ABSTRACT

BENZ, BRANDY LYN. Ground-Layer Vegetation Response to Silvicultural Treatments for Oak (*Quercus*) Regeneration in Southern Appalachian Forests (Under the direction of Dr. Jodi Forrester).

Southern Appalachian forests are highly diverse ecosystems that contain unique microhabitats for ground-layer species due to, in part, their varying topography and geologic history. Ground-layer species play important roles in ecosystem functions including seedling regeneration, nutrient cycling, and wildlife resources. The retention or restoration of species diversity of the ground-layer community has been a growing concern for managers of private and public forestlands, although a more common silvicultural objective is *Quercus* regeneration. Several silvicultural prescriptions have been developed to promote *Quercus* regeneration and it is important to consider the consequences that species-targeted management techniques can have on the survival, productivity, and assemblage of the ground-layer vegetation community, including other woody and herbaceous species.

Our objectives were to compare how silvicultural prescriptions developed for *Quercus* regeneration, including overstory harvest, midstory herbicide applications, or prescribed fire, influence the productivity and diversity of the ground-layer vegetation community. We tested the effects of experimental prescriptions on ground-layer biomass productivity over a decade. We used multivariate analyses to evaluate the treatment versus microhabitat effect on species cover and to evaluate trends in dominance patterns in response to the silvicultural treatments. We hypothesized (1) shelterwood/fire and repeated prescribed fire treatments would increase total ground-layer vegetation biomass production, but that not all lifeforms would respond equally. We expected (2) shelterwood/fire and repeated fire treatments would decrease biomass production of more shade-tolerant, fire-sensitive lifeforms and increase biomass production of more shade-intolerant, pyrophilous lifeforms after a decade. We further hypothesized (3) the shelterwood/fire treatment would lead to the greatest changes in species dominance patterns due to the combination of overstory harvest and prescribed fire treatments.

Results supported our hypotheses and the shelterwood/fire treatment increased total ground-layer biomass by 111% immediately following overstory reductions. Among lifeforms, only ferns declined following overstory reductions and all except vine, woody, and herbaceous lifeforms decreased following the added single fire treatment. Total ground-layer biomass in the repeated fire treatment increased 7% following the first fires, and 60% following the second fires, relative to pre-treatment. Biomass production of woody and shrub lifeforms initially declined following the first fires while all other lifeforms increased, yet following the second fires, only the woody and shrub lifeforms increased biomass production. Total ground-layer biomass in the oak shelterwood treatment showed little change following herbicide treatments (<1%) but increased 34% relative to pre-treatment conditions by year 9. Total ground-layer biomass in the unmanipulated control units had declined 21% after a decade with woody and herbaceous lifeforms showing the most decline.

We also found the most extreme changes in species dominance patterns following the shelterwood/fire treatment, via increased vine biomass of primarily *Rubus* spp. The dense *Rubus* layer was up to twenty times that of pre-treatment conditions and could hinder the regenerative potential of other species, including *Quercus,* if not addressed. *Quercus* biomass (relative to other woody species) increased 16% following repeated fire treatments (versus 11% in oak shelterwood and shelterwood/fire, and 13% in controls) showing the positive potential of reintroducing fire to this landscape for *Quercus* regeneration.

Results suggest the need to monitor changes to species assemblages and dominance patterns in the ground-layer early following treatments for *Quercus* regeneration in case remedial treatments are needed to influence the successional patterns that ensue. In the future, management prescriptions which combine overstory reductions (to increase available light and biomass production), midstory thinning (to reduce undesirable competition), and repeated fires (to maintain desirable woody species assemblages) could be advantageous to meeting objectives for promoting *Quercus* regeneration while maintaining or increasing the diversity of the ground-layer vegetation community of these forests.

Ground-Layer Vegetation Response to Silvicultural Treatments for Oak (*Quercus*) Regeneration in Southern Appalachian Forests

by
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BIOGRAPHY

Brandy Lyn Benz was raised in Supply, North Carolina and grew up climbing the majestic live oaks famous to the state's coastal plain. She moved from sea to mountains to begin earning her Bachelor of Science in Ecology and Environmental Studies degree from the University of North Carolina at Asheville where she received foundational training on plant physiology and phylogeny. After working as a forestry technician for several summers at Bent Creek Experimental Forest in Asheville North Carolina she was accepted at NC State and started earning her Master of Science in Forestry degree where studies focused on increasing her understanding of the ecosystem functions and services provided by the forest and developing her statistical analysis skills. Brandy is fascinated with the unique flora of the Southern Appalachian's biodiverse ecosystems and aspires to work as a botanist one day.

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Vascular species of the *Quercus* L. genus encompass a vastly diverse group of tree and shrub species, with nearly 500 species existing globally (McShea and Healy, 2002), and fossil records dating back at least 50 million years (Tantray et al., 2017). The importance of the genus has been widely documented; being referred to as the “ecological equivalent of manna from heaven” and as “the most important woody genus in the Northern Hemisphere” (McShea and Healy, 2002; Nixon, 1997). Of the 78.5 million hectares of forestland in the US, 51% is of oak forest type making *Quercus* regeneration problems a widespread and major concern (Dey, 2014). Evolutionary adaptations to drought (Kole, 2011; Abrams, 1990), fire (Abrams, 1992; Brose et al., 2014; Hutchinson et al., 2008), and natural disturbances like wind and flooding events (Kushla, 2017; Goldman, 2017) have proved members of the *Quercus* genus to be resilient to many disturbances, natural and anthropogenic, making them able to adapt to a wide variety of habitats.

Despite the genus’ resilience to disturbance and adaptive evolution, scientific research from around the world including: China (Li and Ma, 2003), Sweden (Götmark et al., 2005), Europe (Spinu, 2019), and areas in the Mediterranean (Pulido and Diaz, 2005) report problems with sufficient canopy regeneration of *Quercus* in habitats they once thrived. The lack of *Quercus* regeneration across its native range has been attributed to changes in historical fire disturbance patterns (Abrams, 1992; Hutchinson et al., 2008), oak decline (Greenberg and Collins, 2016; Gottschalk and Wargo, 1996; Colangelo et al., 2018), and the parcellization and conversion of many forest lands to private ownership, which accounts for nearly 83% of the forested land in the Eastern US (McShea et al., 2007; Dey, 2014), among other factors. From 1980 to 2008, the Central Hardwoods Region alone experienced an 87% decrease in *Quercus* density, while volume increased >0.05 m^3 ha^{-1} $year^{-1}$, supporting the theory of insufficient regeneration of *Quercus* in these forests (Fei et al., 2011; Dey, 2014).

Nowacki and Abrams (2008, p.128) coined the term “mesophication” to describe “the escalation of mesic microenvironmental conditions, accompanied by ever-diminishing prospects for fire and fire-dependent heliophytic species.” In Southern Appalachian forests the effects of fire suppression, oak decline, and increased mesophication have resulted in a decline in the number of quality *Quercus* trees that recruit into the canopy, especially on more fertile or mesic sites (Brose, 2011; Elliott and Vose, 2010; Schuler and Miller, 1995; Keyser and Keyser, 2013; Loftis, 1990a). Forest structural and compositional changes are evident in these closed canopy forests where shade-tolerant, fire-sensitive species such as *Acer rubrum* L., *A. saccharum* Marshall, *Fagus grandifolia* Ehrh., and other mesophytic species dominate midstory regeneration layers where disturbance, natural or anthropogenic, is lacking (Holzmueller et al., 2009; Vander Yacht et al., 2019; Lhotka, 2013). Alternatively, in forests where clearcutting or large reductions to overstory stocking levels are part of silvicultural treatments, more shade-intolerant species like *Liriodendron tulipifera* L. or woody members of the *Rubus* L. genus may dominate regeneration layers (Vander Yacht et al., 2019; Lhotka, 2013).

1.2 Silvicultural Management Implications

To combat these structural and compositional changes, silvicultural management techniques are increasingly being developed to favor midstory and ground-layer conditions conducive for the regeneration of *Quercus* in Southern Appalachian forests (Brose et al., 1999; Loftis, 1983, 1990a, 1990b; Shure et al., 2006). Management techniques developed for the regeneration of *Quercus* can create disturbance patterns that alter canopy structure, soil characteristics, and consequently, ground-layer species richness (the number of species per unit area), abundance (cover or biomass per unit area), and composition (the contribution of each species to the total vegetation) (Holzmueller et al., 2009; Elliott et al., 2014). Techniques explored thus far include variable rate harvesting of the overstory, prescribed fire, or midstory herbicide treatments, used individually or combined.

The type and intensity of harvest methods used (clearcutting, shelterwood, or group selection) has varying effects on the recovery of plants in the ground-layer vegetation community in Southern Appalachian forests (Ford et al., 2000; Duguid and

Ashton, 2013; Duffy and Meier, 1992). Changes in canopy structure following overstory reductions alter the light regime, the amount of light available to a plant, of the ground-layer stratum which can affect the growth, survival, and diversity of the of the ground-layer community in different ways. While certain species or lifeforms (functional groups of similar species such as woody or perennial vines) are shade-intolerant and favor high light environments such as *L. tulipifera* and *Rubus* spp., others, such as *A. rubrum* and many ferns are shade-tolerant and favor more low light environments (Shure et al., 2006). Still yet, some species such as *Quercus,* have evolved to take advantage of intermediate light regimes and flourish on the edges of naturally or anthropogenically developed gaps in the forest (Lhotka, 2013). Partial timber harvesting methods, like shelterwood or group selection cuts, often used to promote *Quercus* regeneration in Southern Appalachian forests require repeated logging disturbance which can affect forest floor characteristics by causing soil compaction and altered soil moisture; disturbances from which many vernal (spring) herbs show slow recovery (Meier et al., 1995).

Increasingly, prescribed fire treatments are being used in Southern Appalachian forests to mimic historical fire disturbance patterns thought to have influenced the development of the mixed oak forest types they wish to restore or maintain. The frequency of prescribed fires used to promote *Quercus* regeneration can influence successional stages, and therefore species composition of the ground-layer vegetation community (Burton et al., 2011). Fire intensity (maximum temperature and char height) has varying effects on the recovery of species of the ground-layer community. Low intensity fires may positively influence seedling germination of certain species by reducing leaf litter and fuels on the forest floor and increasing available nutrients, however, intensely hot fires can unfavorably remove litter and duff, completely exposing mineral soil (Elliott et al., 1999). The timing of prescribed fire, performed in either the growing or dormant season, used to regenerate *Quercus* in Southern Appalachian forests can affect ground-layer vegetation differently depending on the most active time of growth and reproduction of the species, as well as the lifeform (fern, herbaceous, shrub, etc.) (Brose et al., 1999).

Herbicides used for midstory competition control can affect ground-layer species composition differently, depending on the type of herbicide used, the timing of application, and the efficacy of the treatment (Hutchinson et al., 2016; Ristau et al., 2011; Vander Yacht et al., 2017). The use of herbicides such as Glyphosate or Triclopyr for midstory competition control in closed canopy, mesophytic forests may increase cover of the ground-layer community, but effects are often short-term due to the intense re-sprouting of species like *A. rubrum* which shade out ground-layer vegetation (Hutchinson et al., 2016; Vander Yacht et al., 2017). The use of herbicides to reduce midstory competition has been shown to be more effective in combination with canopy reduction and/or prescribed fire treatments (Vander Yacht et al., 2017).

1.3 USDA Forest Service: "Regional Oak Study"

A large-scaled field study, the "Regional Oak Study" was established in 2008 by the US Forest Service in the Cold Mountain Game Lands located in the Southern Appalachian Mountains in western North Carolina to test the potential silvicultural treatments developed to increase *Quercus* regeneration (**Figure 1.1**). Study site elevations range from 983 m to 1,271 m above sea level. The terrain is mountainous with gentle to extreme sloping topography where slopes range from 35 to 55 percent (Keyser et al., 2012). Soils in the study area are composed mostly of Plott, Edneyville, and Chestnut soil series types (North Carolina Wildlife Resources Commission (NCWRC, 2020). These loamy soil types tend to exist on steep, sloping terrains, can be strong to moderately deep, and are underlain by igneous and metamorphic rock bases (NCWRC, 2020). Annual precipitation of the study site is approximately 1,060 mm and consistently distributed throughout the year (NCWRC, 2020).

The Cold Mountain Game Lands contain approximately 1,470 ha of land, 89% of which is forested. Oak Forest habitats cover 62% (898 ha) of the Cold Mountain Game Lands, Cove Forests cover 18% (595 ha), Northern Hardwood Forests cover 7% (154 ha), and the remainder is a mixture of forest types (NCWRC, 2020). Dominant canopy species in the game lands include several oaks (*Quercus rubra* L., *Q. alba* L., *Q. prinus* L., and *Q. velutina* Lam.), *A. rubrum*, *A. saccharum* Marshall, *Carya* Nutt., *Prunus serotina* Ehrh., and *L. tulipifera*. The midstory is dominated by many shade-tolerant species such as *Oxydendrum arboreum* (L.) DC.), *Nyssa sylvatica* Marshall, *Halesia tetraptera* Ellis and *A. rubrum* (Greenberg et al., 2016).

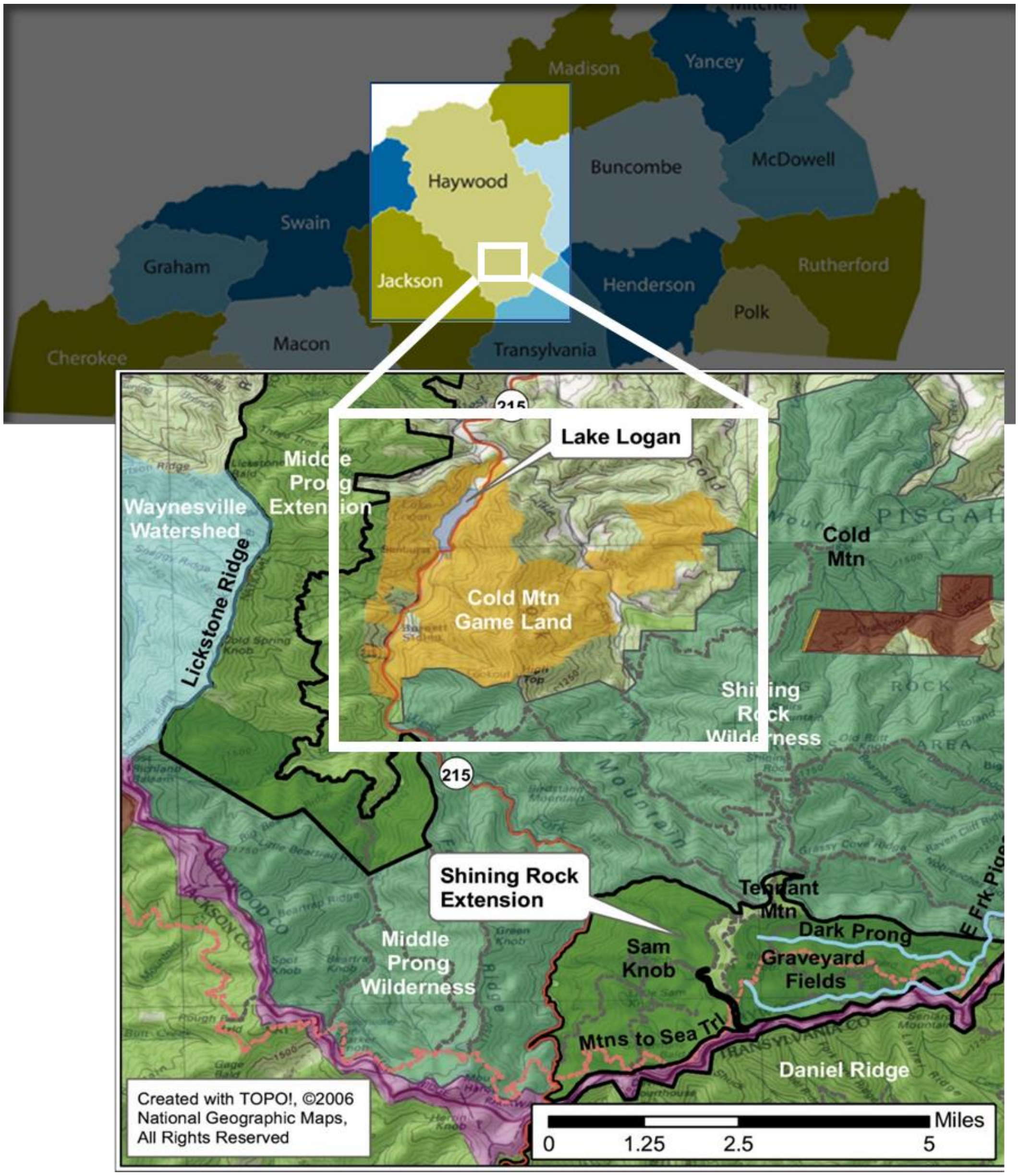

Figure 1.1 Location of the "Regional Oak Study" being conducted by the US Forest Service in the Cold Mountain Game Lands of Haywood County, Western North Carolina. (Adapted from https://alchetron.com/cdn/middle-prong-wilderness-8d455579-833f-41af-b959-8b553185332-resize-750.jpeg, and https://carolinapublicpress.org/296/the-counties-of-western-north-carolina/)

1.3.1 Experimental Design

In 2008, 16 experimental units, hereafter referred to as units, were permanently installed, each approximately 5 ha in size and separated by ≥10 m buffers that would remain untreated. Silvicultural treatments were randomly assigned to 4 of the 16 units, resulting in a completely randomized design, replicated four times (**Figure 1.2**). Treatment unit locations were chosen to avoid history of substantial disturbance within the past 15-20 years and to avoid dominance of ericaceous shrubs in the understory (Greenberg et al., 2016).

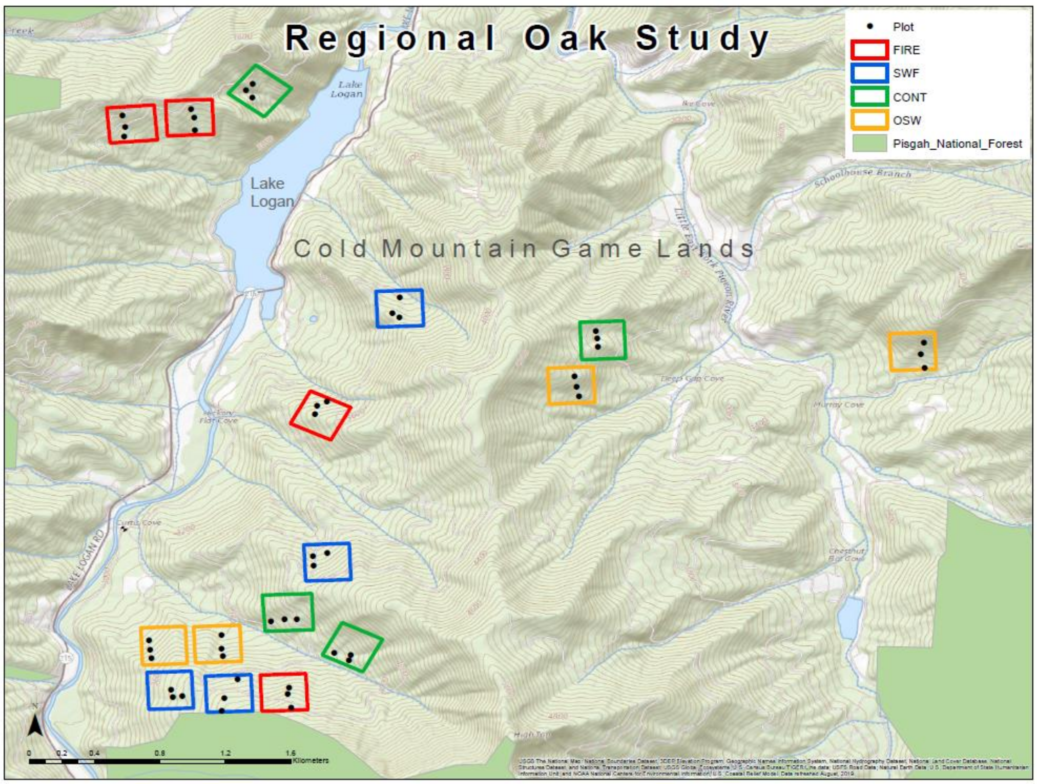

Figure 1.2 Experimental unit map for "Regional Oak Study" sites in the Cold Mountain Game Lands. Units were installed approximately 5 ha in size, separated by ≥10 m untreated buffers, and contain 3 permanent overstory plots. Treatments were randomly assigned and replicated 4 times across the study area. Treatment codes follow: FIRE= repeated fire, SWF= shelterwood and prescribed fire, CONT= unmanipulated control, OSW= oak shelterwood with herbicide.

1.3.2 Silvicultural Treatments

Starting in 2008, four silvicultural treatments aimed at the regeneration of *Quercus* seedlings that are capable of eventual, successful release into the canopy were prescribed (Brose et al., 1999; Loftis, 1990b; Loftis, 1983). The treatments follow:

<u>Repeated Prescribed Fire (FIRE):</u> A dormant-season prescribed fire, scheduled to be repeated every 5-6 years. Two units were burnt before the growing season in 2009, 2014, and 2018, and 2 units were burnt before the growing season in 2010 and 2015 (**Figure 1.3a**).

<u>Oak shelterwood with Herbicide (OSW):</u> A shelterwood prescription following Loftis (1990b) called for the midstory removal of undesirable stems (≥5 cm and <25 cm dbh) using Garlon3A (triclopyr) herbicide and the “hack and squirt” method of application. Treatments were used to reduce the total basal area by 25 - 30% without developing new canopy gaps. Treatment was applied in September of 2008 (**Figure 1.3b**).

<u>Shelterwood and Prescribed Fire (SWF):</u> A shelterwood prescription following Brose et al. (1999) began with a shelterwood harvest removing overstory trees (≥25 cm dbh) while leaving a residual basal area of 30-40% of mostly dominant and co-dominant *Quercus* species. Units were harvested in the spring of 2010 (2 units) or the spring of 2011 (2 units) with residual slash left on site. Prescribed fire was performed prior to the 5th growing season for units harvested in 2011, and prior to the 7th growing season for units harvested in 2010 to control for midstory competition and decrease leaf litter and fine fuels from the forest floor (**Figure 1.3c**).

<u>Control (CONT):</u> Four control units were left unmanipulated throughout the study and served as reference for untreated forest conditions (**Figure 1.3d**).

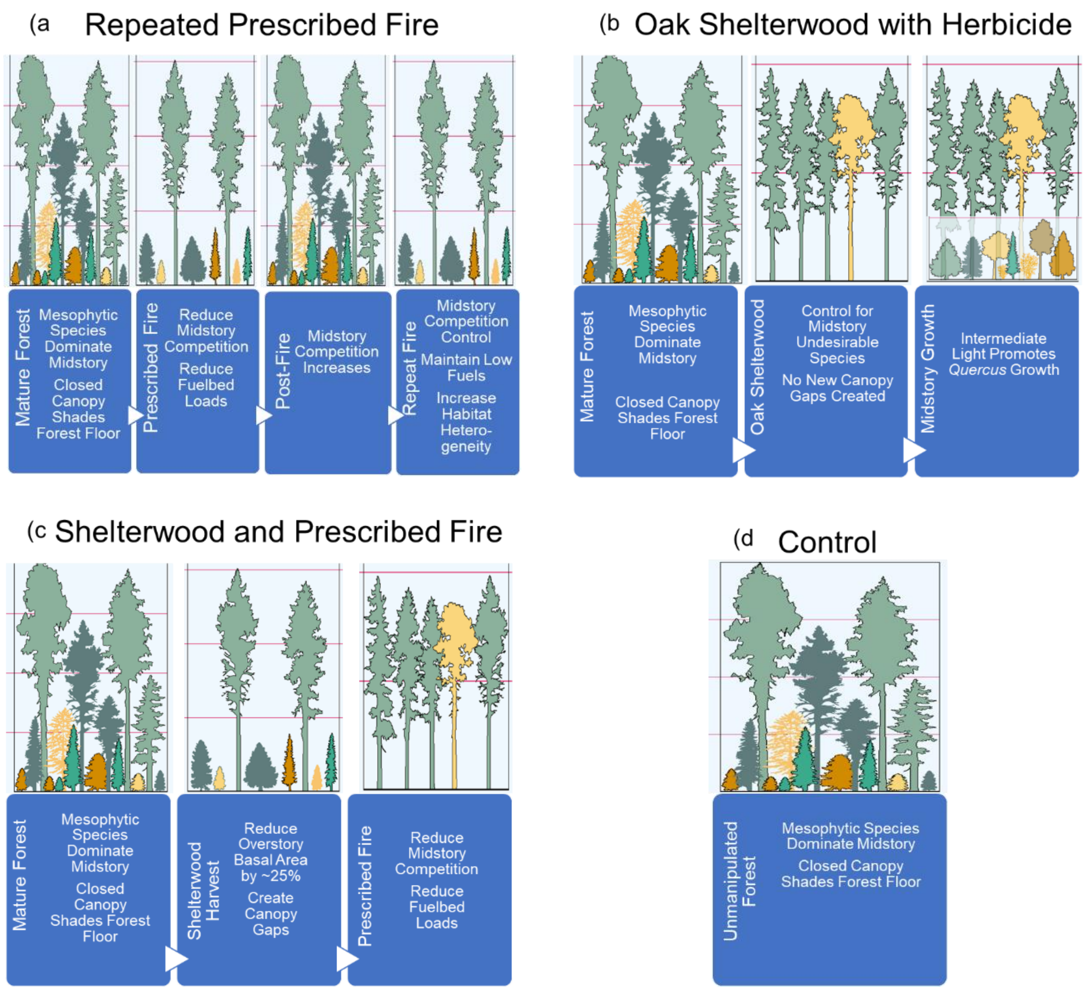

Figure 1.3 Conceptual diagram of silvicultural treatments developed for the “Regional Oak Study” describing expected changes to forest structure and midstory composition (Adapted from Langston, 1995).

Treatment Schedule

Treatment application was asynchronous across and within treatments, primarily because prescribed fire treatments require specific environmental conditions before being conducted. Control and oak shelterwood treatments were synchronous. Fire and shelterwood/fire treatments were asynchronously applied to units. Therefore, data was analyzed on a “years-post initial treatment” basis, hereafter referred to as year (**Table 1.1**). This allowed units that were given the same treatment in different calendar years to be analyzed together to maximize replication and focus on temporal patterns of responses.

Table 1.1 Treatment and ground-layer vegetation measurement schedule as sorted for statistical analysis to address asynchronous calendar year treatments. Cells without calendar years denote no ground-layer measurements were recorded for that treatment year. Treatment codes follow: CONT=control, OSW= oak shelterwood, FIRE= repeated fire, and SWF=shelterwood and fire. Overstory harvest (OH), dormant season prescribed fire (Rx) or midstory thinning with herbicide (MH) are indicated in appropriate years.

