 0.0221$) and DC + B ($t_{1,14} = 6.35$, adjusted $P < 0.0001$), but no significant reduction was detected on MC + B ($t_{1,14} = 1.23$, adjusted $P = 0.9150$). Oe + Oa mass was lower on MC + B than BURN ($t_{1,14} = -3.99$, adjusted $P = 0.0089$) and DC + B ($t_{1,14} = -5.44$, adjusted $P = 0.0002$) before the burn, but Oe + Oa mass did not differ among burn treatments after burning (Table 4). The reduction in total forest floor (Oi + Oe + Oa combined) mass was 29%, 42%, and 27% for BURN, DC + B and MC + B, respectively.

We did not have enough Oi layer remaining on the burned sites for post-treatment nutrient concentration analysis so evaluation of post-burn forest floor nutrient responses are limited to the Oe + Oa layer. Oe + Oa C concentrations were significantly lower on all burned treatments after the fire (BURN, $t_{1,14} = 5.94$, adjusted $P < 0.0001$; DC + B, $t_{1,14} = 5.61$, adjusted $P = 0.0001$; and MC + B, $t_{1,14} = 3.73$, adjusted $P = 0.0168$) (Tables 3 and 4); there were no differences among burn treatments. Oe + Oa N concentration was not changed on any treatment after the burn, and there were no differences among burn treatments. Pre-treatment Oe + Oa Ca concentrations were significantly different among treatments. MC + B had greater Oe + Oa Ca than the other treatments (BURN, $t_{1,14} = 4.92$, adjusted $P = 0.0002$; DC + B, $t_{1,14} = 7.03$, adjusted $P < 0.0001$; and REF, $t_{1,14} = 3.25$, adjusted $P = 0.0150$). Oe + Oa Ca concentrations did not change on any treatments after burning (Tables 3 and 4). Patterns were similar for Oe + Oa K, Mg, and P concentrations with no significant changes on any of the treatments after burning (Table 4).

### 3.3. Soil and soil solution chemistry

Repeated measures analysis of variance showed that total soil C differed significantly among treatments after burning (Table 3); whereas we did not detect a significant difference in total soil N. After the burns, surface soils in DC + B had significantly lower total C concentrations than MC + B ($t_{1,14} = -4.94$, adjusted $P = 0.0007$ for 2006; and $t_{1,14} = -4.37$, adjusted $P = 0.0034$ for 2007) and REF ($t_{1,14} = -1.98$, adjusted $P = 0.0573$ for 2006) (Fig. 2a). Before burning, ECEC, base saturation, and soil cation concentrations were higher in MC + B than the other treatments (Fig. 2c–e). Soil Ca was significantly greater in MC + B than BURN ($t_{1,14} = -4.09$, adjusted $P = 0.0069$), DC + B ($t_{1,14} = -5.29$, adjusted $P = 0.0003$), and REF ($t_{1,14} = 3.83$, adjusted $P = 0.0139$). Soil Mg was greater in MC + B than BURN ($t_{1,14} = 5.70$, adjusted $P < 0.0001$), DC + B ($t_{1,14} = 6.63$, adjusted $P < 0.0001$), and REF ($t_{1,14} = 5.70$, adjusted $P < 0.0001$) before burning. Soil exchangeable Ca and Mg, and extractable $PO_4$–P concentrations also differed significantly among treatments after burning (Table 3). Only DC + B soils responded to burning with increased Ca and $PO_4$–P concentrations (Fig. 2c and f). Soil ECEC, base saturation, and exchangeable K and Mg (Fig. 2d and e) did not change significantly due to burning, on any treatment.

Inorganic soil nitrogen, $NO_3$–N and $NH_4$–N, differed significantly among sampling dates and treatments (Table 3). During the growing season (July 2006) and one year (April 2007) after prescribed burning, DC + B had higher soil $NO_3$–N (Fig. 3a) and $NH_4$–N (Fig. 3b) concentrations than the other treatments; BURN had higher soil $NO_3$–N and $NH_4$–N than MC + B and REF. N-mineralization was higher in the growing season months than in the dormant season (Fig. 3c), but we did not detect any significant differences among treatments (Table 3).

Soil solution $NO_3$–N, $NH_4$–N, $PO_4$–P had significant date, treatment, and date ∗ treatment interaction effects (Table 3). The DC + B treatment had significantly higher concentrations than the other treatments for several months after the restoration treatments (Fig. 4a–f) at both soil depths.

### 3.4. Vegetation responses

Before restoration treatments were implemented, all sites including REF had a large proportion of dead trees (Table 5) due to SPB. After treatment, overstory mortality ranged from 42% to 92%, with the DC + B treatment incurring the greatest mortality. All burn treatments resulted in significantly lower live tree density and basal area when compared to REF (Table 5). On the BURN treatment, densities of blackgum, sourwood, white pine, and red maple were substantially reduced after treatment; chestnut oak (*Q. montana* Willd.) had the highest density, while densities of scarlet oak (*Q. coccinea* Münchh.) and shortleaf pine were unchanged (Appendix A). On the DC + B treatment, all overstory species were reduced substantially, including the oak species and shortleaf pine (Appendix A).

Before the restoration treatment, total understory layer density was high on all treatments including REF, ranging from 14,600 to

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**Table 3**
Mixed model repeated measures analysis of variance of responses to prescribed fire treatments. Probability (*P*) values associated with the variance components for year (pre-burn 2005, post-burn 2006 and 2007) or date (multiple samples per year), treatment (burn only; sub-mesic, cut + burn; dry, cut + burn; and reference sites). *P* values in bold type indicate a significant year or treatment effect, or year ∗ treatment interaction.

| | Date | Treatment | Date ∗ treatment |
|---|---|---|---|
| *Aboveground biomass* | | | |
| Forest floor[a] | | | |
| Oi mass | **$P < 0.0001$** | **$P = 0.0017$** | **$P < 0.0001$** |
| Oe + Oa mass | **$P < 0.0001$** | **$P = 0.0033$** | **$P = 0.0006$** |
| Oe + Oa C | **$P < 0.0001$** | $P = 0.2045$ | **$P = 0.0008$** |
| Oe + Oa N | $P = 0.1762$ | **$P = 0.0110$** | $P = 0.1888$ |
| Oe + Oa Ca | $P = 0.2591$ | **$P < 0.0001$** | $P = 0.8692$ |
| Small wood (< 7.5 cm diameter) | **$P = 0.0117$** | **$P = 0.0128$** | $P = 0.1076$ |
| Large wood (⩾ 7.5 cm diameter) | **$P = 0.0085$** | **$P = 0.0102$** | **$P = 0.0163$** |
| Live trees | **$P < 0.0001$** | $P = 0.1120$ | **$P < 0.0001$** |
| Dead trees | **$P < 0.0001$** | **$P = 0.0485$** | $P = 0.3133$ |
| Live shrubs and tree saplings < 5.0 cm dbh | **$P < 0.0001$** | $P = 0.2838$ | **$P = 0.0035$** |
| *Soil chemistry* | Year | Treatment | Year ∗ Treatment |
| Total C | $P = 0.7972$ | **$P < 0.0001$** | $P = 0.9462$ |
| Total N | $P = 0.8568$ | $P = 0.0718$ | $P = 0.9203$ |
| ECEC | $P = 0.2247$ | **$P < 0.0001$** | $P = 0.3874$ |
| Base saturation | $P = 0.4848$ | **$P = 0.0041$** | $P = 0.1816$ |
| Ca | $P = 0.5697$ | **$P < 0.0001$** | $P = 0.1927$ |
| Mg | $P = 0.5148$ | **$P < 0.0001$** | $P = 0.2138$ |
| K | $P = 0.1212$ | **$P < 0.0001$** | **$P = 0.0552$** |
| $PO_4$– | $P = 0.4536$ | **$P = 0.0478$** | $P = 0.0798$ |
| | Date | Treatment | Date ∗ Treatment |
| $NO_3$–N | $P = 0.0757$ | **$P = 0.0577$** | **$P = 0.0551$** |
| $NH_4$–N | $P = 0.2058$ | **$P = 0.0556$** | **$P = 0.0006$** |
| N–mineralization | **$P = 0.0077$** | $P = 0.7109$ | $P = 0.0214$ |
| *Soil solution chemistry* | | | |
| 30-cm depth | | | |
| $NO_3$–N | **$P < 0.0001$** | **$P < 0.0001$** | **$P < 0.0001$** |
| $NH_4$–N | **$P = 0.0023$** | **$P = 0.0204$** | **$P = 0.0002$** |
| $PO_4$–P | **$P = 0.0305$** | **$P = 0.0447$** | **$P = 0.0064$** |
| $NO_3$–N | **$P < 0.0001$** | **$P = 0.0128$** | **$P < 0.0001$** |
| $NH_4$–N | **$P = 0.0005$** | $P = 0.0670$ | **$P = 0.0003$** |
| $PO_4$–P | **$P = 0.0011$** | $P = 0.1084$ | **$P = 0.0007$** |
| Overstory | Year | Treatment | Year ∗ Treatment |
| Density | **$P < 0.0001$** | **$P < 0.0001$** | **$P < 0.0001$** |
| Basal area | **$P < 0.0001$** | $P = 0.1120$ | **$P < 0.0001$** |
| Density | **$P < 0.0001$** | **$P = 0.0007$** | **$P = 0.0002$** |
| Basal area | **$P < 0.0001$** | **$P = 0.0295$** | **$P = 0.0005$** |
| Herbaceous layer | | | |
| Percent cover | **$P < 0.0001$** | **$P = 0.0004$** | **$P < 0.0001$** |
| $H'_{cover}$ | **$P < 0.0001$** | **$P < 0.0001$** | **$P = 0.0075$** |
| S | **$P < 0.0001$** | **$P < 0.0001$** | **$P = 0.0008$** |
| All graminoids | **$P = 0.0333$** | **$P = 0.0009$** | $P = 0.1811$ |
| Bluestem grasses | **$P = 0.0069$** | **$P = 0.0005$** | **$P = 0.0013$** |

[a] For forest floor, date is pre-treatment (March 2005) and immediately post-treatment (within 2 weeks of the pretreatment collection).

32,200 stems $ha^{-1}$ (Table 6). By the second growing season after treatment, total understory layer density significantly increased on the BURN, DC + B, MC + B treatments (Table 3), whereas density did not change over time on the REF. All restoration treatment sites had significantly higher densities of oaks and shrubs following prescribed burning, but only DC + B and BURN also had higher numbers of red maple and other trees (Table 6). Oaks accounted for 5.8%, 5.4%, 4.2%, and 8.0% of the total density on the BURN, DC + B, MC + B, and REF, respectively. Whereas, average shrub densities ranged from 33.1% to 45.6% of the total density across all sites (Table 6). Densities of shortleaf pine, loblolly pine, and Virginia pine declined following prescribed burning for all burned treatments (Table 6).

We found significant year, treatment and year∗treatment interaction effects for herbaceous layer cover, $H'_{cover}$, and S (Table 3). By the second growing season after the prescribed fires, herbaceous layer cover significantly increased on all of the burned treatments (Table 3, Fig. 5a); REF did not change over time. Much of this increase in herbaceous layer cover on the burned treatments was due to herbaceous species increasing. Forbs and graminoids comprised 19.8%, 14.5%, 32.5%, and 49.1% of the total herbaceous layer cover before treatments and 39.4%, 34.9%, 41.6%, and 42.6% the second growing season after treatments for BURN, DC + B, MC + B and REF, respectively. S increased only on MC + B and DC + B (Fig. 5a) and $H'_{cover}$ increased only on DC + B (Fig. 5b).

