TEMPORAL DYNAMICS AFFECTING GROUND FLORA

RECOVERY AFTER FIRE IN THINNED

PINUS-QUERCUS STANDS

by

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ABSTRACT

The ground flora stratum affects stand structure, resource acquisition, nutrient cycling, and taxonomic richness in forest ecosystems. Disturbances, such as thinning and prescribed fire, alter understory growing conditions that generally increase ground flora cover and richness in stands across the U.S. However, few studies have quantified annual changes in ground flora after a prescribed fire in thinned stands to provide finer temporal resolution of ground flora recovery. I performed a space-for-time study that quantified changes in ground flora assemblages over three growing seasons post-fire in thinned and frequently burned *Pinus-Quercus* stands. My results corroborated trends from other forest types and regions that indicated greater ground flora richness and cover after thinning and burning compared to thin-only treatments. I also found that the stratum experienced relatively rapid succession between growing seasons. Forbs had annual reductions in cover and richness with increasingly difficult growing conditions after the first growing season, while woody plants and shrubs increased in richness over time. The transition from herbaceous to woody dominance in three years was indicative of changing competition dynamics that favored quick growth in the first growing season and long-term investment in vertical growth in the third growing season. Although beneficial for increased ground flora cover, forb taxonomic richness, and reduced fuel levels, the three-year fire return interval did not produce comparable *Pinus* and *Quercus* regeneration to overstory composition. Management of eastern U.S. *Pinus-Quercus* stands may need to account for potential mesophytic dominance in seedling and sapling size classes that occur in thinned and burned stands over time. If

mesophytic dominance becomes an issue, managers could include growing season fires and a secondary thin to foster desired regeneration to recruit into the overstory, although general weather conditions during the growing season could make fires hard to routinely implement.

LIST OF ABBREVIATIONS AND SYMBOLS

α   Alpha, the likelihood that the true population parameter lies outside the sample confidence interval

°   Degrees

%   Percent

>   Greater than

<   Less than

=   Equal to

≥   Greater than or equal to

≤   Less than or equal to

±   Plus or minus

•   Species presence

*   Statistical significance at $p < 0.05$

**   Statistical significance at $p < 0.01$

***   Statistical significance at $p < 0.001$

BNF   Bankhead National Forest

C   Celsius

cm   Centimeters

dbh   Diameter at breast height

FCA   Fourth Corner Analysis

FIA   Forest Inventory Analysis

g	Gram
G.S.	Growing season
ha	Hectare
ISA	Indicator species Analysis
m	Meter
NCVS	North Carolina vegetation survey
NMS	Non-metric multidimensional scaling
p	Probability of occurrence under the null hypothesis of obtaining a value as extreme or more extreme than the observed value
PerMANOVA	Distance-based multivariate analysis of variances
PPFD	Photosynthetic photon flux density
r	Spearman/Pearson correlation coefficient
r^2	Regression coefficient of determination
SE	Standard error
USFS	United States Forest Service

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1. INTRODUCTION

The ground flora stratum (herbaceous and woody plants ≤ 1 m from the forest floor) constitutes a majority of plant diversity and rare species in eastern U.S. forests (Hutchinson 2005, Gilliam 2007). A productive ground flora stratum alters stand structure and increases resource complexity and species diversity. Ground flora change vertical stand development through competition for growing space and resources. As understory competition affects tree regeneration, future overstory composition may be influenced by ground flora (Lorimer *et al.* 1994, Donoso and Nyland 2006, Gilliam 2007). Herbaceous plants in the ground flora stratum have low biomass to net primary productivity ratios to rapidly cycle nutrients through annual senesce and may increase litter decomposition rates, which increase stand productivity and maintain soil fertility (Rochow 1974, Dybzinski *et al.* 2008, Fujii *et al.* 2017). Ground flora richness coincides with higher species diversity in other trophic levels of the food web by providing resources to an array of insects, birds, and mammals in forest ecosystems (Fralish 2004, Hutchinson 2005, Barrioz *et al.* 2013). Ground flora and associated faunal richness add complexity and diversity to stands that indicate enhanced stand resilience to disturbances (Peterson *et al.* 1998).

Disturbances, such as thinning and prescribed surface fires, are discrete events in space and time that alter stand structure and composition (Pickett and White 1985). Silvicultural treatments that impact stand overstory and midstory structure may also promote ground flora diversity (Hutchinson 2005, Waldrop *et al.* 2007). Thinning is an intermediate-scale tending method that increases space and resource availability to enhance desirable tree species

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recruitment to larger size classes, improve stand health, increase the diameter of residual trees, and create wildlife habitat in part from increasing ground flora abundance and richness (Hutchinson 2005, Iverson *et al.* 2008, Nyland 2016). Thinning may also improve seedling establishment and recruitment by increasing photosynthetically active radiation near the forest floor (Lhotka *et al.* 2009, 2013). Increased light availability may promote rapid growth in understory strata because light is often the most limited resource to understory plants in closed canopy stands (Scharenbroch *et al.* 2012, Waldrop *et al.* 2016).

Managers prescribe low-intensity surface fire to reduce unwanted competition and create site conditions that favor specific tree species. Multiple studies have indicated that ground flora richness and cover significantly increases less than two years after fire in hardwood and *Pinus* L. stands (Arthur *et al.* 1998, Hutchinson 2005, Phillips *et al.* 2007, Phillips and Waldrop 2008). Reduced tree density from repeated burns may increase light availability that benefits ground flora establishment over time (Hutchinson 2004, Arthur *et al.* 2012). Ground flora also positively respond to the sudden macronutrient availability of nitrogen, carbon, and phosphorus that may be released by the combustion of duff and litter layers after fire (Gray and Dighton 2009, Scharenbroch *et al.* 2012, Alcañiz *et al.* 2018). Surface fires top-kill fire-intolerant plants and temporarily clear litter to increase space and mineral soil accessibility for ground flora seed germination (Frost 1998, Hiers *et al.* 2007, Moghaddas *et al.* 2008, Schwilk *et al.* 2009).

Effects of combined thinning and prescribed fire on ground flora have recently been a focus of study (e.g. Schwilk *et al.* 2009, Wilms *et al.* 2017). Ground flora richness and cover increased in *Pinus* and hardwood dominated stands that were thinned and burned as compared to thinned-only stands (Waldrop *et al.* 2007, Phillips and Waldrop 2008). Comparisons with burned-only stands did not return conclusive results, potentially because light availability varied

in the understory of burned-only stands between studies (Franklin *et al.* 2003, Hutchinson 2005, Phillips *et al.* 2007). Brewer (2016) reported significant increases in ground flora richness in tornado-disturbed *Pinus-Quercus* L. stands that were burned compared to tornado-disturbed and unburned stands. Fulé *et al.* (2005) and Kinkead *et al.* (2013) found that thinned and burned stands with a high composition of *Pinus* and *Quercus* had significantly greater understory plant cover. Kinkead *et al.* (2013) also reported concerns that a dense layer of woody shrubs, saplings, and vines could inhibit future herbaceous plant development and limit long-term biodiversity. Mixed *Pinus-Quercus* stands are unique in vertical light structure as compared to pine, oak, or other mixed-hardwood dominated stands because of differences in species leaf and canopy architecture and light penetration into the understory (Canham *et al.* 1994, Messier *et al.* 1998). Because overstory composition alters light availability in light-limited forests, ground flora may uniquely respond to thinning and prescribed fire in *Pinus-Quercus* stands with unique light structure compared to *Pinus* or hardwood dominated stands. However, the little research that has occurred in this stand type has not been performed in light-limited eastern U.S. *Pinus-Quercus* stands, indicating a dearth of knowledge for how could ground flora respond to these disturbances. Researchers have also reported a lack of quantitative data that have studied ground floral response to repeated burns beyond a decade and have defined it as an important research gap (Hutchinson 2004, Arthur *et al.* 2012, Matlack 2013).

The ground flora stratum recovers relatively rapidly from a disturbance compared to midstory and overstory strata. Thinning immediately moves energy exchange levels closer to the forest floor (Fahey *et al.* 2016), which in turn increases ground flora photosynthetic productivity (Huang *et al.* 2007). Surface burns generally reduce the aboveground biomass of most understory herbaceous and woody plants, thus immediately increasing resource and space

availability that provide favorable growing conditions for ground flora in subsequent growing seasons. However, midstory and overstory trees outcompete ground flora by moving the level of energy exchange to higher vertical positions that limits ground flora photosynthetic production within five years (Pickett and White 1985, Oliver and Larson 1996, Nyland 2016). Studies of ground flora in thinned and burned eastern U.S. hardwood stands and *Pinus* stands elucidated rapid increases in ground flora cover and richness over a one to three-year period (Phillips *et al.* 2007, Phillips and Waldrop 2008, Outcalt and Brockway 2010, Lettow *et al.* 2014). However, I could find no research that has quantified annual ground flora development in light-limited thinned and burned *Pinus-Quercus* stands, which indicates a lack of data quantifying ground flora recovery at finer temporal scales in a stand type with unique light structure characteristics.