Regional Oak Study: Treatment and Measurement Schedule

Treatment	Units	Pre	1	2	3	5	6	7	8	9
CONT	4	2008	2009	2010	2011			2015		2017
OSW	4	2008 (MH)	2009	2010	2011					2017
FIRE	2	2008	2009 (Rx)	2010	2011		2014 (Rx)	2015	2016	2017
	2	2008	2010 (Rx)	2011	2012		2015 (Rx)	2016	2017	2018
SWF	2	2008	2010 (OH)	2011	2012			(Rx)	2017	2018
	2	2008	2011 (OH)	2012	2013	(Rx)		2017		2019

1.3.3 Preliminary Research

Keyser and Keyser (2013) modeled the expected 50-year response of tree regeneration, basal area (m^2 ha^{-1}), and density (trees ha^{-1}) to *Quercus* regeneration treatments developed for the “Regional Oak Study.” They reported some success in all treatments for increasing dominant/codominant *Quercus* density compared to pre-treatment levels; with the greatest increases in the oak shelterwood and repeated prescribed fire treatments. However, models produced nearly the same response to all treatments for regenerating *Quercus* into dominant/codominant canopy positions after 50 years. In addition, Keyser (unpublished data) is testing the ability of treatments to develop large (i.e., >1.2 m tall), competitive, advanced *Quercus* reproduction necessary to sustain oak recruitment under intense competition from mesic species, including *A. rubrum*, *Betula lenta* L., and *L. tulipifera*. Other preliminary and short-term response studies conducted as part of the “Regional Oak Study” have highlighted pre and post-fire effects on the buried seedbank (Keyser et al., 2012), the short-term responses of breeding birds (Greenberg et al., 2014), and of reptiles and amphibians (Greenberg et al., 2016). No evaluation of the response of the ground-layer vegetation to these silvicultural treatments has been conducted up to this point.

1.4 Objective Statement

It is important to consider the implications that species-targeted silvicultural treatments, like the ones being conducted to promote *Quercus* regeneration in Southern Appalachian forests, can have on the ground-layer vegetation community. Southern Appalachian forests contain unique microhabitats for ground-layer vegetation species due to their varying topography, climate, and geologic history (Simon et al., 2005, Dykeman, 2018), and the region is widely considered a biodiversity hotspot. Consequently, the retention or restoration of species composition and diversity of the ground-layer vegetation community has been a growing concern for private and federal land managers as silvicultural objectives are moving towards managing for multiple objectives and ecosystem services. The objective of this study is to compare how silvicultural treatments used in Southern Appalachian forests, such as repeated prescribed fire, oak shelterwood midstory thinning with herbicide, or shelterwood harvesting followed by prescribed fire affect the productivity, diversity, and successional patterns of the ground-layer vegetation community compared to unmanipulated forest conditions.

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Chapter 2: Ground-Layer Biomass Productivity Following Ten Years of Experimental Oak (*Quercus* spp.) Regeneration Treatments in Southern Appalachian Forests

ABSTRACT

The ground-layer vegetation community plays important roles in ecosystem functions including seedling regeneration, nutrient cycling, and wildlife resources. In fact, species dominance and productivity in this forest layer are important factors in determining the overall species composition and quality of every other layer of the forest. Competitive interactions for resources such as light, water, and nutrients among ground-layer species are complex and vary depending on species composition, forest type, and disturbance patterns. While the productivity and diversity of the ground-layer community is often considered when developing silvicultural objectives, it is not yet well generalized. In this study we evaluated the effects that silvicultural treatments developed to favor *Quercus* regeneration in Southern Appalachian forests, including repeated prescribed fire, oak shelterwood harvesting with herbicide, or shelterwood harvesting followed by prescribed fire have on the biomass productivity of the ground-layer vegetation community. We tested the effects of these treatments on repeated measurements of ground-layer biomass over a decade following initial treatment establishment.

Results show that treatments involving heavy overstory reduction and/or prescribed fire increased total ground-layer biomass relative to treatments that only modify the midstory or leave the forest unmanipulated. Not all ground-layer lifeforms responded equally, and we saw the greatest biomass responses following a decade of shelterwood/fire treatments; especially in the vine lifeform, which increased 10-fold. This was mainly due to increased *Rubus* biomass production (48-86% of vine lifeform following treatments), which without further management could hinder regeneration and biomass productivity of other ground-layer species, including *Quercus*. Repeated fire treatments most favorably increased the proportion of *Quercus* to total woody biomass after a decade of treatments (16% versus 11% in oak shelterwood and shelterwood/fire

treatments, or 13% in controls) showing the advantage of reintroducing a fire regime to these forests for *Quercus* regeneration.

While this study's evaluation of the response of functional groups (lifeforms) gave insight into the effects of treatments on biomass productivity, a more in-depth look at changes to diversity and dominance patterns is needed to capture the full response of such a biodiverse plant community to these *Quercus* regeneration treatments. Furthermore, evaluating the effects of these treatments on microenvironmental parameters (light availability, soil characteristic, and the influence of slope and aspect) that influence ground-layer species diversity and dominance patterns will help to better understand the ground-layer biomass responses following treatments.

2.1 Introduction

Species present in the ground-layer vegetation community play important roles in ecosystem functions such as seedling regeneration (Keyser et al., 2012; Lorimer et al., 1994), nutrient cycling (Zavitkovski, 1976; Welch et al., 2007), and wildlife resources (Ober, 2017; Carey and Johnson, 1995). Forest floor and seedbed conditions can influence the regeneration of germinants, seedlings and sprouts of every species present in the forest community. Seed germination may require direct contact with mineral soil, specific light intensities, cold stratification (a period of freezing temperatures), or even fire (pyrophilous species) to be successful (Eales et al., 2018; Luna et al., 2014).

The ground-layer community also plays an integral role in nutrient cycling. Although the ground-layer's contribution to above-ground net primary productivity (ANPP) may be much less than that of the overstory in temperate forests (Zavitkovski, 1976), its additions to carbon and nutrient cycling in many forest types are greater than that of ANPP because much of the nutrient-rich biomass (deciduous leaves and non-woody plant material) is returned to the forest floor each fall. While studies cite that the ground-layer produces anywhere from <1% - 42% of the annual carbon flux in a forest system, this is largely dependent on the particular ecosystem and the competitive interactions among all layers of the forest (ground-layer, regeneration layer, midstory, and overstory) because species differ relative to their nutrient uptake and allocation efficiency as well as their potential fluxes in carbon (gains and losses in biomass) (Landuyt et al, 2019; Zavitkovski, 1976). Welch et al. (2007) report as much as 5% of the above-ground litter pool in second-growth eastern deciduous forests originated from ground-layer vegetation.

The ground-layer community is also important for wildlife. Forest floor characteristics (light, temperature, and the amount of coarse woody debris) and the species composition of the ground-layer are important factors contributing to the biodiversity of breeding birds, reptiles, and amphibians present in the forest community (Greenberg et al., 2014; 2016). Species present in the ground-layer also provide food and shelter for many small mammals and herpetofauna that are important to the food chain of the forest (Carey and Johnson, 1995). The ground-layer community is also a resource which supports the dynamics of pollinator diversity (Landuyt et al., 2019). For example, certain moth larvae feed solely on the leaves of *Quercus* species (Ober, 2017).

Managers of private and public forest lands are increasingly incorporating the evaluation of the ground-layer community as silvicultural management techniques are being developed not only for sustained timber production, but also to recognize the multiple resources and ecosystem services the forest can provide. The ground-layer community can contribute to species diversity as well as carbon and nutrient cycling of the forest, yet also interfere with natural regeneration and timber production. Competitive interactions among ground-layer vegetation for resources such as light, nutrients, and water are the primary drivers of species composition and dominance in this regenerative forest layer. At this small forest scale (<1 m tall), a dense fern stratum can selectively filter tree seedlings and reduce overall seedling densities (George and Bazzaz ,1999; Engelman and Nyland, 2006). Tall ground-layer vegetation (herbaceous and woody) can inhibit the survival and height growth of planted *Quercus* seedlings (Lorimer et al., 1994). In addition, ruderal (able to quickly colonize disturbed areas) or exotic species, better adapted to disturbances such as overstory reduction or fires (natural or anthropogenic) can quickly outcompete neighboring vegetation post-disturbance, become dominant in the ground-layer, therefore altering successional patterns. *Rubus* species, woody vines generally classified as ruderal, can limit the regeneration of other ground-layer species by more efficiently using total nitrogen from the soil, and ultimately out-growing, and out-shading competitors (Faillace et al., 2018; Gaudio et al., 2008). In these ways, among many others, the ground-layer vegetation community and habitat structure are important factors in determining the overall species composition and quality of every other layer of the forest, from the midstory into the canopy.

Silvicultural treatments can target different aspects of an existing stand to manipulate resources for desired outcomes. Options can include harvesting the overstory to cause more immediate changes in light and growing space resources; thinning the midstory via mechanical or chemical delivery to alter filtered light conditions and reduce undesirable competitors; or burning. Prescribed fire is proposed for use in systems where fire was historically part of the disturbance regime. It exposes mineral soil, reduces mesophytic competitors, and releases a suite of pyrophilous (fire-loving) species more adapted to these conditions. The advancement of oak silviculture relies on a better understanding of the processes and ecosystem effects of the various prescriptions. Additionally, the response of the ground-layer community to these prescriptions is important for evaluating tradeoffs among industrial silvicultural objectives and objectives that support multiple forest ecosystem functions including ground-layer species diversity.

The objective of this study is to compare how silvicultural treatments developed for *Quercus* regeneration in Southern Appalachian forests influence biomass productivity in the ground-layer community, compared to unmanipulated forest conditions. We test the effects of treatments on repeated measurements of ground-layer biomass over a decade following initial treatment establishment. We hypothesize that treatments involving heavy overstory reduction and/or prescribed fire will increase total ground-layer biomass relative to less intensive manipulations that modify the midstory only. The significant change caused by canopy and fuels reduction will alter the available light at the ground-layer and cause a sustained increase in overall productivity.

We further hypothesize that not all components of the ground-layer will respond the same, with varying responses among lifeforms and species. The repeated prescribed fire treatments will decrease lifeform biomass of more shade-tolerant, fire-sensitive lifeforms (herbs, ferns) and increase lifeform biomass of more shade-intolerant, fire-resistant lifeforms (woody, vines) after at least a decade of treatments. The combination of shelterwood harvest and prescribed fire will favor the dominance of shade-intolerant and disturbance-tolerant (ruderal) species.

2.2 Methods

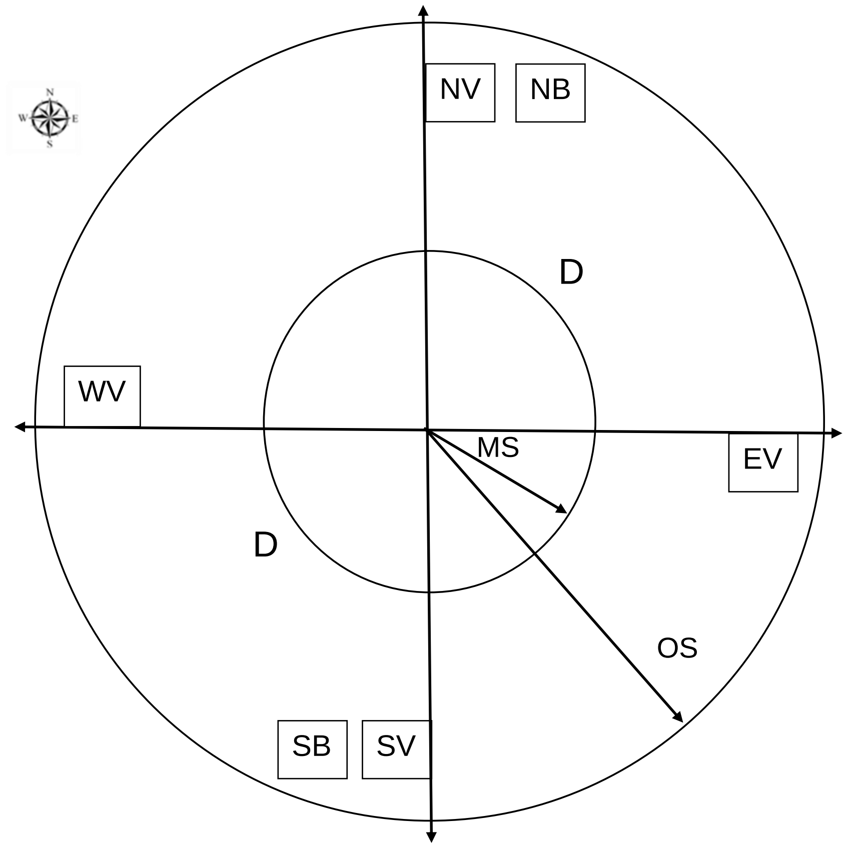
Site Description

This study is being conducted in the Cold Mountain Game Lands of western North Carolina (**Figure 1.1**). Elevations of study sites range from 983 m to 1,271 m above sea level. The terrain is mountainous with slopes ranging from 35 to 55 percent (Keyser et al., 2012). Soils in the study area are mainly Plott, Edneyville, and Chestnut soil series types (North Carolina Wildlife Commission (NCWRC, 2020). Annual precipitation of the study area is ~1,060 mm and consistently distributed throughout the year (NCWRC, 2020). Forests are second-growth, mixed-oak stands approximately 80 years old with dominant canopy species including: *Quercus rubra* L., *Q. alba* L., *Q. prinus* L., and *Q. velutina* Lam., *Acer rubrum* L., *A. saccharum* Marshall, *Carya* Nutt., *Prunus serotina* Ehrh., and *Liriodendron tulipifera* L. Midstory species composition is dominated by shade-tolerant species such as *Oxydendrum arboreum* (L.) DC.), *Nyssa sylvatica* Marshall, and *Halesia tetraptera* Ellis (Greenberg et al., 2016).

Experimental Design

In 2008, 16 experimental units (~5 ha), hereafter referred to as units, were selected, separated by ≥10 m untreated buffers (**Figure 1.2)**. Silvicultural treatments were randomly assigned to 4 of 16 units. Each unit contained three circular overstory plots (0.05 ha), hereafter referred to as plots, and nested midstory plots (0.01 ha) (**Figure 2.1**). Ground-layer vegetation subplots (1 m^2) were established 11 m from plot center in cardinal directions, resulting in 12 subplots per unit (48 per treatment). Supplemental subplots (0.5 m^2) for destructive measurements of plant biomass were established in north and south cardinal directions within 2 m of ground-layer subplots resulting in 6 biomass subplots per unit (24 per treatment).

Regional Oak Study Overstory Plot Layout



OVERSTORY PLOT LAYOUT LEGEND
NV, EV, SV, WV: Ground-layer vegetation subplots (1m^2, 11m from plot center in cardinal directions)
NB and SB: Biomass subplots (0.5x0.5x1m, 2m from respective vegetation subplots)
MS: Midstory plot (5.6m radius, 0.01ha); site of 5-<25cm dbh arboreal measurements
OS: Overstory plot (12.6m radius, 0.05ha); site of ≥25cm dbh arboreal measurements
D: Site of densiometer measurements (8m from plot center at 45° and 225°)

Figure 2.1 Nested experimental design of overstory, midstory, and ground-layer measurement plots developed for the “Regional Oak Study.” Locations of densiometer measurement sites and biomass clipping subplots are also displayed.

Silvicultural Treatments

Treatment application was asynchronous across and within treatments, primarily due to the specific environmental conditions required before prescribed fire treatments can be conducted. Data was therefore analyzed on a “years-post initial treatment” basis, hereafter referred to as year (**Table 1.1**). This allowed units that were given the same treatment in different calendar years to be analyzed together to maximize replication and focus on temporal patterns of responses. Treatments include:

<u>Repeated Prescribed Fire (FIRE):</u> A dormant-season prescribed fire, scheduled to be repeated every 5-6 years. Two units were burnt before the growing season in 2009, 2014, and 2018, and 2 units were burnt before the growing season in 2010 and 2015 (**Figure 1.3 a**).

<u>Oak shelterwood with Herbicide (OSW):</u> A shelterwood prescription following Loftis (1990b) called for the midstory removal of competitive stems (≥5 cm and <25 cm dbh) using Garlon3A (triclopyr) herbicide and the “hack and squirt” method of application. Treatments were used to reduce the total basal area by 25-30% without developing new canopy gaps. Treatment was applied in September of 2008 (**Figure 1.3 b**).

<u>Shelterwood and Prescribed Fire (SWF):</u> A shelterwood prescription following Brose et al. (1999) started with a shelterwood cut to remove overstory trees (≥25 cm dbh), leaving a residual basal area of 30 -40% of mostly dominant and co-dominant *Quercus* species. Units were harvested in the spring of 2010 (2 units) or the spring of 2011 (2 units), and residual slash was left on site. Prescribed fire was performed prior to the 5th growing season for units harvested in 2011, and prior to the 7th growing season for units harvested in 2010 to control for undesirable midstory competition (**Figure 1.3 c**).

<u>Control (CONT):</u> Four control units were left untreated throughout the study and served as reference for unmanipulated forest conditions (**Figure 1.3 d**).

Data Collection

Long-Term Ground-layer Vegetation Subplot Measurements

During intermittent summers (July-August at the time of maximum leaf-out), since 2008, percent cover of all ground-layer vegetation species, defined as all vascular herbaceous and woody species <1 m tall, was visually estimated in each 1 m^2 ground-layer subplot. Ground-layer vegetation was identified to species when possible using nomenclature and identification codes listed in the United States Department of Agriculture: Natural Resource Conservation Service PLANTS database (USDA, NRCS 2020). Cover was recorded using seven classes: 0-<1%, 1%-<5%, 5%-<25%, 25%-<50%, 50%-<75%, 75%-<95%, 95%-100%. Cover class midpoint values were used to calculate average species cover at the plot level, which was used for all further comparative analysis.

A total of 270 species were identified across treatments and years sampled. A separate study explores the individual species responses and overall patterns of compositional change (Benz, Chapter 3). Here we evaluated functional responses to treatments and therefore categorized species into trait-based groups relative to lifeform habits. The 6 plant lifeforms identified in this study include: (1) ferns and fern allies, (2) graminoids including grasses, sedges, and rushes, (3) herbaceous species including flowering forbs and herbaceous vines, (4) shrubs including all non-tree woody species, (5) woody, arboreal species, and (6) perennial vines. Due to the overwhelming flush of *Rubus* spp. that developed post-overstory reduction in the shelterwood/fire treatment, and the importance of *Quercus* as a forest species and the focus of the Regional Oak Study's restoration efforts, we also explored the biomass response of these lifeform subtypes.

Ground-layer Lifeform Biomass Sampling

Cover was visually estimated to the nearest percent in biomass subplots and recorded for each lifeform and lifeform subtype in the summer (July-August) of 2019. All living vegetation rooted in the subplots was clipped and the harvested plant material was oven dried and weighed to 0.001 g. Any vegetation growing taller than 1 m was excluded from cover estimates and not included in biomass samples. Any woody species >5 cm in diameter were excluded from cover measurements and not clipped. Additional biomass subplots were established within treatment units to increase sample sizes for individual lifeforms and to develop a more extensive range of cover values required to develop robust allometric regression equations.

Canopy Openness

Canopy openness at the plot level was estimated intermittently since 2008 by averaging 8 measurements recorded 8 m from plot center in two sub-cardinal directions using a concave spherical densiometer (Forestry Suppliers, Inc., 2008).

Data Analysis

Allometric Relationship of Biomass Regression and Cover

For all lifeforms and lifeform subtypes, power regression equations produced higher R^2 values than linear or quadratic equations for relating summed species cover to lifeform biomass on subplots established specific to biomass estimation (**Table 2.1**). Sample sizes ranged from n=23 for *Rubus* to n=109 for the herbaceous lifeform cover/biomass collections, and R^2 values ranged from 0.57 for woody to 0.898 for ferns. These equations were applied to predict biomass using species cover estimates monitored in the permanent ground-layer subplots, without compromising the long-term data monitoring. Mean ground-layer subplot species cover was summed to lifeform (or subtype) to quantify potential plot lifeform cover. Then, lifeform specific biomass regression equations were applied to estimate potential plot level lifeform biomass ($g\ m^{-2}$), hereafter referred to as biomass.

Table 2.1 Lifeform (and lifeform subtype) specific allometric power regression equations developed to estimate lifeform biomass. Lifeform, sample size (n), equation, fit (R^2), and the standard error of the regression are displayed for each lifeform (and subtype).

Lifeform	n	Power Regression Equation	R^2	StdErr of XY Regression
Fern	29	$y=0.0291x^{1.3438}$	0.898	20.63
Rubus	23	$y = 0.0544x^{1.3566}$	0.810	8.27
Graminoid	39	$y = 0.05x^{1.3163}$	0.765	1.60
Herbaceous	109	$y = 0.0333x^{1.2785}$	0.706	2.76
Vine	65	$y = 0.1497x^{1.0444}$	0.600	10.24
Shrub	30	$y = 0.1946x^{1.0368}$	0.600	8.79
Quercus	39	$y = 0.067x^{1.1905}$	0.596	2.01
Woody	66	$y = 0.0732x^{1.2122}$	0.572	12.02

Lifeform biomass was estimated and analyzed using Statistical Analysis System (SAS version 9.4; Cary, NC). A mixed effect, repeated measures model was used to test for significant effects of treatments on total ground-layer vegetation biomass and specific lifeform biomass over time. Treatment and year were defined as the fixed effects in the model. Plots were nested within treatment by unit and defined as the random effect and as the subject within the repeated statement. A spatial power covariance structure was specified in the model to account for the unequal intervals between sampling periods through time (interdependence of the data). Biomass data were visually assessed for normality and equal variance assumptions and transformed (cube root) to meet model assumptions. P-values <0.05 were considered significant while p-values <0.001 were considered highly significant. Back-transformation of biomass least squares means was performed before reporting significant trends. Due to small sample sizes, woody and *Quercus* biomass estimates were pooled, and vines and *Rubus* biomass estimates were pooled before testing. Although not tested separately with repeated measures we graphed the raw biomass estimates derived from our allometric regressions to calculate the biomass contribution of *Rubus* and *Quercus* lifeform subtypes to lifeform biomass through time (percent *Rubus* to vine, and the percent *Quercus* to woody).

2.3 Results

Pre-Treatment Biomass

Total biomass averaged 19.6 g m^{-2} among experimental units prior to treatments (**Table 2.2**) and was not statistically different ($p \geq 0.1$), making among treatment comparisons thereafter more meaningful. For all lifeforms, except for ferns (CONT versus SWF: $p = 0.03$), biomass prior to treatments was not significantly different among treatment units ($p > 0.5$).

Table 2.2 Total and specific lifeform biomass (g m^{-2}) means ± the standard error (back-transformed). Results are sorted by lifeform for each treatment and year tested with repeated measures.

		Treatment Year							
Lifeform	**Treatment**	**Pre**	**1**	**2**	**3**	**6**	**7**	**8**	**9**
Total	Control	22.2 ± -1.2	20.2 ± -1.6	23.1 ± -1.0	21.2 ± -1.4	N/A	24.6 ± -0.7	N/A	17.6 ± -2.1
	Repeated Fire	16.2 ± -2.4	17.4 ± -2.1	24.4 ± -0.8	21.8 ± -1.3	33.6 ± 1.0	34.1 ± 1.1	31.5 ± 0.6	26.0 ± -0.5
	Oak Shelterwood	21.3 ± -1.4	21.5 ± -1.3	25.4 ± -0.6	27.7 ± -0.1	N/A	N/A	N/A	28.5 ± 0.0
	Shelterwood/Fire	18.8 ± -1.9	39.8 ± 2.2	49.9 ± 4.1	55.6 ± 5.2	N/A	33.5 ± 1.0	42.3 ± 2.7	41.2 ± 2.5
Vine	Control	2.10 ± 0.14	2.40 ± 0.20	2.70 ± 0.26	2.90 ± 0.30	N/A	3.80 ± 0.47	N/A	2.70 ± 0.26
	Repeated Fire	1.00 ± -0.07	2.70 ± 0.26	4.90 ± 0.68	4.00 ± 0.51	4.50 ± 0.60	5.40 ± 0.78	4.90 ± 0.68	3.20 ± 0.35
	Oak Shelterwood	1.80 ± 0.08	3.00 ± 0.32	3.70 ± 0.45	3.30 ± 0.37	N/A	N/A	N/A	5.90 ± 0.87
	Shelterwood/Fire	1.00 ± -0.07	10.10 ± 1.68	13.60 ± 2.36	20.20 ± 3.63	N/A	8.90 ± 1.45	11.80 ± 2.01	11.90 ± 2.03
Woody	Control	8.45 ± 1.36	6.39 ± 0.97	6.27 ± 0.94	5.71 ± 0.84	N/A	7.26 ± 1.13	N/A	4.79 ± 0.66
	Repeated Fire	5.52 ± 0.80	3.47 ± 0.41	4.51 ± 0.60	4.87 ± 0.68	6.61 ± 1.01	6.74 ± 1.04	6.69 ± 1.03	6.92 ± 1.07
	Oak Shelterwood	6.38 ± 0.97	4.62 ± 0.63	7.26 ± 1.13	9.16 ± 1.50	N/A	N/A	N/A	9.46 ± 1.56
	Shelterwood/Fire	5.91 ± 0.88	10.72 ± 1.80	14.69 ± 2.57	13.72 ± 2.38	N/A	7.52 ± 1.19	6.74 ± 1.03	7.10 ± 1.10
Herbaceous	Control	4.02 ± 0.51	4.65 ± 0.63	5.12 ± 0.72	5.00 ± 0.70	N/A	5.04 ± 0.71	N/A	3.22 ± 0.36
	Repeated Fire	2.70 ± 0.26	5.71 ± 0.84	6.96 ± 1.08	5.66 ± 0.83	11.63 ± 1.98	10.95 ± 1.84	8.11 ± 1.30	6.17 ± 0.93
	Oak Shelterwood	6.54 ± 1.00	7.04 ± 1.09	6.97 ± 1.08	6.77 ± 1.04	N/A	N/A	N/A	6.42 ± 0.97
	Shelterwood/Fire	6.68 ± 1.02	12.73 ± 2.19	9.54 ± 1.57	9.44 ± 1.55	N/A	10.03 ± 1.67	10.37 ± 1.73	10.68 ± 1.79
Shrub	Control	0.63 ± -0.14	0.55 ± -0.16	0.57 ± -0.15	0.50 ± -0.17	N/A	1.29 ± -0.01	N/A	0.70 ± -0.13
	Repeated Fire	1.13 ± -0.05	0.99 ± -0.07	2.14 ± 0.15	1.81 ± 0.09	2.55 ± 0.23	2.96 ± 0.31	2.84 ± 0.28	3.15 ± 0.34
	Oak Shelterwood	0.51 ± -0.16	0.21 ± -0.22	0.39 ± -0.19	0.92 ± -0.09	N/A	N/A	N/A	0.97 ± -0.08
	Shelterwood/Fire	0.22 ± -0.22	0.65 ± -0.14	1.19 ± -0.03	3.17 ± 0.35	N/A	2.55 ± 0.23	1.61 ± 0.05	1.20 ± -0.03
Fern	Control	0.09 ± -0.25	0.10 ± -0.24	0.13 ± -0.24	0.16 ± -0.23	N/A	0.25 ± -0.22	N/A	0.14 ± -0.24
	Repeated Fire	0.18 ± -0.23	0.22 ± -0.22	0.26 ± -0.21	0.14 ± -0.24	0.27 ± -0.21	0.25 ± -0.21	0.17 ± -0.23	0.14 ± -0.24
	Oak Shelterwood	0.20 ± -0.22	0.23 ± -0.22	0.51 ± -0.16	0.29 ± -0.21	N/A	N/A	N/A	0.49 ± -0.17
	Shelterwood/Fire	0.91 ± -0.09	0.30 ± -0.20	0.26 ± -0.21	0.36 ± -0.19	N/A	0.53 ± -0.16	0.39 ± -0.19	0.40 ± -0.19
Graminoid	Control	0.04 ± -0.25	0.14 ± -0.23	0.14 ± -0.24	0.14 ± -0.24	N/A	0.05 ± -0.25	N/A	0.03 ± -0.26
	Repeated Fire	0.03 ± -0.26	0.07 ± -0.25	0.15 ± -0.23	0.18 ± -0.23	0.46 ± -0.17	0.40 ± -0.19	0.42 ± -0.18	0.23 ± -0.22
	Oak Shelterwood	0.16 ± -0.23	0.16 ± -0.23	0.27 ± -0.21	0.33 ± -0.20	N/A	N/A	N/A	0.06 ± -0.25
	Shelterwood/Fire	0.01 ± -0.26	0.32 ± -0.20	0.56 ± -0.16	0.32 ± -0.20	N/A	0.16 ± -0.23	0.14 ± -0.24	0.09 ± -0.24

Treatment Effect on Total Ground-Layer Biomass

Total ground-layer vegetation biomass (g m^{-2}) production varied significantly through time depending on the treatment ($F_{(15, 125)} = 4.9$, $p = 0.02$). In the repeated fire treatment, total biomass reached a maximum after the second fires (years 6–7) and exceeded pre-treatment biomass in the controls by 12 g m^{-2} ($p \leq 0.02$, **Figure 2.2, Table 2.2**). Total biomass increased in the shelterwood/fire treatment relative to in the controls for up to three years following overstory harvest (years 1-3: 40-56 g m^{-2} versus 20-23 g m^{-2}, $p \leq 0.003$) and was still greater than pre-treatment control conditions following fire treatments (years 8-9: 41-42 g m^{-2} versus 22 g m^{-2}, $p \leq 0.004$). In year 9, the shelterwood/fire treatment maintained the greatest biomass, though all treatments had significantly higher biomass than the controls (SWF: 41 g m^{-2}, FIRE: 26 g m^{-2} and OSW: 28 g m^{-2} versus CONT: 18 g m^{-2}, $p \leq 0.04$). Total biomass in the oak shelterwood treatment did not differ significantly from controls for any other years.