We found significant year and treatment effects for total graminoids (i.e., native grasses, sedges, and seeded bluestem grasses) and significant year, treatment, and year ∗ treatment interaction effects for seeded bluestem grass cover (Table 3). In 2006, total graminoid cover was higher on MC + B than BURN ($t_{1,7} = 4.79$, adjusted $P = 0.0074$) and REF ($t_{1,7} = 5.05$, adjusted $P = 0.0048$), but there was no difference between MC + B and DC + B ($t_{1,7} = -3.02$, adjusted $P = 0.1307$) (Fig. 6). In 2007, total graminoid cover was higher on MC + B than BURN ($t_{1,7} = 3.74$, adjusted $P = 0.0410$) and REF ($t_{1,7} = 4.00$, adjusted $P = 0.0268$), but no significant differences between DC + B and BURN ($t_{1,7} = 2.75$, adjusted $P = 0.1972$) or REF

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**Table 4**
Aboveground biomass (Mg ha$^{-1}$) for forest floor litter (Oi) and humus (Oe + Oa), small and large down wood, standing live and dead trees, and live understory (shrubs and tree saplings <5.0 cm dbh) before (2005) and after (2006) the restoration treatments: burn only (Burn), dry cut + burn (DC + B), mesic cut + burn (MC + B), and reference (REF).

| | Burn | | | DC + B | | | MC + B | | | REF | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 2005 | 2006 | ±Δ | 2005 | 2006 | ±Δ | 2005 | 2006 | ±Δ | 2005 | 2006 | ±Δ |
| *Forest floor* | | | | | | | | | | | | |
| Litter (Oi) | 2.311 (0.203) | 0.081 (0.037) | −2.23 | 2.313 (0.246) | 0 | −2.31 | 2.730 (0.116) | 0.163 (0.087) | −2.57 | 2.358 (1.022) | – | nc |
| Humus (Oe + Oa) | 36.658 3.789) | 27.143 (5.766) | −9.06 | 43.255 (4.077) | 26.574 (4.279) | −16.68 | 18.499 (1.766) | 15.260 (2.053) | −3.24 | 24.342 (3.048) | – | nc |
| Oe + Oa C (%) | 45.47 (0.76) | 40.44 (1.05) | | 44.43 (0.44) | 39.68 (1.11) | | 45.92 (0.56) | 42.75 (0.55) | | 44.15 (1.30) | – | nc |
| Oe + Oa N (%) | 1.14 (0.04) | 1.26 (0.07) | | 1.18 (0.03) | 1.20 (0.03) | | 1.07 (0.04) | 1.06 (0.03) | | 1.02 (0.06) | – | nc |
| Oe + Oa Ca (%) | 0.49 (0.06) | 0.52 (0.05) | | 0.34 (0.03) | 0.37 (0.04) | | 0.82 (0.06) | 0.90 (0.08) | | 0.63 (0.07) | – | nc |
| Oe + Oa K (%) | 0.05 0.004) | 0.05 (0.003) | | 0.05 (0.004) | 0.06 (0.011) | | 0.07 (0.004) | 0.07 (0.005) | | 0.05 (0.002) | – | nc |
| Oe + Oa Mg (%) | 0.04 (0.003) | 0.04 (0.002) | | 0.03 (0.002) | 0.04 (0.002) | | 0.08 (0.006) | 0.09 (0.010) | | 0.05 (0.004) | – | nc |
| Oe + Oa P (%) | 0.06 (0.004) | 0.05 (0.002) | | 0.05 (0.007) | 0.06 (0.003) | | 0.06 (0.004) | 0.07 (0.002) | | 0.05 (0.004) | – | nc |
| *Small down wood (<7.5 cm diameter)*[a] | | | | | | | | | | | | |
| Pines | 3.267 (1.313) | 1.877 (0.295) | −1.39 | 3.464 (0.044) | 1.929 (0.301) | −1.54 | 3.208 (0.202) | 3.700 (0.536) | +0.49 | 4.025 (0.702) | – | nc |
| Hardwoods | 0.660 (0.062) | 1.183 (0.204) | +0.52 | 1.512 (0.143) | 0.519 (0.084) | −0.99 | 2.544 (1.027) | 1.833 (0.467) | −0.71 | 1.444 (0.232) | – | nc |
| All | 3.927 | 3.060 | −0.87 | 4.977 | 2.394 | −2.58 | 5.752 | 5.533 | −0.22 | 5.469 | – | nc |
| *Large down wood (⩾7.5 cm diameter)*[b] | | | | | | | | | | | | |
| Pines | 19.727 (8.112) | 16.604 (7.520) | −3.12 | 59.640 (14.340) | 25.219 (4.178) | −34.42 | 77.192 (13.773) | 60.798 (10.686) | −16.39 | 57.111 (10.193) | – | nc |
| Hardwoods | 4.068 (1.484) | 2.976 (1.505) | −1.09 | 7.800 (3.726) | 0.559 (0.392) | −7.24 | 4.435 (0.873) | 3.942 (0.980) | −0.49 | 0.439 (0.208) | – | nc |
| All | 23.795 | 19.580 | −4.21 | 67.440 | 25.778 | −41.66 | 81.627 | 64.740 | −16.89 | 57.276 | – | nc |
| *Standing live trees (⩾5.0 cm dbh)*[c] | | | | | | | | | | | | |
| Pines | 0.396 (0.120) | 0.086 (0.046) | −0.31 | 0.803 (0.252) | 0.032 (0.027) | −0.77 | 0.342 (0.138) | 0.281 (0.144) | −0.06 | 0.208 (0.083) | 0.194 (0.090) | −0.01 |
| Hardwoods | 62.492 (15.371) | 46.646 (18986) | −15.85 | 54.338 (9.996) | 9.514 (4.851) | −44.82 | 26.352 (4.647) | 28.140 (5.658) | +1.79 | 62.606 (12.152) | 74.790 (14.917) | +12.18 |
| All | 62.888 | 46.732 | −16.16 | 55.141 | 9.546 | −45.59 | 26.694 | 28.421 | +1.73 | 62.814 | 74.984 | +12.17 |
| *Standing dead trees*[c] | | | | | | | | | | | | |
| Pines | 1.371 (0.259) | 1.804 0.401) | −0.43 | 1.569 (0.454) | 1.346 (0.353) | −0.22 | 1.118 (0.254) | 0.563 0.134) | −0.55 | 1.959 (0.475) | 2.621 (0.711) | +0.66 |
| Hardwoods | 4.968 (3.100) | 15.848 (10.118) | +10.88 | 1.807 (0.795) | 36.720 (8.742) | +34.91 | 1.527 (0.412) | 9.877 (3.358) | +8.35 | 1.498 (0.712) | 0.918 (0.526) | −0.58 |
| All | 6.339 | 17.652 | +11.31 | 3.376 | 38.066 | +34.69 | 2.645 | 10.440 | +7.80 | 3.514 | 3.867 | +0.35 |
| *Live shrubs and tree saplings <5.0 cm dbh*[d] | | | | | | | | | | | | |
| | 7.991 (2.976) | 3.347 (0.872) | −4.64 | 2.643 (1.318) | 2.343 (0.637) | −0.30 | 13.380 (2.615) | 4.722 (1.129) | −8.66 | 5.699 1.967) | 6.858 (2.531) | +1.16 |
| *Total aboveground biomass* | | | | | | | | | | | | |
| | 143.450 | 117.595 | −25.86 | 179.146 | 104.701 | −74.44 | 151.327 | 129.279 | −22.05 | 161.472 | 175.154 | +13.68 |

[a] Small wood mass was estimated using the line-intercept method (Brown, 1974).
[b] Large wood mass was measured within 4 × 20 m belt transects, volume was calculated from circumference and length, and volume was converted to mass using species-specific wood specific gravity (Hubbard et al., 2004).
[c] Standing live and dead tree mass were estimated using allometric equations (Martin et al., 1998); and shrubs and tree saplings (<5.0 cm dbh) mass was estimated using allometric equations (Boring and Swank, 1986; Elliott et al., 2002).
[d] Live shrubs and tree saplings were measured in July before the burn (2005) and the first (2006) growing season after the burn.

($t_{1,7}$ = 3.01, adjusted $P$ = 0.1330) (Fig. 6). For bluestem grass cover, there were no differences among treatments in 2006. By 2007, DC + B had significantly higher bluestem grass cover than BURN ($t_{1,7}$ = 6.49, adjusted $P$ = 0.0006), MC + B ($t_{1,7}$ = 4.40, adjusted $P$ = 0.0138) and REF ($t_{1,7}$ = 6.98, adjusted $P$ = 0.0003) (Fig. 6). DC + B was the only treatment with significantly higher bluestem grass cover in 2007 than 2006 ($t_{1,7}$ = 7.59, adjusted $P$ = 0.0001) (Fig. 6).

### 3.5. Path analysis relating fire to soil nutrients and herbaceous layer responses

The first growing season (June–August 2006) after prescribed burn treatments, soil solution $NO_3$–N at 30 cm soil depth was significantly related to several fire characteristic variables (Appendix B), providing a good fit to the soil solution $NO_3$–N path model ($X^2$ = 8.549, $df$ = 5, $P$ = 0.128, and model goodness of fit CFI = 0.961, NFI = 0.919, and NNFI = 0.882) (Fig. 7). Fire degree-hr, forest floor loss, and fine fuel consumed had direct effects on Δ live trees (pre-burn 2005 mass of live trees – postburn 2006 mass of live trees) and explained 60% of the variation in Δ live trees. Fine fuel consumed and Δ live trees had direct effects and fire degree-hr (standardized path coefficients, 0.52 × 0.24 = 0.12), forest floor loss (standardized path coefficients, 0.21 × 0.24 = 0.05), and fine fuel consumed (standardized path coefficients, 0.18 × 0.24 = 0.04) had indirect effects mediated through Δ live trees on soil $NO_3$–N. Together, these variables explained 29% of the variation in soil $NO_3$–N. In turn, Δ live

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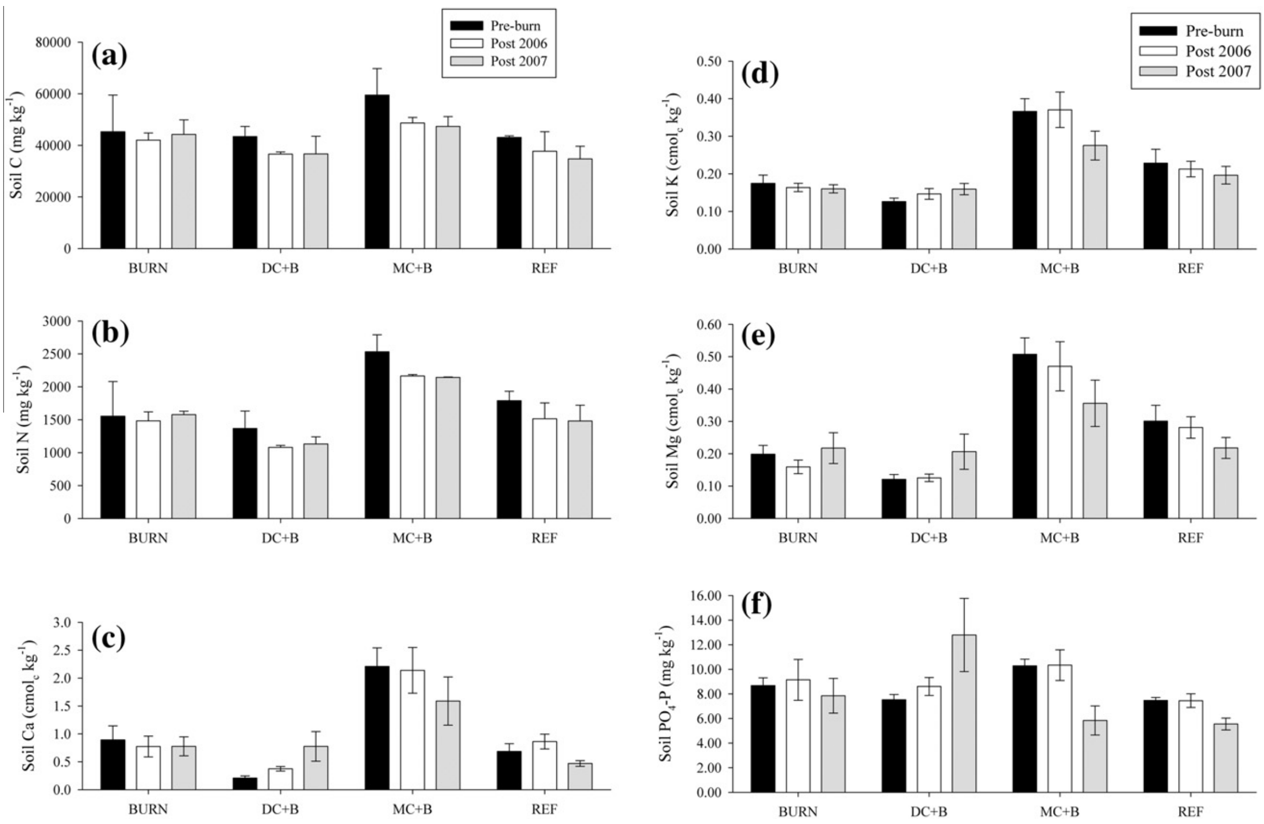


**Fig. 2.** Soil chemistry at 0–10 cm soil depth for the prescribed burn treatments (burn only [BURN]; dry, cut + burn (DC + B); sub-mesic, cut + burn [MC + B], and reference [REF]) before (2005) and after restoration treatments (2006 and 2007): (a) total carbon (mg $kg^{-1}$), (b) total nitrogen (mg $kg^{-1}$), (c) exchangeable calcium, Ca ($cmol_c$ $kg^{-1}$); (d) exchangeable potassium, K ($cmol_c$ $kg^{-1}$); (e) exchangeable magnesium, Mg ($cmol_c$ $kg^{-1}$); and (f) extractable ortho-phosphate, $PO_4$–P concentrations (mg $kg^{-1}$).

trees and soil $NO_3$–N had direct effects on soil solution $NO_3$–N, while fire degree-hr (standardized path coefficients, 0.52 × 0.50 = 0.26), forest floor loss (standardized path coefficients, 0.21 × 0.50 = 0.11), and fine fuel consumed (standardized path coefficients, 0.18 × 0.50 = 0.09) had indirect effects mediated through Δ live trees, and fine fuel consumed (standardized path coefficients, 0.38 × 0.45 = 0.17) and Δ live trees (standardized path coefficients, 0.24 × 0.45 = 0.11) had indirect effects mediated through soil $NO_3$–N on soil solution $NO_3$–N. Total effects (direct + indirect) were 0.32 for fire degree-hr, 0.13 for forest floor loss, 0.28 for fine fuel consumed, 0.45 for soil $NO_3$–N, and 0.61 for Δ live trees on soil solution $NO_3$–N. Direct and indirect effects of these variables explained 64% of the variation in soil solution $NO_3$–N (Fig. 7).