I studied the ground flora stratum over three growing seasons post-prescribed fire in *Pinus-Quercus* stands 12 years after a thinning treatment and four burns that were performed every three years. My overarching goal was to explain how environmental variables affected ground flora in thinned and burned stands. Specific goals included: 1) determine how annual ground flora composition and cover changed in three growing seasons (i.e. annually over the fire rotation) and 2) determine which environmental variables best explained annual changes in composition and cover. I hypothesized that ground flora diversity would increase during the first growing season after fire, then decrease as ground flora cover, sapling density, and tree density increased. I also hypothesized that resource and space metrics, such as tree and sapling density, litter depth, and/or light availability, would explain annual changes in ground flora cover over the three-year burn cycle. My results were also used to develop recommendations for managing *Pinus-Quercus* stands for ground flora assemblages.

2. METHODS

2.1 Study Area

This study was conducted on the William B. Bankhead National Forest (BNF) in northwestern Alabama, which is situated on the southern Cumberland Plateau (Fenneman 1938, Figure 1). The Cumberland Plateau corresponds with the Southwest Appalachian level III ecoregion (Griffith *et al.* 2001). Braun (1950) classified the region as a transition between mixed-mesophytic forest to the north and *Pinus-Quercus* forest to the south. The underlying bedrock is the Pennsylvania Pottsville formation, which includes sandstone, stratified shale, and siltstone (Szabo *et al.* 1988). Soil is classified as Typic Hapludults and Dystrudepts, which are well drained, moderately deep, strongly acidic, and low in nutrients (U.S. Department of Agriculture Soil Conservation Services 1959). Regional climate is classified as humid mesothermal, consisting of long, hot summers and short, mild winters (Thornthwaite 1948). Annual precipitation averages 138 cm, with a monthly mean of 13.8 cm in January and 11.3 cm in July (PRISM Climate Group, 2017). Average annual temperature is 15 °C, with a monthly means of 26 °C in July and 5 °C in January. Smalley (1979) determined the region to have an average growing season of 220 days a year, spanning from late-March to late-November.

Land in BNF was previously cut over and farmed for agriculture until the early 1920s (Addor and Birkhoff 2004). The U.S. Forest Service (USFS) purchased and began to manage stands in Alabama national forests as *Pinus* plantations in the 1930s (USFS 2004). BNF managers planted the current overstory *Pinus taeda* L. (loblolly pine) between 1972 and 1979, which went largely unmanaged for 30 years post-establishment (Schweitzer *et al.* 2016).
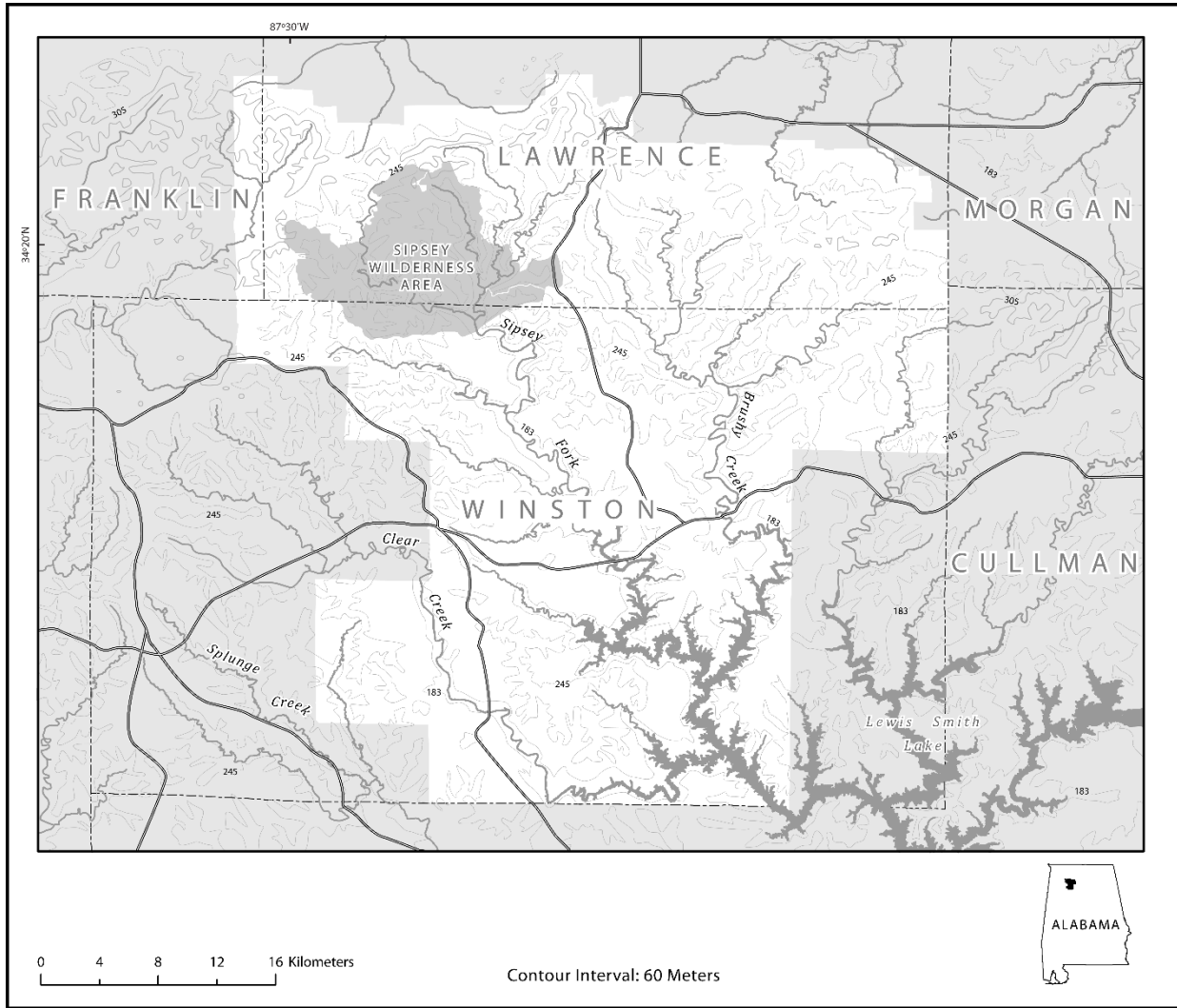
Figure 1. Map of Bankhead National Forest and the Sipsey Wilderness in northwestern Alabama.

Following a *Dendroctonus frontalis* Zimmermann (southern pine beetle) outbreak that caused high mortality in southern pine forests, BNF managers decided to restore the plantations to historical *Pinus-Quercus* mixed composition (Addor and Birkhoff 2004). Managers also implemented a prescribed burn program to reduce litter and fuel loads and prepare the *P. taeda* plantations for regeneration and transition to mixed species stands. In 2004, a study was initiated to quantify how thinning and prescribed burning affected stand composition and structure. A randomized 3×3 factorial experiment was created to test combinations of three thinning levels (control: none; low intensity: basal area reduced to 17.2 m^2 ha^{-1}; high intensity: basal area reduced to 11.5 m^2 ha^{-1}) and three fire frequencies (control: none; infrequently burned: once every nine years; frequently burned: once every three years), which were replicated four times each (Schweitzer *et al.* 2016). Over the following 12 years, understory *Quercus* were released into the overstory and currently comprise of 18% of basal area in frequently burned treatments.

Our study plots included replicates from the above study by Schweitzer *et al.* (2016) that experienced a high intensity thin and burned every three years or not burned at all. Because replicates were initially burned in sequential years, three blocks were at different stages of recovery after the most recent fire, which enabled a space-for-time study design to be imposed on the original design. Thinning operations were done in 2005 as a free thin using a wheeled feller-buncher with a hydro-axe attachment and crawler mounted feller bunch to cut trees and a forwarder with a loader bucket to move felled trees to the landing. Slash was left on site. Operators targeted trees of all merchantable size classes and removed 457 stems ha^{-1} across studied stands. Study plots have been burned four times since 2006, with fires set during the dormant months from January–March (Schweitzer *et al.* 2016). Temperatures were recorded 25 cm above the ground surface using 30 HOBO temperature probes (HOBO TCP6-K12 Probe

Thermocouple Sensor, Onset Computer Corporation, Cape Cod, Massachusetts, USA) distributed across the stand. Burns were ignited with hand strip fires at eight-meter intervals and aerial ignitions using potassium permanganate. Fires averaged 95.5 °C during the first burn, 123.2 °C for the second burn, 208.4 °C for the third burn, and 195.6 °C during the fourth and most recent burn (Schweitzer *et al.* 2016). Temperatures averaged over 32 °C for approximately 55% of the time during the most recent fire.

2.2 Field Methods

Plots were established in three treatments identified by growing season since burn: first growing season (G.S. 1, burned Spring 2017), second growing season (G.S. 2, burned Spring 2016), and third growing season (G.S. 3, burned Spring 2015). Plots were also established in stands that had a high intensity thin, but were not burned as a control. I randomly selected plots using a fishnet overlay in ArcMap v.10.3 (Environmental Systems Research Institute, Redlands, CA, U.S.) clipped to each stand. A random number generator was used to select numbers within the range of the fishnet to determine plot location. Plots were relocated if placed within 15 m of other plots, on sites near streams or with steep slopes, or within 25 m of the stand boundary. Field surveys and sampling occurred from June through August 2017.