Within the control treatment, total biomass varied from a maximum of 7 g m^{-2} across the decade, with the lowest value observed in year 9 (significantly lower than pre-treatment, years 2 and 7, $p \leq 0.05$). Total biomass increased gradually following the oak shelterwood treatment, with a significant increase of 6-7 g m^{-2} from pre-treatment to years 3 and into year 9 ($p \leq 0.02$). The repeated fire treatment caused the most significant variation in total biomass through time (**Figure 2.2, Table 2.2**). Biomass increased significantly ($p \leq 0.02$) following the first prescribed fires (years 2-3: 22-24 g m^{-2} relative to pre-treatment and year 1: 16–17 g m^{-2}), and after the second prescribed fires (years 6-9: 26-34 g m^{-2}). The second prescribed fire caused a more significant increase in total biomass relative to the first fires (years 6-9 versus 2-3, $p \leq 0.04$), with biomass reaching a maximum 32-34 g m^{-2} in years 6-8 and slowly declining again by year 9 ($p < 0.02$). The shelterwood/fire treatment caused biomass to more than double following overstory harvest (years 1-3: 40-56 g m^{-2}, $p < 0.001$). Although biomass declined relative to the post-harvest peak (from 56 g m^{-2} in year 3 to 33 g m^{-2} in year 7, $p = 0.0096$) the subsequent single fire treatment maintained elevated productivity relative to pre-treatment rates (years 7-9: 33-41 g m^{-2} $year^{-1}$, $p \leq 0.01$).

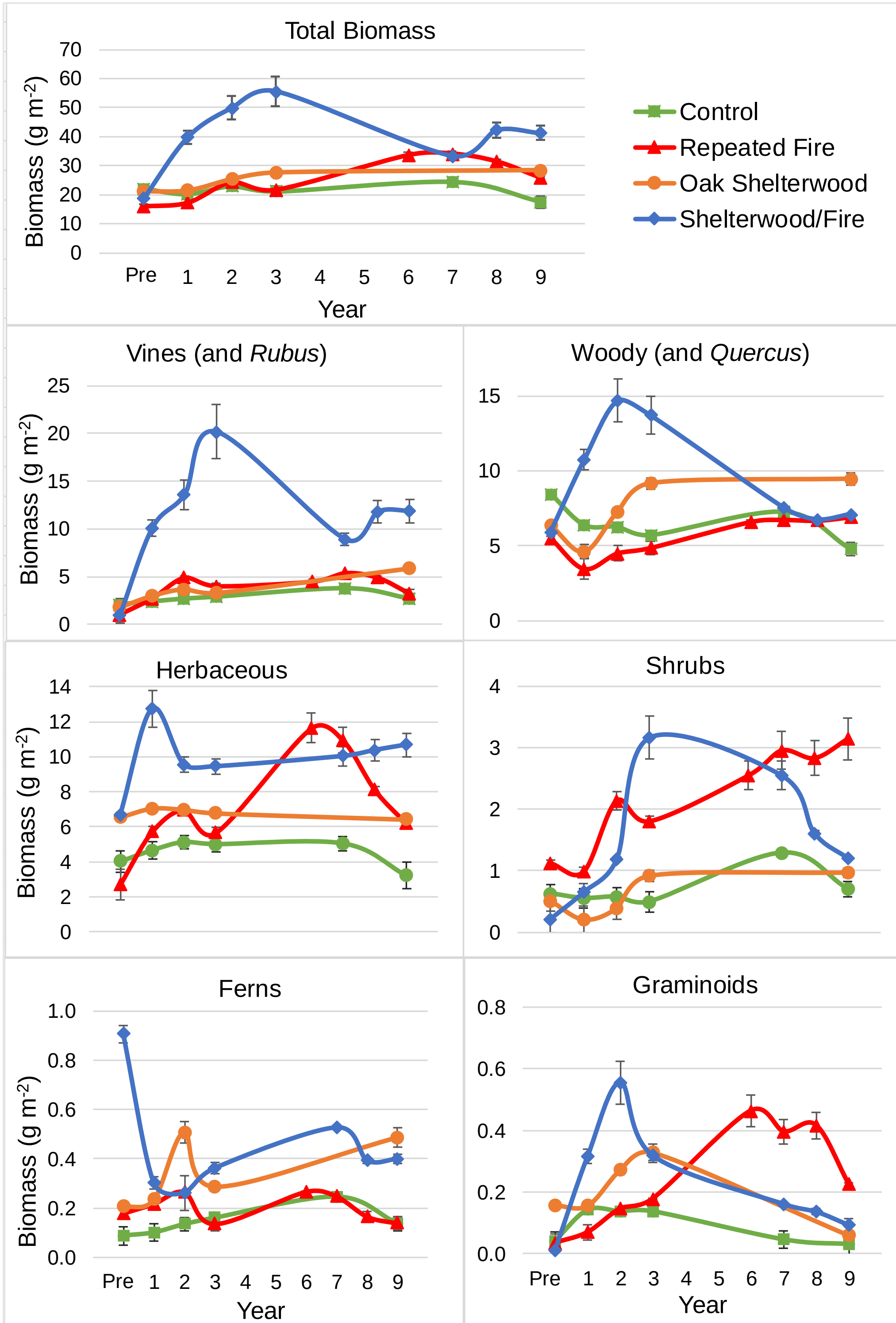


Figure 2.2 Ground-layer biomass (g m^{-2}) least square means results showing the change in total and individual lifeform biomass by treatment and year. Results were back-transformed from cube root transformation of lifeform biomass estimates. Error bars display the standard error of the mean. Note the differences in the maximum y-axis value for biomass (g m^{-2}).

Biomass by Lifeform

Vine Response

The effect of treatments on perennial vine (vine lifeform) biomass varied significantly through time depending on the treatment ($F_{(15, 134)} = 4.9$, $p < 0.0001$), and contributed the most to total biomass overall in all years following treatments (**Table 2.4**). The shelterwood/fire treatment increased vine biomass ten-fold following overstory harvest (pre-treatment: 1 g m^{-2} to year 1: 10.1 g m^{-2}, p < 0.0001, **Figure 2.2**). Thereafter, biomass in the shelterwood/fire treatment remained higher than all other treatments for years 1-3 (13.6-20.2 g m^{-2} versus CONT: 2.4-2.9 g m^{-2}, FIRE: 2.7-4.9 g m^{-2}, and OSW: 3-3.7 g m^{-2}, p ≤ 0.01). In year 9, vine biomass in the shelterwood/fire treatment (11.9 g m^{-2}) was significantly greater than in the control (2.7 g m^{-2}, p = 0.0002) and repeated fire (3.2 g m^{-2}, p = 0.005) treatments.

Vine biomass fluctuated within the control treatment from 2.1 g m^{-2} pre-treatment to 3.8 g m^{-2} by year 7 (p = 0.02), yet by year 9 did not differ significantly from pre-treatment levels (2.7 g m^{-2}, p = 0.3). The repeated fire treatment increased vine biomass for all years following treatments (from pre-treatment: 1 g m^{-2} to years 1-9: 2.7-5.4 g m^{-2}, p ≤ 0.03), with the peak two years after the second prescribed fires (year 7). Overall, vines in the repeated prescribed fire treatment increased 1-2 years following fire treatments and began decreasing 3-4 years post-fires, being still greater than pre-treatment conditions by year 9 (3.2 g m^{-2}, p = 0.003). The oak shelterwood treatment caused a gradual increase in vine biomass with the peak at 5.9 g m^{-2} in year 9 (from 1.8 g m^{-2} pre-treatment, p < 0.02). The shelterwood/fire treatment increased vine biomass 10-fold following overstory harvest (pre-treatment: 1 g m^{-2} versus years 1-3: 10.1-20.2 g m^{-2} , p ≤ 0.02), peaking in year 3 and resulting in the highest response in the study (**Figure 2.2**). The subsequent prescribed fire reduced vines biomass more than 50% by year 7 (8.8 g m^{-2} versus year 3: 20.2 g m^{-2}, p = 0.03), which remained stable into year 9.

Although the *Rubus* spp. lifeform subtype was included in the vine biomass estimates before testing the overall lifeform response to treatments, personal observations made during field surveys of the ground-layer vegetation afforded the assumption/prediction that it was the growth and abundance of *Rubus* species in particular that were driving the vine biomass response. We identified three *Rubus* species across treatments and years including: *R. odoratus*, *R. occidentalis*, and *R. allegheniensis*, but *R. allegheniensis* was by far the most prevalent. Overstory removal in the shelterwood/fire treatment increased *Rubus* biomass from 7% of total vine biomass pre-treatment, to 56% in treatment year 1 and 71% in treatment year 3 (**Figure 2.3**). Subsequent, single prescribed fire treatments reduced *Rubus* percentages to 48% by year 7, yet percentages increased again to 74% by treatment year 9. Although these species were found across the study site prior to treatments, only the shelterwood/fire treatment increased the proportion of *Rubus* to total vine lifeform biomass in such a way.

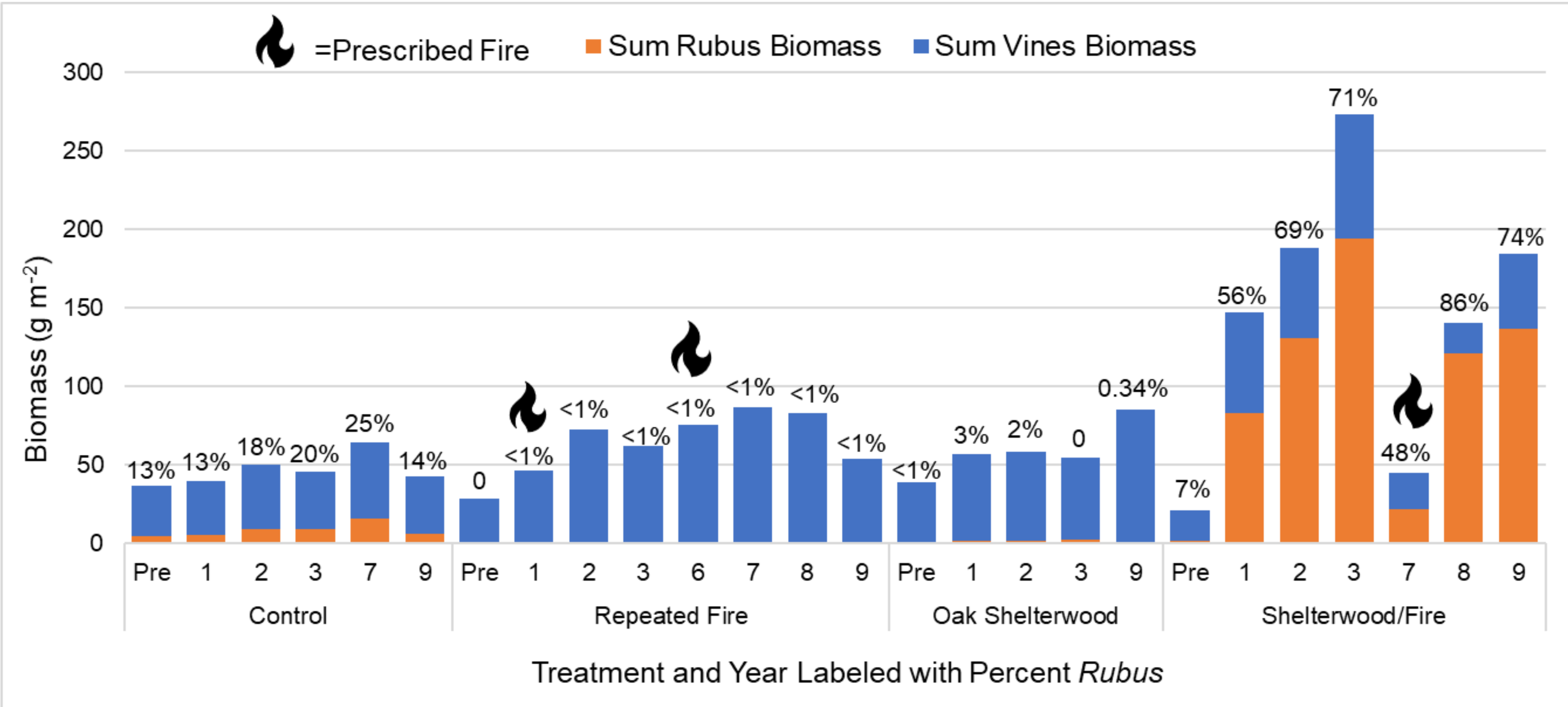


Figure 2.3 Percent of *Rubus* spp. within vine lifeform biomass (g m^{-2}) by treatment and year. Data were derived from raw biomass estimates from allometric regression of lifeform cover (summed plot means). Stacked bars represent the sum of *Rubus* spp. and the sum of vine biomass (*Rubus* excluded). Bars are labeled with the percent of *Rubus* in overall (*Rubus* included) vine biomass.

Woody Response

The effect of treatments on the biomass of tree seedlings and sprouts (woody lifeform) also varied significantly through time depending on the treatment ($F_{(15, 131)}$ = 3.2, $p < 0.0002$) and contributed the second-most to total biomass. The shelterwood/fire treatment resulted in higher woody biomass relative to the controls 2-3 years following overstory harvest (13.7-14.7 g m^{-2} versus CONT years 2-3: 5.7-6.3 g m^{-2}, p = 0.01, **Figure 2.2**). The shelterwood/fire treatment also increased woody biomass the three years following overstory harvest (years 1-3: 10.7-14.7 g m^{-2}) relative to the three years following the first prescribed fires in the repeated fire treatment (years 1-3: 3.5-4.9 g m^{-2}, p ≤ 0.04).

Woody biomass fluctuated in the controls but had declined nearly 50% by year 9 (8.4 g m^{-2} pre-treatment to 4.8 g m^{-2} year 9, p = 0.01) retaining the least woody biomass relative to other treatments. The repeated fire treatment reduced woody biomass production following the first prescribed fires (pre-treatment: 5.5 g m^{-2} to year 1: 3.5 g m^{-2}, p = 0.01). Thereafter, woody biomass remained stable into year 3, increased in year 6 to 6.6 g m^{-2} (p = 0.1), and remained constant into year 9 despite secondary fire treatments (years 6-9: 6.6-6.9 g m^{-2}). Initial midstory thinning with herbicide in the oak shelterwood treatment slightly reduced woody biomass from 6.4 g m^{-2} pre-treatment to 4.6 g m^{-2} in year 1, though differences in time were not statistically significant (p = 0.2). Biomass increased into years 3 and 9 (9.2-9.5 g m^{-2}, p ≤ 0.01), but did not differ from pre-treatment levels (p = 0.1). The shelterwood/fire treatment increased woody biomass for three years following overstory harvest (years 1-3: 10.7-14.7 g m^{-2}, p ≤ 0.02) resulting in the greatest woody biomass response in the study (**Figure 2.2**). Additional prescribed fire treatments decreased woody biomass by year 7 (13.7 g m^{-2} to 7.5 g m^{-2}, p ≤ 0.04) and biomass levels remained constant into year 9 when biomass in the shelterwood/fire treatment did not differ from pre-treatment conditions (p = 0.5).

We isolated the *Quercus* species from the pooled woody lifeform to test how the focal management species responded to treatments. We found the greatest percentage of *Quercus* to total woody biomass in the repeated fire treatments, particularly following the second prescribed fires (years 6-9: 25-33%, **Figure 2.4**). We also found the greatest increase in percent *Quercus* to total woody biomass from pre-treatment to year 9 (16%) in the repeated fire treatment, although this was a similar pattern with pre-treatment to year 9 (13% increase) in the control treatment. Both shelterwood treatments increased *Quercus* biomass relative to total woody biomass by 11%.

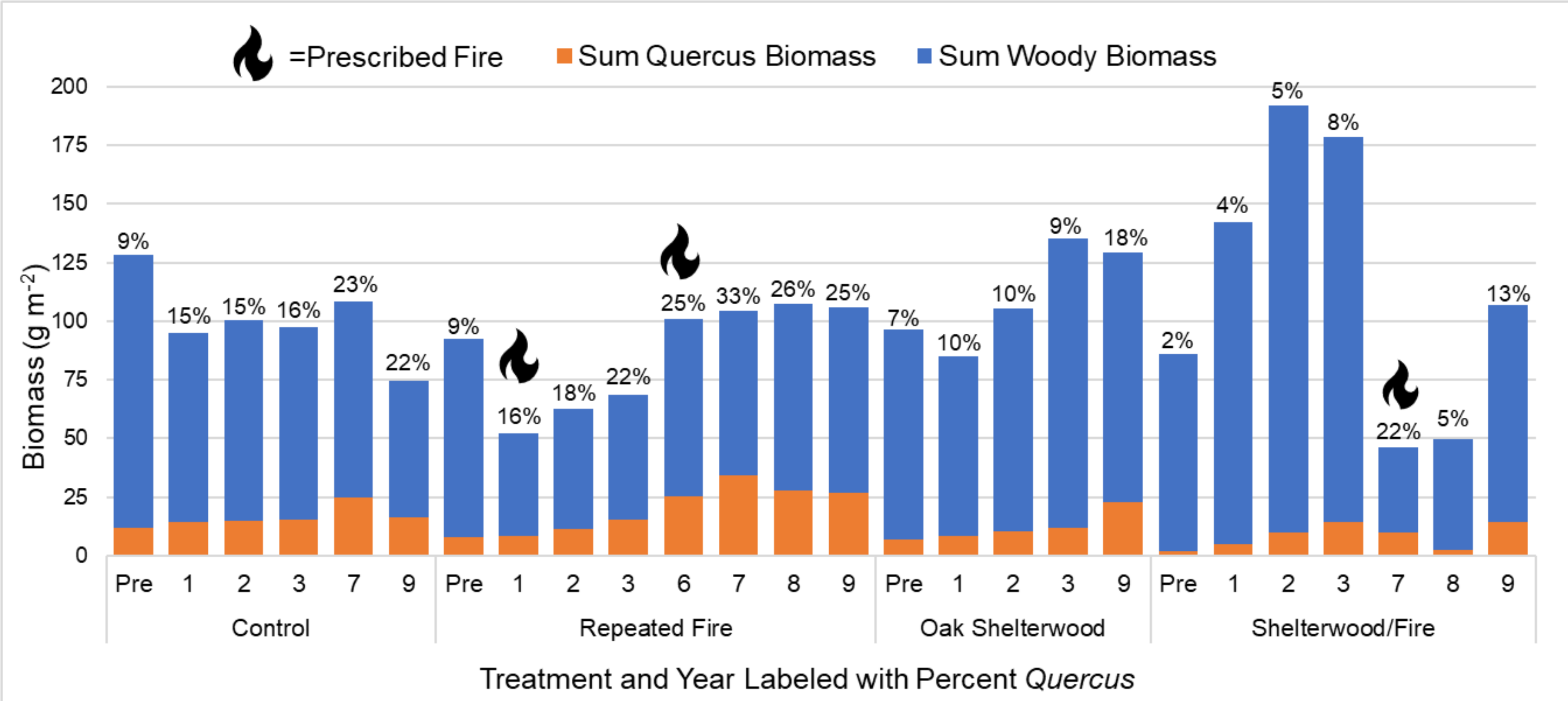


Figure 2.4 Percent of *Quercus* spp. within the woody lifeform biomass (g m^{-2}) by treatment and year. Data were derived from raw biomass estimates from allometric regression of lifeform cover (summed plot means). Stacked bars represent the sum of *Quercus* spp. and the sum of woody biomass (*Quercus* excluded). Bars are labeled with the percent of *Quercus* in overall (*Quercus* included) woody biomass.

Herbaceous Response

The effect of treatments on flowering forbs and herbaceous vines (herbaceous lifeform) biomass varied significantly by treatment and through time ($F_{(15, 209)} = 3.4$, $p < 0.0001$), contributing the third-most to total biomass. Among treatments, the shelterwood/fire treatment caused the largest increase (5.7 g m^{-2}) in herbaceous biomass the year following initial treatments (relative to CONT: 4.7 g m^{-2}, FIRE: 5.7 g m^{-2}, and OSW: 7 g m^{-2}, $p \leq 0.04$, **Figure 2.2**). Herbaceous biomass in the shelterwood/fire treatment remained higher than in controls for years 3, 7, and 9 (10-10.7 g m^{-2} versus CONT: 3.2-5 g m^{-2}, $p \leq 0.05$). The repeated fire treatment increased herbaceous biomass two growing seasons after the second prescribed fires relative to controls (year 7: 10.9 g m^{-2} versus CONT: 5 g m^{-2}, $p \leq 0.05$).

Herbaceous biomass in the control treatment declined after nearly a decade (years 2-7: 4-5.1 g m^{-2} versus year 9: 3.2 g m^{-2}, $p \leq 0.03$) and had the lowest herbaceous productivity among treatments in the final year (**Figure 2.2**). In the repeated fire treatment, biomass nearly doubled following the first fires (pre-treatment: 2.7 g m^{-2} versus years 1-3: 5.7-7 g m^{-2}, $p < 0.0001$), peaked following the second fires, at 11.6 g m^{-2} in year 6 ($p \leq 0.001$), and gradually declined into year 9 (years 8-9: 8.1-6.2 g m^{-2}, $p \leq 0.01$). In the shelterwood/fire treatment, biomass nearly doubled (6.7 g m^{-2} to 12.7 g m^{-2}, $p < 0.0001$) following the overstory harvest, producing the highest herbaceous biomass. Biomass declined the next year to 9.5 g m^{-2} ($p = 0.01$) and remained stable into year 9 despite subsequent fire treatments (years 2-9: 9.4-10.7 g m^{-2}). The oak shelterwood treatment produced no significant differences in herbaceous biomass through time.

Shrub Response

The main effect of year was highly significant for non-tree woody species (shrub lifeform) ($F_{(8, 125)} = 4.9$, $p < 0.0001$), but the treatment by year interaction was not identified ($F_{(15, 122)} = 1.49$, $p = 0.12$). Shrub biomass in the controls varied slightly through time ($p > 0.08$) and peaked in year 7 at 1.3 g m^{-2} (**Figure 2.2**). The repeated fire treatment increased shrub biomass relative to pre-treatment conditions in the second year following the first prescribed fires (0.99-1.1 g m^{-2} to 2.1 g m^{-2}, $p \leq 0.04$), and continued to increase biomass following the second fires (years 6-9: 2.6-3.2 g m^{-2}, $p \leq 0.02$). The oak shelterwood treatment reduced shrub biomass by nearly half (pre-treatment: 0.51 g m^{-2} to year 1: 0.21 g m^{-2}, p = 0.1). Thereafter, shrubs increased into years 3 and 9 (0.92-0.97 g m^{-2}, $p \leq 0.04$), but did not differ from pre-treatment biomass (p = 0.3). The shelterwood/fire treatment started with the lowest biomass (0.22 g m^{-2}) which increased 5-fold by the second year after the overstory harvest (1.2 g m^{-2}, p = 0.04) and gained an additional 2 g m^{-2} by year 3. Additional, single prescribed fires reduced shrub biomass to 1.2 g m^{-2} by year 9, still a 6-fold increase from pre-treatment levels (p = 0.053).

Fern Response

Fern and fern allies (fern lifeform) biomass production varied significantly through time depending on the treatment ($F_{(15, 119)} = 2$, $p = 0.02$), but contributed a relatively small amount to total biomass overall. Before treatments, fern biomass in the shelterwood/fire treatment (0.91 g m^{-2}) was the highest in the study and was significantly higher than in the controls (0.09 g m^{-2}, p = 0.03), the lowest fern biomass in the study (**Figure 2.2**). Otherwise, pre-treatment fern biomass was statistically similar among all other treatments.

Fern biomass increased moderately throughout years in the control treatments from pre-treatment and year 1 (0.09-0.1 g m^{-2}) to a high of 0.25 g m^{-2} in year 7 ($p \leq 0.04$) but was returning to pre-treatment levels by year 9 (0.14 g m^{-2}, p = 0.35). The repeated fire treatment decreased fern biomass nearly 50% three years after the first prescribed fires (year 2: 0.26 g m^{-2} versus year 3: 0.14 g m^{-2}, p = 0.02). Fern biomass nearly doubled again by year 6 and decreased again, nearly to pre-treatment levels by year 9, yet neither change was significant. This trend shows an increase in fern biomass in the growing seasons just after prescribed fires, with a slow decrease in ferns as time since fire increases. The oak shelterwood treatment caused a doubling of fern biomass within two years (pre-treatment: 0.2 g m^{-2} to year 2: 0.51 g m^{-2}, $p \leq 0.02$). This peak in biomass occurred following midstory thinning and fluctuated in years following treatment from 0.3 to 0.5 g m^{-2} but remained significantly (p = 0.04) higher than pre-treatment levels. The shelterwood/fire treatment caused the most change in fern biomass. The initial overstory harvest reduced ferns biomass by nearly 2/3 (pre-treatment: 0.91 g m^{-2} versus year 1: 0.3 g m^{-2}, p = 0.003). There was a general pattern of increasing biomass following this reduction with biomass reaching 0.5 g m^{-2} just after the final prescribed fires conducted (year 7), yet fern biomass never regained pre-treatment levels.