The first growing season after prescribed burning, none of the path variables were correlated with herbaceous layer response (Appendix B), and the data did not fit a path model. For the second growing season after treatment, however, path variables were correlated with herbaceous layer response (Appendix C) and a significant path model was developed ($X^2$ = 9.348, $df$ = 7, $P$ = 0.229, and model goodness of fit CFI = 0.970, NFI = 0.905, and NNFI = 0.909) for herbaceous layer response (Δ herbaceous layer cover = preburn 2005 herbaceous layer cover – postburn 2007 herbaceous layer cover) and soil solution $NO_3$–N (Fig. 8). Fire degree-hr, forest floor loss, and fine fuel consumed had direct effects on Δ live tree mass; these three variables explained 60% of the variation in Δ live trees (Fig. 8). Forest floor loss, fine fuel consumed, and Δ live trees had direct effects and fire degree-hr (standardized path coefficients, 0.52 × −0.15 = −0.08), forest floor loss (standardized path coefficients, 0.21 × −0.15 = −0.03), and fine fuel consumed (standardized path coefficients, 0.18 × −0.15 = −0.03) had indirect effects mediated through Δ live trees on Δ herbaceous layer cover (Fig. 8). Total effects (direct + indirect) were −0.08 for fire degree-hr, −0.37 + −0.03 = −0.40 for forest floor loss, −0.29 + −0.03 = −0.32 for fine fuel consumed, and −0.15 for Δ live trees. Direct and indirect effects of these variables explained 46% of the variation in Δ herbaceous layer cover (Fig. 8). Fine fuel consumed and Δ live trees had direct effects on soil $NH_4$–N, and fire degree-hr (standardized path coefficients, 0.52 × 0.08 = 0.04), forest floor loss (standardized path coefficients, 0.21 × 0.08 = 0.02), and fine fuel consumed (standardized path coefficients, 0.18 × 0.08 = 0.01) had indirect effects on soil $NH_4$–N mediated through Δ live trees. Direct and indirect effects of these variables explained 13% of the variation in soil $NH_4$–N (Fig. 8). Soil $NH_4$–N and Δ live trees had direct effects and fire degree-hr (standardized path coefficients, 0.52 × −0.15 × −0.11 = 0.01), forest floor loss (standardized path coefficients, −0.37 × −0.11 = 0.04), fine fuel consumed (standardized path coefficients, −0.29 × −0.11 = 0.03), and Δ live trees (standardized path coefficients, −0.15 × −0.11 = 0.02) had indirect effects mediated through Δ herbaceous layer cover on soil solution $NO_3$–N. Direct and indirect effects of these variables explained 32% of the variation in soil solution $NO_3$–N (Fig. 8).

We found significant correlations between Δ herbaceous layer cover and Δ S (preburn 2005 species richness – postburn species richness) for both years after the prescribed fires ($r$ = 0.6821, $P$ = 0.0001 for 2006, Appendix B; $r$ = 0.6828, $P$ = 0.0001 for 2007, Appendix C). For the second growing season after treatment, we used the same model structure as that for Δ herbaceous layer cover to test the path model for ΔS (preburn 2005 – postburn 2007 species richness). A significant path model was generated for ΔS ($X^2$ = 2.072, $df$ = 2, $P$ = 0.150, and model goodness of fit CFI = 0.981, NFI = 0.969, and NNFI = 0.809; model diagram not shown). The model was slightly less explanatory than for Δ herbaceous layer cover, as direct and indirect effects of these variables explained 42% of the variation in ΔS.

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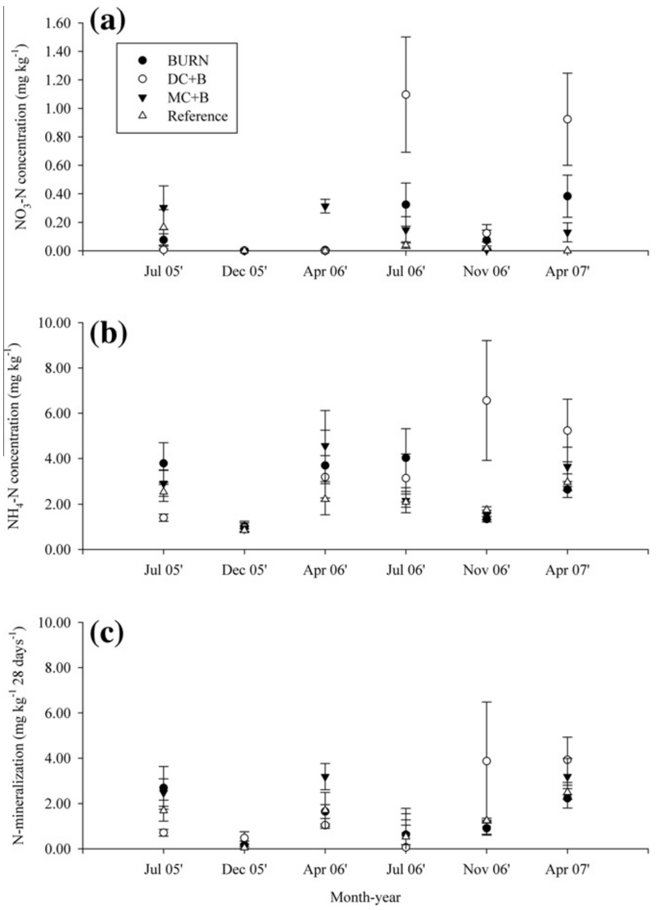


**Fig. 3.** Available soil nitrogen: (a) nitrate-nitrogen ($NO_3$–N) and (b) ammonium-nitrogen ($NH_4$–N) concentrations (mg kg$^{-1}$) and (c) N-mineralization (mg kg$^{-1}$ 28 days$^{-1}$) for the restoration treatments (burn only [BURN]; dry, cut + burn (DC + B); sub-mesic, cut + burn [MC + B], and reference [REF]) before (2005) and after treatments (2006 and 2007):

## 4. Discussion

### 4.1. Fire and aboveground biomass consumption

Fire severity, a function of fire intensity (upward heat pulse produced by the fire) and duration (length of time burning occurs at a particular point); and the combination of fire intensity and duration explain increases in soil temperature (downward heat pulse) (Ryan and Noste, 1985). Fire severity describes the magnitude of disturbance, and highly influences the response of ecosystem processes to burning (Neary et al., 2005; Keeley, 2009). Ecosystem effects of fires are a combination of conditions during burning (especially fire intensity, residency time, and biomass consumption) and resiliency of ecosystem components (typically soils and vegetation) to these conditions (Pyke et al., 2010). We calculated an index of fire severity by integrating the area below a temperature response curve using degree-hr; this measure incorporates fire intensity and duration into a single measure. In our study, fire severity based on degree-hr was highest at the DC + B sites and lowest at the MC + B sites. The DC + B sites also had the highest tree mortality, forest floor loss, and large and small wood consumption, compared to the other treatments, even though fuel load was highest on the MC + B treatment.

We quantified aboveground mass and biomass by individual components before and after the prescribed fires to estimate fuel load and consumption. Prior to the burn treatments, fuel load was high on all sites including the REF sites, ranging from 27.7 to 87.4 Mg ha$^{-1}$ for small plus large down wood mass. All sites had substantial pine mortality due to SPB and some of the dead pines had fallen over and small hardwoods were taken down in their descent. Not surprisingly, the two cut treatments had the highest down large wood mass, with an average of 67.4 Mg ha$^{-1}$ on the DC + B sites and 81.6 Mg ha$^{-1}$ on the MC + B sites. Large wood consumption differed between these two treatments, however, with 62% of the large wood consumed on the DC + B treatment sites and only 20% consumed on the MC + B sites.

Generally, with prescribed burning in the southern Appalachians, the forest floor humus (Oe + Oa) layer remains largely intact, which mitigates surface erosion and movement of sediment and nutrients off-site (Clinton et al., 1996; Elliott and Vose, 2005a; Vose et al., 2005). The longer a fire persists in one place the more severe the fire and the more likely there will be significant consumption of the Oe + Oa layer. Minimizing consumption of the forest floor layer has important implications for near-term site recovery and long-term site productivity, as this layer is typically the largest pool of site nutrients in these ecosystems. In our study, 18–39% of the Oe + Oa layer was consumed during the burn treatments, whereas several studies of low to moderate severity prescribed fires have shown little to no loss of the Oe + Oa layer (Vose et al., 1999; Hubbard et al., 2004; Clinton and Vose, 2007). Findings from burn studies in the southern Appalachians are mixed regarding mass and nutrient loss from wood and forest floor pools. For example, Knoepp et al. (2009) reported large forest floor losses after understory prescribed fires in mesic, mixed-oak forests; 82–92% mass loss of the Oi layer and 26–46% of the Oe + Oa layer. On the other hand, Vose and Swank (1993) reported a range of 47–61% for total aboveground mass consumption, 63–94% for the Oi layer, but only 2–14% of the Oe + Oa layer was consumed across pine-hardwood sites after fell-and-burn treatments. In another study of pine-hardwoods on ridge-tops without felling, Vose et al. (1999) found large reductions in forest floor small wood (80% loss) and Oi layer mass (65% loss) while observing little change in the Oe + Oa layer (7% loss). Kodama and Van Lear (1980) reported that understory burning in loblolly pine plantations resulted in 60% combustion of the Oi layer, but only 6% loss of the Oe + Oa layer. In other studies across the eastern US, low severity fires resulted in moderate and comparable combustion losses of the Oi layer; New Jersey pine barrens (30%; Boerner, 1983), Kentucky oak-pine forest (32%; Blankenship and Arthur, 1999), and Kentucky oak-hickory forest (37%, Trammell et al., 2004). The wide range of responses are likely due to variations in environment, fuel load, fuel conditions, fire intensity and duration, all of which influence fire severity or the magnitude of the response.

In addition to large mass losses, total aboveground N losses from fire can be large and variable (Wan et al., 2001; Nave et al., 2011). For burn only treatments in southern Appalachian pine-hardwood forests, Hubbard et al. (2004) reported losses of 62 kg N ha$^{-1}$ following understory burning and Vose et al. (1999) measured 75 kg N ha$^{-1}$ loss from heavily burned ridge tops. Our findings were similar to those reported by Vose and Swank (1993) who found N losses from fell-and-burn treatments ranged from 193 to 480 kg N ha$^{-1}$ across three xeric, pine-hardwood sites. We estimated total aboveground N losses as 164, 311, and 86 kg N ha$^{-1}$ for BURN, DC + B, and MC + B treatments, respectively. We calculated total N by multiplying Oi and Oe + Oa N concentrations by mass of that component; and assumed an average N concentration of 0.15% for wood, and multiplied N concentration by mass of wood components (see Table 4). The lower N loss on the MC + B treatment compared to the other burned treatments was primarily due to the lower Oe + Oa layer mass loss. In fact, N loss on the BURN treatment was twice that of the MC + B treatment, even though large down wood loss was three times higher due to cutting on MC + B.