To quantify litter, light availability, ground flora, sapling, and overstory tree variables, twenty 0.05-ha (500-m^2) fixed-radius plots were established in each block. In each plot, saplings (woody stems $\geq$ 1m in height and $\leq$ 5 cm in diameter at breast height (dbh)) were identified to species and counted for density. Trees larger than 5 cm dbh were identified to species, measured for basal area, counted for density, and assigned a crown position. Crown positions were based on light interception compared to adjacent overstory trees and included dominant, co-dominant,

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intermediate, and overtopped trees (Oliver and Larson 1996). Hemispherical photos were taken at plot center using a Nikon fisheye lens attached to an Olympus Stylus TG-3 camera mounted on a self-leveling tripod using a Mid-O Mount 10MP (Regent Instruments, 2011) at 1 m from the ground to capture light availability at the top of the ground flora stratum. Photos were oriented north and collected at dawn, dusk, or in overcast conditions to maintain consistency and reduce glare and sun fleck error during photo analysis.

I established three 12.4 m transects at 0 degrees (north), 120 degrees (southeast), and 240 degrees (southwest), along which ten 1×1 m subplots (10-m^2) were placed. Within subplots, all ground flora species were identified to the lowest taxonomic level possible given available reproductive structures. To ensure all plants were properly inventoried and identified, new and/or unidentifiable species were collected as voucher specimens. Plants accurately identified to species occurred in genera that also contained unidentified species. However, these species and genera were analyzed as distinct groups for taxonomic richness and non-metric multidimensional scaling (NMS) tests. For example, *Solidago arguta* Aiton (goldenrod) and *Solidago odora* Aiton (licorice goldenrod) were analyzed separately from the genus *Solidago*, in which other species were found, but unidentifiable to species. Species authorities and taxonomic classification were determined using Weakley (2015).

I estimated percent cover of ground flora using the North Carolina Vegetation Survey (NCVS) protocol, where 0 = absent, 1 = solitary or few, 2 = 0–1%, 3 = 1–2%, 4 = 2–5%, 5 = 5–10%, 6 = 10–25%, 7 = 25–50%, 8 = 50–75%, 9 = 75–95%, and 10 = 95–100% (Peet *et al.* 1998). Seedlings (woody plants ≤ 1 m in height) were also identified to species, given a cover class, and counted for density within each subplot. Ground cover classes were given to for categories derived from the USFS (2016) grade scale, which included bare ground, *Pinus* litter, broadleaf

litter, coarse woody debris (woody material ≥ 10 cm diameter), fine woody debris (woody material < 10 cm not connected to coarse woody debris), moss, and rock. Every category was assigned a NCVS cover class in each subplot.

Litter was defined as undecomposed or partially decomposed organic material readily identifiable, which included forest floor leaves, needles, twigs, cones, bark, flower parts, and dead moss, lichen and ground flora stems as demarcated by the FIA protocol (Woodall and Monlean 2008). Four 0.25 m^2 quadrats were established to collect litter samples five meters from plot center in the four cardinal directions that were bulked per plot. Litter depth was measured at the four corners of each litter sample plot before litter was collected and averaged for each plot. Slope and aspect were collected to determine if either variable was associated with differences between plots and treatments.

2.3 Analyses

To calculate plot-level NCVS cover classes for ground flora and ground cover, cover classes for each species were converted to the midrange value, averaged across the 10 subplots, and converted back to the corresponding cover class (Peet *et al.* 1998). Ground flora were also analyzed for taxonomic richness and Shannon Weiner's diversity index measures. As ground cover was expected to total ca. 100 percent, the total midrange value was calculated for each plot, averaged across the treatment, and relativized to 100 percent before reconverting values back to NCVS classes to ensure comparable assessments of ground cover variables between treatments.

PC-ORD v. 7.0 was used to run non-metric multidimensional scaling (NMS) to evaluate annual differences between ground flora assemblages (Peck 2016). Distance-based multivariate

analysis of variances (PerMANOVAs) were used to determine if there were significant differences in species assemblages between all treatments. Species that occurred in fewer than two plots were removed from analyses to reduce extraneous error within NMS analyses and prioritize species that represented unique communities. Plot-level cover class values were relativized to each species' maximum cover class to reduce influence of naturally large plants and increase influence of smaller plants in ground flora assemblage analyses (Peck *et al.* 2016). Eleven environmental variables were tested for correlation with ground flora composition and abundance: 1) light availability (percent photosynthetic photon flux density, % PPFD), 2) tree density, 3) sapling density, 4) overstory *P. taeda* relative importance value (average of relative dominance and relative density), 5) litter depth, 6) litter mass, 7) bare ground cover, 8) broadleaf litter cover, 9) *Pinus* litter cover, 10) coarse woody cover, and 11) fine woody cover. An NMS scree plot was used to determine an optimal number of axes to use in the final solution (Peck 2016). Sørensen (Bray-Curtis) distance interpolation was used with 250 runs and was repeated with other solutions to ensure consistency of interpretation. A biplot overlay assessed correlations between axes and environmental variables and were included on ordination plots when r > 0.5.

An indicator species analysis (ISA) determined the most representative species for each growing season post-burn. The ISA used average relative frequency and relative abundance to calculate an indicator value of each species per treatment (Dufrêne and Legendre 1997; Peck 2016). Fourth Corner Analysis (FCA) was used to quantify correspondence between ground flora assemblages by growth habit and environmental variables. To ensure the observed differences between growth habit and environmental variables were statistically significant, randomization

was performed within columns to determine how species by growth habit responded to annual environmental change.

Using the U.S. Department of Agriculture plant classification system (https://plants.usda.gov/java/, accessed: November 2017), ground flora data were classified into four life-form groups to indirectly observe annual changes in ground flora competition dynamics post-fire. Categories included forbs, graminoids, vines, and woody plants (defined as shrubs and trees). Species considered to have multiple growth habits were categorized by growth strategy observed *in situ* (i.e. all *Toxicodendron radicans* L. (poison ivy) were observed as forbs and not as vines). Plants identified to family or genus that include multiple growth habits were removed from this analysis (i.e. *Rubus, Fabaceae*). Average total cover for each growth habit was calculated for each plot by adding the midpoints of the cover for each species plot average and converting the values back to the corresponding NCVS cover class to obtain an average cover class for each season.

Tree data were calculated for total density ha^{-1}, density ha^{-1} by crown position, total live basal area, and relative importance for each species. Seedling counts were summed across the ten quadrats and scaled to hectare level density. Total sapling and tree counts per plot were scaled to hectare level density. Hemispherical photos were analyzed using WinSCANOPY version 2014a (Reagents Instruments 2014) to measure canopy openness and percent PPFD in each plot. Litter was air-dried in the laboratory for 21 days and weighed to measure litter mass.

Data were not normal when first analyzed. Kruskal-Wallis and Mann-Whitney U tests were used to determine if differences in data were significant between treatments. Post-hoc Dunn's test pairwise comparisons were used to determine significant differences of the variables between treatments. Spearman correlations were used to determine significant correlations

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between variables. Total ground flora cover and taxonomic richness, light availability, tree density, and bare ground cover achieved normality via Jaque-Bera tests (Jaque and Bera 1980) and homogeneity of variance via Levene's test after a logarithmic transformation. Highly correlated normalized data were run for single linear and multilinear regressions. Tests for normality were performed using R v. 3.2.2 (R Core Team. Released 2015. R: A Language and Environment for Statistical Computing, Version 3.2.2. Vienna, Austria, https://www.R-project.org) and all other statistical analyses were performed in SPSS v. 22 (IBM Corp. Released 2013. IBM SPSS Statistics for Windows, Version 22.0. Armonk, NY: IBM Corp.).

3. RESULTS

3.1 Ground Flora

I documented a total of 151 ground flora taxa across the four treatments. The control treatment had 75 taxa, G.S. 1 had 107 taxa, G.S. 2 had 98 taxa, and G.S. 3 had 93 taxa. Average aggregated taxonomic richness per plot was significantly higher in burned plots compared to the control ($p < 0.001$). Taxonomic richness per plot decreased from G.S. 1 (35 taxa) to the latter two growing seasons (31 taxa, Table 1), but were not significantly different. Shannon Weiner's diversity index mirrored average taxonomic richness trends and did not indicate any nuanced results compared to taxonomic richness.

3.2 Growth Habit

Burned treatments had significantly more forbs, graminoids, and woody plant taxa per plot compared to the control ($p < 0.001$). Average forb richness was highest in G.S. 1 at 14 taxa per plot (Table 1). Forb richness decreased to nine forb taxa per plot by G.S. 2 and five forb taxa by G.S. 3, which was significantly lower as compared to G.S. 1 ($p < 0.001$). Forb trends were reversed in woody taxa, with significant increases in average richness from 14 taxa per plot in G.S. 1 and G.S. 2 to 18 taxa per plot by G.S. 3 ($p < 0.01$). Vine ground flora richness did not significantly change between the control and any of the three growing seasons.

Ground flora cover significantly increased from an average cover range of 5–10% in the control to 50–75% in burned plots (Table 2). Forb, graminoid, vine, and woody cover were all significantly higher in burned treatments as compared to the control. Ground flora cover did not significantly change over three growing seasons, maintaining cover ranges of either 25–50% or

Table 1. Kruskal-Wallis results summarizing the mean values ($\pm$ SE) of ground flora taxonomic richness by growth habit. Dunn's post-hoc pairwise comparison test letters indicate significance when $\alpha < 0.05$ within individual growing seasons and the control.