Graminoid Response

The effect of treatments on the biomass of grasses, sedges, and rushes (graminoid lifeform) also varied significantly through time depending on the treatment ($F_{(15,145)}$ = 2.5, p = 0.003). The graminoid lifeform contributed minimally to total biomass overall (**Figure 2.2**). In the controls, graminoid biomass significantly increased into year 3, relative to pre-treatment (0.04 vs 0.14 g m^{-2}, p ≤ 0.03), then decreased into year 9 (0.03 g m^{-2}, p ≤ 0.02), showing the natural ebb and flow of graminoid growth in these unmanipulated forests. Two growing seasons after overstory removal in the shelterwood/fire treatment, graminoid biomass was significantly higher than in the controls (year 2: 0.56 g m^{-2} versus CONT: 0.14 g m^{-2}, p = 0.04).

The shelterwood/fire treatment increased biomass of graminoids from pre-treatment levels, peaking in year 2 (0.01 g m^{-2} versus 0.09-0.56 g m^{-2}, p ≤ 0.03). Graminoid biomass had begun to decrease before fires (year 3) and significantly decreased following fires (year 3: 0.32 g m^{-2} to year 9: 0.09 g m^{-2}, p ≤ 0.04). The repeated fire treatment increased graminoids up to three years following the second prescribed fires relative to pre-treatment (0.03 g m^{-2} versus years 6-8: 0.4-0.46 g m^{-2}, p ≤ 0.02), and at times was significantly higher than in the controls (year 7: 0.05 g m^{-2}, p = 0.04). The oak shelterwood treatment caused minor increases to graminoid biomass two and three years following herbicide treatment (year 2-3: 0.27-0.33 g m^{-2}, versus pre-treatment: 0.16 g m^{-2}, p = 0.02), but then decreased significantly in by year 9 (from years 2 and 3 to 0.06 g m^{-2} p ≤ 0.04), lower than even the initial biomass (p =0.03).

Canopy Openness

As to be expected, the effect of treatments on canopy openness through time showed the greatest change in the shelterwood/fire treatment after overstory reduction

(**Figure 2.5**). Canopy openness increased from 5% pre-treatment, to just over 51% following overstory removal (years 1-2). Canopy closure occurred quickly, with openness declining to 19% by year 7, yet it was still the treatment with the greatest canopy openness by this time. Minimal changes were seen in the oak shelterwood treatment as pre-treatment canopy openness (3.7%) increased in treatment year 1 to 12.7% but decreased to just 5.4% by year 9. Slight changes were also seen in the repeated fire treatment following the second prescribed fires (6.5% year 6 to 16.6% in year 7), but this response was short-lived and was nearly equal to pre-fire levels by year 8.

While canopy openness immediately increased following overstory reductions in the shelterwood/fire treatment, *Rubus* biomass increased more slowly and peaked one year after canopy openness started to decline (year 3, **Figure 2.6**). Even though the following prescribed fire failed to increase canopy openness, the flush of *Rubus* was still evident post-fire (years 7-9) in the shelterwood/fire treatment. *Quercus* biomass showed no response to changes in canopy openness through time.

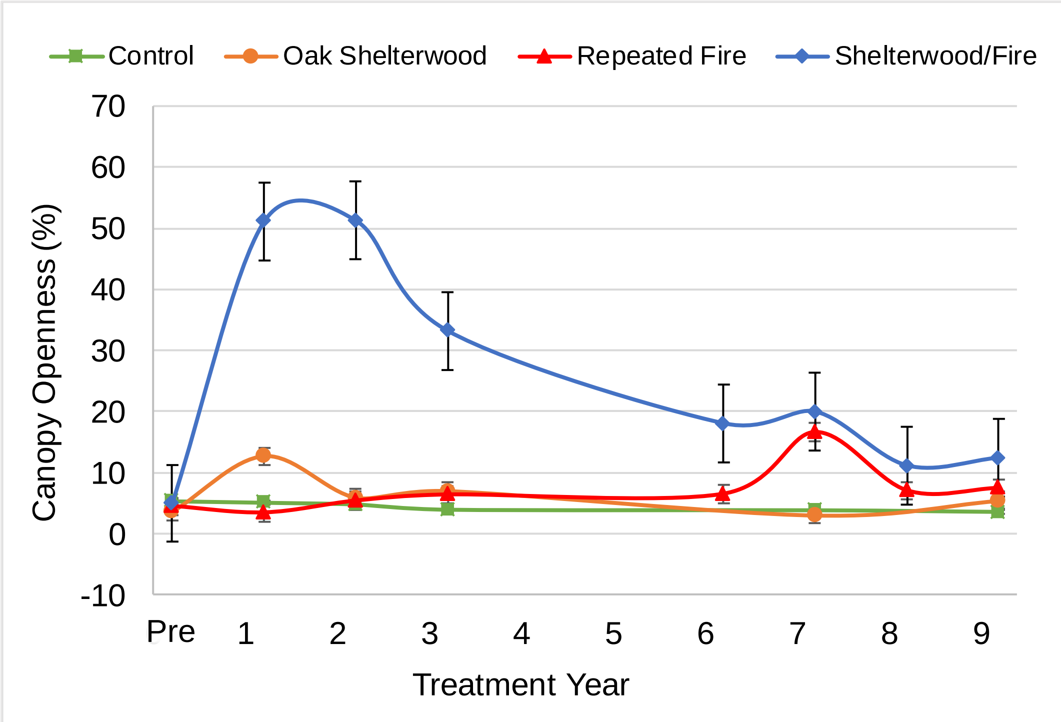


Figure 2.5 Mean canopy openness by treatment and year showing possible changes to ground-layer light availability via changes to overstory canopy structure. Error bars display the standard error of the mean.

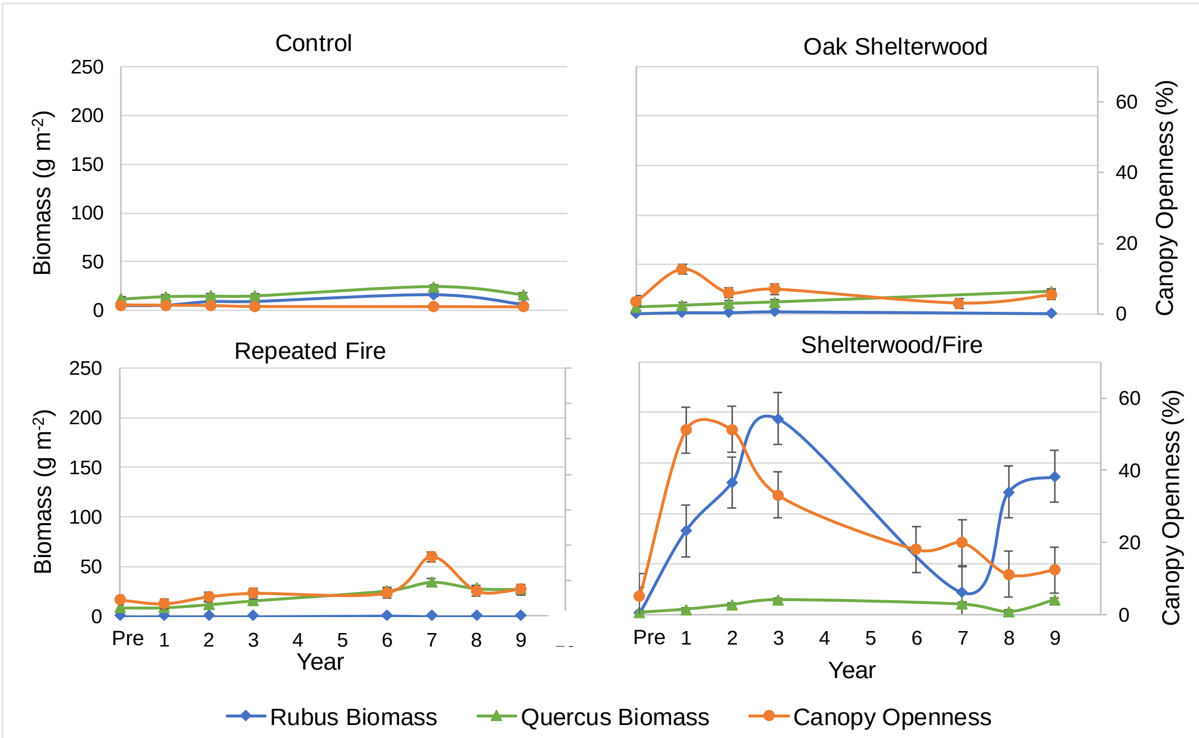


Figure 2.6 Associations between canopy openness and ground-layer biomass (g m^{-2}) of *Rubus* and *Quercus* species by treatment, through treatment years (x-axis). Raw biomass estimates were derived from lifeform subtype specific allometric regression of long-term cover data. Biomass of *Rubus* spp. or *Quercus* spp. are on the primary y-axis and canopy openness (%) is on the secondary y-axis.

2.4 Discussion

Results from testing repeated measures of the effects of treatments on total ground-layer biomass (g m^{-2}) supported our hypothesis that treatments involving overstory reduction (shelterwood/fire) and/or prescribed fire (shelterwood/fire or repeated fire) would increase total ground-layer biomass. Total biomass in the shelterwood/fire treatment was greater than in the control treatment for all years-post treatment and was most extreme three years following overstory reduction when total biomass peaked at 56 g m^{-2}, the highest response in the study (**Figure 2.2**). Dyer et al. (2010) found a positive relationship with total ground-layer biomass (all vegetation <1.4 m tall) and increasing gap size in mesic, northern hardwood forests of Wisconsin. The selective shelterwood harvest prescribed in this study, which left only 30-40% residual basal area, can be compared to the largest size of the experimental group selection harvests tested in Dyer et al. (2010) due to the large amount of overstory basal area removed. Shure et al. (2006) also found significant increases in total ground-layer biomass (herbaceous and woody species <30 cm tall) in mid-successional, mixed-oak forests in western North Carolina following gap creation, with responses declining 4-6 years post-treatment. Our results indicate a decreased response of total ground-layer biomass in the shelterwood/fire treatment by year 7, although this is probably a combined result of a natural decline in biomass production and reductions due to prescribed fires conducted in treatment year 5 (2 units) or 7 (2 units). Lack of data for years 4-6 limits our interpretation of biomass levels just before fires, however, total ground-layer biomass in the shelterwood/fire treatment post-fires never again reached the lower pre-treatment levels (**Figure 2.2**).

We also found less intense, yet significant, increases in total ground-layer biomass in the repeated fire treatment 1-2 years following the second prescribed fires, relative to controls, when total biomass peaked at 34 g m^{-2} (**Figure 2.2**). Although data to quantify the fire intensity of the second prescribed fire conducted in these treatment units is lacking, Keyser et al. (2012) report that the first prescribed fires conducted (year 1) were of low intensity, with maximum litter surface temperatures ranging from 79-316 °C, scorch heights averaging 0.3 m, and low litter and fuels consumption from fires. This type of low intensity prescribed fire still positively influences forest soil nutrient availability and can reduce fuel loads on the forest floor (Knoepp et al. 2009). Repeated fires can also increase habitat heterogeneity and alter the ground-layer light regime (Iverson et al., 2008). The greater response of total ground-layer biomass after the second prescribed fires is likely due to a combination of different fire intensities, the reduction of, at least some, forest floor fuels from the combination of two fires, and decreased resource competition among persisting ground-layer vegetation. When repeated, even low intensity fires can kill non-pyrophytic woody species which are not well adapted to fire disturbances (Iverson et al., 2008; Lafon et al., 2017; Keyser, 2019). This reduced competition may allow more biomass allocation to persisting woody species, which in this study contributed the second-most to total biomass overall.

We found fewer significant responses within the oak shelterwood treatment as total biomass gradually increased into treatment year 9 (**Figure 2.2**). Despite finding no significant differences in total biomass between the oak shelterwood treatment and our unmanipulated controls up to year 8, by year 9, total ground-layer biomass in the control treatment was significantly lower than all other treatments, showing the lasting (11 year) positive response of total ground-layer biomass productivity to all silvicultural treatments prescribed.

As with total ground-layer biomass, the shelterwood/fire treatment resulted in the most extreme changes to lifeform biomass, followed by the repeated fire treatment. Besides ferns, biomass of all lifeforms responded positively to overstory harvest in the shelterwood/fire treatment (**Figure 2.2**). Without finding any bias in pre-treatment fern biomass data, aside from large patches of *P. acrostichoides* in our ground-layer subplots, we can only conclude that the direct effects of logging damage are to blame for the drop (0.91-0.3 g m^{-2}) in fern biomass immediately following treatment implementation, and not the indirect effects of logging (increased light from the canopy reduction or forest floor fuels reduction). Biomass response varied by lifeform in the shelterwood/fire treatment after the single prescribed fires conducted by year 7. The biomass of herbaceous and vines lifeforms increased, while all other lifeforms decreased post-fire (**Figure 2.2**).

We found only partial agreement with our second hypothesis that repeated prescribed fire treatments would decrease lifeform biomass of more shade-tolerant, fire-sensitive lifeforms (herbs and ferns) and increase lifeform biomass of more shade-intolerant, fire-resistant lifeforms (woody and vines) after a decade of treatments. Within the repeated fire treatment, biomass of herbaceous, graminoid and shrub lifeforms all increased from repeated prescribed fires, with greater responses to the second fires conducted (**Figure 2.7**). While the biomass response of herbaceous and graminoid lifeforms peaked the growing season after the second fires were conducted, it began to quickly decrease and was nearly at pre-fire levels four years post-fire. Contrary to expected outcomes, the response of woody and vine lifeform biomass to repeated prescribed fire treatments was minimal. Biomass of both lifeforms responded much more to the overstory reduction associated with the shelterwood/fire treatment than to repeated prescribed fires (**Figure 2.7**). Fire intensity (temperature, flame height, duration, etc.) can have a major influence on vegetation responses (Elliott et al., 1999; Elliott and Vose, 2010; Holzmueller et al., 2009), and the low intensity fires reported for the first prescribed fires (Keyser et al., 2012) may be telling of the intensity of the second fires as well.

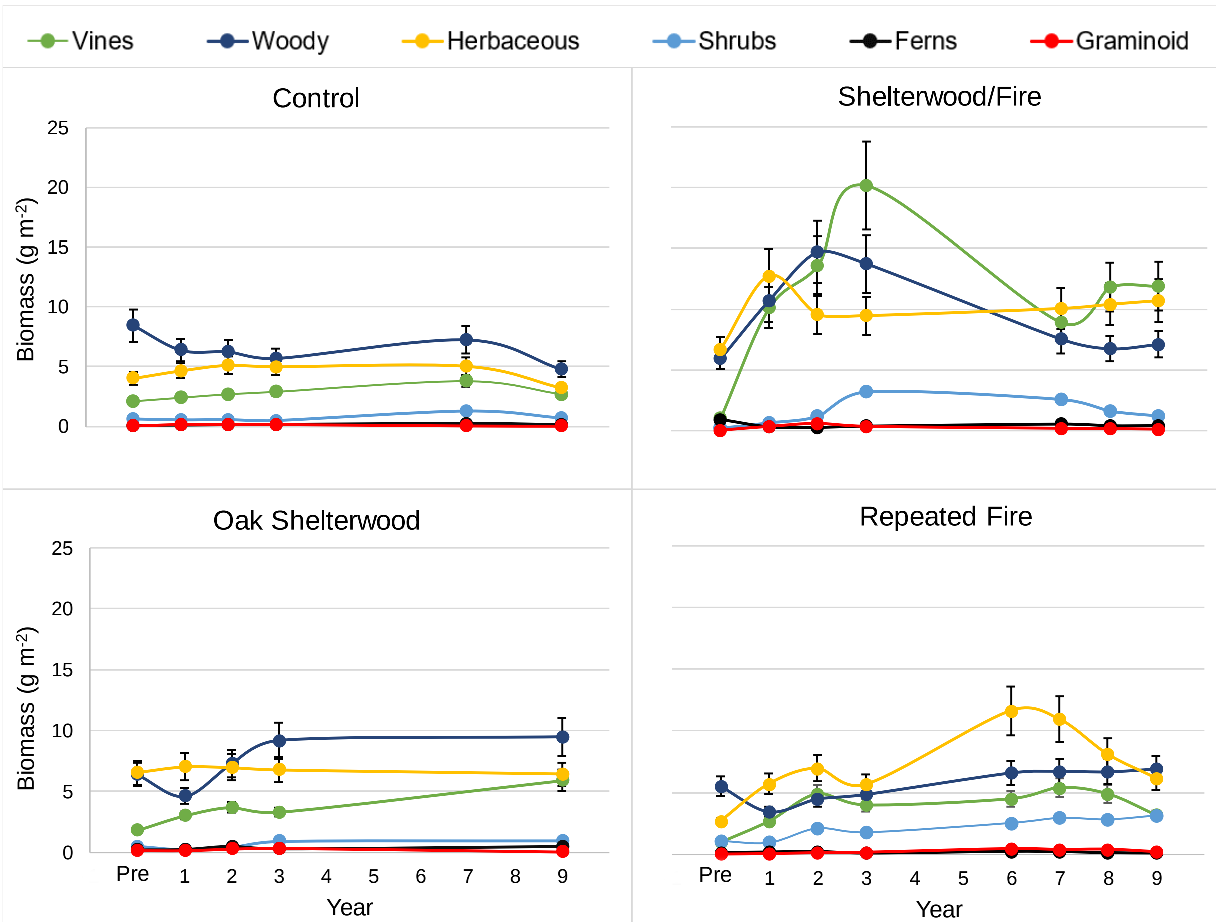


Figure 2.7 Changes to lifeform biomass (g m^{-2}) least square means by treatment through time. Error bars represent the standard error of the mean.

Quercus and *Rubus* Lifeform Subtypes

As previously stated, the overwhelming flush of *Rubus* spp. biomass after overstory reduction in the shelterwood/fire treatment was evident from pre-treatment to year 3 (1.5 -194 g m^{-2}), when *Rubus* biomass outweighed (in grams) all other ground-layer lifeform and lifeform subtypes. By year 7, *Rubus* biomass was greatly reduced from prescribed fires, but quickly increased again by year 9. *Rubus* biomass responded to no other treatments with the same intensity. This was also evident from graphing the percentage of *Rubus* spp. to total vine biomass in the shelterwood/fire treatment, as *Rubus* biomass contributed up to 86% to total vine biomass in year 8 (**Figure 2.3**). The next highest percentage of *Rubus* in any other treatment was in the control treatment for year 7 (25%).

Rubus species, especially *R. allegheniensis*, are ruderal, or pioneer species which can respond quickly to disturbances that increase ground-layer light availability. Comparing changes to *Rubus* biomass to changes in canopy openness through time showed a delayed yet intense response of *Rubus* biomass to increased canopy openness, a proxy for increased light availability to the forest ground-layer (**Figure 2.6**). Increased frequency, density, basal area, and importance values (percent affinity) for *R. allegheniensis* has also been seen in response to shelterwood harvest treatments in comparable Southern Appalachian forests (Elliott and Knoepp, 2005). *Rubus* spp. abundance also increased in response to uneven-aged harvest methods in mesic hardwood forests of Northern Wisconsin (Scheller and Mladenoff, 2002).

We found the greatest change in woody biomass (*Quercus* spp. included) in the shelterwood/fire treatment after overstory reduction when woody biomass nearly tripled, increasing by 10 g m^{-2} (**Figure 2.2**). However, the percentage of *Quercus* spp. to total woody biomass derived from raw biomass estimates was greatest in the repeated fire treatment, namely after the second fires, and *Quercus* percentage peaked at 33% in year 7 (**Figure 2.4**). The repeated fire treatment also resulted in the greatest percentage of *Quercus* to woody biomass (25%) after a decade of treatments. The use of prescribed fire to increase *Quercus* regeneration and abundance in Southern Appalachian forests has increased in recent years as land managers attempt to restore some of the historical fire regime patterns thought to have helped shape the *Quercus* dominated forest canopies present today (Lafon et al., 2017; Brose et al., 2014; Abrams, 1992; Hutchinson et al., 2008). There has been some reported success with repeated prescribed fires increasing *Q. rubra* and *Q. alba* in the ground-layer (<1.4 m tall) of oak-hickory forest types in the Great Smokey Mountains National Park, USA (Holzmueller et al., 2009). Elsewhere in the Southern Appalachian region, repeated prescribed fires led to mixed results for regeneration of red vs white oak group in the ground-layer (<1 cm basal area) and mortality post-fire was partially dependent on topographic moisture gradients (Elliott et al. 1999). Still, results are not consistent, with another example reporting little success with single, low intensity prescribed fires, suggesting that more intense or repeated fires will be necessary to develop sufficient *Quercus* regeneration in the ground-layer of these mesic forest types (Elliott and Vose 2010).

2.5 Conclusions

Ground-layer biomass in this mesic, Southern Appalachian forest responded positively to shelterwood/fire and repeated fire treatments which increased available light to the forest floor and periodically reduced ground-layer competition with prescribed fires. Biomass of vine and woody lifeforms did not respond the way we expected with little change in response from repeated fire treatments. While the shelterwood/fire treatment did produce the greatest biomass response relative to other treatments, it may have had unintended consequences relative to individual lifeforms. We hypothesized that woody and vine lifeforms would increase, and this was the case. However, *Rubus* species dominated vine lifeform biomass totals in the shelterwood/fire treatment, even after a decade, and produced the highest biomass recorded for any functional group in the ground-layer. Without follow-up treatments to control this dense *Rubus* layer, the regenerative potential of all other lifeforms will decline (Engelman and Nyland, 2006; Dosono and Nyland, 2006; Kern et al., 2014).

The intended purpose of the silvicultural treatments prescribed in this study was to increase *Quercus* regeneration. Results suggest that the repeated fire treatment increased the proportion of *Quercus* species in the woody lifeform more than any other treatment after a decade, showing positive results from reintroducing fire to this landscape. While the oak shelterwood treatment also increased woody biomass in the ground-layer, the proportion of *Quercus* within the woody lifeform was lower in this treatment than in the unmanipulated controls after a decade. Other studies report that although *Quercus* regeneration can benefit from midstory thinning treatments, other woody species, particularly those which are shade-tolerant, may benefit more, ultimately hindering *Quercus* regeneration (Schweitzer, 2019; Schweitzer and Dey, 2017; Hackworth et al., 2020). The single application of Garlon3A to undesirable midstory stems in this study may not have created the filtered light conditions sufficient to favor *Quercus* productivity in the ground-layer, or the species already present in the ground-layer and seedbank outcompeted *Quercus* cohorts for resources. Regardless, further treatments in these units will be necessary if increasing *Quercus* regeneration is still the main future objective of the study.

Grouping ground-layer species into functional lifeform groups helped to characterize the biomass response to the treatments prescribed but may have not told the whole story. For one, herbaceous species are vastly diverse and have different light and resource requirements, and height growth limitations. Therefore, grouping all herbaceous species into one lifeform probably limited our interpretation of more defined herbaceous biomass responses to the treatments. A better understanding of species-specific resource requirements would allow ground-layer species to be categorized into functional groups specific to these requirements, not just a lifeform. Further work evaluating the above- and below-ground competitive interactions among ground-layer species would also give insight into these fine scale relationships that help determine the regenerative potential of the future forest. Work that focuses on the nutrient availability of the soil at different ecological gradients could also shed light on the productivity potential of specific species in the ground-layer of these forests.

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Chapter 3: A Decade of Change in Ground-Layer Species Assemblages and Successional Patterns Following Oak (*Quercus* spp.) Regeneration Treatments in Southern Appalachian Forests

Abstract

The decline in midstory dominance and canopy recruitment of *Quercus* spp. in most of its native range is recognized, especially in mesic, Southern Appalachian forests of the Eastern US, and silvicultural prescriptions are often developed to create forest conditions conducive to the regeneration of these keystone species. It is important to consider how these species-targeted silvicultural prescriptions can influence the ground-layer vegetation community as Southern Appalachian forests contain unique ground-layer microhabitats due to their varying topography and geologic history, among other characteristics. We test how certain silvicultural prescriptions developed to promote *Quercus* regeneration in Southern Appalachian forests (repeated prescribed fire, oak shelterwood thinning with herbicide, or shelterwood harvesting followed by prescribed fire) along with microenvironmental metrics, influence long-term species diversity (richness and abundance), and turnover, and if species show affinity to particular treatments using multivariate analyses.

We hypothesize that species composition would shift from more shade-tolerant, fire-sensitive species to more shade-intolerant, pyrophilous species in the shelterwood/fire and repeated prescribed fire treatments as a result of increased light and reduction of leaf litter and dead wood on the forest floor, and increased soil nutrient availability post-fire. We further hypothesized that the shelterwood/fire treatment would lead to the greatest changes in species dominance patterns due to the combination of overstory disturbance and following prescribed fire treatments. After a decade, species richness was increased by all silvicultural treatments (+13 species following repeated fire and oak shelterwood treatments, and +9 species following shelterwood/fire treatments) relative to controls (+5 species), without drastic species turnover. Shelterwood/fire treatments caused the most significant changes in successional patterns, evident from dissimilarities seen among treatment years in non-metric multidimensional scaling ordinations, and most evident the year following overstory

reduction, supporting our hypothesis that this combination of treatments would result in the greatest changes to species diversity and turnover. Comparing changes to ground-layer species composition post-treatment is important for future restoration efforts and for evaluating whether these silvicultural prescriptions can meet traditional management goals while maintaining ground-layer vegetation diversity. For this, managing the disturbance intensity of silvicultural prescriptions for a broader range of species may allow land managers to meet objectives for canopy recruitment of desirable woody species while also incorporating the consideration of ground-layer species diversity.

3.1 Introduction

Quercus Diversity and Regeneration Concerns

The *Quercus* L. genus encompasses an incredibly diverse group of nearly 500 vascular tree and shrub species which exist globally and has been referred to as the "ecological equivalent of manna from heaven" (McShea and Healy, 2002). Members of the genus have developed evolutionary adaptations making them resilient to many types of disturbance including drought (Kole, 2011; Abrams, 1990), fire (Abrams, 1992; Brose et al., 2014; Hutchinson et al., 2008), and wind and flooding events (Kushla, 2017; Goldman, 2017) allowing them to adapt to a wide variety of habitats. Despite this, scientific research from around the world including China (Li and Ma, 2003), Sweden (Gotmark et al., 2005), Central Europe (Spinu, 2019), and areas in the Mediterranean (Pulido and Diaz, 2005) report problems with sufficient canopy recruitment of *Quercus* spp. in habitats they once thrived. In North American forests, fire suppression (Nowacki and Abrams, 2008; Abrams, 1992; Hutchinson et al., 2008), disease complexes such as oak decline (Greenberg and Collins, 2016; Gottschalk and Wargo, 1996), land-use practices such as agricultural abandonment (Vander Yacht et al., 2017; 2018) and clearcutting (Lhotka, 2013), and the parcelization or conversion of forested lands in the Eastern US into private ownership (McShea et al., 2007; Dey, 2014) are just some of the factors thought to hinder *Quercus* regeneration.