In our study, pre-treatment fuel load was not related to forest floor loss or fine fuel loss (Appendix B). While MC + B had the larg-

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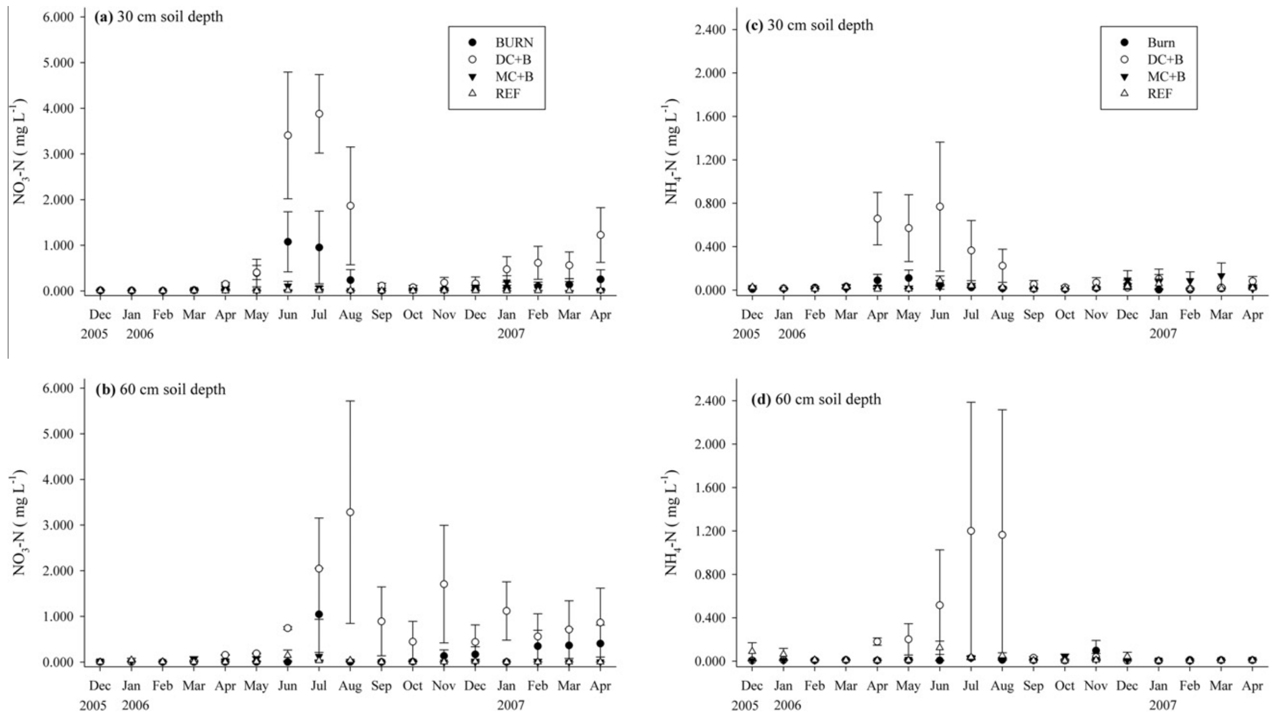


**Fig. 4.** Soil solution chemistry for the restoration treatments (burn only [BURN]; dry, cut + burn (DC + B); sub-mesic, cut + burn [MC + B], and reference (REF) four months before (December 2005- March 2006) and thirteen months (April 2006 – April 2007) after treatments: nitrate-nitrogen, $NO_3$–N (a) 30 cm soil depth, (b) 60 cm soil depth; ammonium-nitrogen, $NH_4$–N (c) 30 cm soil depth, (d) 60 cm soil depth; and ortho-phosphate, $PO_4$–P concentrations (e) 30 cm soil depth, (f) 60 cm soil depth.

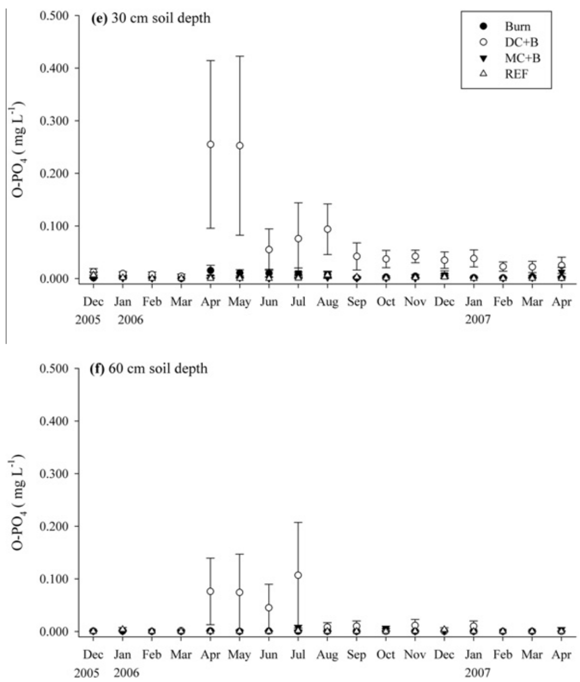


**Fig. 4** (*continued*)

est fuel load, these sites were sub-mesic and therefore had the lower fire severity (based on degree-hr) compared to the other burned sites. The higher site moisture on MC + B likely offset the potentially large mass and total N loss that would be expected from cutting and burning on drier sites, as seen on DC + B.

### 4.2. Soil and soil solution nutrient responses

Exchangeable cations pools in soil and total cations in forest floor material can both be impacted by fire through ash deposition (ash-bed effect) and leaching (Nobles et al., 2009), and the magnitude of the response depends on fire severity (Knoepp et al., 2005). Some studies have reported no response or a transient increase in plant available nutrients following prescribed fire in mixed-hardwood forests in Appalachian forests (Vose et al., 1999; Boerner et al., 2000, 2004; Hubbard et al., 2004; Coates et al., 2008). Others have reported significant increases in available nutrients following burning (Knoepp et al., 2004; Boerner and Brinkman, 2005). In our study, the most severely burned sites (DC + B) had increased soil Ca, Mg, $PO_4$–P, $NH_4$–N, and $NO_3$–N for up to two years after the burn treatment. Following an intense fell-and-burn treatment in xeric, pine hardwood forests, soil $NH_4$–N immediately increased by an order of magnitude (from an average 0.55 mg $kg^{-1}$ to 4.5 mg $kg^{-1}$); and remained elevated for 3 years (Knoepp et al., 2004). More transient responses have also been reported. For example, understory burning in a mixed-oak community resulted in increased K, Ca, Mg, $PO_4$–P, $NH_4$–N, and $NO_3$–N availability in soil on the burned area compared with the control, but the response lasted for less than one year (Elliott et al., 2004). In a longleaf-shortleaf pine forest in central Florida, Lavoie et al. (2010) found that forest floor $NH_4$–N, $PO_4$–P, Ca, Mg and K decreased immediately after fire, but increased in the surface mineral soil (0–5 cm depth); Ca, Mg, and K remained elevated for the first year after fire. Liechty et al. (2005) found a greater than 60% increase in surface soil Ca concentrations in shortleaf pine stands following harvesting with the retention of large amounts woody debris and prescribed fire. Similarly, Masters et al. (1993) found that Ca, Mg, and K in soil increased only slightly if harvesting was not followed by a prescribed fire or prescribed fire was not proceeded by some type of harvesting activity in shortleaf pine-hardwood stands. When harvesting and prescribed fire were combined, Ca, Mg, and K concentrations in surface soils significantly increased.

We also found higher soil solution $NH_4$–N, and $NO_3$–N for five months and higher $PO_4$–P for 13 months at the DC + B sites. Knoepp and Swank (1993) found no significant increases in soil solution $NH_4$–N concentrations after fell-and-burn treatments in

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**Table 5**
Overstory average density (stems $ha^{-1}$) of dead and live trees, percent mortality, and basal area ($m^2\ ha^{-1}$) of live trees within each treatment before (2005) and after (2006) restoration treatments: burn only (Burn), dry cut + burn (DC + B), mesic cut + burn (MC + B), and reference (REF). Different lower case letters in a column indicate significant ($\alpha$ = 0.05) differences among treatment.

| Treatment | Pre-treatment (2005) | | | | Post-treatment (2006) | | | |
|---|---|---|---|---|---|---|---|---|
| | Dead | Live | Mortality[a] (%) | Live tree basal area | New Dead | Live | Mortality[b] (%) | Live tree basal area |
| Burn | 403 (59) | 478 (57) | 45.7 | 11.23 (1.71) | 306 (90) | 175 b (55) | 63.6 | 6.30 b (2.26) |
| DC + B | 412 (52) | 816 (62) | 33.6 | 16.72 (2.24) | 634 (97) | 68 c (30) | 91.5 | 1.83 c (0.91) |
| MC + B | 575 (60) | 753 (61) | 43.3 | 10.56 (1.74) | 319 (57) | 438 b (73) | 42.1 | 8.43 b (2.10) |
| REF | 446 (41) | 847 (107) | 34.5 | 13.74 (1.51) | 34 (5) | 838 a (107) | 3.9 | 14.44 a (1.52) |

[a] Mortality in 2005 was estimated by measuring standing dead and down pines that were recently killed by SPB and other hardwoods that were broken by falling pine trees.
[b] Mortality in 2006 was attributed to the treatments (burn only or cut + burn) and was based on dead trees that were tagged as live trees in 2005 before the cutting.
Standard errors are in parentheses.

**Table 6**
Average density (stems $ha^{-1}$) of understory shrubs and tree saplings (woody stems <5.0 cm dbh, >0.5 m height); before (2005) and the first (2006) and second (2007) growing seasons after restoration treatments: burn only (BURN), dry cut + burn (DC + B), mesic cut + burn (MC + B), and reference (REF). Different lower case letters in a row indicate significant ($\alpha$ = 0.05) differences among years within a treatment.

| Treatment | Type | Before treatment | After treatment | |
|---|---|---|---|---|
| | | 2005 | 2006 | 2007 |
| Burn | Pines[a] | 450 (450) | 50 (50) | 150 (50) |
| | Oaks[b] | 850 (350) a | 1900 (400) b | 3000 (900) b |
| | Red maple[c] | 3550 (1350) a | 6750 (1450) b | 7800 (3800) b |
| | Sassafras[c] | 4850 (1658) a | 11400 (5015) b | 14450 (6570) b |
| | Other trees[d] | 1850 (427) a | 5200 (2115) a | 5300 (1655) a |
| | Shrubs[e] | 5550 (3150) a | 13150 (8250) b | 20900 (2200) b |
| | Total | 17100 (2100) a | 38450 (1550) b | 51600 (14700) b |
| DC + B | Pines[a] | 950 (850) | 0 | 300 (300) |
| | Oaks[b] | 300 (200) a | 4250 (3850) b | 2300 (100) b |
| | Red maple[c] | 750 (250) a | 2650 (450) b | 4850 (1050) b |
| | Sassafras[c] | 2300 (1112) ab | 1850 (848) a | 6000 (2464) b |
| | Other trees[d] | 3800 (1361) a | 6971 (2031) ab | 9657 (2383) b |
| | Shrubs[e] | 18150 (7550) a | 4500 (400) b | 19350 (6550) a |
| | Total | 24150 (3850) b | 19350 (50) a | 42450 (4150) c |
| MC + B | Pines[a] | 350 (250) | 0 | 50 (50) |
| | Oaks[b] | 1100 (100) a | 2750 (150) b | 2300 (100) b |
| | Red maple[c] | 7950 (2450) a | 9000 (2800) a | 10000 (900) a |
| | Sassafras[c] | 1500 (1247) a | 1350 (956) a | 850 (639) a |
| | Other trees[d] | 8400 (1149) a | 18150 (3065) b | 16700 (2968) b |
| | Shrubs[e] | 13650 (2850) a | 22650 (150) b | 24650 (3950) b |
| | Total | 32200 (1900) a | 53900 (1400) b | 54550 (7850) b |
| REF | Pines[a] | 350 (250) a | 650 (550) a | 500 (400) a |
| | Oaks[b] | 1400 (900) a | 1550 (950) a | 1700 (600) a |
| | Red maple[c] | 3100 (500) a | 2500 (500) a | 2750 (350) a |
| | Sassafras[c] | 400 (169) a | 600 (262) a | 350 (140) a |
| | Other trees[d] | 5550 (1397) a | 7550 (1986) a | 8950 (2627) a |
| | Shrubs[e] | 3800 (1500) a | 5950 (650) a | 7050 (450) a |
| | Total | 14600 (4400) a | 18800 (5300) a | 21300 (6800) a |