Growth Habit	Control	G.S. 1	G.S. 2	G.S. 3	Significance
Forb	1.70 ($\pm$ 0.55)[a]	14.40 ($\pm$ 0.89)[b]	9.30 ($\pm$ 0.94)[bc]	5.35 ($\pm$ 1.05)[c]	$p < 0.001$
Graminoid	1.35 ($\pm$ 0.18)[a]	2.05 ($\pm$ 0.05)[b]	2.00 ($\pm$ 0.00)[b]	1.85 ($\pm$ 0.11)[b]	$p < 0.001$
Woody	11.25 ($\pm$ 0.68)[a]	13.80 ($\pm$ 0.71)[ab]	14.45 ($\pm$ 0.73)[b]	17.90 ($\pm$ 0.57)[c]	$p < 0.001$
Vine	4.50 ($\pm$ 0.22)	4.40 ($\pm$ 0.26)	5.10 ($\pm$ 0.26)	5.00 ($\pm$ 0.23)	$p = 0.105$
Total	18.85 ($\pm$ 0.97)[a]	35.15 ($\pm$ 1.14)[b]	31.00 ($\pm$ 1.31)[b]	31.10 ($\pm$ 1.49)[b]	$p < 0.001$

Table 2. Kruskal-Wallis results summarizing the mean values ($\pm$ SE) of ground flora cover category by growth habit. To remain conservative, cover values were rounded down to determine specific range, where 0 = absent, 1 = solitary or few, 2 = 0–1%, 3 = 1–2%, 4 = 2–5%, 5 = 5–10%, 6 = 10–25%, 7 = 25–50%, 8 = 50–75%, 9 = 75–95%, and 10 = 95–100%. Dunn's post-hoc pairwise comparison test letters indicate significance when $\alpha < 0.05$ within individual growing seasons and the control.

Growth Habit	Control	G.S. 1	G.S. 2	G.S. 3	Significance
Forb	1.45 ($\pm$ 0.27)[a]	5.85 ($\pm$ 0.18)[b]	4.10 ($\pm$ 0.24)[c]	3.65 ($\pm$ 0.38)[c]	$p < 0.001$
Graminoid	1.70 ($\pm$ 0.21)[ac]	3.40 ($\pm$ 0.29)[b]	3.95 ($\pm$ 0.23)[ab]	2.70 ($\pm$ 0.22)[c]	$p < 0.001$
Woody	4.45 ($\pm$ 0.17)[a]	6.70 ($\pm$ 0.13)[b]	7.00 ($\pm$ 0.10)[b]	6.75 ($\pm$ 0.10)[b]	$p < 0.001$
Vine	4.50 ($\pm$ 0.18)[a]	4.85 ($\pm$ 0.20)[ac]	5.80 ($\pm$ 0.22)[b]	5.55 ($\pm$ 0.14)[bc]	$p < 0.001$
Total	5.65 ($\pm$ 0.11)[a]	8.20 ($\pm$ 0.16)[b]	8.20 ($\pm$ 0.12)[b]	7.45 ($\pm$ 0.11)[b]	$p < 0.001$

50–75% throughout all burned plots. However, forb cover significantly decreased after G.S. 1

from 5–10% to 1–2% by G.S. 2 and 0–1% in G.S. 3 ($p < 0.01$). Graminoid cover maintained

cover of 1–2% in G.S. 1 and G.S. 2 before significantly decreasing to 0–1% in G.S. 3 ($p = 0.02$).

Vine cover significantly increased from 2–5% to 5–10% cover by G.S. 2 and maintained higher

cover through G.S. 3 ($p = 0.01$). Woody cover did not significantly change over three growing

seasons post-fire.

3.3 NMS Ordination

The three-dimensional NMS projections had significant differences between all four

treatments (PerMANOVA, $p < 0.001$). Final stress for the three axes solution was 17.8% and

explained a cumulative 78% of variance between assemblages (NMS, McCune and Grace 2002).

Both plots indicated that G.S. 1 was most different from the control, while G.S. 2 and G.S 3

trended closer to control composition (Figure 2). Axis 1 explained 48% of variance within

ground flora composition and projected differences between G.S. 1, G.S. 2 and G.S. 3, and the

control. Axis 1 was most correlated with tree density ($r = -0.717$) and bare ground cover ($r = 0.740$). Axis 2 explained 12% of the variance, but the projection with axis 1 indicated no

difference between G.S. 2 and G.S. 3. Axis 3 explained 18% of the variance and showed a

difference between G.S. 2 and G.S. 3. However, no highly correlated environmental variable

explained the difference.

The ISA resulted in 45 indicator species: three in the control, 18 in G.S. 1, nine in G.S. 2,

and 15 in G.S. 3 (Table 3). When categorized by growth habit, fifteen G.S. 1 indicator species

were categorized as forbs, one as graminoid, and two as woody plants (Figure 3). G.S. 2 had four

woody and forb indicator species each and one vine indicator. By G.S. 3, most indicator species
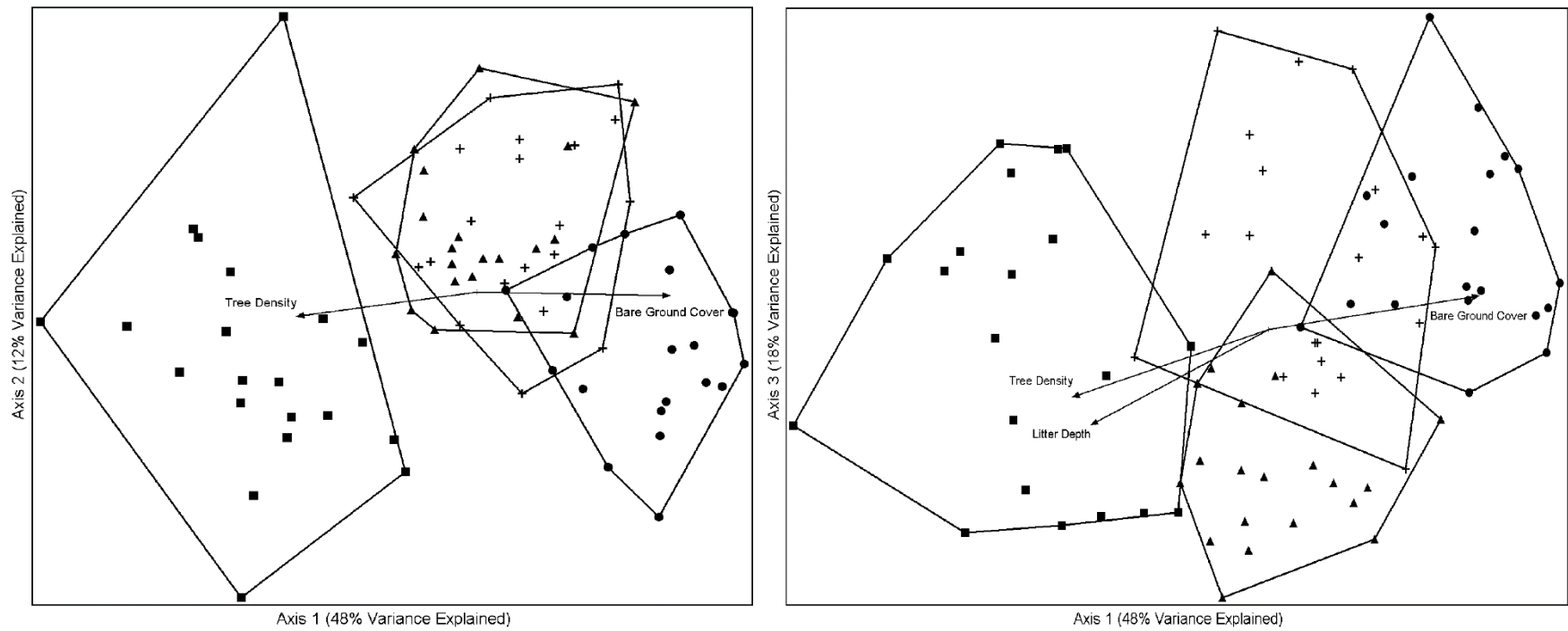
**Figure 2.** Three-dimensional non-metric multidimensional scaling projections based on ground flora abundance in the control (squares), G.S. 1 (circles), G.S. 2 (plus signs), and G.S. 3 (triangles) plots. Convex hulls connect plots in the same growing season and biplot overlays indicate the strength and direction of correlations (r ≥ 0.5) between environmental factors and ordination axes.

Table 3. Indicator Species Analysis results assessing the representative species for each growing season and the control. * indicates α < 0.05, ** indicates α < 0.01, *** indicates α < 0.001, and • indicates presence of the species in the treatment. Bold signifies unique indicator species to the specific treatment.