Canopy recruitment of *Quercus* species in mesic, Southern Appalachian forests is problematic and silvicultural prescriptions are increasingly being developed to promote forest conditions which favor advanced *Quercus* regeneration. Shelterwood harvest techniques are used to reduce overstory basal area, increasing available light to the midstory and forest floor, and are often followed by prescribed fires to reduce competition from undesirable species in the midstory. Shelterwood studies report successes (Brose and Van Lear, 1998), failures (Shure et al., 2006; Loftis, 1983), and mixed outcomes (Loftis, 1990a) for *Quercus* regeneration, with results often dependent on existing environmental factors and the size and amount of advanced *Quercus* regeneration present at the site prior to treatments.

The use of herbicides to control for midstory competition of undesirable, often mesophytic species in closed canopy forests has also been shown to promote advanced *Quercus* regeneration, but results are often short-lived without additional follow-up herbicide treatments or in conjunction with later overstory removal (Loftis, 1990b; Schuler and Miller, 1995; Schweitzer, 2019; Hackworth et al., 2020). The use of repeated prescribed fire to promote *Quercus* regeneration by reducing competition from more shade-tolerant and/or less fire-resistant species present in forest regeneration layers has led to inconclusive results with successes (Brose and Van Lear, 1998) and failures (Elliott and Vose, 2010). These mixed results highlight the complexity of *Quercus* regeneration dynamics in Southern Appalachian forests and how success is dependent on many factors including preexisting species composition and environmental parameters, as well as the timing of disturbance events.

Southern Appalachian Ground-Layer Biodiversity

The retention or restoration of ground-layer species composition and diversity is equally important as timber production and has become a growing concern for managers of private and federal forest lands who are increasingly incorporating the evaluation of this community as silvicultural treatments are being developed. Southern Appalachian forests contain unique microhabitats for ground-layer vegetation due to their varying topography and geologic history, among other characteristics. Elevations in the Southern Appalachians range from 500 m above sea level in Murphy, NC, to 2,037 m above sea level at Mount Mitchel, the highest peak in the eastern United States (Simon et al., 2005; Dykeman, 2018). The region's contrasting elevations produce strong gradients in topographic slopes going from valley to ridge tops. The Southern Appalachian's mountainous terrain also creates strong differences in slope aspects that can change significantly within a single stand of trees. Slope aspect can influence the growth of many ground-layer species by affecting temperature and the light regime, or the amount of sunlight plants are exposed to, at the forest floor in specific microhabitats (Small and McCarthy, 2003; Huebner et al., 1995; Schafale and Weakley, 1990).

There are several hundred state-listed species and many federally listed species of concern in North Carolina (Krings et al., 2012), many residing in the Southern Appalachian region. Glaciation events, such as those of the Pleistocene Epoch, caused the southern migration of many ground-layer species that were more typical of high latitudes, and some of these species remained in their current habitats even after glacial retreat (Clark, 2001). For instance, Southern Appalachian high-elevation outcrops are home to several rare herbaceous species, including *Geum radiatum* Michx., *Liatris helleri* Porter, and *Houstonia purpurea* var. *montana* (Small) Terrell, that are endemic to their respective habitats, largely due to the aforementioned glaciation events (Wiser, 1994). Species rich cove forests exhibiting high soil fertility also exist along mid to upper slopes and are known to be locations of high endemism and niche specialists (Braun, 1950; Whittaker, 1956; Ulrey, 2002).

Managing for Greater Diversity

Given the extraordinary ecological significance of both *Quercus* species that dominate the forest canopy, and so many species of the ground-layer community, management objectives in such a biodiverse ecosystem cannot be constrained to favoring just one genus, even *Quercus*. While competition for resources such as light, water, and nutrients are often studied for regeneration (midstory) and dominant (overstory) forest layers, competition for these resources among ground-layer species is less studied, less predictable, and more dependent on short-term responses to disturbance (natural and anthropogenic), and on the complex competitive interactions with neighboring vegetation.

The fern stratum has been shown to selectively filter tree seedlings and reduce overall seedling densities (George and Bazzaz,1999; Engelman and Nyland, 2006). Tall ground-layer vegetation, including both herbaceous and woody species, can reduce height growth and survival of planted *Quercus* seedlings (Lorimer et al., 1994). *Rubus* species, woody vines generally classified as ruderal (able to quickly colonize disturbed areas), can limit the regeneration of other ground-layer species by more efficiently using total nitrogen from the soil, and ultimately out-growing, and out-shading competitors (Faillace et al., 2018; Gaudio et al., 2008).

Disturbances which increase available light at the forest floor, such as overstory reduction or fire, can disproportionately favor the regeneration of more shade-intolerant species, such as *Liriodendron tulipifera* L., and *Rubus* L. spp. in the ground-layer (Lhotka, 2013; Kolb and Steiner, 1990; Hutchinson et al., 2005). Fire disturbance, natural or anthropogenic, can reduce leaf litter and fine fuels on the forests floor which can reduce physical barriers to the soil and increase germination rates of many species (Hutchinson et al., 2005), and often results in short-term increases in available soil nutrients (Knoepp et al., 2009; Hutchinson et al., 2005). Repeated fires can also promote the long-term survival of pyrophytic species (Hammond et al., 2015), partially by reducing the competitive status of more mesophytic and fire-sensitive species (Hutchinson et al., 2016; Nowacki and Abrams, 2008; Knoepp et al., 2009).

Disturbance processes that increase light availability to the ground-layer may also lead to the formation of recalcitrant vegetation layers, particularly when multiple processes are combined (Royo and Carson, 2006). Disturbance can lead to large increases in the cover or density of just one or a couple of native species that form a persistent and monodominant layer termed a “recalcitrant understory layer” (sensu Royo and Carson, 2006). The formation of these recalcitrant layers can act as a strong filter on ground-layer vegetation, including the success of the *Quercus* regeneration. In the southeastern United States, examples of recalcitrant interference include primarily *Kalmia latifolia* L. and *Rhododendron* L. species (Brose, 2017). Competition for resources among species in the ground-layer community is a major factor determining species composition, dominance, and species response to variations in resource availability. Dominance or evenness patterns are important but not the sole metrics to consider when attempting to quantify and characterize the response of vegetation to disturbance. An in-depth look at which particular species, if any, become dominant following silvicultural treatments is necessary to monitor objective success and alter management strategies when necessary. Monitoring changes to ground-layer species dominance early can help to avoid dominance of undesirable (often invasive) species in the long-term.

Studies that have examined the effects of natural and anthropogenic disturbances on the survival and diversity of the ground-layer community are vast, citing species richness, composition, and abundance as suitable indicators of diversity (Brose et al., 1999; Ford et al., 2000; Duguid and Ashton, 2013; Holzmueller et al., 2009; Meier et al., 1995). Species richness is a simple yet inadequate measure of species diversity and is best when considered in conjunction with other measures. Species composition, the contribution of each species to the total vegetation community, is particularly important when describing diversity in Southern Appalachian forests due to the exceptional number of endemic and rare species found in the region (Krings et al., 2012; Wiser, 1994). Species abundance, often measured in percent cover, is an important measure of productivity which is used to estimate the ground-layer's contributions to the seedbank, net primary productivity, fuel bed conditions, and soil nutrient loads (Zavitkovski, 1976; Welch et al., 2007).

The objective of this study is to test how silvicultural treatments used to promote *Quercus* regeneration in Southern Appalachian forests, including repeated prescribed fire, oak shelterwood thinning with herbicide, or shelterwood harvesting followed by prescribed fire, influence the ground-layer vegetation community, compared to unmanipulated forest conditions. We test if treatments influence 1) species diversity (richness and abundance), turnover, and dominance patterns, and 2) if resource availability patterns promote or change species' affinities to certain silvicultural treatments. We evaluate the effects of the large-scale treatment relative to the microenvironmental influences on long-term species abundance using multivariate analyses. We hypothesize that species composition will shift from more shade-tolerant, fire-sensitive species to more shade-intolerant, pyrophilous species in the shelterwood/fire and repeated prescribed fire treatments as a result of increased light and reduction of leaf litter and dead wood on the forest floor, and higher soil nutrient availability post-fire. We further hypothesize that the shelterwood/fire treatment will lead to the greatest changes in species dominance patterns due to the combination of overstory disturbance and following prescribed fire treatments.

3.2 Methods

Study Site

This study area is located in the Cold Mountain Game Lands of western North Carolina (**Figure 1.1**). Experimental plot elevations range from 983 m to 1,271 m above sea level, with slopes ranging from 35 to 55 percent (Keyser et al., 2012). Soils found in the Cold Mountain Game Lands consist mostly of Plott, Edneyville, and Chestnut soil series types (N. C. Wildlife Commission (NCWRC, 2020). Annual precipitation averages 1,060 mm and is consistently distributed throughout the year (NCWRC, 2020). Forests are second-growth, mixed oak stands, approximately 80 years old, with dominant canopy species including: *Quercus rubra* L., *Q. alba* L., *Q. prinus* L., and *Q. velutina* Lam., *Acer rubrum* L., *A. saccharum* Marshall, *Carya* Nutt., *Prunus serotina* Ehrh., and *Liriodendron tulipifera* L. (Keyser et al., 2012). The midstory is dominated by shade-tolerant species including *Oxydendrum arboreum* (L.) DC.), *Nyssa sylvatica* Marshall, and *Halesia tetraptera* Ellis (Greenberg et al., 2016).

Experimental Design

Sixteen experimental units (~5 ha), hereafter referred to as units, were selected in 2008, separated by ≥10 m untreated buffers (**Figure 1.2**). Four treatments were randomly assigned to units and replicated four times. Three silvicultural treatments developed for *Quercus* regeneration were tested and compared with unmanipulated controls for reference. Treatment application was asynchronous across and within treatments, mainly due to the nature of prescribed fire treatments which require specific environmental conditions before conducted. Therefore, data was analyzed on a “years-post initial treatment” basis, hereafter referred to as year (**Table 1.1**). This allowed units that were given the same treatment in different calendar years to be analyzed together to maximize replication and focus on temporal patterns of responses. Treatments include:

Repeated Prescribed Fire (FIRE): repeated, prescribed fire (3 times, every 5-6 years) conducted in the dormant season. Two units were burnt in the dormant season of 2009, 2014, and 2018, and 2 units were burnt in the dormant season of 2010 and 2015 (**Figure 1.3 a)**.

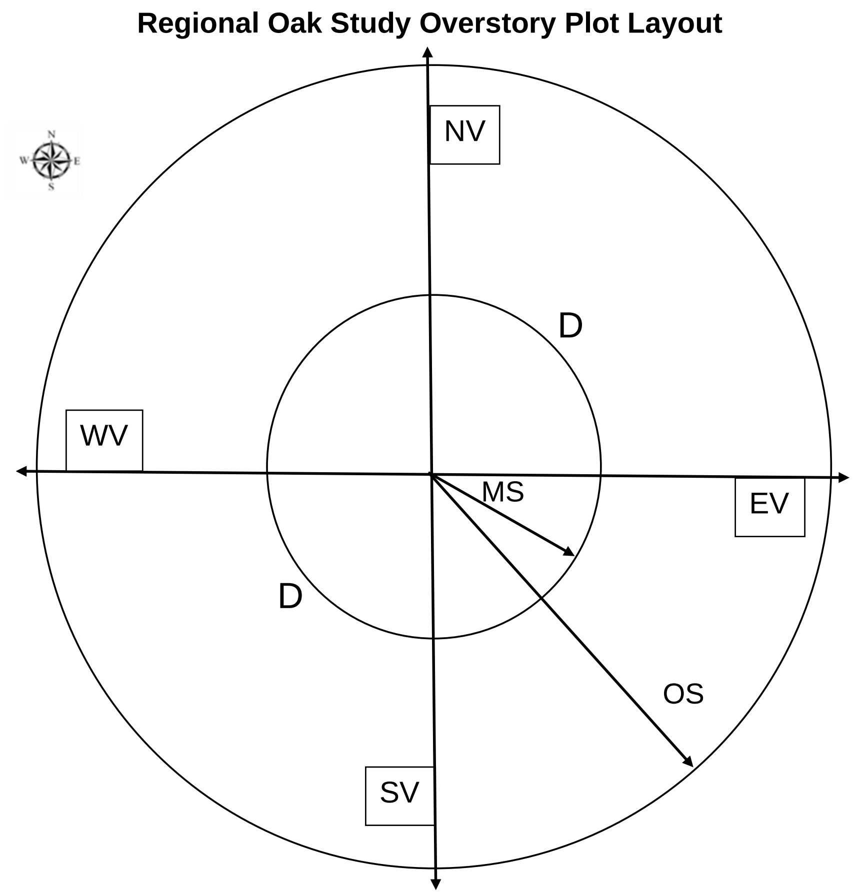
Oak Shelterwood with Herbicide (OSW): prescription following Loftis (1990b) consisting of a midstory thinning with herbicide (Garlon3A- triclopyr) and the “hack and squirt” method of application to remove competitive stems (≥5 cm and ≤25 cm dbh) of undesirable species. Objectives were to reduce the total basal area by 25-30% without creating new canopy gaps. Treatment was applied in September of 2008 (**Figure 1.3 b**).

Shelterwood and Prescribed Fire (SWF): shelterwood harvest and single, dormant season prescribed fire prescription following Brose et al. (1999) consisting of the removal of overstory trees (≥25 cm dbh), leaving a residual BA of 30-40% of mostly dominant and co-dominant *Quercus* species. Residual slash was left on site. Two units were harvested in the spring of 2010 and burnt 7 years post-harvest, and 2 units were harvested in the spring of 2011 and burnt 5 years post-harvest. Prescribed fire objectives were to control for midstory competition and decrease leaf litter and fine fuels on the forest floor (**Figure 1.3 c**).

Control (CONT): Four control units were left untreated throughout the study to serve as reference for unmanipulated forest conditions (**Figure 1.3 d**).

Field measurements

Three permanent, circular, overstory plots were installed in each unit (0.05 ha with a 12.5 m radius), hereafter referred to as plots (**Figure 3.1**). Overstory basal area (OSBA: m^2 ha^{-1}) and density (OStph: trees ha^{-1}) were recorded for trees ≥12 cm dbh in the 12 plots. Nested midstory plots (0.01 ha) shared the overstory plot centers. Midstory basal area (MSBA: m^2 ha^{-1}) and density (MStph: trees ha^{-1}) were recorded for trees 5 to <12 cm dbh. Permanent ground-layer vegetation subplots (1 m^2) were established 11 m from plot center in cardinal directions, resulting in 12 subplots per unit (48 per treatment). Canopy openness (%OPEN) was measured for varying years throughout the study using a concave spherical densiometer 8 m from plot center at 45° and 245° azimuth and calculated from the mean of 16 measurements averaged to plot level (Forestry Suppliers, Inc., 2008, “D” in **Figure 3.1**).



LEGEND

NV, EV, SV, WV: Ground-layer vegetation subplots (1m^2, 11m from plot center in cardinal directions), 2019 ceptometer measurements, 2019 soil sampling (≤2m from subplot)
MS: Midstory plot (5.6m radius, 0.01ha); site of 5-<25cm dbh arboreal measurements
OS: Overstory plot (12.6m radius, 0.05ha); site of ≥25cm dbh arboreal measurements
D: Site of densiometer measurements (8m from plot center at 45° and 225°)

Figure 3.1 Nested experimental design of overstory, midstory, and ground-layer subplots developed for the Regional Oak Study. Locations of ceptometer, densiometer and soil data collection are also depicted.

Spatial data, including plot level latitude, longitude, and elevation (m) was recorded using GPS equipment (Garmin etrex 20). To evaluate the influence of slope and aspect on species diversity, we used plot level terrain shape index (TSI) and landform index (LFI), which quantify landform shape from convex (low) to concave (high) on a micro (TSI) or macro (LFI) scale. Indices were evaluated using a clinometer following McNab (1989, 1993).

In 2019, an ACCUPAR LP-80 ceptometer was used to evaluate photosynthetically active radiation (PAR in µmol m^{-2} s^{-1}) at the ground-layer. Measurements were recorded at 0.3 m, 0.6 m, and 1 m above the center of each ground-layer subplot (12 per plot) and averaged to plot level. Soil samples were collected in the summer of 2019 (July-August) using 10 cm diameter core to a depth of 15 cm. Four cores were composited by plot to evaluate soil and nutrient concentrations. Samples were air dried and submitted to Brookside Labs (New Bremen, OH) for chemical analyses.

Ground-layer vegetation surveys were conducted during the summer (July-August), semi-annually since one year before treatments (2008) and percent cover of all ground-layer vegetation species (vascular, herbaceous, and woody, <1 m tall) was visually estimated in each 1 m^2 ground-layer subplot. Vegetation was identified to species when possible using nomenclature and identification codes listed in the United States Department of Agriculture: Natural Resource Conservation Service PLANTS database (USDA, NRCS 2020). Percent cover was recorded in seven classes: 1 (<1%), 2 (1%-<5%), 3 (5%-<25%), 4 (25%-<50%), 5 (50%-<75%), 6 (75%-<95%), 7 (95%-100%). Cover class midpoint values were used to calculate mean plot species cover, which was used for all further comparative analysis.

Data Analysis

Generalized linear model with a Tukey's HSD (honest significance test) was used to test if treatments influenced canopy openness after treatments occurring in year 1 and after repeated treatments by year 9. We used the same model to test for differences in the coefficient of variation of mean canopy openness at the unit level to evaluate if silvicultural treatments resulted in a more, or less, homogenous canopy cover following treatments. All analyses unless indicated otherwise were conducted using Statistical Analysis System (SAS version 9.4; Cary, NC)

Species richness was calculated as the count of species per treatment (48 m^2) for each year. To support richness patterns, species turnover was calculated as the total number of species lost versus the total number of species gained in each treatment after at least a decade of silvicultural manipulations (pre-treatment to year 9).

Multivariate analyses were performed on all datasets at the plot level using PC-ORD 7 (Corvallis, OR) to evaluate changes in species composition through time. Multi-response permutation procedures (MRPP) tested the hypothesis of no differences in species occurrence (presence/absence), or abundance (cover), among treatments through time (pre-treatment through year 3, and year 9) (Peck, 2016). The option to make pairwise comparisons was chosen to perform randomization tests on between treatment differences. Although not corrected for multiple comparisons, this test is still a useful way to explore the data for possible dissimilarities between species composition, related to silvicultural treatments (Peck, 2016).

We used nonmetric multidimensional scaling (NMS) to compare species composition by ordinating plots in species space and overlaying our biotic and abiotic environmental parameters to show the effects of large-scale treatments versus microenvironmental influence on species abundance before, just after, and at least a decade post-initial treatment (pre-treatment, year 1, and year 9). Environmental parameters in the second matrix included: latitude, longitude, elevation (m), TSI, LFI, OSBA, OStph, MSBA, MStph, and canopy openness (%OPEN). In addition, we used NMS to evaluate the influence of at least a decade (2019) of silvicultural treatments on the difference in light measured as PAR (in µmol $m^{-2}s^{-1}$) at 1 m and 0.3 m from the ground surface (dPAR) and plot level soil characteristics relative to year 9 species abundance.

We performed indicator species analysis on species abundance data to evaluate the percent affinity of a species to certain silvicultural treatments before, just after, and at least a decade post-initial treatment. We deleted species that were present in <5% of our plots reduce noise in the data (Peck, 2016). Sorensen’s distance measure was applied, and treatment was used as the grouping variable. The procedure uses a Monte Carlo permutation test (p <0.05) to test the hypothesis that the observed indicator values of species do not differ from those of a randomized run. The formula used for calculating species indicator values (IV; based on Dufrene and Legendre, 1997) takes into account the relative frequency and relative abundance of a species, and is calculated as follows:

$IV_{KJ}= 100(RA_{KJ} * RF_{KJ})$

where IV= Indicator Value

RA= Relative Abundance

RF= Relative Frequency

JK= Species J in Group K

To discuss how disturbances associated with our silvicultural treatments (overstory reduction, fire, herbicide treatment) influenced species abundance we researched tolerance characteristics for indicator species relative to the species tolerance to shade (shade-tolerant or shade-intolerant), fire (pyrophytic or non-pyrophytic), and general disturbance (primary succession/ruderal or secondary succession/non-ruderal). Species tolerance information was developed from available botanical databases and specialized to the region when possible.

Mantel tests were performed on species abundance data, using environmental variables as the second matrix to test if the observed dissimilarities in species abundance were related to the observed dissimilarities in the environmental patterns, and if this changed through time (pre-treatment through year 3, and year 9 (Peck, 2016). Environmental variables included: latitude, longitude, elevation (m), TSI, LFI, OSBA and OStph, MSBA and MStph, and %OPEN. Sorensen's distance measure was applied to species cover matrices and Euclidean distance measure was applied to environmental variable matrices. Mantel's asymptotic approximation, which standardizes the results, was used for randomization runs (Peck, 2016).

Delta PAR (dPAR) was calculated as the difference in light measured as PAR (in μmol $m^{-2}s^{-1}$) at 1 m and 0.3 m from the ground surface and included in the environmental matrix of the year 9 NMS analysis. In addition, ceptometer measurements were normalized [n-min/(max-min)] at the quad level to account for varying sky conditions and averaged by plot to calculate the linear slope of change in PAR from 0.3 m-0.6 m and from 0.6 m-1 m. A generalized linear model and Levene's test of homogeneity at the plot level was used to test for differences in the linear slope of change among treatments at the different ground-layer stratum. We also tested the coefficient of variation for the separate slopes among treatments to evaluate if the silvicultural treatments resulted in a more, or less, homogenous ground-layer light environment following treatments.

Nonmetric multidimensional scaling was performed on combined species abundance data for pre-treatment through year 3, and year 9 to display successional trajectories, or changing patterns of species abundance through time. Auto pilot mode was used to select an appropriate number of axes for graphing ordinations and Sorensen's distance method was applied to the species cover matrix.

3.3 Results

Overstory Change and Influence

Prior to treatments, overstory structure including basal area and density of the overstory and midstory trees (and canopy openness) were relatively similar among treatments (**Table 3.1**). However, the shelterwood/fire treatment had considerably lower midstory density with 185 fewer stems than any other treatment (**Table 3.1**). Midstory density declined through time in all treatments, yet the immediate effects of silvicultural manipulations (year 1) were most similar between the oak shelterwood and the shelterwood/fire treatments with decreases of 200 and 175 MStph, respectively, versus repeated fire and control treatments with decreases of 16 and 50 MStph, respectively (**Table 3.1**). Following overstory harvest in the shelterwood/fire treatment (year 1) the reductions in OSBA (24 m^2 ha^{-1}), OStph (163 trees ha^{-1}), and MStph (175 trees ha^{-1}) resulted in a 10-fold increase in canopy openness from 5% to 51.2% (**Table 3.1**). The oak shelterwood treatment increased canopy openness by 16.5% the year following herbicide treatments (year 1) but it was reduced by 14.3% again the following year. In the repeated fire treatment, canopy openness increased by 10.2% following the second prescribed fires (year 6) but was largely unchanged by the fires conducted in year 1.

Differences in overstory basal area and density were minimal following the repeated burns (OSBA: 0, OStph: -21 trees ha^{-1}) and the oak shelterwood (OSBA: -1 m^2

ha^{-1}, OStph: -20 trees ha^{-1}) treatments, and were similar to patterns of natural change in the controls (OSBA: -2 m^2 ha^{-1}, OStph: -17 trees ha^{-1}) (**Table 3.1**). Differences in the shelterwood/fire treatment relative to all other treatments were still evident by year 9 with the lowest OSBA (17 m^2 ha^{-1} less than any other treatment) and OStph (145 trees ha^{-1} less than any other treatment), and the greatest canopy openness (4.9% greater than any other treatment). By year 9, midstory density was more similar between oak shelterwood and shelterwood/fire treatments with 75 and 33 trees ha^{-1}, respectively, and between repeated fire and control treatments with 300 and 383 trees ha^{-1}, respectively (**Table 3.1).**

Pre-treatment mean canopy openness did not differ among treatments ($F_{(3,44)}$ = 0.68, p = 0.57) and was approximately 5%, yet openness was more variable within the repeated fire treatment, and was 29–45 higher than any other treatment (CV: $F_{(3,12)}$ = 5.14, p = 0.016). Just after initial treatments (year 1) mean canopy openness differed among treatments ($F_{(3,38)}$ = 68.4, p < 0.001) with the shelterwood/fire treatment having 39–49% greater canopy openness than any other treatment. However, variation within treatments in year 1 did not differ among treatments (CV: $F_{(3,10)}$ = 0.21, p = 0.89), nor did it in year 9 (CV: $F_{(3,12)}$ = 0.28, p = 0.84). Still, by year 9 mean canopy openness continued to differ among treatments ($F_{(3,44)}$ = 13.02, p < 0.001) with the shelterwood/fire having 5–9% greater canopy openness than any other treatment.

Table 3.1 Treatment means and the standard error (SE) for parameters influenced by treatments through time. Parameter codes follow: OSBA=overstory basal area (m^2 ha^{-1}), OStph= overstory trees per hectare (tress ha^{-1}), MSBA= midstory basal area (m^2 ha^{-1}), MStph= midstory trees per hectare (tress ha^{-1}). Canopy openness (%OPEN) was calculated from densiometer measurements. The percent change by year 9 from pre-treatment conditions (%CHG) is given for each treatment.