[a] Pines included: *P. virginiana*, *Pinus echinata*, *P. taeda*.
[b] Oaks included: *Quercus coccinea*, *Q. montana*, *Q. velutina*, *Q. alba*, *Q. rubra*, *Q. marilandica*, *Q. falcata*, *Q. nigra*, *Q. stellata*.
[c] Red maple (*Acer rubrum*), Sassafras (*Sassafras albidum*).
[d] Other trees included: *Oxydendrum arboreum*, *Nyssa sylvatica*, *Liriodendron tulipifera*, *Pinus strobus*, *Liquidambar styraciflua*, *Prunus serotina*, *Diospyros virginiana*, *Carya* spp. (*glabra* and *tomentosa*), *Fraxinus pennsylvanica*, *Cornus florida*, *Betula lenta*, *Crataegus* sp., *Amelanchier arborea*, *Carpinus caroliniana*, *Castanea pumula*, *Aesculus flava*, *Fagus grandifolia*, *Tsuga canadensis*, *Robinia pseudoacacia*, *Magnolia fraseri*.
[e] Shrubs and vines included: *Rubus* spp., *Vaccinium* spp. (*arboreum*, *corymbosum*, *stamineum*, *vacillans*), *Calycanthus floridus*, *Smilax* spp. (*glauca*, *rotundifolia*), *Vitis* spp. (*aestivalis*, *rotundifolia*), *Ilex opaca*, *Rhus* spp. (*copallina*, *glaba*), *Kalmia latifolia*, *Aralia spinosa*, *Ilex ambigua*, *Gaylussacia baccata*, *Euonymous americanus*, *Parthenocissus quinquefolia*, *Viburnum acerifolium*, *Pyrularia pubera*, *Toxicodendron radicans*, *Hydrangea arborescens*. Within a group, species list is ranked by abundance across all sites. All species nomenclature follows Gleason and Cronquist (1991).

pine-hardwoods, but they did find an increase in soil solution $NO_3$–N concentrations and the increase was roughly proportional to the intensity of the burn. Knoepp and Swank (1993) explained that even though the response to treatment was significant and quite striking graphically, actual concentrations in solutions ranged between 0.02 and 0.50 mg $L^{-1}$. In our study, soil solution $NO_3$–N concentrations were much higher after burning treatments than those reported by Knoepp and Swank (1993), well above 3.0 mg $L^{-1}$ on DC + B and above 1.0 mg $L^{-1}$ on BURN, for several months after the burn. In contrast, in similar shortleaf pine-mixed hardwood ecosystems as those in our study, Elliott and Vose (2005a) found no detectable differences between control and burned sites for soil solution $NH_4$–N, $NO_3$–N, and $PO_4$–P after low severity fire, and concentrations remained low (<0.02 mg $L^{-1}$) for 10 months. Examin-

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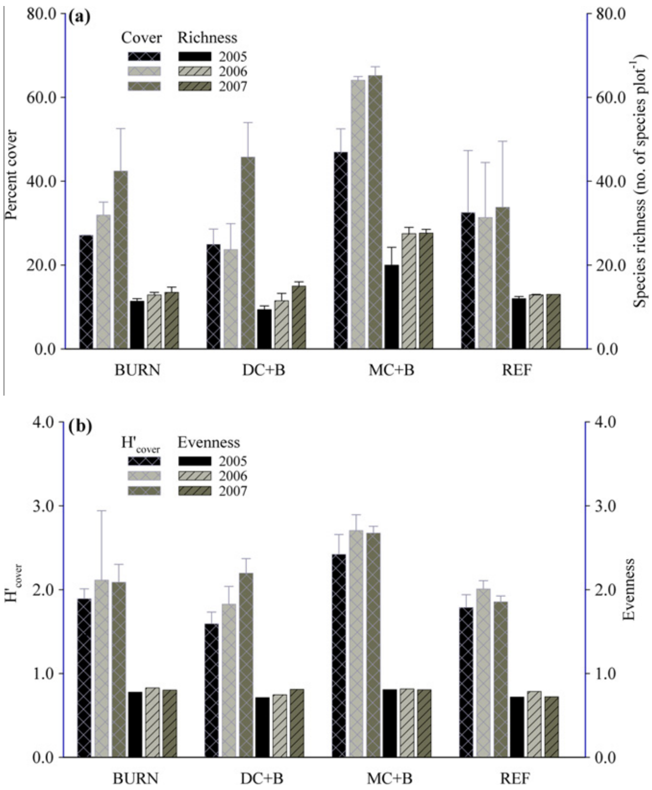


**Fig. 5.** Herbaceous layer response for the restoration treatments (burn only [BURN]; dry, cut + burn (DC + B); sub-mesic, cut + burn [MC + B], and reference (REF) before (2005) and the first two growing seasons (2006, 2007) after treatments: (a) percent cover and species richness and (b) diversity based on percent cover ($H'_{cover}$, Shannon's index) and evenness of species distribution.

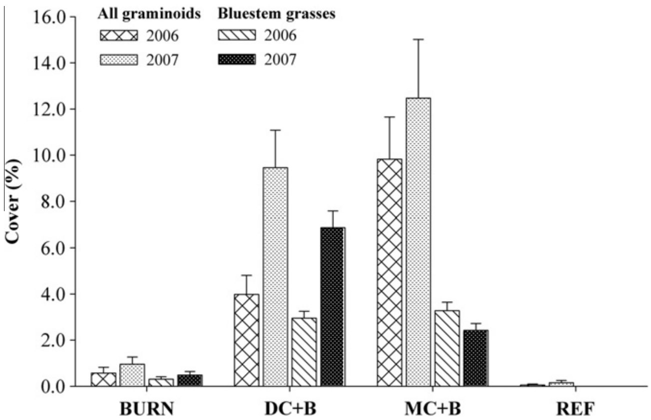


**Fig. 6.** Grass cover on the restoration treatments (burn only [BURN]; dry, cut + burn (DC + B); sub-mesic, cut + burn [MC + B], and reference (REF) and the first two growing seasons (2006, 2007) after treatments.

ing prescribed fire impacts in Jeffrey pine (*Pinus jeffreyi* Grev. & Falf.) stands of the Sierra Nevadas; Murphy et al. (2006) found no effect of burning on soil solution $NO_3$–N, $NH_4$–N, or $PO_4$–P. In another study in the Sierra Nevadas, Caldwell et al. (2009) found that fire effects on $PO_4$–P were mixed with increases in one site with andesitic parent material and decreases in the other with granitic parent material. They hypothesized that the decreasing trend in $PO_4$–P at the granitic site was due to increases in Ca and pH, and subsequent $PO_4$–P immobilization. In our study, soil Ca increased after burning on the DC + B sites, but likely not high enough to immobilize $PO_4$–P allowing for higher soil solution $PO_4$–P for several months after the fire.

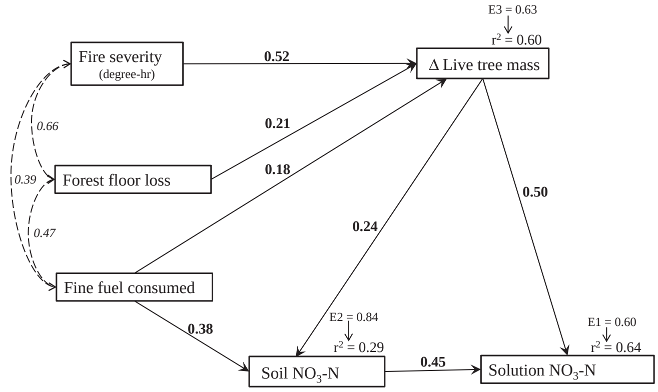


**Fig. 7.** Final structural equation models with standardized path coefficients for soil solution nitrate-nitrogen at 0–30 cm soil depth for June–August 2006 ($NO_3$–N $_{2006}$) ($X^2$ = 8.49, *df* = 5, *P* = 0.128, and model goodness of fit CFI = 0.961, NFI = 0.919, and NNFI = 0.882). Variables used in the model are: fire severity as estimated by degree-hr; forest floor loss = preburn Oi + Oe + Oa forest floor – postburn Oi + Oe + Oa forest floor; fine fuel consumed = preburn fine fuel (down small wood <7.5 cm diameter) – postburn fine fuel; Δ live tree = preburn live tree biomass – postburn live tree biomass; soil $NO_3$ = soil nitrate-nitrogen concentration in 2006; and solution $NO_3$ = soil solution $NO_3$ at 30 cm soil depth in 2006.

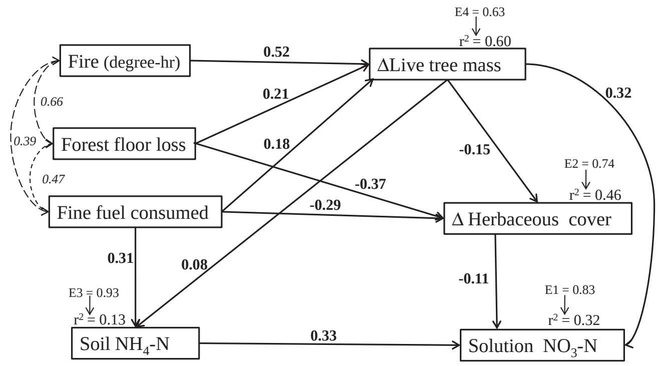


**Fig. 8.** Final structural equation models with standardized path coefficients for soil solution nitrate-nitrogen at 0–30 cm soil depth for March–April 2007 ($NO_3$–N 2007) and herbaceous layer cover change between preburn-2005 and postburn-2007 ($X^2$ = 9.348, *df* = 7, *P* = 0.229, and model goodness of fit CFI = 0.970, NFI = 0.905, and NNFI = 0.909). Variables used in model are described in Fig. 7, and soil $NH_4$ = soil ammonium-nitrogen concentration in 2007; solution $NO_3$ = soil solution $NO_3$ at 30 cm soil depth in 2007; and Δ herbaceous cover = herbaceous layer cover 2005 – herbaceous layer cover 2007.

### *4.3. Vegetation responses*

In general, vegetation is responsive to prescribed fire in the southern Appalachians, but the magnitude of response depends on numerous factors (e.g., timing, fuel load, topography, and fire characteristics). In our study, overstory mortality was high on all the burned treatments, particularly the most severely burned treatment, DC + B. The cutting prior to the prescribed burning was designed to favor oaks and yellow pines, however, the high severity burns on the DC + B treatment substantially reduced all species, including the oak species and shortleaf pine. On the BURN treatment, comparatively more oaks and pines (Virginia and shortleaf pine) survived the burn.

The vegetation layer most responsive to dormant season, prescribed fire is the understory and small size class trees. Even low severity fires in mesic forests result in topkill of small woody stems and rapid recruitment from sprouting stems can alter species composition (Elliott et al., 2004; Elliott and Vose, 2010). In our study, understory stem density increased after the prescribed fires over the two year period. In contrast, understory biomass decreased on all of the burned sites the first growing season after the prescribed

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fires with the greatest loss on the MC + B sites. However, recovery was rapid and by 2007, the second growing season postburn, understory biomass had doubled on MC + B (10.42 ± 2.30 Mg $ha^{-1}$) and was nearly threefold higher on BURN (8.53 ± 2.55 Mg $ha^{-1}$) and DC + B (9.08 ± 2.27 Mg $ha^{-1}$).

Many studies have shown an increase in understory stem density in Eastern mixed-hardwood forests following a single fire disturbance (Clinton et al., 1993; Elliott et al., 1999; Kuddes-Fischer and Arthur, 2002; Elliott and Vose, 2005b, 2010; Alexander et al., 2008; Hutchinson et al., 2008; Iverson et al., 2008). Even though survival of existing seedlings and saplings is low because most aboveground stems (<3.0 m height) are burned (Alexander et al., 2008; Hutchinson et al., 2008), rapid and prolific sprouting response of shrubs and trees results in higher densities within the first year after the fire. Even with repeated low severity fire that reduces understory density (Jenkins and Jenkins, 2006); multiple fires do not necessarily discriminate between oaks and other tree species (Alexander et al., 2008; Green et al., 2010).