Species	Growth Habit	Control	G.S. 1	G.S. 2	G.S. 3
Berchemia scandens (Hill) K. Koch	Vine	*	•	•	•
Bignonia capreolata Linnaeus	Vine	*			•
***Callicarpa americana* Linnaeus**	Woody	***			
***Agalinis tenuifolia* (Vahl) Rafinesque**	Forb		*		
Chamaecrista fasciculata (Michaux) Greene	Forb		***	•	
***Chimaphila maculata* (Linnaeus) Pursh**	Forb		*		
***Clitoria mariana* Linnaeus**	Forb		***		
Coreopsis major Walter	Forb		**	•	•
Erechtites hieraciifolius (Linnaeus) Rafinesque ex A.P. de Candolle	Forb		***	•	
Eupatorium rotundifolium Linnaeus	Forb		**	•	•
Helianthus hirsutus Rafinesque	Forb		*	•	•
Iris verna* Linnaeus *var. smalliana	Forb		***		
***Lespedeza hirta* (Linnaeus) Hornemann**	Forb		***		
Lespedeza procumbens Michaux	Forb		***	•	•
Lespedeza repens (Linnaeus) W. Barton	Forb		***	•	•
Lespedeza violacea (Linnaeus) Persoon	Forb		***	•	•
Quercus stellata Wangenheim	Woody		*	•	•
Rhus copallinum Linnaeus var. *copallinum*	Woody		***	•	•
Scleria oligantha Michaux	Graminoid		***	•	
Solidago odora Aiton	Forb		***	•	•
Symphyotrichum patens (Aiton) G.L. Nesom	Forb		*	•	
Carya glabra (P. Miller) Sweet	Woody	•	•	***	•
Galactia volubilis (Linnaeus) Britton	Vine	•		*	•
Helianthus strumosus Linnaeus	Forb			*	•
Liriodendron tulipifera Linnaeus	Woody	•	•	*	•
Oxalis stricta Linnaeus	Forb		•	**	•
Prunus serotina Ehrhart	Woody	•	•	*	•
Solidago arguta Aiton	Forb		•	*	•
Styrax grandifolius Aiton	Woody		•	*	
Toxicodendron radicans (Linnaeus) Kuntze	Forb	•	•	*	•
Amelanchier arborea (Michaux f.) Fernald	Woody	•			**
Asimina triloba (Linnaeus) Dunal	Woody	•	•	•	*
Carya tomentosa (Lamark) Nuttall	Woody	•	•	•	***
Dioscorea villosa	Graminoid		•	•	*
Hydrangea quercifolia Bartram	Woody		•		**
Muscadinia rotundifolia (Michaux) Small	Vine	•	•	•	*
Nyssa sylvatica Marshall	Woody	•	•	•	*
Quercus alba Linnaeus	Woody	•	•	•	**
Quercus velutina Lamarck	Woody	•	•	•	***
Sassafras albidum (Nuttall) Nees	Woody	•	•	•	***
Vaccinium arboreum Marshall	Woody	•	•	•	**

Species	Growth Habit				
Vaccinium corymbosum **Linnaeus**	Woody				*
Vaccinium pallidum **Aiton**	Woody				***
Vaccinium stamineum Linnaeus *var. stamineum*	Woody	•	•	•	***
Vitis aestivalis Michaux *var. aestivalis*	Vine		•	•	**
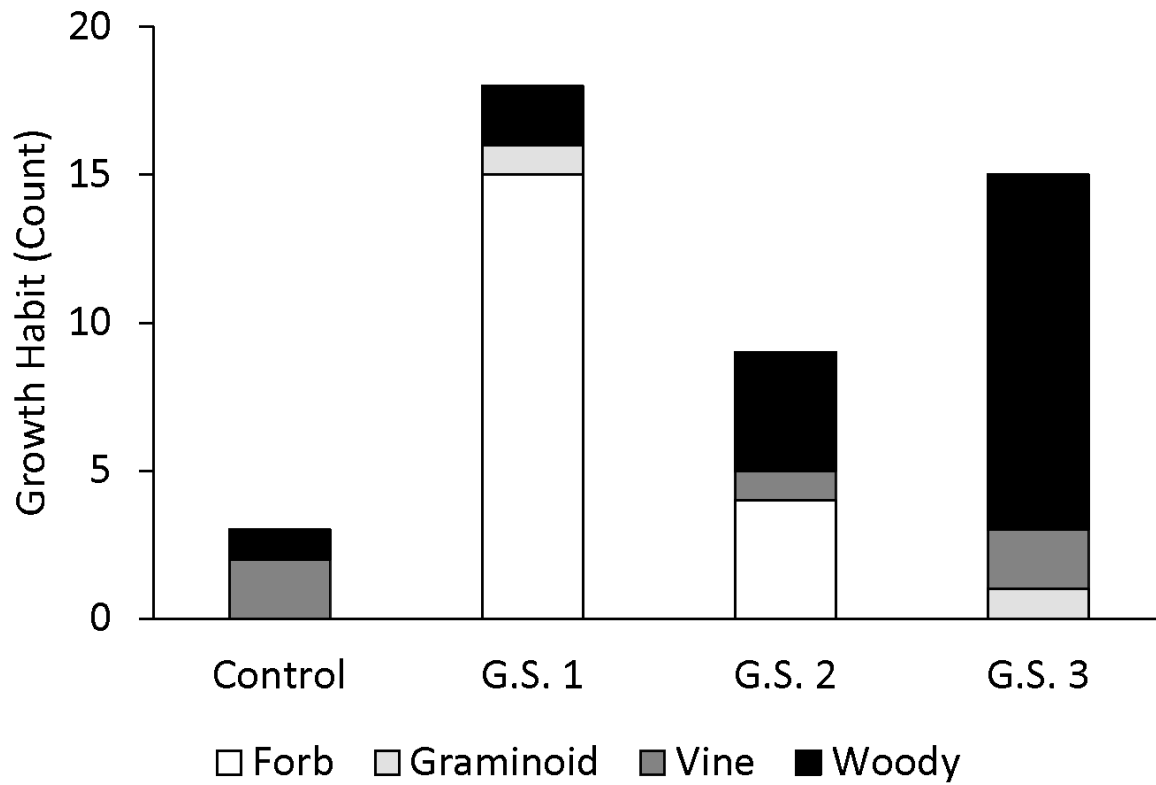
Figure 3. Indicator species results categorized by growth habit for each growing season and the control. Altered competition dynamics for each growing season are indicated by the shift in indicator species assemblages from forbs in G.S. 1 to woody plants by G.S. 3.

were woody (12), with no forbs, one graminoid, and two vine indicator species. Unique indicator species followed a similar progression, with all unique indicator species categorized as forbs in G.S. 1, all categorized as woody plants in G.S. 3, and no unique indicator species in G.S. 2 (Table 3).

Fourth Corner Analysis identified significant correlations in three of the four growth habits with the 11 environmental variables used in PC-ORD. Forb assemblages were most correlated with litter depth ($r = -0.253$), light availability ($r = 0.227$), and tree density ($r = -0.223$, $p < 0.01$). Vine assemblages were most correlated with bare ground cover ($r = -0.118$) and tree density ($r = 0.114$, $p < 0.001$). Woody assemblages were most correlated with litter depth ($r = 0.178$), *P. taeda* importance ($r = -0.175$), and light availability ($r = -0.167$, $p < 0.001$). Graminoid assemblages were not significantly correlated with any variables measured.

3.4 Overstory Stand Composition and Structure

All stands averaged approximately 19 m^2 ha^{-1} and were primarily composed of *P. taeda* (67% basal area, BA), *Quercus* species (18% BA), and *Liriodendron tulipifera* (tulip poplar, 7% BA). *Quercus montana* Willd. (chestnut oak, 8% BA), *Q. alba* (6% BA), and *Q. coccinea* Münchh. (scarlet oak, 2% BA) had the highest basal areas of *Quercus* species. Overstory relative dominance was not significantly different between control and burned treatments within most species.

Tree density significantly decreased in burned plots as compared to the control ($p < 0.001$). Tree density in burned plots significantly increased over time, from approximately 280 trees ha^{-1} in G.S. 1 and G.S. 2 to 600 trees ha^{-1} in G.S. 3 ($p < 0.001$). Most trees were categorized as intermediate (446 stem/ha) or overtopped (251 stem/ha) compared to codominant trees (190

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stem/ha) in the control treatment. In burned treatments, intermediate (125 stems/ha) and overtopped (75 stems/ha) tree densities were significantly lower than in the control (p < 0.001). However, codominant tree density (182 stems/ha) in burn treatments was not significantly different than the control. Tree density was highly correlated with nine of eleven variables tested and was most positively correlated with litter depth and broadleaf cover (Table 4). Tree density was most negatively correlated with ground flora cover, bare ground cover, ground flora taxonomic richness and *P. taeda* importance value. A multiple linear regression used tree density and bare ground cover to moderately predict total annual ground flora cover (r^2 = 0.688, p < 0.001).

Pinus taeda was the most important tree, with an average importance value of 55.10 ± 2.95 SE. *Quercus* species totaled the second highest importance value at 21.75 ± 2.03 SE. *Pinus taeda* importance values significantly increased in G.S. 1 compared to the control (p < 0.001), as tree abundance and basal area of non-*P. taeda* trees decreased. However, *P. taeda* importance values significantly decreased over time with increased hardwood density and basal area (p < 0.001). *Pinus taeda* importance value was most positively correlated with *Pinus* litter cover, light availability, and ground flora taxonomic richness and cover, while most negatively correlated with litter depth and broadleaf litter cover (Table 4).

3.5 Advanced Reproduction

Seedling density significantly increased from 34,400 ± 3,390 SE seedlings ha^{-1} in the control treatment to 57,830 ± 3,310 SE in burned treatments (p < 0.001). Seedling density decreased in G.S. 2, but increased back to comparable G.S. 1 density by G.S. 3. Seedling density was positively correlated with total ground flora cover and bare ground cover (Table 4). Sapling

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Table 4. Results of a Spearman Correlation analysis that determined the strength and significance of correlations between light availability, tree, sapling, and seedling density, overstory *P. taeda* importance value, ground flora taxonomic richness and cover, litter depth, bare ground cover, broadleaf litter cover, and *Pinus* litter cover. * indicates α < 0.05, ** indicates α < 0.01, and *** indicates α < 0.001.