Treatment	Year	OSBA	Ostph	MSBA	MStph	%OPEN
Control	Pre	27(2)	202(19)	6(1)	550(62)	5.4(0.6)
	1	26(2)	198(19)	6(1)	500(67)	1.9(0.5)
	2	26(2)	198(19)	6(1)	500(67)	4.8(0.6)
	3	26(2)	195(18)	6(1)	467(59)	3.9(0.6)
	7	25(2)	187(20)	6(1)	433(63)	3.8(0.7)
	9	25(2)	185(19)	5(1)	383(53)	3.5(0.6)
	%CHG	**-7.4**	**-8.4**	**-16.7**	**-30.4**	**-35.2**
Repeated Fire	Pre	29(3)	216(23)	8(1)	533(78)	4.5(1.3)
	1	29(3)	215(23)	8(1)	517(76)	3.4(0.7)
	2	28(3)	210(21)	7(1)	442(75)	5.4(0.7)
	3	28(3)	210(21)	6(1)	417(76)	6.4(0.5)
	7	29(3)	203(19)	6(1)	325(65)	16.6(7.4)
	9	29(3)	195(19)	6(1)	300(66)	7.5(0.8)
	%CHG	**0**	**-9.7**	**-25**	**-43.7**	**66.7**
Oak Shelterwood	Pre	30(3)	220(15)	7(1)	467(77)	3.7(0.8)
	1	29(3)	218(15)	4(1)	267(62)	20.2(2.9)
	2	29(3)	211(16)	3(1)	175(45)	5.9(0.7)
	3	29(3)	208(15)	2(1)	125(33)	7(0.7)
	7	30(3)	201(13)	2(1)	75(25)	3.1(0.5)
	9	29(3)	200(13)	2(1)	75(25)	5.4(0.7)
	%CHG	**-3.3**	**0.4**	**-71.4**	**-83.9**	**45.9**
Shelterwood /Fire	Pre	32(2)	210(16)	4(1)	283(73)	5(0.8)
	1	8(2)	47(8)	1(0)	108(58)	51.2(4.1)
	2	8(2)	45(8)	1(0)	100(58)	51.3(7.8)
	3	9(2)	45(8)	1(1)	92(50)	33.2(7.5)
	7	8(2)	37(8)	1(1)	42(19)	19.9(4.6)
	9	8(2)	40(9)	1(1)	33(19)	12.4(1.7)
	%CHG	**-75**	**-81.0**	**-75**	**-88.3**	**148**

Ground-layer Species Richness and Turnover

We accounted for a total of 270 species over a decade's worth of ground-layer vegetation surveys. Richness counts may be slightly inaccurate as some specimens were only reliably identified to genus (*Poa* spp., *Carex* spp., *Sanicula* spp., *Imaptiens* spp., *Agrimonia* spp., *Prenanthes* spp., *Cuscuta* spp., and others) and some specimens were only reliably identified to lifeform and recorded as "unknown species." However, these specimens tended to have very low cover values, thus not significantly biasing richness or species abundance data. Species richness increased more following all silvicultural prescriptions (+13 species in oak shelterwood and repeated fire, +9 species in shelterwood/fire), relative to controls (+5 species) over nearly a decade (**Table 3.2**). The oak shelterwood treatment had the greatest species richness among treatments for most years, with 123 species before treatments and 136 species a decade following herbicide applications (**Table 3.2**). Before and after silvicultural treatments richness in the ground-layer community of these forests was overwhelmingly dominated by herbaceous species (≥46%), and secondly by woody species (≥16%), with other lifeforms individually making up ≤10% of the total species pool in each treatment (**Table A.3.1**).

Relative to species turnover, the number of species lost between pre-treatment and treatment year 9 was relatively similar among treatments and less than the number of species gained in each treatment (**Table 3.2**). The oak shelterwood treatment resulted in the most gains in species turnover (32 species versus 31 species in repeated fire and shelterwood/fire treatments, and 20 species in the controls) and more species were gained following all silvicultural treatments, supporting total richness patterns. Species occurrence significantly differed among treatments through time (Overall MRPP, $p < 0.001$, **Table A.3.2**). Species assemblages were similar only between the repeated fire and oak shelterwood treatments prior to treatment ($p = 0.1$), and assemblages remained similar between these treatments into year 9 ($p = 0.07$). Otherwise, species occurrence differed between all other treatments until year 9 ($p < 0.05$), when differences converged between the control and repeated fire treatments ($p = 0.07$).

Table 3.2 Species richness (count per 48 m^2) and turnover by treatment through time. Richness represents the total number of species for that treatment and year. Turnover represents the number of species lost or gained between pre-treatment (Pre) and year 9. Asterisk indicate years when only 2 (of 4) shelterwood/fire treatment units were measured (year 7: 3 years post-fire, year 8: 2 years post-fire).

	Treatment Year								Turnover	
Treatment	**Pre**	**1**	**2**	**3**	**6**	**7**	**8**	**9**	**Loss**	**Gain**
Control	100	108	106	104		93		105	17	20
Repeated Fire	108	128	117	115	125	115	119	121	18	31
Oak Shelterwood	123	117	132	132				136	19	32
Shelterwood/Fire	107	122	126	119		*79	*84	116	24	31

Ground-Layer Species Composition

Species evenness among treatments was relatively similar in both years for common species (ranked <60), but less similar among treatments and between years for more rare species (ranked >90, **Figure 3.2**). Relative abundance of more rare species increased by year 9 for all treatments, chiefly in the repeated fire treatment. Inspection of the year 9 species abundance data suggests that *R. allegheniensis* is primarily responsible for the higher dominance pattern in the shelterwood/fire treatment relative to all other treatments.

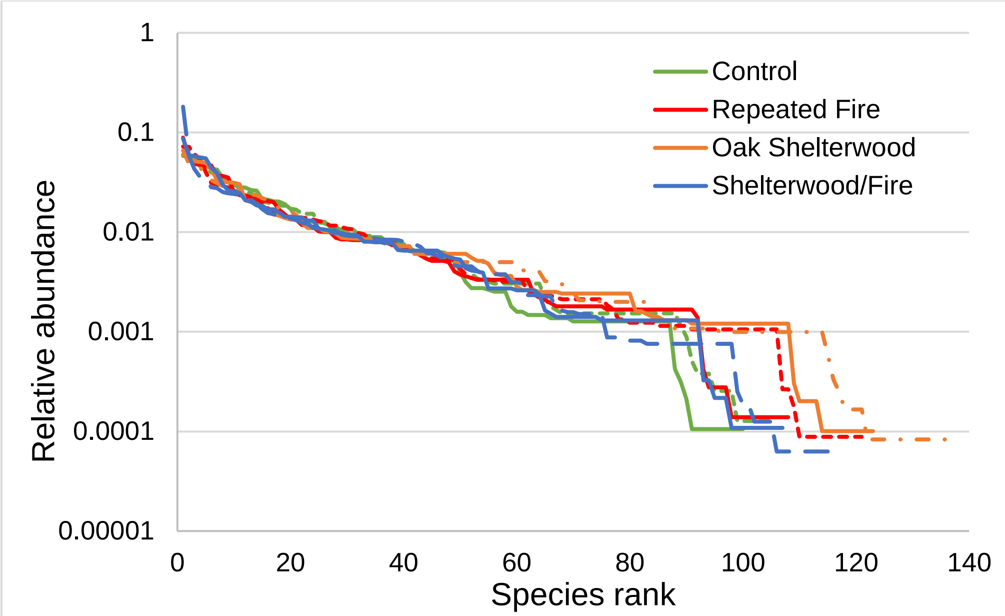


Figure 3.2 Rank abundance curve with solid lines representing richness and evenness the year prior to silvicultural treatments (pre-treatment) and dashed lines indicating conditions at least a decade after treatments (year 9). Relative abundance is presented on a log scale.

Treatments caused significant change to species abundance patterns through time (Overall MRPP, $p < 0.001$, **Table A.3.2**). Prior to treatments, species composition differed between the control and oak shelterwood treatments ($p = 0.008$), and the repeated fire and shelterwood/fire treatments ($p = 0.02$). Following treatments, species abundance patterns varied between treatments, and all treatment combinations differed by year 9 ($p \leq 0.046$). These differences are evident in the distribution of plots in the NMS ordination space for pre-treatment, year 1, and year 9 (**Figure 3.3**). Most of the variation in species assemblages was explained by axis 1 (shown for all years). Axes 2 and 3 explained nearly equal variance through time. Three axes solutions cumulatively represented 66-69% of the variance explained in ordinations for all years. Prior to silvicultural manipulation, treatments were not organized into discrete clusters in the ordination space. Axis 1 had the most associated species ($r^2 > 0.2$), including seven species that remained associated into year 1 (**Table A.3.3).** These included *Polystichum acrostichoides* (Michx.) Schott ($r = -0.55$), *Chimaphila maculata* (L.) Pursh ($r = 0.48$), *Dichanthelium boscii* (Poir.) Gould and C.A. Clark ($r = 0.46$), *Laportea* *canadensis* (L.) Weddell (r = -0.45), *Actaea racemosa* L. (r = -0.45), *Sanguinaria canadensis* L. (r = -0.45), and *Smilax glauca* Walter (r = 0.47). Species associated with axis 2 included *Kalmia latifolia* L. (r = -0.47), and *Eutrochium purpureum* (L.) E.E. Lamont (r = 0.47). Species associated with axis 3 included *Dryopteris marginalis* (L.) A. Gray (r = -0.47), and *Carya cordiformis* (Wangenh.) K. Koch (r = 0.49).

Before silvicultural manipulations, each treatment had a unique set of indicator species ranging from 1 species in the repeated fire treatment to 7 species in the shelterwood/fire treatment (**Table 3.3**). Indicators were a mix of woody and herbaceous species and included one vine. *Carya cordiformis*, highly associated with axis 3, was a pre-treatment indicator for the shelterwood/fire treatment, as were many herbaceous species including *Polygonatum biflorum* (Walter) Elliott, *Thalictrum dioicum* L., *Sanicula* L., *Uvularia grandiflora* Sm., and *Conopholis americana* (L.) Wallr. F., and one other woody species, *Fraxinus americana* L. The five pre-treatment indicators in the control treatment included several woody species such as *Acer rubrum L.*, *Quercus prinus L.*, and *L. tulipifera, and Castanea dentata* (Marshall) Borkh., and one herbaceous species, *Galium latifolium* Michx. The oak shelterwood treatment had two pre-treatment indicators, *Symphyotrichum cordifolium* (L.) G.L. Nesom and *Parthenocissus quinquefolia* (L.) Planch., the latter remaining and indicator with increasing importance values into year 9. Only one pre-treatment repeated fire indicator, *Quercus coccinea* Muenchh., remained an indicator for that treatment into year 9.

The year following initial silvicultural treatments, the shelterwood/fire treatment moved higher on axis 2, while other treatments shifted lower on axis 2 in ordination space (**Figure 3.3**). Some repeated fire plots (left side of ordination space) shifted and spread wider along axis 2, while others (right side of ordination space) shifted only slightly. A complete separation of the shelterwood/fire treatment relative to others occurred on axis 3. In addition to the seven previously mentioned species, three more species were associated with axis 1 including *Desmodium nudiflorum* (L.) DC. (r = 0.56), *Arisaema triphyllum* (L.) Schott (r = -0.48), and *Aristolochia macrophylla* Lam. (r = -0.45) (**Table A.3.3**). No species were highly ($r^2 > 0.2$) associated with axis 2, but some top associations included two vines, *R. allegheniensis* (r = 0.35), and *P. quinquefolia* (r

= 0.32), yet these species were more highly associated with axis 3 (*R. allegheniensis*: r = 0.57, and *P. quinquefolia* (r = -0.45), as were vines *Vitis aestivalis* Michx. (r = 0.56) and *R. odoratus* L. (r = 0.46).

Nine more indicator species were associated with the shelterwood/fire treatment than any other treatment in year 1, including *Carex* spp., *R. allegheniensis*, and *C. lyonii*, which were all highly associated with axis 2 (**Table 3.3, Table A.3.3**). Additional indicators solely significant in year 1 included *Erechtites hieraciifolius* (L.) Raf. ex DC., *Robinia pseudoacacia* L., *Betula lenta* L., *Phytolacca americana* L., and *Ligusticum canadense* (L.) Britton. Four additional herbaceous species became oak shelterwood treatment indicators following herbicide treatment (year 1) with *Arisaema triphyllum* (L.) Schott, *Sedum ternatum* Michx., and *Viola pubescens* Aiton significant in only that year. Other indicator species included *P. quinquefolia*, which was highly associated with axis 3, *Polygonatum pubescens* (Willd.) Pursh, and *L. canadensis*. The repeated fire treatment had three new indicators in addition to *Q. coccinea*, including *Polygonatum biflorum* (Walt.) Ell., *Uvularia puberula* Michx., and *Pyrularia pubera* Michx. Minor changes were seen to indicators for the controls. Two woody species (*A. rubrum* and *Q. prinus*) were retained, and one new herbaceous species, *Goodyera pubescens* (Willd.) R. Br. Ex Ait. F. became significant.

The shelterwood/fire treatment moved even higher on axis 2 after at least a decade (year 9) and was more distinctly separated from other treatments in ordination space (**Figure 3.3**). Two species that were highly associated with axis 1 just after treatments (year 1) were still associated (*A. macrophylla*: r = -0.46 and *D. nudiflorum:* r = 0.56), and four species that were highly associated with axis 1 pre-treatment were again associated (*D. boscii*: r = 0.47, *S. canadensis*: r = -0.56, *S. glauca*: r = 0.52, and *S. rotundifolia*: r = 0.64, **Table A.3.3**). In addition, *Q. velutina* (r = 0.48), *Sanicula* L. (r = -0.45), and *Vaccinium pallidum* Aiton (r = 0.51) were highly associated with axis 1. High axis 2 species associations included one shrub (*Viburnum acerifolium* L.: r = -0.41) and two vines (*V. aestivalis*: r = 0.47 and *R. allegheniensis:* r = 0.56). No species were highly associated with axis 3, but strong associations ($r^2 > 0.17$) included *Prunus serotina* Ehrh. (r = -0.41) and *M. racemosum* (r = 0.42).

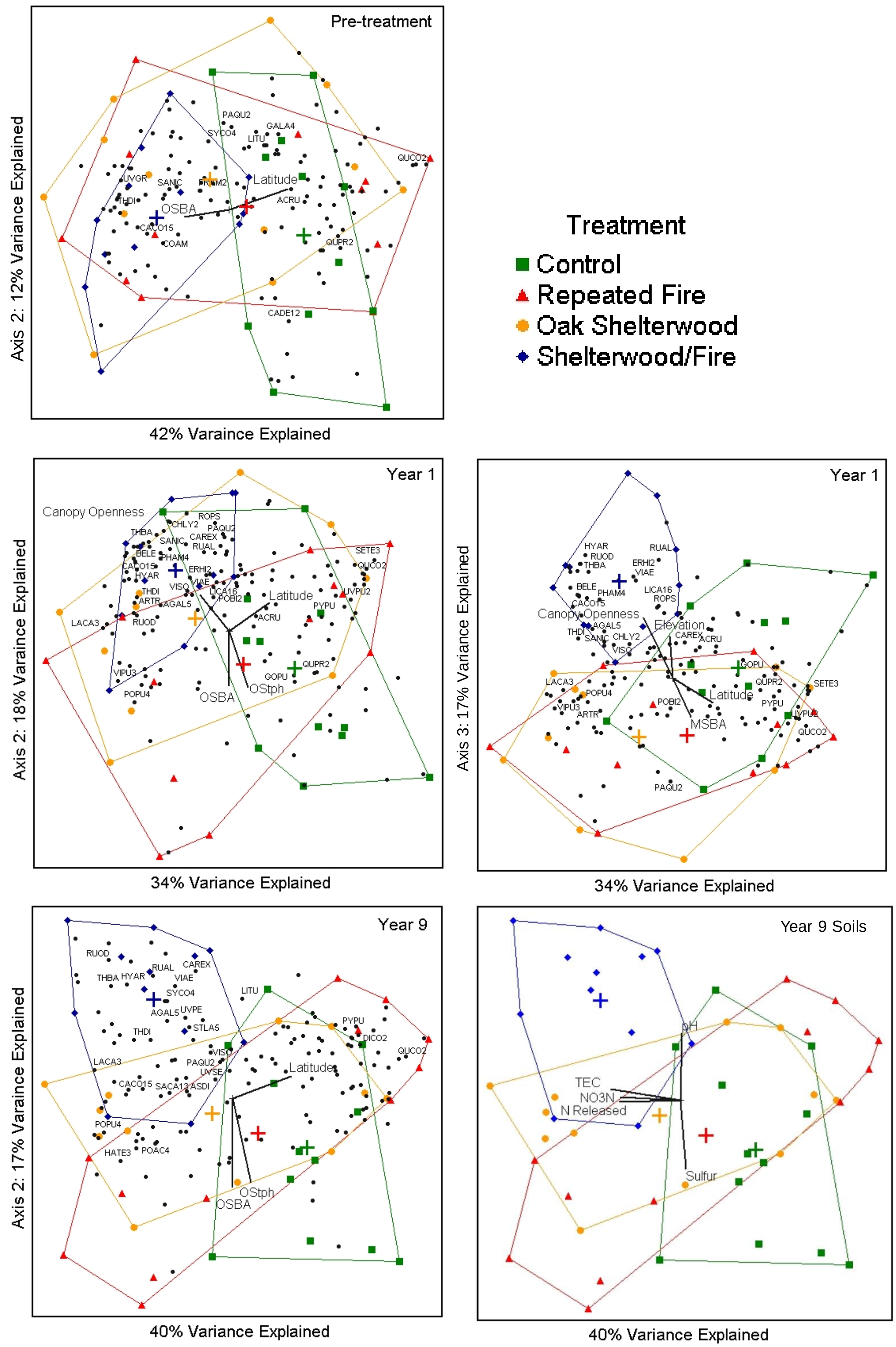
At least a decade after treatments only the shelterwood/fire treatment retained a high number of indicators (16), and indicators associated with the control treatment had vanished (**Table 3.3**). Five new indicators of the shelterwood/fire treatment in year 9 included several herbaceous species (*Aster divaricatus* L., *S. cordifolium*, *Uvularia perfoliata* L., *Uvularia sessilifolia* L., *S. canadensis,* and *Stachys latidens* Small ex Britton) and one woody species (*L. tulipifera).* Persistent shelterwood/fire indicators included two vines, *R. allegheniensis* and *V. aestivalis*, which were highly associated with axis 2 in ordination space, as well as *Carex* L., *Ageratina altissima* (L.) R.M. King and H. Rob., *T. dioicum*, *Viola sororia* Willd., and *Hydrangea arborescens* L.

Species Composition Relative to the Environment

Prior to silvicultural treatments, patterns of dissimilarities in species abundance were not strongly related to abiotic or biotic environmental parameters (Mantel, $p = 0.5$). Species composition after the silvicultural manipulations was highly correlated with environmental parameters and the strong relationships remained apparent into year 9 ($p < 0.001$). Strong differences in composition due to latitude were apparent in all years increasing along axis 1 in all ordinations (pre-treatment: $r=0.55$, year 1: $r=0.46$, year 9: $r=0.55$) (**Figure 3.3, Table A.3.4**). Biotic structural parameters such as overstory basal area (OSBA, Axis 1: $r = -0.48$) also significantly influenced species abundance prior to treatments.

Species compositional responses to decreasing OSBA (axis 2: $r = -0.53$) and OStph (axis 2: $r = -0.54$), and increasing canopy openness (%OPEN, axis 2: $r = 0.44$, axis 3: $r = 0.56$), direct effects of heavy overstory reductions associated with the shelterwood/fire treatment, were evident in ordination space just after treatments (year 1) and explained some of the separation of the shelterwood/fire treatment in ordination space. Axis 3 also correlated with decreasing midstory basal area (MSBA, $r = -0.45$) and elevation ($r = 0.47$) just after treatments (year 1), but not by year 9. Only the influence of latitude (axis 1: $r = 0.55$) and the effects of treatments on OSBA (axis 2: $r = -0.66$) and OStph (axis 2: $r = -0.68$) were still evident by year 9.

Figure 3.3 Nonmetric multidimensional scaling ordination of plots in species space comparing changes to species composition in the year before, immediately after and 9 years after treatment. Environmental joint biplot vectors display changes to environmental parameters through time ($r^2 > 0.2$). Axis 1 accounted for the most variance explained in ordinations for all years. Three axes solutions cumulatively explained 66-69% of the variation explained for all ordinations. The year 9 ordination is displayed twice with the display on left highlighting species and static environmental correlations and the display to the right including important soil and light variables ($r^2 > 0.3$) measured in 2019.



Pre-treatment
Axis 2: 12% Variance Explained
42% Varaince Explained
PAQU2
SYCO4
GALA4
LITU
QUCO2
UVGR
SANIC
PRUM2
Latitude
THDI
ACRU
OSBA
CACO15
COAM
QUPR2
CADE12
Treatment
Control
Repeated Fire
Oak Shelterwood
Shelterwood/Fire
Year 1
Axis 2: 18% Varaince Explained
34% Variance Explained
Canopy Openness
ROPS
CHLY2
PAQU2
THBA
CAREX
SANIC
RUAL
SETE3
BELE
PHAM4
QUCO2
CACO15
ERHI2
HYAR
VIAE
UVPU2
VISO
THDI
LICA16
Latitude
ARTR
POBI2
PYPU
AGAL5
LACA3
RUOD
ACRU
QUPR2
VIPU3
GOPU
OStph
POPU4
OSBA
Year 1
Axis 3: 17% Variance Explained
34% Variance Explained
HYAR
RUAL
RUOD
THBA
ERHI2
VIAE
BELE
LICA16
PHAM4
ROPS
CACO15
Canopy Openness
Elevation
AGAL5
THDI
CAREX
SANIC
CHLY2
ACRU
VISO
GOPU
LACA3
QUPR2
SETE3
POPU4
Latitude
VIPU3
POBI2
PYPU
ARTR
UVPU2
MSBA
QUCO2
PAQU2
Year 9
Axis 2: 17% Varaince Explained
40% Variance Explained
RUOD
RUAL
CAREX
THBA
HYAR
VIAE
SYCO4
LITU
AGAL5
UVPE
STLA5
PYPU
THDI
DICO2
QUCO2
VISO
LACA3
PAQU2
Latitude
UVSE
CACO15
SACA13
ASDI
POPU4
HATE3
POAC4
OStph
OSBA
Year 9 Soils
40% Variance Explained
pH
TEC
NO3N
N Released
Sulfur

Table 3.3 Results from Indicator Species Analysis (ISA) performed on species abundance (% cover) data showing differences in indicator species by treatment and treatment year. Numbers reflect the species importance values (IV), which indicate the percent affinity to respective treatments for that year. Species were deemed significant at p ≥ 0.5.

Treatment and Year:		**CONT**			**FIRE**			**OSW**			**SWF**		
Genus Species Authority	**USDA Code**	**Pre**	**1**	**9**	**Pre**	**1**	**9**	**Pre**	**1**	**9**	**Pre**	**1**	**9**
Acer rubrum L.	ACRU	60	56										
Galium latifolium Michx.	GALA4	43											
Quercus prinus L.	QUPR2	41	50										
Castanea dentata (Marshall) Borkh.	CADE12	29											
Goodyera pubescens (Willd.) R. Br. ex Ait. f.	GOPU		44										
Liriodendron tulipifera L.	LITU	25											38
Quercus coccinea Muenchh.	QUCO2				33	38	44						
Polygonatum biflorum (Walt.) Ell.	POBI2					38					36		
Uvularia puberula Michx.	UVPU2					33							
Pyrularia pubera Michx.	PYPU					27	39						
Quercus alba L.	QUAL												
Dichanthelium commutatum (J.A. Schultes) Gould	DICO2						34						
Parthenocissus quinquefolia (L.) Planch.	PAQU2							43	68	70			
Symphyotrichum cordifolium (L.) G.L. Nesom	SYCO4							33					43
Arisaema triphyllum (L.) Schott	ARTR								40				
Polygonatum pubescens (Willd.) Pursh	POPU4								37	41			
Laportea canadensis (L.) Weddell	LACA3								36	37			
Sedum ternatum Michx.	SETE3								20				
Viola pubescens Aiton	VIPU3								20				
Polystichum acrostichoides (Michx.) Schott	POAC4									35			
Halesia tetraptera Ellis	HATE3									24			
Thalictrum dioicum L.	THDI										62	48	44
Fraxinus americana L.	FRAM2										48		
Carya cordiformis (Wangenh.) K. Koch	CACO15										43		
Sanicula L.	SANIC										41	54	
Uvularia grandiflora Sm.	UVGR										34		
Conopholis americana (L.) Wallr. f.	COAM										32		
Erechtites hieraciifolius (L.) Raf. ex DC.	ERHI2											83	
Vitis aestivalis Michx.	VIAE											81	65
Rubus allegheniensis Porter	RUAL											81	93
Robinia pseudoacacia L.	ROPS											69	
Phytolacca americana L.	PHAM4											58	
Viola sororia Willd.	VISO											58	44
Betula lenta L.	BELE											57	
Carex L.	CAREX											44	54
Rubus odoratus L.	RUOD											42	33
Hydrangea arborescens L.	HYAR											42	47
Ageratina altissima (L.) R.M. King & H. Rob.	AGAL5											38	59
Chelone lyonii Pursh	CHLY2											32	
Ligusticum canadense (L.) Britton	LICA16											25	
Thaspium barbinode (Michx.) Nutt.	THBA											25	25
Aster divaricatus L.	ASDI												47
Uvularia perfoliata L.	UVPE												45
Sanguinaria canadensis L.	SACA13												39
Uvularia sessilifolia L.	UVSE												25
Stachys latidens Small ex Britton	STLA5												25
Number of Indicator Species:		**5**	**3**	**0**	**1**	**4**	**3**	**2**	**6**	**5**	**7**	**16**	**16**

Abiotic Change and Influence

Dissimilarities in soil characteristics existed among our plots and explained some of the differences in ground-layer species composition (**Figure 3.3**). Soil variables that were significant (biplot cut-off $r^2 > 0.3$), and negatively correlated with axis 1 include total exchange capacity (TEC, r = -0.6), nitrate nitrogen (NO_3N, r = -0.56), and available soil nitrogen (N released, r = -0.56). Axis 2 was positively correlated with pH (r = 0.58) and negatively with sulfur (S, r = -0.6) (**Table A.3.6**).

After at least a decade of silvicultural treatments, treatment differences in the percent change in the vertical light profile descending from 1 m - 0.3 m above the forest floor, quantified here as dPAR (% µmol m^{-2} s^{-1}), was most pronounced in the shelterwood/fire treatment (-32% reduction in PAR) and least pronounced in the repeated fire treatment (-12% reduction in PAR, **Figure 3.4**). Both shelterwood treatments led to a more variable light profile relative to the control, but these differences were not significant ($F_{(3,44)} = 0.81$, p = 0.49, Levene's Test for Homogeneity $F_{(3,44)} = 1.29$, p = 0.29). Treatment differences in dPAR were not evident in ordination space ($r^2 > 0.3$) (**Figure 3.3**).

Extensive testing of differences in linear slopes of normalized PAR measurements from 0.3 m to 0.6 m ($F_{(3,44)} = 1.14$, p = 0.34, Levene's Test for Homogeneity $F_{(3,44)} = 0.78$, p = 0.5), from 0.6 m to 1 m ($F_{(3,44)} = 0.72$, p = 0.55, Levene's Test for Homogeneity $F_{(3,44)} = 1.1$, p = 0.36), and from 0.3 m to 1 m ($F_{(3, 44)} = 0.48$, p = 0.68; Levene's Test for Homogeneity $F_{(3,44)} = 0.68$, p = 0.57) among treatments were also not significant.