In the understory, we found a significant increase in the density of oak species (*Quercus alba, Q. coccinea*, *Q. montana*, *Q. rubra*, and *Q. velutina*) on all burn treatments. However, oaks accounted for a small proportion of the total stem density, with only 5.8%, 5.4%, 4.2%, and 8.0% on the BURN, DC + B, MC + B, and REF treatments, respectively. Whereas, averaged across all burn treatments, red maple comprised 15%, other tree species 37%, and shrubs made up 44% of the total stem density. Oak seedlings were also present in herbaceous layer (stems < 0.5 m height) accounting for 20% of the total number of tree seedlings averaged across treatments. The high densities of woody species other than oaks, coupled with the fast growth rates of some of these species, suggests that oaks will continue to be at a competitive disadvantage in these pine-hardwood communities through time, without further intervention. Other studies have shown that low intensity, dormant season prescribed fire does not alter the competitive status of oak seedlings relative to shade tolerant seedlings (Hutchinson et al., 2005b; Albrecht and McCarthy, 2006; Chiang et al., 2008).

Pine regeneration was not improved on any of our burned sites. We found little to no recruitment of pines into the understory after two years and the pine saplings that were present before the burns were killed by fire on all sites. In addition, we did not observe any seed germination of shortleaf, pitch or Virginia pines after fire even though overstory basal area was reduced enough on all of the burned sites to allow for pine seedling establishment. Guidelines for successful regeneration of shortleaf pine are 10–14 $m^2$ $ha^{-1}$ of overstory basal area (Shelton and Cain, 2000) and all of our burned sites had <10 $m^2$ $ha^{-1}$ residual basal area. An earlier study by Elliott and Vose (2005b) found that low severity prescribed fires did not reduce overstory basal area and prepare a seedbed for successful pine germination. In our study, poor pine regeneration may have been due to drought (the lowest rainfall year on record occurred in 2007), poor seed production, and hardwood competition in the understory. Poor seed production was likely because nearly all overstory pines were dead due to the SPB infestation prior to treatments.

Herbaceous layer composition and diversity may be altered with prescribed fire, but the relative magnitude of the response depends on fire severity. For example, Phillips et al. (2007) found that a combined treatment of thinning from below followed by prescribed fire resulted in increased herbaceous layer cover and richness because fire was more severe and the canopy was more open in the combined treatment than the burn only treatment. In a southern Appalachians pine-oak community, Elliott et al. (1999) found herbaceous layer composition was altered following moderate-severity prescribed fire. Evergreen shrub density was significantly reduced, while deciduous shrubs, forbs, and grasses increased within two growing seasons following fire (Elliott et al., 1999). Ten years after burning, forbs and grasses were more abundant than they were before the prescribed fire treatment (Elliott et al., 2009). In contrast, after low-severity, understory fires, little to no changes in herbaceous layer diversity were found (Elliott and Vose, 2005b, 2010; Hutchinson et al., 2005a; Jackson et al., 2006). Low severity prescribed fires coupled with dormant-season ignition, allow the root systems and seedbanks of herbaceous layer species to survive; thus, species are able to re-emerge in the spring and summer following the burn treatments. Whereas, with higher severity fires, early successional species may colonize a site and post-burn herbaceous layer diversity may be altered. For example, after a severe wildfire in Linville Gorge, western North Carolina, Dumas et al. (2007) found that post-disturbance colonizers occurred only in burned plots; their abundance probably resulted from a dormant seedbank that flourished following the fire. In our study, we also found recruitment of early successional forbs (*Erechtites hieracifolia* and *Phytolacca americana* L.), which contributed 5.6% and 7.0% to the herbaceous layer cover on the BURN and DC + B, respectively. Other research has suggested that an initial increase in N availability after fire can contribute to increases in herbaceous layer cover (Gilliam, 1988; Elliott et al., 2004; Knoepp et al., 2009), but this short-term N pulse may not alter species richness or diversity. After low severity fire, even though herbaceous layer species richness and diversity were not affected (Elliott and Vose, 2005b, 2010), percent cover increased. The authors attributed this increase to the observed short term pulse of available N. In our study, with more severe fires, we found an increase in herbaceous layer cover as well as species richness and diversity two years following fire treatments.

Seeding bluestem grasses was relatively successful on both dry and sub-mesic cut-and-burn treatments, but not effective on burn only and reference sites. Native grasses also had higher cover on the cut-and-burn sites than the other sites. With few exceptions, native grasses and bluestem grasses require high light for germination and growth. Even though fire intensity and forest floor consumption were greater on the BURN treatment than on the MC + B treatment, light levels were lower due to residual standing dead trees and remaining live trees on BURN and the relatively closed canopy on references sites.

### *4.4. Path analysis relating fire to soil nutrients and herbaceous layer responses*

Grace et al. (2010) reviewed the use of structural equation modeling (SEM) for ecological systems. SEM has appeal because it can be used as a framework for interpretation when there are large numbers of predictors and responses with complex causal connections. Indeed, some authors have found SEMs useful in interpreting their results from fire studies (Grace and Keeley, 2006; Hiers et al., 2007; Keeley and McGinnis, 2007; Keeley et al., 2008; Kilpatrick et al., 2010). We used SEMs to estimate causal effects through path analysis and were able to construct good-fit models for fire effects on overstory response, soil and soil solution N response, and herbaceous layer response.

In our conceptual model, we hypothesized that fuel load and fire severity would have direct effects on fuels consumed, overstory and understory responses, and soil nutrient responses (Fig. 1). Our results supported our hypothesis and showed that fire severity (measured as degree-hr, forest floor loss, and fine fuel consumed) explained a large proportion of the variation in overstory response (i.e., Δ live tree biomass), and fire severity and overstory response partially explained soil $NO_3$–N response. These variables combined, directly and indirectly, explained a large portion of the soil solution $NO_3$–N at 30 cm soil depth (within the rooting zone for most plants). Thus, with high fire severity more N is available for plant uptake during the first two growing seasons following fire in these pine-hardwood ecosystems. Vose and Swank

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(1993) calculated large total ecosystem N losses following a fell-and-burn treatment in pine-hardwoods; we estimated similar aboveground N loss in our study. Knoepp and Swank (1993) found an increase in soil solution $NO_3$–N following burning for these same study sites, but the magnitude of response was much less than we found in our study.

In our path analyses, we found no significant correlation between understory response (i.e., Δ shrub biomass) and fire degree-hr ($r = 0.010$, $P = 0.959$) or fuel load ($r = 0.080$, $P = 0.664$), nor did understory response contribute to explanation of soil nutrients or herbaceous layer responses. In our theoretical model, we explored the potential for a direct path from soil nutrients to the herbaceous layer response. However, herbaceous layer response was not significantly correlated with any soil nutrient parameter (see Appendices B and C). In addition, none of the soil nutrient variables contributed to our path model for herbaceous layer response. Other factors, such as increased soil moisture and light availability following prescribed burning, most likely outweigh the observed increase in available N (i.e., $NO_3$–N and $NH_4$–N) and cations in the first year following fire.

In the first growing season after fire, herbaceous layer cover and diversity responses (i.e., Δ herbaceous layer cover and ΔS) were not related to the potential predictor variables (i.e., fire characteristics, overstory and understory live and dead biomass, and soil resources). Keeley et al. (2008) found that fire severity in chaparral systems was not a good predictor of vegetation regeneration in the first year or subsequent years after fire. In our study, we found a good-fit model for herbaceous layer response in the second growing season, where fire severity (as measured by fire degree-hr, forest floor loss, and fine fuel consumed) had direct effects on live tree mass and herbaceous layer response and indirect effects on herbaceous layer response mediated through remaining live tree mass. Overall, our path model explained 46% and 42% of the variation in herbaceous layer response for Δ cover and ΔS, respectively. The loss of forest floor mass and lower residual live tree mass (less overstory biomass) resulted in increased herbaceous layer cover and S. Surprisingly, we did not find any significant correlations between herbaceous layer responses and soil nutrients or soil nutrient changes (i.e., preburn – postburn), so these variables were not included in the path model for herbaceous layer response.

Our results found that herbaceous layer cover and S were highest where overstory biomass was lowest and forest floor loss was greatest. These findings are similar to those of Laughlin et al. (2007) for a ponderosa pine (*P. ponderosa* L.) ecosystem in northern Arizona. Hiers et al. (2007) also found that the light environment and forest floor depth were the overriding factors affecting understory communities, particularly grasses and legumes, in longleaf pine ecosystems. Reduced overstory canopy would increase light availability, and, in turn, recruitment opportunities for shade-intolerant species. Reduced forest floor mass (or depth) would allow seed germination, particularly from dormant seedbanks, and resprouting from basal meristems, such as perennial grasses.

### 4.5. Implications for management

We examined the effects of cut-and-burn, burn only, and no treatment on ecosystem structure and function in degraded shortleaf pine-hardwood forests heavily impacted by SPB induced tree mortality. We also seeded the treated sites with bluestem grass seeds to accelerate recruitment of this understory component. We found differences among treatments in fire severity, soil and soil solution nutrient responses, vegetation recovery and the interactions among these response variables. Fire severity was highest at the dry, cut-and-burn sites even though fuel load was highest on the sub-mesic, cut-and-burn treatment.

Soils in the dry, cut-and-burn sites responded with increased $NO_3$–N, $NH_4$–N Ca, Mg, and $PO_4$–P concentrations as well as higher soil solution $NO_3$–N, $NH_4$–N, $PO_4$–P concentrations for several months after the restoration treatments. High soil solution $NO_3$–N, $NH_4$–N, $PO_4$–P concentrations after burning were due to combustion of organic matter, ash inputs, and increased soil microbial activity. Increased microbial N mineralization resulted in elevated ammonium concentrations, higher rates of nitrification, and increased soil solution N concentrations (Neary et al., 2005). Vegetation mortality after fire reduced plant nutrient uptake and increased the potential for leaching losses.

Fire did not stimulate pine recruitment even though the overstory basal area was sufficiently reduced to allow light penetration to the understory. Poor pine regeneration was due to a combination of factors: drought, poor seed production, and a dense understory layer.

Seed production was limited because nearly all overstory pines were dead due to the SPB infestation prior to treatments. Without a seed source, pines are not likely to become re-established in these degraded forests, and planting shortleaf pine seedlings will be required. Seeding bluestem grasses was relatively successful on both dry and sub-mesic cut-and-burn treatments, but not effective on burn only sites suggesting that open canopies are required for seed germination. Increased fire severity resulted in increased herbaceous layer cover as well as species richness and diversity two years following fire treatments. Density of oak species increased significantly on all burn treatments; however, oaks accounted for a relatively small proportion of the total stem density in the understory. The higher densities of woody species other than oaks, coupled with the fast growth rates of some of these species, suggests that oaks will continue to be at a competitive disadvantage in these pine-hardwood communities through time, without further intervention.

We found a good-fit path model for herbaceous layer response in the second growing season, showing that fire severity had direct effects on live tree mass and herbaceous layer response and indirect effects on herbaceous layer response mediated through residual live tree mass. We concluded that the combination of forest floor removal by fire and increased penetration of light associated with the loss of the aboveground biomass were responsible for the increased abundance and diversity of herbaceous layer vegetation observed by the second growing season post-treatment.

Our study shows that cutting followed by prescribed fire can reduce fuel loads, increase soil nutrient availability, open the canopy by reducing overstory basal area, and stimulate vegetative growth. Although the cut-and-burn treatments have positioned these degraded ecosystems on a restoration trajectory, clearly, further silvicultural treatments are needed to fully restore these sites to shortleaf pine/bluestem communities. Additional treatments, such as herbicide, thinning, and prescribed fire, will be necessary to reduce understory density and increase light to the forest floor. Herbicide treatments could target sprouting maples and sassafras to favor oaks and bluestem grass cover. A fire-free period of 10–15 years will be needed for oaks to grow large enough to survive additional fire treatments and be competitive post-fire (Brose and Van Lear, 2004). Planting shortleaf pine seedlings will be necessary because adequate cone crops were absent in these areas due to high mortality of overstory pine; even with adequate seed production, overstory canopies need to remain open to allow for successful seed germination and seedling growth (Shelton and Cain, 2000). Following successful regeneration, thinning treatments could be designed to favor pines and oak, maintain low basal area, and promote a bluestem grass ground cover. Future research that addresses fire coupled with silvicultural treatments, fire seasonality, and the longer term effects will be particularly useful to gain a better understanding of how a combination of management practices affect restoration of shortleaf pine ecosystems.