	1.	2.	3.	4.	5.	6.	7.	8.	9.	10.
1. Light Availability	–									
2. Tree Density	-0.669***	–								
3. *P. taeda* Importance Value	0.633***	-0.679***	–							
4. Sapling Density	0.097	-0.366**	0.021	–						
5. Seedling Density	0.106	-0.165	-0.001	0.115	–					
6. Ground Flora Richness	0.512***	-0.583***	0.293**	0.255*	0.157	–				
7. Ground Flora Cover	0.573***	-0.831***	0.497***	0.415***	0.239*	0.609***	–			
8. Litter Depth	-0.663***	0.737***	-0.638***	-0.059	-0.195	-0.541***	-0.621***	–		
9. Bare Ground Cover	0.642***	-0.677***	0.503***	0.102	0.252*	0.528***	0.617***	-0.836***	–	
10. Broadleaf Litter Cover	-0.561***	0.546***	-0.824***	0.132	-0.113	-0.361**	-0.379**	0.673***	-0.573***	–
11. *Pinus* litter Cover	0.448***	-0.495***	0.816***	-0.021	-0.033	0.301**	0.374**	-0.522***	0.407***	-0.811***

density was not statistically different from the control to G.S. 1. Sapling density significantly increased from 3,750 saplings ha^{-1} in G.S. 1 to 7,111 saplings ha^{-1} in G.S. 2 (p < 0.001), but significantly decreased to 4,806 saplings ha^{-1} in G.S. 3 (p = 0.031). Sapling density was positively correlated with ground flora richness and cover and negatively correlated with tree density (Table 4).

3.6 Litter

Litter depth decreased by 3.6 cm from the control to G.S. 1 (p < 0.001, Table 5). Litter depth significantly increased two years after fire to an average depth of 3.7 cm by G.S. 3 (p < 0.01). Corresponding litter weights followed depth trends, with an average litter mass of 1,611 g in the control, 479 g in G.S. 1, and 1,400 g by G.S. 3 (Table 5). Ground cover also reflected changes in litter depth and weight, as litter depth was negatively correlated with bare ground cover (Table 4). Bare ground cover was highest in G.S. 1 at an average cover of 5–10%, which decreased to 0–1% by G.S. 2, was solitary by G.S. 3, and was generally absent in the control. Ground cover changed from mostly *Pinus* litter to mostly broadleaf litter in three growing seasons. *Pinus* litter covered 50–75% of the ground in G.S. 1, but decreased to 5–10% cover in G.S. 3. Conversely, broadleaf cover increased from 1–2% cover in G.S. 1 to 50–75% cover by G.S. 3 (Table 5).

3.7 Light availability

Light availability increased from 15% ± 2 SE in the control to 32% ± 2 SE in burned treatments (p < 0.001). Percent PPFD was greatest in G.S. 1 at 45% and decreased to 30% and 20% by G.S.2 and G.S. 3, respectively (Figure 4, p < 0.001). Light availability was most

Table 5. Kruskal-Wallis results summarizing the mean values (± SE) of litter depth and mass, bare ground cover, *Pinus* litter cover, and broadleaf litter cover by growing season and the control. To remain conservative, cover values were rounded down to determine specific range, where 0 = absent, 1 = solitary or few, 2 = 0–1%, 3 = 1–2%, 4 = 2–5%, 5 = 5–10%, 6 = 10–25%, 7 = 25–50%, 8 = 50–75%, 9 = 75–95%, and 10 = 95–100%. Dunn's post-hoc pairwise comparison test letters indicate significance when $\alpha < 0.05$ within individual growing seasons and the control.

Variable	Control	G.S. 1	G.S. 2	G.S. 3	Significance
Litter depth (cm)	4.2 (± 0.3)[a]	0.5 (± 0.0)[b]	2.1 (± 0.1)[c]	3.7 (± 0.2)[a]	$p < 0.001$
Litter mass (g)	1,611 (± 111)[a]	479 (± 50)[b]	768 (± 85)[b]	1,400 (± 82)[a]	$p < 0.001$
Bare ground cover	0.55 (± 0.22)[a]	5.05 (± 0.23)[b]	2.65 (± 0.21)[c]	1.10 (± 0.23)[a]	$p < 0.001$
Pinus litter cover	6.55 (± 0.26)[ac]	8.35 (± 0.25)[b]	7.15 (± 0.22)[ab]	5.80 (± 0.32)[c]	$p < 0.001$
Broadleaf litter cover	7.90 (± 0.14)[a]	3.85 (± 0.25)[b]	7.40 (± 0.20)[a]	8.30 (± 0.18)[a]	$p < 0.001$
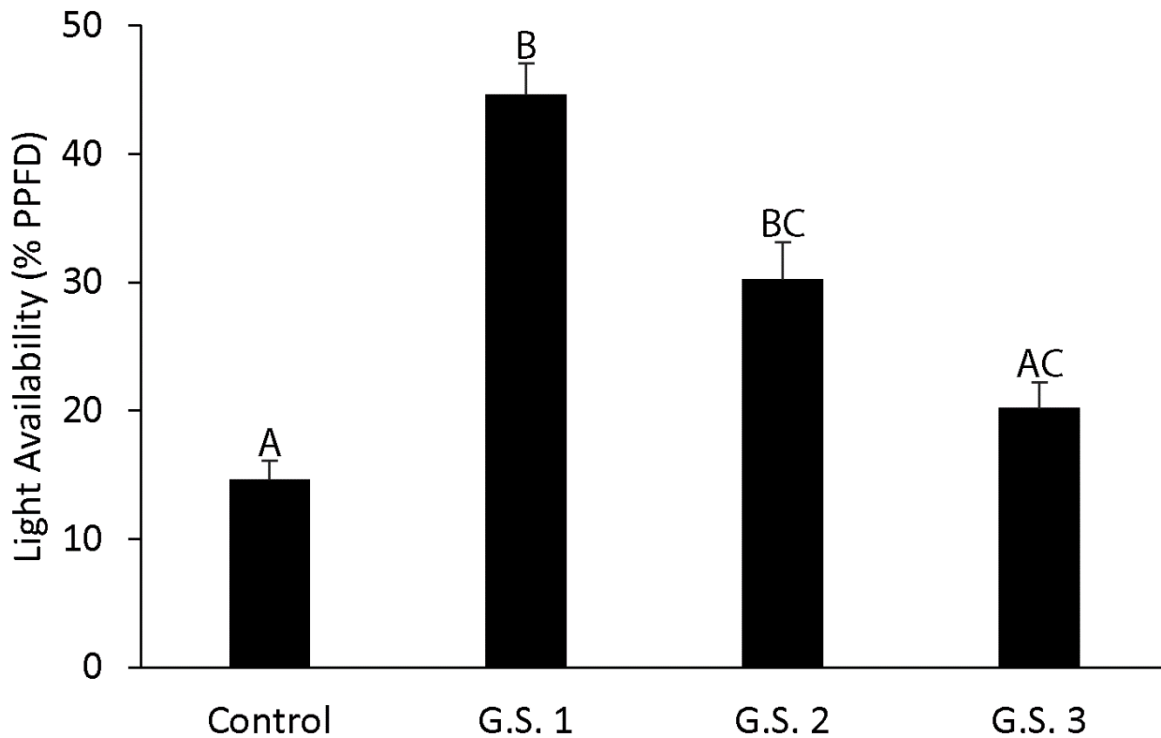
Figure 4. Light availability, measured in percent photosynthetic photon flux density, of each growing season and the control. Error bars indicate standard error for each treatment. Dunn's post-hoc pairwise comparison test letters indicate significance when $\alpha < 0.05$ within individual growing seasons and the control.

positively correlated with bare ground cover and *Pinus* litter and negatively correlated with litter

depth and broadleaf cover (Table 4). Light availability explained 23% of variability in taxonomic

richness throughout all four treatments ($p < 0.001$). Decreases in % PPFD were most strongly

explained by increased tree density ($r^2 = 0.431$, $p < 0.001$).

4. DISCUSSION

4.1 Ground Flora and Rapid Succession

Ground flora richness and cover immediately increased in my burned and thinned *Pinus-Quercus* stands compared to the thin-only treatment, which is consistent with other results in *Pinus*-dominated and hardwood-dominated stands across the U.S. (Phillips *et al.* 2007, Phillips and Waldrop 2008, Outcalt and Brockway 2010, Willms *et al.* 2017). Although Phillips and Waldrop (2008) reported that taxonomic richness continuously increased in mixed-*Pinus* stands on the South Carolina Piedmont, my taxa totals peaked in G.S. 1 and decreased in G.S. 2 and G.S. 3. Differences in taxonomic richness patterns may be attributed to different stand types and ecoregions between studies, as the *Pinus* dominated stands likely had different canopy specific leaf area and structure compared to the mixed *Pinus-Quercus* stands. Increased richness was partially explained by increased light availability after fire, as past studies in other stands types had found (Phillips *et al.* 2007, Phillips and Waldrop 2008, Barrioz *et al.* 2013, Bowles *et al.* 2017). As light availability is generally considered a limiting resource for ground flora in closed canopy stands, increased light availability caused by thinning and maintained by frequent burning provided adequate conditions for ground flora germination (Scharenbroch *et al.* 2012, Waldrop *et al.* 2016). Fire-induced increases in richness and cover also indicated a greater ground flora response to forest disturbances such as thinning followed by repeated fire that changes in structure following thinning alone could not emulate (Kinkead *et al.* 2013, Waldrop *et al.* 2016).