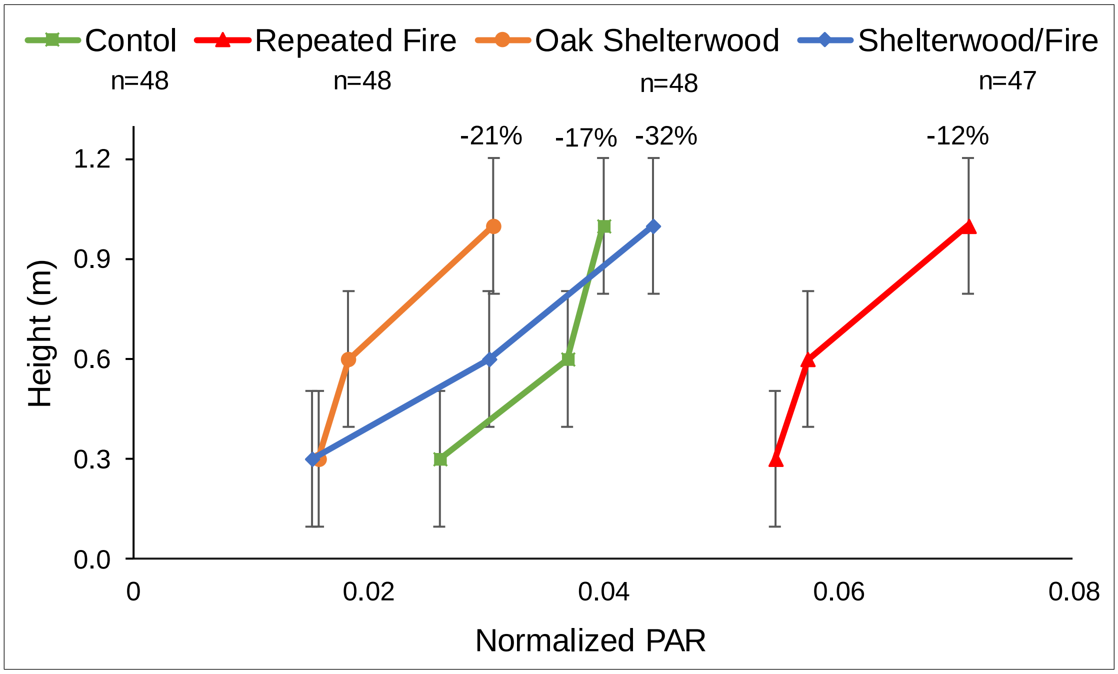


Figure 3.4 Vertical PAR intensity (measured as μmol m^{-2} s^{-1} and normalized to 1) ascending ground-layer subplots for each treatment. Error bars display the standard error of the mean. For all treatments n=48, except in shelterwood/fire n=47. Labels above treatment groups indicate mean dPAR (μmol m^{-2} s^{-1}) in the vertical light profile (descending from 1 m -0.3 m above the forest floor).

Changing Successional Patterns

Nonmetric multidimensional scaling of plots in species abundance space through time (pre-treatment through year 3, and year 9) developed a 3 axis solution which cumulatively explained 64% of the variation in the ordinations. Several of the species that were highly associated (r^2 = 0.2) with axis 1 in individual year ordinations above were again highly associated with axis 1 here. These included one fern (*P. acrostichoides:* r = -0.56), four herbaceous species (*S. canadensis:* r = -0.51, *A. racemosa*: r = -0.45, *L. canadensis*: r = -0.47, and *D. nudiflorum:* r = 0.55), and two vines (*S. rotundifolia:* r = 0.52 and *S. glauca*: r = 0.51) (**Table A.3.5**). The only species highly associated with axis 2 was *R. allegheniensis* (r=0.51). Axis 3 had no highly associated species and the two strongest associated species were *Sassafras albidum* (Nutt.) Nees: r = 0.41 and *R. allegheniensis:* r = 0.41.

The shelterwood/fire treatment resulted in the greatest temporal changes to species composition, which can be seen from the length of vector lines joining plots chronologically and was most evident from vector lines joining plots pre-treatment to plots in year 1 (**Figure 3.5**). Changes in species composition through time for all other silvicultural treatments were similar to that in the controls. There was less movement of plots along ordination axes, and less distance from pre-treatment conditions by year 9.

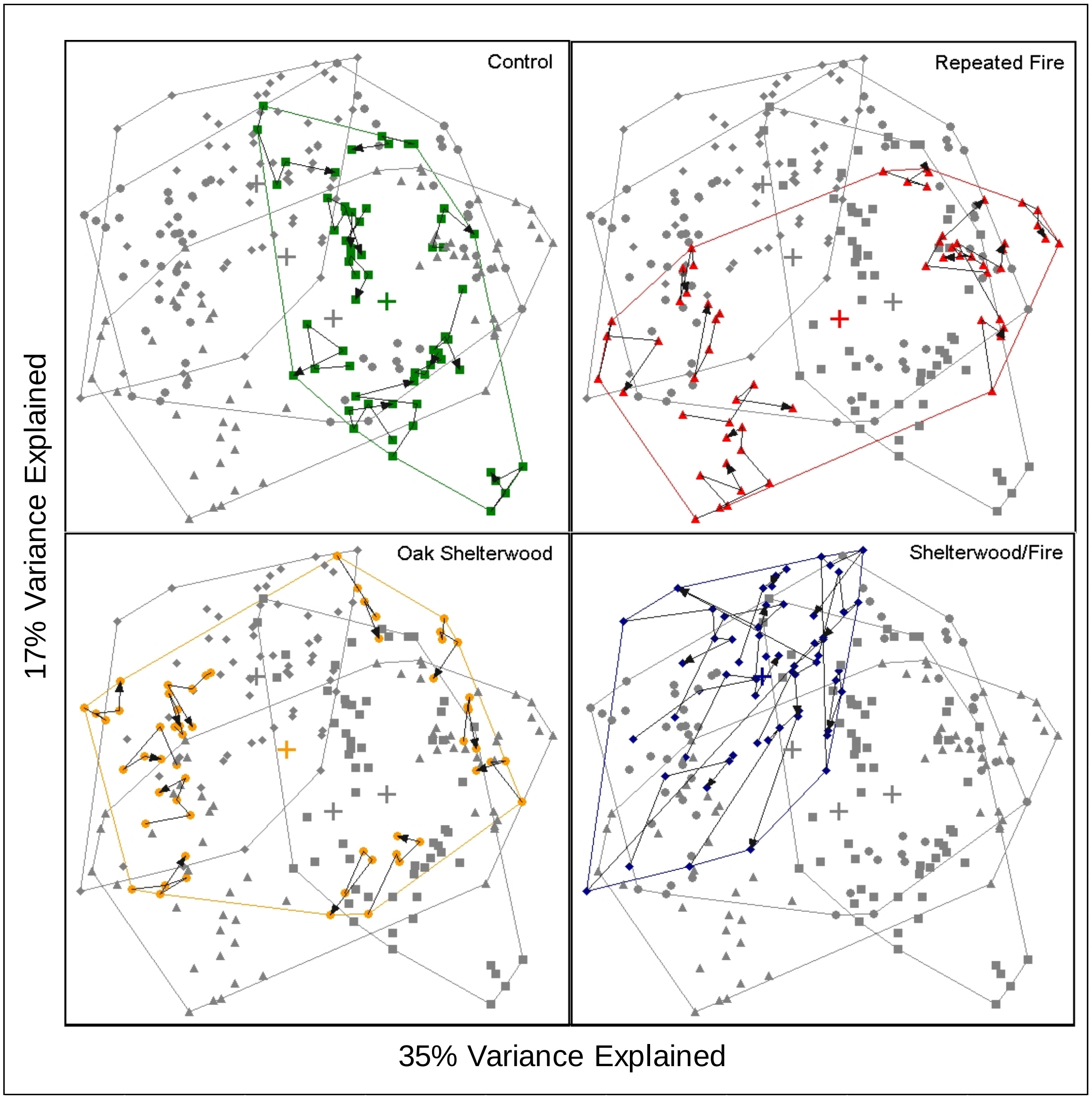


Figure 3.5 Nonmetric multidimensional scaling (NMS) ordination of plots in species space with treatment specific successional vectors chronologically linking plots from pre-treatment through treatment year 3, and treatment year 9 (black arrows) to show successional trajectories, or changes in redundant patterns of species abundance through time. Axis 1 and 2 are displayed which jointly represent the most variance explained in the ordination. Addition of axis 3 cumulatively accounted for 64% of the variance explained in ordination.

3.4 Discussion

The silvicultural treatments prescribed to promote *Quercus* regeneration in these mesophytic, Southern Appalachian forests increased ground-layer species richness compared to the unmanipulated controls. This was primarily seen following the oak shelterwood treatment which resulted in the least changes to overstory structure and light availability. Changes in species richness alone cannot account for how many species were gained and lost through time (species turnover) following silvicultural manipulations, which, in this study was relatively similar among treatments, but with more species gained after a decade, relative to controls. Species richness was increased the most from midstory thinning (OSW) and repeated fire (FIRE) treatments, and secondly by overstory reduction followed by fire (SWF treatment) implying that silvicultural treatments had an overall positive influence relative to leaving the forest unmanipulated.

Increases in ground-layer species richness are known to be associated with treatments that reduce woody plant cover, which in turn increases available light to the forest floor and reduces resource competition, yet richness often declines quickly with canopy closure or in the absence of repeated disturbance (Glasgow and Matlack, 2007; Elliott et al., 1999). Species richness may be more greatly increased with a combination of thinning and fire treatments (Barefoot et al., 2019), and although the shelterwood/fire treatment conducted in this study did not increase overall richness more than repeated fire or oak shelterwood treatments, it resulted in one more species gained after nearly a decade. Although the species which newly colonized the shelterwood/fire treatment were not non-native exotics, they were not necessarily desirable species, especially the recalcitrant layer of *Rubus* that formed in the ground-layer (Royo and Carson, 2006).

We hypothesized that ground-layer species composition would shift from more shade-tolerant, fire-sensitive species to more shade-intolerant, pyrophilous species in the shelterwood/fire and repeated prescribed fire treatments as a result of increased light and reduction of leaf litter and dead wood on the forest floor, and increased soil nutrient availability post-fire. Furthermore, we hypothesized that the shelterwood/fire treatment would lead to the greatest changes in species dominance patterns due to the combination of overstory disturbance and following prescribed fire treatments. Before and after silvicultural treatments, richness in the ground-layer community of these forests was overwhelmingly dominated (≥46%) by herbaceous species, and secondly by woody species (≥16%) in all treatments (**Table A.3.1**). Classifying ground-layer species relative to their tolerance to disturbances (shade, fire, drought) allowed some interpretation of the effects of treatments on ground-layer species composition. The greatest changes in the affinity of certain species to a certain treatment (indicator species) were seen the year following overstory reduction in the shelterwood/fire treatment. Increased importance values of several shade-intolerant or intermediate vines (*V. aestivalis*, *R. allegheniensis*, *R. odoratus*) and one shrub (*H. arborescens*), and at least one disturbance-tolerant species (*E. hieraciifolius*) were seen, with all except *E. hieraciifolius* persisting as important indicators into year 9. These findings supported our hypothesis that the shelterwood/fire treatment would lead to the greatest changes in species dominance patterns due to the combination of overstory disturbance and following prescribed fire treatments.

Two *Rubus* species (*R. allegheniensis* and *R. odoratus*) species known to colonize disturbed areas (ruderal) became indicator species following shelterwood/fire treatments and *R. allegheniensis* had the highest importance value of any species among all treatments by year 9 (93 versus 83 for *E. hieraciifolius* in year 1, also in the shelterwood/fire treatment). Elliott and Knoepp (2005) also reported increasing dominance and importance values for *Rubus* species following shelterwood harvest in sub-mesic Southern Appalachian forests. In addition, Elliott and Vose (2010) report increased importance values for *Rubus* species following two rounds of annual prescribed fires in similar forest types. *Rubus* are nitrophilic species well studied for their ability to hinder regeneration of other ground-layer species by more efficiently using available soil nitrogen and growing quickly, out-shading competing vegetation (Faillace et al., 2019; Gilliam, 2019). The dominant relative abundance of *R. allegheniensis* in the ground-layer following the shelterwood/fire treatment could be a factor contributing to this treatment having the greatest vertical percent change in PAR (dPAR) at ground-layer subplots even though this treatment resulted in the highest percent canopy openness after a decade. The *Rubus* in these treatment units has developed into a dense, low-canopy recalcitrant understory layer which has grown to out-shade most other competing vegetation, causing less light to reach lower ground-layer levels (Royo and Carson, 2006). If not managed for, this recalcitrant *Rubus* layer could slow regeneration processes and ultimately alter the species composition of woody seedlings in the ground-layer.

The shelterwood/fire treatment also resulted in three species switching treatment affinities by year 9. Early successional, shade-intolerant *L. tulipifera* was a pre-treatment control indicator yet switched treatment affinities to the shelterwood/fire treatment by year 9, probably due to increased light availability following the overstory reduction. While Loftis (1990b) found that shelterwood cuts could produce intermediate light that should favor *Quercus* regeneration over that of *L. tulipifera*, results from our study show that the shelterwood cuts performed increased *L. tulipifera* dominance. Increased *L. tulipifera* was also seen following a 60% residual overstory cut and herbicide treatment in West Virginia, with little advantage to the *Quercus* regeneration the treatment was meant to favor (Schuler and Miller, 1995). Lhotka (2013) also found increasing seedling density and importance values for *L. tulipifera* with increasing gap size showing the importance of light availability in relation to competitive advantages among ground-layer species following overstory disturbance events. *Symphyotrichum cordifolium* was a pre-treatment oak shelterwood indicator, yet this shade-intolerant, early successional species also showed greater affinity to the shelterwood/fire treatment following the prescribed fires conducted in year 5 or 7. These findings supported our hypothesis that ground-layer species composition would shift from more shade-tolerant, fire-sensitive species to more shade-intolerant, pyrophilous species in the shelterwood/fire treatment, but we did not see species switch affinities in favor of the repeated fire treatment.

Three *Quercus* species showed significant affinity to certain silvicultural treatments. *Q. prinus* L. was a control treatment indicator only for the first two years before completely losing significance. *Q. coccinea* was a consistent repeated fire treatment indicator with importance values increasing through time (33-44). *Q. alba* L. (IV: 31, not in table) showed affinity to the repeated fire treatment solely in year 3. Repeated fire is a widely used silvicultural method for favoring the regeneration of

Quercus species and seemed to be the best candidate for *Quercus* regeneration in these forests. Holzmueller et al. (2009) found that *Q. alba* and *Q. rubra* in the ground-layer showed affinity to repeated fire treatments over that of single fire treatments, even after at least 15 years with no fire, while other *Quercus* species showed no differences in fires frequency. *Quercus alba* seedling densities also increased following repeated fires (Holzmueller et al., 2009). Barefoot et al. (2019) report increased *Quercus* seedling density in the ground-layer following a combination of thinning and repeated fire treatments. This treatment combination was not prescribed in the "Regional Oak Study" but could give a further advantage to the oak shelterwood treatment that was prescribed in favoring *Quercus* regeneration.

Ground-Layer Light

Treatment differences in the vertical percent reduction in PAR (dPAR) descending ground-layer subplots ranged 20% after at least a decade of silvicultural treatments, however dPAR did not significantly vary among treatments. Tsai et al. (2018) found that nine years following variable retention overstory thinning treatments, light availability to the ground-layer did not differ among treatments but variation in the light environment was twice as high in thinned versus un-thinned treatments. Increasing available light heterogeneity in the ground-layer may increase species diversity as it creates different microhabitats which can favor a larger number of species with varying light requirements. Despite the initially heavy overstory reduction in the shelterwood/fire treatment, after a decade this treatment resulted in the greatest dPAR descending ground-layer subplots, implying greater overall ground-layer density. Increased ground-layer density implies more competition among ground-layer species for resources such as light, water, and soil nutrients. Species that can utilize these resources faster and more efficiently (such as *Rubus*) will persist and thrive, helping to determine successional patterns post-disturbance.

Conversely, two or three low intensity fires conducted over a decade (repeated fire treatment) decreased dPAR the most relative to other treatments. Repeated, low intensity, dormant season prescribed fire can reduce midstory tree density by a third, which can increase light availability to the ground-layer by 10-20% full sunlight, although these effects may only last 3-5 years (Johnson et al., 2019). These findings show that repeated, low intensity prescribed fires can have lasting effects on the reduction of midstory/ground-layer density, therefore reducing competition among ground-layer species, as well as favoring the long-term survival of more pyrophytic species.

Changing Dominance Patterns

Changes to dominance patterns relative to species composition and abundance were most extreme following the overstory reduction associated with the shelterwood/fire treatment. These results supported our hypothesis that the shelterwood/fire treatment would lead to the greatest changes in species dominance patterns from the combination of overstory reduction and fire treatments. Changes to species trajectories were relatively similar in all other treatments, including in the controls. Extreme and unfavorable changes to dominance patterns and successional trajectories of ground-layer communities may have long-lasting recourses against silvicultural objectives, and ultimately forest resilience, leading to a departure from a “safe operating space” and possibly leading to irreversible species dominance patterns (Johnstone et al., 2016). The recalcitrant *Rubus* layer which now dominates the ground-layer following the shelterwood treatment will have negative effects on the regeneration of other species, including desirable *Quercus* regeneration, which may last for long periods of time, essentially arresting succession, as very few species have the competitive ability to grow through this dense layer (Royo and Carson, 2006).

The shelterwood/fire treatment had the greatest direct influence on overstory basal area and density, and canopy openness, two important factors controlling light availability to the forest floor, arguably the most important and limiting resource for many ground-layer species. Studies that evaluate the effects of timber harvesting in the Appalachian region (Elliott and Knoepp, 2006) and elsewhere (Belote et al., 2012) show that shifts in species composition are related to the disturbance intensity of the treatment (amount of residual basal area left uncut which influences light availability), but that harvesting generally increases species diversity, with the influence of treatments generally lasting 10 or more years. In our study, effects from the shelterwood/fire treatment were still seen in dominance patterns after a decade, and the plots in these treatment units never reverted back to their pre-treatment locations in ordinations.

3.5 Conclusions

At least a decade after the single herbicide application (oak shelterwood) and repeated, low intensity fires (repeated fire) prescribed for *Quercus* regeneration in these mesic, Southern Appalachian forests species diversity and environmental parameters had changed minimally. Greater compositional changes were evident a decade after shelterwood/fire treatments, but this treatment also increased dominance of undesirable species, namely *Rubus* spp. in the ground-layer, potentially hindering the development of the woody regeneration and altering successional patterns. While the shelterwood/fire treatment had the quickest impact on successional trajectories, it also had the highest likelihood of unintended consequences.

While problems with successful canopy recruitment of *Quercus* species in Southern Appalachian forests are well studied, the influence that silvicultural prescriptions developed to address these issues can have on the ground-layer vegetation community is less studied, yet critical since the ground-layer will competitively interact with and influence the success of *Quercus* spp. regeneration. We found that the ground-layer community responds differently to changes in available light, and possibly soil nutrients following treatments of varying disturbance patterns. Management objectives following silvicultural disturbance should include monitoring the ground-layer vegetation annually and minimizing competition from undesirable species, which can have lasting (at least a decade) effects on successional patterns and species composition. Developing silvicultural prescriptions which manage for disturbance intensities relative to the disturbance-tolerances of species already present in the ground-layer community can help influence ensuing competitive interactions among vegetation and help better predict which species will dominate post-disturbance.

Comparing changes to ground-layer species composition post-treatment is important for future retention/restoration efforts and for evaluating whether certain silvicultural prescriptions can meet traditional management objectives while maintaining or restoring diversity of the ground-layer community. Managing for disturbance intensities when developing silvicultural prescriptions for a broader range of species may allow land managers to meet objectives for canopy recruitment of desirable woody species while also favoring the successful regeneration and survival of desirable ground-layer species. This study represents only a decade of post-disturbance responses and continual monitoring of species composition at this site is necessary to evaluate the effects of treatments on long-term successional patterns and trajectories. A follow-up to initial silvicultural treatments, including competition control of undesirable species, should be conducted with the added objectives of maintaining or increasing species diversity of the ground-layer vegetation community.

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Chapter 4: Synthesis and Future Recommendations

Southern Appalachian forests are highly diverse ecosystems whose geological history and varying microtopography have created unique microhabitats for a vast suite of ground-layer species. Ground-layer vegetation species play crucial roles in a variety of ecosystem functions and services including, but not limited to, seedling regeneration, nutrient cycling, and wildlife resources. While the retention and restoration of species composition and diversity has been a growing concern for private and non-private forestland owners, the more pressing concern for land managers in Southern Appalachian forests in recent decades has been promoting the advanced regeneration of *Quercus* species, which have considerably declined in midstory forest layers due to the suppression of historical fire regimes leading to increasing mesophication in these forest types.

While problems with successful canopy recruitment of *Quercus* species in Southern Appalachian forests are well studied, the influence that silvicultural prescriptions developed to address these issues can have on the ground-layer vegetation community is less studied, yet critical since the ground-layer will competitively interact with and influence the success of *Quercus* spp. regeneration. In such a biodiverse landscape, it is also important to consider the consequences that species-targeted management techniques can have on the survival, productivity, and assemblage of the ground-layer community, including other woody and herbaceous species. Competitive interactions for resources such as light, water, and nutrients among ground-layer species are complex and vary depending on species composition, forest type, and disturbance patterns.

We set out to compare how silvicultural management techniques developed for *Quercus* regeneration (repeated prescribed fire, oak shelterwood thinning with herbicide, or shelterwood harvesting followed by prescribe fire) in combination with microenvironmental influences altered the productivity, diversity, and species assemblages of the ground-layer vegetation community. We hypothesized that shelterwood/fire and repeated prescribed fire treatments would increase total biomass production, but that not all functional groups (lifeforms) would respond the same way.

We expected that repeated prescribed fire treatments would decrease dominance and biomass production of more shade-tolerant, fire-sensitive lifeforms (herbs, ferns) and increase dominance and biomass production of more shade-intolerant, pyrophilous lifeforms (woody, vines), and that the shelterwood/fire treatment would increase dominance of shade-intolerant lifeforms after a decade. Furthermore, we expected that the shelterwood/fire treatment would lead to the greatest changes in species dominance patterns due to the combination of overstory disturbance and prescribed fire treatments which more drastically alter ground-layer light, temperature, and soil nutrient availability, driving competitive interactions which help determine the ensuing species assemblages and dominance patterns.

Measuring and visualizing changes in plant communities composed of numerous sometimes shifting species through time is a complex undertaking. I found that a two-part approach was necessary to assess first the broadscale pattern and then follow with the finer species details. I found complementary patterns in the separate analyses (Table 4.1). Species richness was increased by all silvicultural treatments, relative to the unmanipulated controls, without drastic species turnover, showing the somewhat positive effects from all *Quercus* regeneration management strategies. Results also supported our hypothesis of increased total biomass following shelterwood/fire treatments, less so following repeated fire treatments. We also found that treatments that only modified the midstory (oak shelterwood) or leave the forest unmanipulated (controls) did very little to alter species assemblages and dominance patterns after a decade. The shelterwood/fire treatment resulted in the greatest changes in species dominance patterns, via increased biomass of vine (primarily *Rubus* spp.), herbaceous, and woody lifeforms following treatments. However, the dense *Rubus* layer that formed in the ground-layer following shelterwood/fire treatments could hinder regeneration of other species, including *Quercus,* if not addressed. The greatest increases in *Quercus* biomass proportions (of the woody lifeform) were seen following a decade of repeated fire treatments showing the positive effects of reintroducing a fire regime to this landscape. While the oak shelterwood treatment also increased woody biomass in the ground-layer, *Quercus* proportions were lower in this treatment than in the unmanipulated controls after a decade.

Table 4.1 Patterns of change in ground-layer vegetation dynamics of Southern Appalachian forests 9 years following silvicultural treatments developed for *Quercus* regeneration.

	Variable	Control	Repeated Fire	Oak Shelterwood	Shelterwood /Fire
	Total Biomass	↓	↑	↑	↑
Lifeform Biomass	Vine	↑	↑	↑	↑
	Woody	↓	↑	↑	↑
	Herbaceous	↓	↑	↑	↑
	Shrub	↑	↑	↑	↑
	Fern	↑	↓	↑	↓
	Graminoid	↓	↑	↓	↑
Metrics	Species Richness	↑5	↑13	↑13	↑9
	Species Turnover	↓17, ↑20	↓18, ↑31	↓19, ↑32	↓24, ↑31
	Evenness	↓	↓	↓	↓
	Indicators	↓5	↑2	↑3	↑9
	Trajectories	Minor Shift	Minor Shift	Minor Shift	Major Shift

Future Recommendations

Understanding how ground-layer species composition is modified by silvicultural treatments is important for future retention/restoration efforts and for evaluating whether certain silvicultural prescriptions can meet traditional management objectives such as timber production, while maintaining or restoring the diversity of the ground-layer community. Results suggest the need to monitor changes to species assemblages and dominance patterns in the ground-layer early-on following treatments for *Quercus* regeneration in case follow-up treatments are needed to influence the successional patterns that ensue. While this study's evaluation of the biomass response of functional groups (lifeforms) gave insight into the effects of treatments on biomass productivity, a more in-depth look at biomass productivity of individual species would further enhance our understanding of the competitive interactions among ground-layer species and help to predict the dominance patterns that would ensue. A better understanding of species-specific resource requirements would also allow ground-layer species to be categorized into functional groups specific to these requirements, not just a lifeform.

This study represents only a decade of post-disturbance responses and continual monitoring of species assemblages at this site is necessary to evaluate the effects of treatments on long-term successional patterns. Further work evaluating the above and below ground competitive interactions of the ground-layer would also give insight into these fine scale relationships that help determine the regenerative potential of the future forest. With a baseline dataset for soil nutrients now recorded, future work that focuses on the nutrient availability of the soil at different ecological gradients could also shed light on the productivity potential of specific species in the ground-layer of these forests.

A follow-up to initial silvicultural treatments, including competition control of undesirable species in the ground-layer and midstory, should be conducted with the added objectives of maintaining or increasing species diversity of the ground-layer vegetation community. Management objectives following silvicultural disturbance should include monitoring the ground-layer vegetation annually and minimizing competition from undesirable species, which can have lasting (at least a decade) effects on successional patterns and species composition. Developing silvicultural prescriptions which manage for disturbance intensities relative to the disturbance-tolerances of species already present in the ground-layer community can help influence ensuing competitive interactions among vegetation and help to better predict which species will dominate post-disturbance, and also allow land managers to meet objectives for canopy recruitment of desirable woody species while favoring the successful regeneration and diversity of desirable ground-layer species.

APPENDIX

Appendix A

Table A.3.1 Species richness (count of species per 48 m^2) by treatment, lifeform (and subtype), and treatment year. The proportional contribution of each lifeform (%LF/All) within a treatment is given for pre-treatment (Pre) and the final full year of measurements (year 9). Asterisk in the shelterwood/fire treatment indicate years when only 2 (of 4) shelterwood/fire treatment units were measured (year 7: 3 years post-fire, year 8: 2 years post-fire).