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## Appendix A

Average density (stems $ha^{-1}$), basal area (BA, $m^2\ ha^{-1}$) and importance value (IV = (relative density + relative basal area)/2)

| | Pre-burn 2005 | | | Post-burn 2006 | | |
|---|---|---|---|---|---|---|
| | Density | BA | IV | Density | BA | IV |
| *Burn only* | | | | | | |
| *Quercus Montana* | 53 | 3.34 | 20.45 | 34 | 2.54 | 29.96 |
| *Oxydendrum arboretum* | 112 | 1.34 | 17.76 | 28 | 0.55 | 12.39 |
| *Nyssa sylvatica* | 78 | 1.06 | 12.88 | 56 | 0.96 | 23.68 |
| *Pinus strobes* | 53 | 1.54 | 12.39 | 9 | 0.06 | 3.16 |
| *Acer rubrum* | 59 | 0.46 | 8.25 | 6 | 0.14 | 2.90 |
| *Pinus virginiana* | 22 | 1.04 | 6.94 | 12 | 0.46 | 7.20 |
| *Quercus coccinea* | 6 | 1.31 | 6.47 | 6 | 1.28 | 11.91 |
| *Sassafras albidum* | 28 | 0.16 | 3.64 | 6 | 0.02 | 1.92 |
| *Pinus echinata* | 3 | 0.26 | 1.50 | 3 | 0.26 | 2.97 |
| *Dry, cut + burn* | | | | | | |
| *Pinus strobus* | 253 | 3.95 | 23.33 | 9 | 0.26 | 15.96 |
| *Pinus virginiana* | 84 | 3.12 | 14.51 | 6 | 0.04 | 6.62 |
| *Acer rubrum* | 112 | 2.29 | 13.75 | 19 | 0.59 | 34.28 |
| *Nyssa sylvatica* | 88 | 1.51 | 9.87 | 9 | 0.28 | 16.69 |
| *Oxydendrum arboreum* | 103 | 1.10 | 9.62 | 3 | 0.02 | 3.11 |
| *Quercus coccinea* | 53 | 1.95 | 9.09 | – | – | – |
| *Quercus montana* | 40 | 1.28 | 6.32 | 9 | 0.39 | 20.01 |
| *Quercus velutina* | 12 | 0.62 | 2.61 | – | – | – |
| *Pinus echinata* | 9 | 0.35 | 1.62 | – | – | – |
| *Sassafras albidum* | 16 | 0.12 | 1.33 | 3 | 0.02 | 3.32 |
| *Sub-mesic, cut + burn* | | | | | | |
| *Liriodendron tulipifera* | 212 | 2.42 | 25.55 | 125 | 2.16 | 27.07 |
| *Acer rubrum* | 128 | 1.86 | 17.31 | 75 | 1.33 | 16.47 |
| *Pinus virginiana* | 65 | 1.07 | 9.44 | 34 | 0.75 | 8.38 |
| *Pinus strobus* | 25 | 1.57 | 9.09 | 22 | 1.58 | 11.84 |
| *Liquidambar styraciflua* | 53 | 0.87 | 7.66 | 34 | 0.58 | 7.36 |
| *Oxydendrum arboreum* | 59 | 0.54 | 6.47 | 19 | 0.23 | 3.51 |
| *Cornus florida* | 59 | 0.25 | 5.11 | 34 | 0.16 | 4.84 |
| *Prunus serotina* | 38 | 0.28 | 3.84 | 16 | 0.16 | 2.72 |
| *Quercus alba* | 25 | 0.24 | 2.78 | 19 | 0.20 | 3.35 |
| *Quercus velutina* | 12 | 0.16 | 1.58 | 6 | 0.11 | 1.35 |
| *Quercus montana* | 9 | 0.05 | 0.87 | 6 | 0.04 | 0.93 |
| *Quercus rubra* | 9 | 0.06 | 1.23 | – | – | – |
| *Quercus coccinea* | 6 | 0.15 | 1.12 | 6 | 0.17 | 1.71 |
| *Quercus falcata* | 6 | 0.06 | 0.69 | 3 | 0.03 | 0.56 |
| *All Quercus* | 67 | 0.72 | 8.27 | 40 | 0.55 | 7.90 |
| *Reference* | | | | | | |
| *Acer rubrum* | 216 | 2.99 | 23.60 | 219 | 3.21 | 24.16 |
| *Quercus montana* | 106 | 3.26 | 18.14 | 103 | 3.38 | 17.88 |
| *Quercus alba* | 94 | 1.73 | 11.84 | 94 | 1.86 | 12.03 |
| *Oxydendrum arboreum* | 88 | 0.98 | 8.73 | 88 | 1.04 | 8.81 |
| *Pinus strobus* | 53 | 1.04 | 6.93 | 50 | 1.02 | 6.52 |
| *Cornus florida* | 62 | 0.36 | 4.99 | 62 | 0.37 | 5.02 |
| *Quercus coccinea* | 19 | 0.99 | 4.72 | 19 | 1.06 | 4.79 |
| *Nyssa sylvatica* | 47 | 0.34 | 4.02 | 44 | 0.36 | 3.85 |
| *Pinus virginiana* | 38 | 0.24 | 3.09 | 34 | 0.27 | 2.98 |
| *Pinus echinata* | 3 | 0.43 | 1.75 | 3 | 0.44 | 1.71 |

Species are ranked the highest eight based on importance value in either year. Other less abundant species not listed were: *Betula lenta*, *Carya* spp., *Diospyros virginiana*, *Fagus grandifolia*, *Ilex opaca*, *Magnolia acuminata*, *Quercus falcata*, *Quercus rubra*, *Quercus stellata*, *Tsuga canadensis*, and *Vaccinium aboreum*. All species nomenclature follows Gleason and Cronquist (1991).

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## Appendix B

Bivariate correlations (Pearson coefficients with *P*-values, *df* = 32) among variables evaluated for path analysis for the first year after restoration treatments (2006).

| | Fire severity | Load | Fine fuel loss | FF loss | Δ shrub mass | Live tree | Δ Live tree | Dead tree | Δ Dead tree | Soil $NO_3$ | Soil $NH_4$ | Δ Soil N | Δ Soil Ca | Solution $NO_3$ | Solution $NH_4$ | Herb cover | Δ Herb cover | Herb S |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Fire (degree-hr) | 1.000 | | | | | | | | | | | | | | | | | |
| Load | 0.1836 | 1.000 | | | | | | | | | | | | | | | | |
| | 0.3144 | | | | | | | | | | | | | | | | | |
| Fine fuel loss | **0.3941** | −0.2623 | 1.000 | | | | | | | | | | | | | | | |
| | **0.0256** | 0.1469 | | | | | | | | | | | | | | | | |
| FF loss | **0.6572** | −0.1201 | **0.4747** | 1.000 | | | | | | | | | | | | | | |
| | **<0.0001** | 0.5126 | **0.0061** | | | | | | | | | | | | | | | |
| Δ shrub mass | 0.0095 | 0.0799 | **−0.3848** | 0.2307 | 1.000 | | | | | | | | | | | | | |
| | 0.9590 | 0.6638 | **0.0297** | 0.2040 | | | | | | | | | | | | | | |
| Live tree | **−0.5689** | 0.0054 | **−0.5081** | **−0.6490** | −0.0916 | 1.000 | | | | | | | | | | | | |
| | **0.0007** | 0.9765 | **0.0030** | **<0.0001** | 0.6181 | | | | | | | | | | | | | |
| Δ Live tree | **0.7301** | 0.1450 | **−0.4819** | **0.6361** | −0.1396 | **−0.6413** | 1.000 | | | | | | | | | | | |
| | **<0.0001** | 0.4284 | **0.0052** | **<0.0001** | 0.4459 | **0.0001** | | | | | | | | | | | | |
| Dead tree | **0.6126** | 0.1061 | **0.4507** | **0.5011** | −0.1808 | **−0.4786** | **0.9375** | 1.000 | | | | | | | | | | |
| | **0.0002** | 0.5631 | **0.0096** | **0.0035** | 0.3219 | **0.0056** | **<0.0001** | | | | | | | | | | | |
| Δ Dead tree | **−0.6360** | −0.1135 | **−0.4770** | **−0.5096** | 0.1922 | **0.5486** | **−0.9377** | **−0.9742** | 1.000 | | | | | | | | | |
| | **<0.0001** | 0.5363 | **0.0058** | **0.0029** | 0.2918 | **0.0012** | **<0.0001** | **0.0001** | | | | | | | | | | |
| Soil $NO_3$ | 0.2505 | −0.0893 | **0.4927** | 0.3345 | −0.1871 | **−0.3986** | **0.4232** | **0.4496** | **−0.4523** | 1.000 | | | | | | | | |
| | 0.1667 | 0.6269 | **0.0042** | 0.0613 | 0.3052 | **0.0238** | **0.0158** | **0.0098** | **0.0093** | | | | | | | | | |
| Soil $NH_4$ | **0.5927** | 0.1083 | 0.1934 | **0.5199** | 0.0750 | **−0.5257** | **0.4864** | **0.4608** | **−0.4910** | 0.3019 | 1.000 | | | | | | | |
| | **0.0004** | 0.5551 | 0.2889 | **0.0023** | 0.6833 | **0.0020** | **0.0048** | **0.0080** | **0.0043** | 0.0931 | | | | | | | | |
| Δ Soil N | 0.2179 | −0.1115 | 0.1144 | 0.1723 | 0.2788 | 0.2625 | 0.0180 | −0.0339 | −0.0031 | 0.1164 | 0.3691 | 1.000 | | | | | | |
| | 0.2309 | 0.5435 | 0.5330 | 0.3457 | 0.1223 | 0.1467 | 0.9222 | 0.8537 | 0.9866 | 0.5258 | 0.0376 | | | | | | | |
| Δ Soil Ca | −0.0961 | −0.0318 | −0.1069 | 0.0082 | 0.0696 | 0.2782 | −0.0757 | −0.0756 | 0.1669 | −0.1578 | −0.3106 | **0.6483** | 1.000 | | | | | |
| | 0.6008 | 0.8484 | 0.5603 | 0.9646 | 0.7052 | 0.1232 | 0.6807 | 0.6811 | 0.3612 | 0.3884 | 0.0836 | **<0.0001** | | | | | | |
| Solution $NO_3$ | **0.4392** | −0.0674 | **0.5060** | 0.2726 | −0.3165 | **−0.4265** | **0.6925** | **0.7099** | **−0.7305** | **0.6606** | 0.1664 | −0.2270 | −0.1457 | 1.000 | | | | |
| | **0.0119** | 0.7139 | **0.0031** | 0.1311 | 0.0776 | **0.0149** | **<0.0001** | **<0.0001** | **<0.0001** | **<0.0001** | 0.3628 | 0.2116 | 0.4262 | | | | | |
| Solution $NH_4$ | **0.4826** | 0.2540 | 0.1443 | 0.3187 | 0.0098 | −0.2864 | **0.7063** | **0.7414** | **−0.7309** | 0.0526 | **0.5807** | 0.1192 | −0.1567 | 0.2704 | 1.000 | | | |
| | **0.0051** | 0.1607 | 0.4306 | 0.0754 | 0.9574 | 0.1120 | **<0.0001** | **<0.0001** | **<0.0001** | 0.7749 | **0.0005** | 0.5158 | 0.3918 | 0.1345 | | | | |
| Herb cover | −0.2710 | 0.1552 | −0.1337 | −0.0070 | **0.4067** | 0.0213 | −0.2267 | −0.2121 | 0.2284 | −0.1348 | −0.1991 | 0.1231 | −0.0119 | −0.1978 | −0.1910 | 1.000 | | |
| | 0.1336 | 0.3963 | 0.4656 | 0.9695 | **0.0209** | 0.9079 | 0.2121 | 0.2439 | 0.5086 | 0.4619 | 0.2747 | 0.5022 | 0.9485 | 0.2778 | 0.2951 | | | |
| Δ Herb cover | 0.1748 | −0.1770 | −0.2271 | −0.1996 | −0.1908 | 0.1078 | 0.0319 | 0.1524 | −0.1408 | 0.1703 | 0.2927 | −0.0948 | −0.3016 | 0.1579 | 0.2156 | **−0.5339** | 1.000 | |
| | 0.3386 | 0.3326 | 0.2112 | 0.2733 | 0.2954 | 0.5571 | 0.8626 | 0.4050 | 0.4419 | 0.3513 | 0.1040 | 0.6059 | 0.0934 | 0.3880 | 0.2360 | **0.0016** | | |
| Herb S | −0.3071 | 0.2998 | −0.1380 | 0.0504 | **0.3949** | −0.0969 | −0.2083 | −0.2578 | 0.2324 | −0.1262 | −0.2222 | −0.0618 | 0.0739 | −0.2441 | −0.2254 | −0.6339 | **0.8665** | 1.000 |
| | 0.0873 | 0.0955 | 0.4512 | 0.7842 | **0.0253** | 0.5979 | 0.2526 | 0.1544 | 0.2006 | 0.4911 | 0.2215 | 0.7369 | 0.6877 | 0.1783 | 0.2149 | 0.0001 | **0.0001** | |
| Δ Herb S | 0.1160 | −0.3929 | −0.1001 | −0.2057 | **−0.3579** | 0.2771 | 0.0282 | 0.1536 | −0.1008 | 0.1142 | 0.1745 | 0.0571 | −0.0053 | 0.1430 | 0.1348 | **0.7869** | **−0.6821** | **−0.8662** |
| | 0.5272 | 0.0261 | 0.5856 | 0.2587 | **0.0443** | 0.1247 | 0.8781 | 0.4011 | 0.5831 | 0.5337 | 0.3394 | 0.7563 | 0.9772 | 0.4349 | 0.4619 | **0.0001** | **0.0001** | **0.0001** |