Changes in taxonomic richness and cover by growth habit were indicative of relatively rapid succession in ground flora. Total forb cover and richness were highest in G.S. 1 and decreased with waning light availability, which were similar to other studies (Phillips and Waldrop 2008, Waldrop *et al.* 2008, Lettow *et al.* 2014) and are indicative of high light requirements that forbs need to persist. Similar trends in forb indicator species and unique indicator species suggested that competition dynamics favored quick growth and resource acquisition in the growing season directly after fire. This trend indicates that fire is an important driver that promotes herbaceous cover and richness in *Pinus-Quercus* stands, as found in other studies that have a *Pinus* and/or *Quercus* component across the U.S. (Fulé *et al.* 2005, Phillips and Waldrop 2008, Outcalt and Brockway 2010, Kinkead *et al.* 2013, Lettow *et al.* 2014).

Although woody cover did not statistically change in three growing seasons, woody biomass likely increased, as woody plants had grown above the 1 m delineation of ground flora by G.S. 3 (personal observation). Competition dynamics changed by G.S. 3 to favor growth habits that invested energy and resources into long-term vertical growth exhibited in the shift of ISA species to woody indicator species by G.S. 3. Increased woody competition for space and resources correlated with decreased forb and graminoid cover and richness, which was a concern stated by Kinkead *et al.* (2013) for maintaining future herb diversity. Phillips *et al.* (2007) and Phillips and Waldrop (2008) recorded similar increases in high woody cover several years after treatment that may indicate an analogous succession to woody dominant cover in the ground flora stratum post-thinning and fire disturbance. Many of these woody plants were saplings that re-sprouted in G.S. 1 and blocked light from reaching ground flora by G.S. 2. Continued re-sprouting in my study supported results from Knapp *et al.* (2015), who found that saplings re-

sprouted more successfully in stands burned in the dormant season every four years as compared to saplings in stands burned annually.

Vine cover was the only growth form to have peak cover in G.S. 2. Vines may have taken longer to grow because many taxa observed *in situ* depended on taller shrubs and trees. This was corroborated by positive correlations between vines and tree density in FCA results. Once woody plants grew above the ground flora stratum, vines could grow up stems and outcompete other ground flora for light. Graminoid cover was comparable to results from Phillips and Waldrop (2008) in mixed-*Pinus* stands, with significantly higher cover and richness in plots that were thinned and burned compared to thinned-only plots. However, graminoid cover decreased by G.S. 3, likely from greater competition by woody plants and vines for light capture. Specifically, lower graminoid cover may have occurred because of reduced light availability levels, which generally needs to remain high for many graminoids to persist. In general, total ground flora cover did not change until light availability decreased below 30% PPFD, although the change in total cover did not statistically change in the latter two growing seasons.

A lack of unique indicator species in G.S. 2 was also symptomatic of rapid succession in ground flora assemblages. I interpreted G.S. 2 as a transition from herbaceous to woody dominance, with a mix of species found in either G.S. 1 or G.S. 3 and an even split of four indicator species for each growth habit. Transitions from forb to woody cover could have effects on species in other trophic levels of the food web. As ground flora feed insects, birds, and mammals for habitat and food supply, changes in ground flora assemblages towards woody plants will likely affect animals that eat specific forbs, grasses, vines and woody plants (Fralish 2004, Hutchinson 2005, Barrioz *et al.* 2013).

Only 16 of my 80 plots contained an invasive plant and all invasive species occurred at low cover. After twelve years, thinned stands burned four times had three invasive species (*Lespedeza bicolor* Turcizainow (bicolor lespedeza), *Lespedeza cuneata* (Dum. Cours.) G. Don (sericea lespedeza), and *Lonicera japonica* Thunberg (Japanese honeysuckle)) that often occurred in areas that experienced continuous human presence and disturbance. Both *Lespedeza* species are capable of surviving fire and may benefit from low intensity surface burns over time. However, neither species occurred at covers above 0–1% across a plot and did not indicate any capability to increase dominance or abundance with the current silvicultural prescription. The highest average cover class of *L. japonica* occurred in the control treatment near old rock walls indicative of a homestead that was abandoned when the land came into federal ownership, at which time it began converting back to forest. Invasive plants did not significantly contribute to the cover in any treatment or indicate signs of future dominance within the ground flora stratum. Though not specified, differences in land uses may have also impacted ground flora composition, abundance, and invasive species cover over time that could have altered results across all compared studies (Gilliam 2007).

4.2 Biotic effects on Ground Flora

Greater tree density was indicative of increased competition for space and resources, explaining annual decreases in light availability and ground flora cover. Fewer canopy trees created a relatively open overstory that increased light availability and growing space at the forest floor for smaller plants. Increased tree density in the understory with time since fire decreased resources and space available for ground flora as the hardwood trees in higher strata outcompeted smaller plants for light. Because light availability partially explained changes in

ground flora richness ($r^2 = 0.22$), tree density also indirectly affected ground flora richness. As prescribed fire removed vegetation in understory strata, ground flora likely had enhanced photosynthetic productivity and performance (Huang *et al.* 2007) that caused increased cover. Fire also affected litter accumulation that likely influenced ground flora germination and growth, as litter depth correlated with ground flora cover and taxonomic richness (Table 4). However, my results did not align with Phillips *et al.* (2007), who reported a delayed response in cover in stands of the central Appalachian Plateau in Ohio and southern Appalachian Mountain in North Carolina that were thinned and burned compared to the thin-only treatment. Method collection differences could have caused differences in results, as Phillips *et al.* (2007) collected their data directly after the disturbances, while I collected data four months post-fire. Variations in stand type, site quality, and past land use history may have also affected ground flora recovery post-disturbance and caused difference between the two studies. If stands continue to transition from *P. taeda-Quercus* stands to mixed-hardwood stands, decreased light transmission into the understory may cause a decline in ground flora cover.

Dominant litter cover was also symptomatic of annual changes in ground flora growing conditions that affected competition over time. Annual shifts from pine to broadleaf litter cover correlated to of increasingly difficult growing conditions for smaller plants. Greater *Pinus* litter cover correlated with low litter depth and greater bare mineral soil accessibility, both of which are favorable for ground flora germination (Hiers *et al.* 2007, Moghaddas *et al.* 2008, Schwilk *et al.* 2009). Increases in broadleaf cover correlated with increased litter depth and diminished bare mineral soil accessibility, and both correlated with reduced ground flora establishment. Growing season three had litter depths and masses that, if extrapolated to G.S. 4, would likely return to pre-burn depths and weights (i.e. the control treatment).

Litter recovery time post-fire seem to be quicker than reported in Stambaugh *et al.* (2006), which reported that litter depths recovered to 75% accumulation after four years and took 12 years to return to comparable litter depths in mixed hardwood stands in the Missouri Ozarks. However, accumulation was slower than reported by Arthur *et al.* (2017), who determined that litter recovered to comparable pre-burn masses within one growing season in mixed hardwood stands in the Cumberland Plateau of eastern Kentucky. In southern Appalachian mixed oak stands, Waldrop *et al.* (2016) had deeper litter depths on average, but found concurring results that litter in thinned and burned treatments approached thin-only litter levels after three growing seasons before the next burn in the fourth dormant season. As changes in average litter depth and mass correlated with ground flora richness and cover over three growing seasons in my study, differences in litter may also help explain variability in ground flora assemblages and succession rates between my study and other studies in the eastern U.S.

Of similar interest, litter composition may have affected ground flora competition dynamics because of effects litter has on fire characteristics and ground moisture (Kane *et al.* 2008, Alexander and Arthur 2014). For example, *Pinus* species needles generally cause hot fires with quick rates of spread because of lower moisture levels in the needle, relatively fast litter drying rates post-precipitation event, and long decomposition rates (Williamson and Black 1981, Fonda 2001). In comparison, mesic species, such as *Acer rubrum L.*, drop litter that decomposes relatively quickly, hold more moisture for longer time periods, requires more energy to ignite, and does not burn as intensely as *Pinus* or *Quercus* litter (Kreye *et al.* 2013, Alexander and Arthur 2014). Some *Quercus* species have litter that has combustion comparable to fire tolerant *Pinus palustris* Mill. (longleaf pine), but generally have traits that indicate moderate fire tolerance with lobed leave, moderate decomposition rates, and moderate moisture retention

compared to *Pinus* and *A. rubrum* litter (Kane *et al.* 2008). Alterations in fire severity, intensity, and duration and soil moisture retention and availability affect tree seedling and resprouting capabilities and likely affect herbaceous ground flora response, composition, and cover. These differences may have also caused unique burning and environmental conditions that could account for variability in my *Pinus-Quercus* ground flora assemblages as compared to other stand types that were thinned and burned. However, this study did not analyze litter composition by functional burning characteristics. I also did not find research that has attempted to relate ground flora assemblages with litter and fuels composition, a literature gap should be studied to better elucidate ground flora response to prescribed fire.

4.3 Advanced Reproduction

My thinned and burned plots had significantly higher seedling and sapling densities than thinned-only plots, as found in other studies within BNF (Schweitzer *et al.* 2016) and eastern U.S. stand types (Albrecht and McCarthy 2006, Phillips and Waldrop 2008, Waldrop *et al.* 2008, Iverson *et al.* 2017). My seedling data revealed incongruities in trends between treatments, decreasing in density from G.S. 1 to G.S. 2 and recovering by G.S. 3. This trend may have occurred from seedlings growing into sapling size classes in favorable growing conditions. Sapling density may have decreased by G.S. 3 because of decreased light availability in the lower midstory that occurred with greater small tree density, as sapling density was positively correlated with light availability. A second possible reason for declined sapling density was recruitment into larger size classes, as sapling density was negatively correlated with tree density. These reasons may explain why my seeding and sapling densities did not significantly

increase between G.S. 1 and G.S. 3 as has been observed in other studies (Albrecht *et al.* 2006, Phillips and Waldrop 2008).

After four fire rotations in these treatments, I did not observe a decrease in *A. rubrum* re-sprouts as was described in Albrecht and McCarthy (2006). *Acer rubrum* saplings likely maintained high density because the three-year fire return interval allowed for resprouts that quickly grew into saplings in the high light environment of thin *Pinus-Quercus* stands. Arthur *et al.* (1998) and Knapp *et al.* (2015) reported similar trends across other species, with higher sapling re-sprouting in stands with longer fire return intervals compared to stands burned on shorter fire rotations. *Quercus* seedlings outcompeted *A. rubrum* seedlings, but failed to recruit to the sapling class, possibly because *A. rubrum* saplings were preventing enough light from reaching the ground flora. However, few *A. rubrum* resprouts successfully recruited into tree size classes because most saplings were top-killed from the fire, with only 40 *A. rubrum* trees recorded in burned plots and only eight greater than 20 cm dbh.

Successful re-sprouting of competitor species may have also occurred because fire in these stands has previously been set during the dormant season when carbon stores are primarily underground and are unaffected by fire. Resource allocation differences, such as distinctions between *Acer*, *Quercus*, and *L. tulipifera* rooting networks, alter re-sprout response by species after fire (Burns and Honkala 1990). *Quercus* advanced reproduction tend to grow conservatively, promoting root growth and protecting dormant buds more than other tree species (Lorimer *et al.* 1994, Brose and Van Lear 2004). These adaptions generally lead to higher probabilities of successful resprouting compared to other competitor species (Kruger and Reich 1997, Brose and Van Lear 1998). However, species with more aggressive growth strategies like *A. rubrum* have been seen to continually resprout after multiple burns, as was seen in my study

and other studies in eastern US forests (Blankenship and Arthur 2006). Burns during the growing season may return different results, when species with different resource allocation strategies have varied levels of carbons stores above and belowground (Brose *et al.* 2013). However, burning at a three-year return interval for 12 years has caused clumps of *A. rubrum* to have enough stems to insulate the inner stems from being damaged by fire, regardless of when a fire is introduced to the stand (C.J. Schweitzer, personal communication: 09 February 2018). Managers may want to consider the long-term response of mesic saplings to frequent prescribed fire for long time periods when determining stand management methods.

4.4 Importance and Future Research

The ground flora stratum adds diversity, habitat and resource availability, and competitive interactions to increase ecosystem complexity within stands (Gilliam 2007). As small plants are sensitive to stand-scale disturbances, a quantitative representation of annual changes in ground flora assemblages could provide practical information to describe stand characteristics after a disturbance (Onaindia *et al.* 2004). Although research has occurred to study changes in the ground flora stratum from thinning and prescribed fire, limited research has quantified effects of these specific disturbances on ground flora in *Pinus-Quercus* stands (Fulé *et al.* 2005). Other ground flora studies have analyzed the effects of disturbance on the ground flora stratum in Alabama (Outcalt and Brockway 2010, Kleinman *et al.* 2017), but I could find no research that studied ground flora response to thinning and burning treatments in *Pinus-Quercus* stands in Alabama, the ecoregion, or across the southeastern U.S. Furthermore, many studies that have studied ground flora response to thinning and burning have lacked a temporal component. Studies that included an initial temporal component generally studied ground flora changes after

one burn without quantifying long-term changes after repeated burns. None of the cited studies that have included a temporal aspect included a chrono-sequence across consecutive growing seasons. Though time was replaced with space, my study provides finer temporal resolution results of long-term changes in ground flora after repeated fire compared to past research.

A similar type of study should be performed over larger areas and across more stand treatments to validate my results. This study replaced space for time and made assumptions about equivalent stand composition, residual basal area, past fire history, and initial ground flora assemblages that could uniquely affect each individual treatment. However, the significant results of my study provide precedent for a continuous longitudinal study that analyzes changes in ground flora assemblages in *Pinus-Quercus* stands to corroborate my findings.

A number of other stand types also exist in different ecoregions of the U.S. that have had few or no thin and burn studies performed to analyze annual ground flora community response. Research has indicated similar responses by the understory after prescribed fire (Taft 2003, Hartman and Heumann 2004, Knapp et al 2015), thinning (Harrington and Edwards 1999), and both (Schwilk *et al.* 2009, Willms *et al.* 2017) in a variety of stand types and ecoregions. However, more intensive research with finer temporal resolution will ensure that extrapolations of outcomes from these other studies are accurate. More data sets will also help delineate broad trends of ground flora recovery within eastern stands that could be useful for future management.

4.5 Management Implications

Managers are becoming increasingly interested in promoting stand biodiversity (Lindenmayer *et al.* 2000, USFS 2000), which can be accomplished in many stand types by managing for a diverse ground flora stratum. Thinning and prescribed burning are methods to

increase ground flora taxonomic richness and understory cover in *Pinus-Quercus* stands. My

results were comparable with thinned and burned stands with large *Pinus* and/or *Quercus*

components in other regions of the U.S., which may indicate a general trend across *Pinus-*

Quercus stands in North America. Fire seemed to perpetuate herbaceous plant richness and cover

that a one-time thin could not continue to maintain, which likely affected resource availability

for herbivores and omnivores (Fralish 2004, Barrioz *et al.* 2013). Succession from herbs to

woody plants occurs quickly and fire would have to occur annually or biannually to maintain

long-term herb richness and cover for plant and animal biodiversity. If stands are burned

annually, sapling re-sprouting may cease to occur (Knapp *et al.* 2015) and could allow continual

forb availability. However, annual burning may not be possible in these stand types because fuel

loading may not be great enough to carry fires every dormant season. To increase ground flora

richness while meeting long-term management goals, managers may want to consider

maintaining a portion of stands in the stand initiation or understory reinitiation stages across the

landscape to conserve beta and gamma diversity that is indicative of ecosystem resilience

(Peterson 1998).

Litter is another important consideration for ground flora assemblages and fuels

management, a concern for managers of fire-influenced forests across the world (Waldrop *et al.*

2016). I found that burning every three years maintained reduced litter depths that kept fuel loads

below control levels over all three growing seasons. Litter also became more mesic as time since

burn increased, changing from pine in G.S. 1 to hardwood (specifically *A. rubrum* litter, personal

observation) by G.S. 3 (Nowacki and Abrams 2008). This may affect fire characteristics (i.e. fire

line intensity and rate of spread) in these stands that managers should be aware of for the future

(Kreye *et al.* 2013, Alexander and Arthur 2014), as fire characteristics could have long-term effects on ground flora assemblages and advanced regeneration.

Restoring stands from uniform structure and composition (e.g. plantations) to historical composition depends on advanced regeneration to create and maintain desired stand conditions. Although thinning and fire treatments released *Quercus* stems to create general *Pinus-Quercus* overstory composition, advanced reproduction surveyed in frequently burn treatments had few *Pinus* seedlings, no *Pinus* saplings, few *Quercus* saplings, and an abundance of *A. rubrum* saplings that will likely maintain dominance in smaller size classes. Of similar concern, few small trees survived a fire recurrence interval of every three years. As overstory *P. taeda* die, a true C stratum (see Oliver and Larson 1996) does not exist in one observed stand to be released into the canopy if managers maintain a three-year fire recurrence interval.

Though beneficial for ground flora biodiversity, dormant season prescribed fires at a three-year recurrence interval may not be the best course of action if managers want to maintain a *Pinus-Quercus* stand. If regeneration composition is dominated by mesic reproduction, I would recommend performing at least one growing season burn (Arthur *et al.* 2012) and a second burn within two years to reduce species like *A. rubrum* in the understory and change competition dynamics to favor *Quercus* advanced reproduction. However, managers should be aware of potential issues that can arise while attempting prescribed growing season fires in regions that experience high humidity during the growing season.

Pinus advanced reproduction is often more prevalent in large canopy gaps (Palik and Pederson 1996, Stambaugh and Muzika 2004, Weber *et al.* 2014) and a second thin may be needed for *Pinus* regeneration if overstory lateral growth has reduced gap sizes over 12 years. Combined with a dormant season burn, *Pinus* advanced reproduction will benefit from greater

increased bare mineral soil accessibility and light to outcompete other fast-growing tree species (Cain and Sheldon 2002). Once *Quercus* and *Pinus* saplings become more abundant than non-*Quercus* broadleaf saplings, a 10 to 30-year fire-free period would be needed to encourage *Quercus* and *Pinus* growth to reach 15 cm dbh, a size where most the trees could tolerate surface fire and release into the canopy when an opening is created (Arthur *et al.* 2012). By including a focus on herbaceous and woody ground flora assemblages, managers can use prescribed fire post-thinning to increase stand resilience and diversity and manipulate woody advanced reproduction to reflect desired future overstory composition that accomplish multiple management goals across many stand types.

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