Fire severity as estimated by degree-hr; load is preburn (2005) down dead biomass = down large wood (⩾7.5 cm diameter) + down small wood (<7.5 cm diameter) + forest floor (Oi + Oe + Oa layers); Fine fuel loss = preburn fine fuel (down small wood < 7.5 cm diameter) − postburn (2006) fine fuel; FF loss = preburn Oi + Oe + Oa forest floor − postburn Oi + Oe + Oa forest floor; Δ shrub mass = preburn shrub layer (woody stems <5.0 cm dbh, and >0.5 m height) biomass − postburn shrub layer biomass; live tree = postburn biomass of standing live trees; Δ live tree = preburn live tree biomass − postburn live tree biomass; dead tree = postburn biomass of standing dead trees; Δ dead tree = preburn dead tree biomass − postburn dead tree biomass; soil $NO_3$ = soil nitrate-nitrogen concentration in 2006; soil $NH_4$ = soil ammonium-nitrogen concentration in 2006; Δ Soil N = soil N 2005 − soil N 2006; Δ Soil Ca = soil exchangeable Ca concentration 2005 − soil exchangeable Ca concentration 2006; solution $NO_3$ = soil solution $NO_3$ at 30 cm soil depth in 2006; solution $NH_4$ = soil solution $NH_4$ at 30 cm soil depth in 2006; herb cover = herbaceous layer cover in 2006; Δ herb cover = herbaceous layer cover 2005 − herbaceous layer cover 2006; herb S = herbaceous layer richness in 2006; Δ herb S = herbaceous layer richness 2005 − herbaceous layer richness 2006. Pre-treatment data were collected in 2005 and post-treatment (following the prescribed fires) data was collected in 2006.

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**Appendix C**

Bivariate correlations (Pearson coefficients with *P*-values, *df* = 32) among variables evaluated for path analysis for the second year after restoration treatments (2007).

| | Fire severity | Load | Fine fuel loss | FF loss | Δ shrub mass | Live tree | Δ Live tree | Dead tree | Δ Dead tree | Soil $NO_3$ | Soil $NH_4$ | Δ Soil N | Δ Soil Ca | Solution $NO_3$ | Solution $NH_4$ | Herb cover | Δ Herb cover | Herb S |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Fire (degree-hr) | 1.000 | | | | | | | | | | | | | | | | | |
| Load | 0.1836 | 1.000 | | | | | | | | | | | | | | | | |
| | 0.3144 | | | | | | | | | | | | | | | | | |
| Fine fuel loss | **0.3941** | −0.2623 | 1.000 | | | | | | | | | | | | | | | |
| | **0.0256** | 0.1469 | | | | | | | | | | | | | | | | |
| FF loss | **0.6572** | −0.1201 | **0.4747** | 1.000 | | | | | | | | | | | | | | |
| | **0.0001** | 0.5126 | **0.0061** | | | | | | | | | | | | | | | |
| Δ shrub mass | −0.2383 | 0.1502 | **0.3847** | −0.1454 | 1.000 | | | | | | | | | | | | | |
| | 0.1890 | 0.4120 | **0.0297** | 0.4271 | | | | | | | | | | | | | | |
| Live tree | **−0.5689** | 0.0054 | **−0.5081** | **−0.6490** | 0.2435 | 1.000 | | | | | | | | | | | | |
| | **0.0007** | 0.9765 | **0.0030** | **0.0001** | 0.1793 | | | | | | | | | | | | | |
| Δ Live tree | **−0.7301** | 0.1450 | **−0.4819** | **0.6361** | −0.3384 | **−0.6413** | 1.000 | | | | | | | | | | | |
| | **0.0001** | 0.4284 | **0.0052** | **0.0001** | 0.0581 | **0.0001** | | | | | | | | | | | | |
| Dead tree | **0.6126** | 0.1061 | **0.4507** | **0.5011** | **−0.3586** | **−0.4786** | **0.9375** | 1.000 | | | | | | | | | | |
| | **0.0002** | 0.5631 | **0.0096** | **0.0035** | **0.0438** | **0.0056** | **<0.0001** | | | | | | | | | | | |
| Δ Dead tree | **0.6360** | −0.1135 | **0.4770** | **−0.5096** | **0.3775** | **0.5486** | **−0.9377** | **−0.9742** | 1.000 | | | | | | | | | |
| | **0.0001** | 0.5363 | **0.0058** | **0.0029** | **0.0332** | **0.0012** | **<0.0001** | **0.0001** | | | | | | | | | | |
| Soil $NO_3$ | **0.5668** | 0.1241 | 0.2215 | **0.4163** | −0.2471 | **−0.4270** | **0.5321** | **0.5048** | **−0.5312** | 1.000 | | | | | | | | |
| | **0.0007** | 0.4987 | 0.2232 | **0.0178** | 0.1727 | **0.0148** | **0.0017** | **0.0032** | **0.0018** | | | | | | | | | |
| Soil $NH_4$ | 0.2731 | −0.1050 | **0.3503** | 0.2986 | −0.1172 | −0.3314 | 0.2291 | 0.2382 | −0.2927 | 0.2809 | 1.000 | | | | | | | |
| | 0.1304 | 0.5673 | **0.0493** | 0.0970 | 0.5229 | 0.0639 | 0.2073 | 0.1893 | 0.1040 | 0.1194 | | | | | | | | |
| Δ Soil N | −0.2504 | 0.1794 | −0.0468 | −0.1635 | −0.1313 | 0.1414 | 0.0205 | 0.1141 | −0.0738 | −0.2930 | −0.2726 | 1.000 | | | | | | |
| | 0.1669 | 0.3259 | 0.7991 | 0.3712 | 0.4738 | 0.4401 | 0.9114 | 0.5341 | 0.6883 | 0.1037 | 0.1311 | | | | | | | |
| Δ Soil Ca | −0.3376 | 0.1520 | 0.1262 | −0.1681 | 0.2460 | 0.2841 | −0.3345 | −0.2571 | 0.3294 | **−0.5105** | −0.0627 | **0.4314** | 1.000 | | | | | |
| | 0.0588 | 0.4062 | 0.4914 | 0.3578 | 0.1749 | 0.1151 | 0.0613 | 0.1554 | 0.0656 | **0.0028** | 0.7331 | **0.0137** | | | | | | |
| Solution $NO_3$ | 0.1512 | 0.0349 | **0.4799** | 0.3277 | −0.2294 | −0.2557 | **0.4446** | **0.5038** | **−0.5155** | 0.0333 | **0.4307** | 0.0500 | −0.1503 | 1.000 | | | | |
| | 0.4089 | 0.8575 | **0.0084** | 0.0671 | 0.2065 | 0.1578 | **0.0108** | **0.0033** | **0.0025** | 0.8563 | **0.0139** | 0.7856 | 0.4116 | | | | | |
| Solution $NH_4$ | 0.2386 | 0.0555 | 0.0144 | 0.1748 | 0.1774 | −0.1629 | −0.0092 | 0.0344 | −0.0748 | 0.1587 | 0.3095 | 0.0375 | 0.0847 | 0.0928 | 1.000 | | | |
| | 0.1884 | 0.7790 | 0.9420 | 0.3387 | 0.3314 | 0.3730 | 0.9603 | 0.8515 | 0.6841 | 0.3858 | 0.0847 | 0.8386 | 0.6447 | 0.6133 | | | | |
| Herb cover | 0.1106 | 0.2115 | 0.1405 | 0.3307 | −0.1266 | −0.3120 | 0.1831 | 0.1914 | −0.1691 | −0.0556 | 0.1793 | 0.0802 | 0.0828 | 0.0389 | 0.0251 | 1.000 | | |
| | 0.5467 | 0.2452 | 0.4431 | 0.0645 | 0.4899 | 0.0821 | 0.3157 | 0.2939 | 0.3549 | 0.7622 | 0.3261 | 0.6628 | 0.6522 | 0.8328 | 0.8917 | | | |
| Δ Herb cover | **−0.3762** | 0.3054 | **0.5397** | **−0.6026** | **0.4169** | **0.5265** | **−0.5229** | **−0.4222** | **0.4232** | −0.0363 | −0.2766 | −0.1666 | 0.0368 | −0.3575 | −0.0110 | **−0.5602** | 1.000 | |
| | **0.0338** | 0.0892 | **0.0014** | **0.0003** | **0.0176** | **0.0020** | **0.0021** | **0.0161** | **0.0158** | 0.8438 | 0.1255 | 0.3620 | 0.8413 | 0.0445 | 0.9525 | **0.0009** | | |
| Herb S | −0.0912 | 0.2278 | 0.0831 | 0.2962 | 0.1137 | −0.3033 | 0.0552 | −0.0146 | −0.0088 | −0.1565 | 0.1184 | 0.1592 | 0.2375 | 0.0148 | 0.0174 | **−0.3984** | **0.7708** | 1.000 |
| | 0.6197 | 0.2098 | 0.6510 | 0.0998 | 0.5354 | 0.0915 | 0.7643 | 0.9368 | 0.9620 | 0.3922 | 0.5188 | 0.3842 | 0.1907 | 0.9361 | 0.9247 | **0.0239** | **0.0001** | |
| Δ Herb S | −0.2872 | **0.3692** | **0.4735** | **−0.5670** | 0.1177 | **0.5701** | **−0.4218** | −0.2740 | 0.3192 | −0.0594 | −0.1644 | −0.0488 | 0.0988 | −0.2282 | −0.0541 | **−0.5661** | **0.6828** | **−0.7363** |
| | 0.1110 | **0.0376** | **0.0062** | **0.0007** | 0.5211 | **0.0007** | **0.0162** | 0.1291 | 0.0749 | 0.7468 | 0.3686 | 0.7908 | 0.5904 | 0.2090 | 0.7688 | **0.0008** | **0.0001** | **0.0001** |

Fire severity as estimated by degree-hr; load is preburn (2005) down dead biomass = standing dead trees + down large wood (⩾7.5 cm diameter) + down small wood (<7.5 cm diameter) + forest floor (Oi + Oe + Oa layers); Fine fuel loss = preburn fine fuel (down small wood <7.5 cm diameter) – postburn (2006) fine fuel; FF loss = preburn Oi + Oe + Oa forest floor – postburn Oi + Oe + Oa forest floor; Δ shrub mass = preburn shrub layer (woody stems <5.0 cm dbh, and >0.5 m height) biomass – postburn shrub layer biomass; live tree = postburn biomass of standing live trees; Δ live tree = preburn live tree biomass – postburn live tree biomass; dead tree = postburn biomass of standing dead trees; Δ dead tree = preburn dead tree biomass – postburn dead tree biomass; soil $NO_3$ = soil nitrate-nitrogen concentration in 2007; soil $NH_4$ = soil ammonium-nitrogen concentration in 2007; Δ Soil N = soil N 2005 – soil nitrogen 2007; Δ Soil Ca = soil exchangeable Ca concentration 2005 – soil exchangeable Ca concentration 2007; solution $NO_3$ = soil solution $NO_3$ at 30 cm soil depth in 2007; solution $NH_4$ = soil solution $NH_4$ at 30 cm soil depth in 2007; herb cover = herbaceous layer cover in 2007; Δ herb cover = herbaceous layer cover 2005 – herbaceous layer cover 2007; herb S = herbaceous layer richness in 2007; Δ herb S = herbaceous layer richness 2005 – herbaceous layer richness 2007. Pre-treatment data were collected in 2005 and post-treatment (following the prescribed fires) data were collected in 2007.

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of live overstory species; pre-burn (2005) and post-burn (2006) for each of the restoration treatment.

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