		Treatment Year									
Treatment	**Lifeform**	**Pre**	**%LF /All**	**1**	**2**	**3**	**6**	**7**	**8**	**9**	**%LF /All**
Control	Vine	6	**6%**	7	7	7	N/A	6	N/A	8	**8%**
	Rubus	1	**1%**	1	1	1	N/A	1	N/A	1	**1%**
	Woody	18	**18%**	18	18	18	N/A	20	N/A	20	**21%**
	Quercus	5	**5%**	5	5	5	N/A	5	N/A	5	**5%**
	Herbaceous	46	**46%**	50	51	49	N/A	42	N/A	48	**46%**
	Shrub	6	**6%**	6	5	5	N/A	6	N/A	8	**8%**
	Fern	8	**8%**	8	8	8	N/A	8	N/A	8	**8%**
	Graminoid	10	**10%**	13	11	11	N/A	5	N/A	5	**5%**
	TOTAL	**100**	N/A	**108**	**106**	**104**	N/A	**93**	N/A	**105**	N/A
Repeated Fire	Vine	6	**6%**	6	8	6	6	6	5	5	**4%**
	Rubus	0	0	1	1	1	1	1	2	1	**1%**
	Woody	22	**20%**	22	20	20	20	18	20	20	**17%**
	Quercus	5	**5%**	5	5	5	5	5	5	5	**4%**
	Herbaceous	55	**51%**	69	60	60	68	60	65	67	**55%**
	Shrub	6	**6%**	8	6	6	7	8	7	6	**5%**
	Fern	7	**6%**	7	7	7	7	8	6	6	**5%**
	Graminoid	7	**6%**	10	10	10	11	9	9	11	**9%**
	TOTAL	**108**	N/A	**128**	**117**	**115**	**125**	**115**	**119**	**121**	N/A
Oak Shelterwood	Vine	4	**3%**	5	5	5	N/A	N/A	N/A	6	**4%**
	Rubus	1	**1%**	1	1	1	N/A	N/A	N/A	1	**1%**
	Woody	20	**16%**	21	22	22	N/A	N/A	N/A	23	**17%**
	Quercus	3	**2%**	4	4	4	N/A	N/A	N/A	4	**3%**
	Herbaceous	68	**55%**	65	71	70	N/A	N/A	N/A	76	**56%**
	Shrub	8	**7%**	5	8	9	N/A	N/A	N/A	9	**7%**
	Fern	7	**6%**	5	8	7	N/A	N/A	N/A	7	**5%**
	Graminoid	12	**10%**	11	13	14	N/A	N/A	N/A	10	**7%**
	TOTAL	**123**	N/A	**117**	**132**	**132**	N/A	N/A	N/A	**136**	N/A
Shelterwood /Fire	Vine	5	**5%**	6	5	6	N/A	6	3	7	**6%**
	Rubus	1	**1%**	2	2	3	N/A	2	2	2	**2%**
	Woody	18	**17%**	15	18	18	N/A	11	12	15	**13%**
	Quercus	3	**3%**	3	4	4	N/A	2	2	2	**2%**
	Herbaceous	61	**57%**	75	74	67	N/A	42	55	72	**62%**
	Shrub	4	**4%**	3	4	4	N/A	6	1	3	**3%**
	Fern	7	**7%**	7	7	8	N/A	3	5	7	**6%**
	Graminoid	8	**7%**	11	12	9	N/A	7	4	8	**7%**
	TOTAL	**107**	N/A	**122**	**126**	**119**	N/A	**78***	**84***	**116**	N/A

Table A.3.2 Results from multi-response permutation procedures (MRPP) performed on species occurrence (presence/absence), and species abundance (% cover) data showing significant overall and pairwise differences in response by treatment year.

Multi-response Permutation Procedures (MRPP) by Treatment Year															
Species Presence/Absence:															
Treatment Year	**Overall**		**Pairwise Treatment Differences:**												
			CONT vs SWF		**CONT vs OSW**		**CONT vs FIRE**		**FIRE vs SWF**		**FIRE vs OSW**		**OSW vs SWF**		
	A	**p=**	**A**	**p=**	**A**	**p=**	**A**	**p=**	**A**	**p=**	**A**	**p=**	**A**	**p=**	
Pre	0.048	**<0.001**	0.081	**<0.001**	0.026	**0.02**	0.026	**0.03**	0.034	**0.02**	0.013	0.1	0.02	**0.04**	
1	0.064	**<0.001**	0.089	**<0.001**	0.036	**0.01**	0.03	**0.01**	0.056	**0.001**	0.014	0.1	0.036	**0.005**	
2	0.062	**<0.001**	0.086	**<0.001**	0.028	**0.02**	0.026	**0.02**	0.065	**0.001**	0.014	0.1	0.041	**0.003**	
3	0.057	**<0.001**	0.071	**<0.001**	0.025	**0.03**	0.024	**0.03**	0.068	**<0.001**	0.013	0.1	0.037	**0.006**	
9	0.062	**<0.001**	0.085	**<0.001**	0.025	**0.02**	0.017	0.07	0.07	**<0.001**	0.022	0.07	0.042	**0.001**	
Species Cover (%):															
Treatment Year	**Overall**		**Pairwise Treatment Differences:**												
			CONT vs SWF		**CONT vs OSW**		**CONT vs FIRE**		**FIRE vs SWF**		**FIRE vs OSW**		**OSW vs SWF**		
	A	**p=**	**A**	**p=**	**A**	**p=**	**A**	**p=**	**A**	**p=**	**A**	**p=**	**A**	**p=**	
Pre	0.026	**<0.001**	0.041	**<0.001**	0.017	**0.008**	0.01	0.08	0.02	**0.02**	0.009	0.1	0.008	0.1	
1	0.055	**<0.001**	0.056	**<0.001**	0.024	**0.005**	0.013	**0.04**	0.066	**<0.001**	0.013	0.09	0.054	**<0.001**	
2	0.061	**<0.001**	0.061	**<0.001**	0.012	0.07	0.013	0.06	0.084	**<0.001**	0.012	0.1	0.075	**<0.001**	
3	0.061	**<0.001**	0.067	**<0.001**	0.005	0.2	0.01	0.08	0.096	**<0.001**	0.009	0.1	0.07	**<0.001**	
9	0.066	**<0.001**	0.074	**<0.001**	0.025	**0.006**	0.023	**0.01**	0.071	**<0.001**	0.019	**0.046**	0.064	**<0.001**	

Table A.3.3 Species axis correlations for the nonmetric multidimensional scaling of species abundance before, just after, and at least a decade following initial silvicultural treatments (pre-treatment, year 1, and year 9). Species with significant associations ($R^2 \geq 0.2$) are listed and **bolded** relative to the most highly associated axis for that year.

Species Code	Year	Axis 1 r	Axis 1 tau	Axis 2 r	Axis 2 tau	Axis 3 r	Axis 3 tau
ACRA7	Pre	**-0.453**	**-0.456**	0.165	0.202	0.049	-0.029
ACRA7	1	**-0.539**	**-0.459**	0.118	0.17	-0.155	-0.03
ACSA3	Pre	**-0.48**	**-0.549**	-0.381	-0.233	0.388	0.263
ARMA7	1	**-0.449**	**-0.325**	0.001	-0.122	-0.354	-0.31
ARMA7	9	**-0.455**	**-0.313**	-0.222	-0.307	0.377	0.25
ARTR	1	**-0.483**	**-0.49**	0.093	0.114	-0.253	-0.158
CACO15	Pre	-0.313	-0.333	-0.11	-0.081	**0.49**	**0.356**
CHMA3	Pre	**0.475**	**0.487**	-0.128	-0.173	-0.073	-0.184
CHMA3	1	**0.522**	**0.581**	-0.225	-0.148	0.061	-0.184
DENU4	1	**0.556**	**0.59**	0.31	0.132	-0.187	-0.193
DENU4	9	**0.559**	**0.586**	0.29	0.179	0.174	0.131
DIBO2	Pre	**0.461**	**0.473**	0.196	0.204	-0.1	-0.115
DIBO2	1	**0.486**	**0.46**	0.312	0.265	-0.28	-0.207
DIBO2	9	**0.465**	**0.446**	0.228	0.249	0.253	0.125
DRMA4	Pre	-0.157	-0.087	-0.132	-0.137	**-0.471**	**-0.286**
EUPU21	Pre	0.148	0.221	**0.473**	**0.368**	0.093	0.157
KALA	Pre	0.3	0.334	**-0.47**	**-0.314**	0.028	0.151
LACA3	Pre	**-0.454**	**-0.525**	0.002	0.02	0.207	0.114
LACA3	1	**-0.505**	**-0.589**	0.011	-0.026	-0.073	-0.069
LITU	9	0.039	-0.126	**0.449**	**0.435**	-0.132	-0.009
PAQU2	1	-0.007	-0.282	0.321	0.295	**-0.452**	**-0.186**
POAC4	Pre	**-0.547**	**-0.5**	-0.126	-0.104	-0.094	-0.211
POAC4	1	**-0.55**	**-0.481**	-0.199	-0.301	-0.141	-0.1
POPU4	Pre	**-0.538**	**-0.466**	0.06	0.075	-0.062	-0.077
QUVE	9	**0.477**	**0.424**	0.046	-0.005	0.136	0.087
RUAL	1	-0.061	-0.136	0.345	0.237	**0.569**	**0.566**
RUAL	9	-0.336	-0.242	**0.577**	**0.494**	-0.317	-0.244
RUOD	1	-0.333	-0.293	0.058	0.024	**0.46**	**0.354**
SACA13	Pre	**-0.449**	**-0.477**	0.232	0.199	0.208	0.112
SACA13	1	**-0.587**	**-0.552**	-0.021	-0.065	-0.182	-0.079
SACA13	9	**-0.564**	**-0.502**	0.025	0.063	0.259	0.146
SANIC	9	**-0.452**	**-0.343**	0.284	0.343	0.058	0.103
SMGL	Pre	**0.47**	**0.556**	0.086	0.101	0.022	-0.041
SMGL	1	**0.541**	**0.472**	0.18	0.228	-0.074	-0.045
SMGL	9	**0.521**	**0.51**	0.3	0.278	-0.014	0.065
SMRO	Pre	**0.47**	**0.513**	0.032	0.033	0.342	0.225
SMRO	9	**0.635**	**0.568**	0.161	0.118	0.358	0.264
VAPA4	9	**0.508**	**0.533**	-0.003	0.025	0.026	0.034
VIAE	1	-0.192	-0.094	0.189	0.285	**0.557**	**0.371**
VIAE	9	-0.216	0.044	**0.468**	**0.28**	-0.273	-0.117

Table A.3.4 Nonmetric multidimensional scaling axis correlations for environmental variables related to species abundance before, just after, and at least a decade following initial silvicultural treatments. Variables are sorted according to their association (r) with axes. **Bolded** associations were significant ($R^2 \geq 0.2$) environmental biplot vectors in ordinations.

Environmental Parameters	Year	Axis 1		Axis 2		Axis 3	
		r	tau	r	tau	r	tau
Latitude	Pre	**0.552**	**0.365**	-0.333	-0.238	-0.051	-0.005
	1	**0.457**	**0.275**	0.386	0.223	-0.359	-0.223
	9	**0.552**	**0.314**	0.338	0.238	0.079	0.099
Overstory Basal Area	Pre	**-0.48**	**-0.313**	0.23	0.155	-0.211	-0.162
	1	-0.009	0.013	**-0.534**	**-0.388**	-0.393	-0.223
	9	-0.022	-0.025	**-0.679**	**-0.516**	0.122	0.05
Overstory tph	Pre	0.007	0.028	0.326	0.198	-0.18	-0.064
	1	0.312	0.22	**-0.54**	**-0.375**	-0.415	-0.218
	9	0.31	0.21	**-0.66**	**-0.498**	0.065	0.03
Canopy Openness	Pre	0.082	0.112	0.081	0.071	-0.022	0.021
	1	-0.39	-0.268	0.435	0.326	**0.559**	**0.283**
	9	-0.282	-0.163	0.391	0.245	-0.373	-0.223
Elevation	Pre	-0.242	-0.133	0.394	0.324	-0.13	-0.089
	1	-0.131	-0.059	-0.405	-0.243	**0.468**	**0.414**
	9	-0.187	-0.074	-0.279	-0.179	-0.302	-0.324
Midstory Basal Area	Pre	0.194	0.224	0.088	0.004	-0.064	-0.11
	1	0.305	0.33	-0.204	-0.196	**-0.451**	**-0.348**
	9	0.339	0.28	-0.357	-0.222	0.038	0.075
Terrain Shape Index	Pre	0.075	0.086	-0.082	-0.05	-0.094	-0.046
	1	0.001	0.037	-0.089	-0.097	-0.046	-0.052
	9	0.034	0.077	-0.144	-0.128	0.329	0.267
Landform Index	Pre	0.129	0.063	0.05	-0.008	-0.078	-0.029
	1	0.11	0.014	-0.203	-0.122	-0.16	-0.031
	9	0.057	-0.026	-0.224	-0.138	0.124	0.111
Longitude	Pre	0.217	0.08	-0.24	-0.016	-0.217	-0.145
	1	0.185	0.043	0.172	-0.028	-0.229	-0.028
	9	0.223	0.074	-0.005	-0.076	0.072	-0.055
Midstory tph	Pre	0.276	0.227	0.161	0.088	-0.096	-0.097
	1	0.338	0.273	-0.261	-0.236	-328	-0.246
	9	0.308	0.306	-0.405	-0.271	-0.038	0.062

Table A.3.5 Species axis correlations for the nonmetric multidimensional scaling of species abundance through time (pre-treatment-year 3, and year 9). Species with significant associations ($R^2 \geq 0.2$) are listed and **bolded** relative to the most highly associated axis.

Species Code	Axis 1		Axis 2		Axis 3	
	r	tau	r	tau	r	tau
POAC4	**-0.561**	**-0.484**	-0.135	-0.223	0.005	0.059
DENU4	**0.545**	**0.566**	0.211	0.099	-0.043	-0.1
SMRO	**0.516**	**0.504**	0.123	0.068	-0.303	-0.252
SACA13	**-0.514**	**-0.501**	0.119	0.099	-0.128	-0.09
SMGL	**0.511**	**0.526**	0.089	0.118	0.045	0.021
LACA3	**-0.467**	**-0.504**	0.105	0.074	-0.129	-0.06
ACRA7	**-0.452**	**-0.447**	0.07	0.068	-0.205	-0.155
RUAL	-0.099	-0.107	**0.507**	**0.415**	0.411	0.416

Table A.3.6 Nonmetric multidimensional scaling axis correlations for soil characteristics and vertical percent change in PAR (dPAR) at ground-layer subplots in 2019. Variables are sorted according to their association (r) with axes. **Bolded** associations were significant ($R^{2} = \geq 0.3$) environmental biplot vectors in ordinations.

2019 Soils and dPAR	Description	Axis 1		Axis 2		Axis 3	
		r	tau	r	tau	r	tau
TEC	Total Exchange Capacity	**-0.60**	**-0.43**	0.23	0.19	-0.18	-0.11
Nrel	Nitrogen Released	**-0.56**	**-0.38**	-0.08	-0.14	-0.11	-0.06
NO_3N	Nitrogen Nitrate	**-0.56**	**-0.43**	0.12	0.18	-0.10	-0.14
S	Sulfur (ppm)	0.18	0.19	**-0.60**	**-0.39**	0.33	0.26
pH	Acidity	0.09	0.06	**0.58**	**0.44**	-0.21	-0.17
Al	Aluminum (mg/kg)	-0.16	-0.08	-0.31	-0.18	0.00	0.08
B	Boron (mg/kg)	-0.26	-0.33	0.16	0.09	-0.27	-0.16
Ca	Calcium (mg/kg)	-0.46	-0.32	0.38	0.29	-0.18	-0.13
Cu	Copper (mg/kg)	-0.37	-0.29	-0.08	0.12	0.23	0.18
Fe	Iron (mg/kg)	0.25	0.15	-0.43	-0.25	0.34	0.26
K	Potassium (mg/kg)	-0.20	-0.06	0.33	0.22	-0.07	-0.01
Mg	Magensium (mg/kg)	-0.37	-0.26	0.36	0.32	-0.29	-0.21
Mn	Manganese (mg/kg)	-0.09	-0.05	0.52	0.34	-0.11	-0.14
Na	Sodium (mg/kg)	-0.03	-0.04	-0.06	-0.09	0.07	0.06
NH_4N	Ammonium (ppm)	-0.24	-0.18	-0.26	-0.17	-0.23	0.00
OM	Organic Matter	-0.52	-0.38	-0.29	-0.14	-0.21	-0.04
P	Phosphorus (mg/kg)	-0.21	-0.14	-0.17	-0.15	0.14	0.12
Zn	Zinc (mg/kg)	-0.26	-0.22	-0.06	-0.09	0.04	0.17
dPAR	Vertical PAR % Change	0.22	0.13	-0.13	-0.14	-0.23	-0.16

Table A.3.7: Cover (%) values for species present pre-treatment, year 1, and year 9 sorted alphabetically, by lifeform. The overall change in species percent cover from pre-treatment to year 9 (Pre:9) is given.

Treatment/Year:	**Control**				**Oak Shelterwood**				**Repeated Fire**				**Shelterwood/Fire**			
Species	**Pre**	**1**	**9**	**Pre:9**	**Pre**	**1**	**9**	**Pre:9**	**Pre**	**1**	**9**	**Pre:9**	**Pre**	**1**	**9**	**Pre:9**
Ferns																
Adiantum pedatum	0.63	0.63	0.84	**0.22**	0.07	0.13	0.38	**0.30**	0.38	0.94	0.44	**0.06**	0.50	0.44	0.69	**0.19**
Athyrium filix-femina	0.06	0.31	0.31	**0.25**												
Botrychium biternatum	0.06	0.01	0.06	**0.00**	0.01		0.06	**0.06**	0.01	0.01	0.01	**0.00**			0.01	**0.01**
Botrychium virginianum	0.07	0.01	0.06	**-0.01**	0.45	0.07	0.20	**-0.24**	0.13	0.13	0.19	**0.07**	0.51	0.13	0.14	**-0.38**
Deparia acrostichoides							0.38	**0.38**						0.38	0.69	**0.69**
Dryopteris marginalis									0.13	0.38		**-0.13**				**0.00**
Osmunda cinnamomea	0.31	0.31	0.78	**0.47**									0.38			**-0.38**
Osmunda claytoniana									0.31	0.84	0.85	**0.54**	0.63	0.13	0.63	**0.00**
Phegopteris hexagonoptera	0.44	0.69	0.44	**0.00**	0.13	0.38	0.13	**0.01**	0.31	0.06	0.13	**-0.19**	0.38	0.81		**-0.38**
Polystichum acrostichoides	0.44	0.19	0.19	**-0.25**	2.63	2.82	3.07	**0.44**	1.76	1.19	0.94	**-0.81**	2.69	1.44	1.59	**-1.10**
Thelypteris noveboracensis	0.63	0.69	1.63	**1.00**	0.06	0.13		**-0.06**					0.44	0.19	0.06	**-0.38**
Unknown spp.					0.01		0.06	**0.06**								**0.00**
Graminoids																
Brachyelytrum erectum	0.07	0.07		**-0.07**									0.13	0.19	0.01	**-0.12**
Bromus									0.01			**-0.01**				
Bromus pubescens					0.06	0.13		**-0.06**								
Carex	0.07	0.01		**-0.07**	0.15	0.07	0.02	**-0.13**	0.06	0.08	0.01	**-0.06**	0.02	0.51	0.34	**0.32**
Carex blanda	0.01	0.06		**-0.01**										0.07	0.13	**0.13**
Carex communis					0.06	0.06	0.06	**0.00**		0.01	0.07	**0.07**		0.06		**0.00**
Carex digitalis	0.02	0.09	0.26	**0.23**	0.13	0.13	0.02	**-0.11**	0.01	0.07	0.15	**0.14**	0.01	0.44	0.26	**0.26**
Carex pensylvanica	0.07	0.13		**-0.07**	0.31		0.31	**0.00**	0.06	0.06	0.13	**0.06**				
Carex virescens		0.06		**0.00**	0.07	0.01	0.19	**0.12**						0.06		**0.00**
Danthonia	0.06			**-0.06**									0.02			**-0.02**
Danthonia compressa					0.13	0.25	0.06	**-0.06**		0.01	0.06	**0.06**	0.01	0.06		**-0.01**
Danthonia spicata									0.06			**-0.06**				**0.00**

Treatment/Year:	**Control**				**Oak Shelterwood**				**Repeated Fire**				**Shelterwood/Fire**			
Species	**Pre**	**1**	**9**	**Pre:9**	**Pre**	**1**	**9**	**Pre:9**	**Pre**	**1**	**9**	**Pre:9**	**Pre**	**1**	**9**	**Pre:9**
Dichanthelium	0.01	0.01	0.06	**0.05**					0.01	0.07	0.06	**0.06**	0.01	0.01		**-0.01**
Dichanthelium boscii	0.16	0.27	0.09	**-0.07**	0.27	0.32	0.32	**0.06**	0.26	0.34	0.38	**0.11**	0.06	0.06	0.01	**-0.06**
Dichanthelium commutatum						0.01	0.07	**0.07**		0.02	0.83	**0.83**		0.69	0.32	**0.32**
Dichanthelium dichotomum		0.06	0.01	**0.01**	0.13	0.07	0.01	**-0.13**		0.03	0.39	**0.39**				
Dichanthelium sphaerocarpon		0.01		**0.00**												
Luzula echinata		0.07		**0.00**	0.13			**-0.13**								
Muhlenbergia tenuiflora	0.06	0.06		**-0.06**	0.07	0.01		**-0.07**								
Poa	0.01	0.07	0.01	**0.01**		0.01	0.08	**0.08**		0.14	0.19	**0.19**			0.07	**0.07**
Unknown spp.					0.13			**-0.13**			0.02	**0.02**	0.01	0.07	0.06	**0.05**
Herbaceous																
Actaea pachypoda						0.06	0.31	**0.31**								**0.00**
Actaea racemosa	0.31	0.31	0.38	**0.06**	2.25	2.03	1.72	**-0.53**	0.75	0.63	0.69	**-0.06**	1.44	1.06	1.03	**-0.41**
Ageratina altissima	0.01	0.06		**-0.01**	0.19	0.13	0.25	**0.06**			0.06	**0.06**	0.06	0.39	1.14	**1.08**
Agrimonia					0.13	0.06		**-0.13**		0.01		**0.00**				
Amphicarpaea bracteata			0.01	**0.01**	0.19	0.19	0.20	**0.01**	0.13	0.19	2.36	**2.24**	0.31			**-0.31**
Antennaria plantaginifolia					0.01	0.01		**-0.01**								
Arabis laevigata										0.06	0.01	**0.01**				
Aralia racemosa												**0.00**	0.06			**-0.06**
Arisaema triphyllum	0.01	0.07	0.14	**0.14**	0.41	0.67	0.56	**0.16**	0.07	0.40	0.11	**0.04**	0.21	0.15	0.48	**0.27**
Aristolochia serpentaria										0.06	0.01	**0.01**				
Arnoglossum atriplicifolium									0.06	0.06		**-0.06**				
Aruncus dioicus					0.31			**-0.31**							0.31	**0.31**
Asarum canadense					0.01	0.31	0.38	**0.37**					0.19	0.06	0.78	**0.59**
Asclepias													0.06			**-0.06**
Asclepias exaltata			0.31	**0.31**												
Asclepias quadrifolia		0.06	0.13	**0.13**												
Aster	0.06			**-0.06**									0.01			**-0.01**
Aster divaricatus	1.01	1.01	0.39	**-0.61**	0.57	0.75	0.38	**-0.19**	0.56	1.76	1.02	**0.46**	0.32	1.01	2.29	**1.97**

Treatment/Year:	Control				Oak Shelterwood				Repeated Fire				Shelterwood/Fire			
Species	**Pre**	**1**	**9**	**Pre:9**	**Pre**	**1**	**9**	**Pre:9**	**Pre**	**1**	**9**	**Pre:9**	**Pre**	**1**	**9**	**Pre:9**
Aster lowrieanus			0.06	**0.06**			0.01	**0.01**			0.13	**0.13**				
Astilbe biternata		0.63		**0.00**	1.63	2.08	1.09	**-0.53**			0.06	**0.06**	0.63	0.94	1.09	**0.47**
Aureolaria laevigata		0.06	0.06	**0.06**	0.07	0.06	0.13	**0.06**	0.07	0.01	0.19	**0.12**				
Bidens frondosa															0.06	**0.06**
Cacalia atriplicifolia											0.31	**0.31**				
Campanula divaricata							0.07	**0.07**		0.06	0.14	**0.14**				
Caulophyllum thalictroides									0.44	0.76	0.51	**0.06**	0.81	0.50	0.81	**0.00**
Chelone lyonii	0.06	0.13	0.06	**0.00**	0.01	0.01	0.13	**0.12**					0.13	0.44	0.13	**-0.01**
Chimaphila maculata	0.09	0.09	0.05	**-0.04**	0.08	0.02	0.17	**0.09**	0.09	0.05	0.07	**-0.02**			0.01	**0.01**
Circaea lutetiana					0.07	0.13	0.13	**0.06**	0.06	0.01	0.06	**0.00**	0.07	0.06	0.01	**-0.06**
Cirsium vulgare														0.78		**0.00**
Clintonia umbellulata															0.01	**0.01**
Collinsonia canadensis	0.13	0.13	0.06	**-0.06**	0.31	0.31	0.31	**0.00**					0.13	0.81	0.75	**0.63**
Conopholis americana	0.14	0.13	0.13	**-0.01**	0.38	0.14	0.19	**-0.19**	0.13	0.01	0.06	**-0.06**	0.76	0.06	0.06	**-0.69**
Coreopsis major									0.07	0.13	0.13	**0.06**			0.13	**0.13**
Crepis														0.01		**0.00**
Cuscuta														0.06	0.31	**0.31**
Desmodium nudiflorum	1.58	2.60	2.01	**0.42**	3.09	2.22	2.47	**-0.61**	1.39	2.94	3.56	**2.18**	0.13	0.06	0.06	**-0.07**
Desmodium rotundifolium					0.06	0.06		**-0.06**								
Dioscorea quaternata	0.13	0.32	0.14	**0.01**	0.19	0.50	0.56	**0.38**		0.08	0.07	**0.07**	0.19	0.33	0.13	**-0.06**
Doellingeria infirma									0.07	0.19	0.13	**0.06**	0.06			**-0.06**
Erechtites hieraciifolius						0.01		**0.00**		0.01		**0.00**		1.58		**0.00**
Erigeron pulchellus	0.06	0.31		**-0.06**			0.06	**0.06**			0.06	**0.06**				
Eupatorium purpureum	0.56	0.69	0.44	**-0.13**	0.69	0.44	0.31	**-0.38**	0.07	0.51	0.82	**0.75**	0.38	0.69	0.26	**-0.11**
Euphorbia corollata	0.01	0.06		**-0.01**					0.06			**-0.06**				
Eurybia chlorolepis						0.06		**0.00**								
Eurybia macrophylla	0.06	0.06	0.06	**0.00**												
Fragaria virginiana					0.01			**-0.01**							0.01	**0.01**
Galax urceolata	0.44	0.38	0.13	**-0.31**												

Treatment/Year:	**Control**				**Oak Shelterwood**				**Repeated Fire**				**Shelterwood/Fire**			
Species	**Pre**	**1**	**9**	**Pre:9**	**Pre**	**1**	**9**	**Pre:9**	**Pre**	**1**	**9**	**Pre:9**	**Pre**	**1**	**9**	**Pre:9**
Galearis spectabilis							0.07	**0.07**			0.01	**0.01**				
Galinsoga quadriradiata														0.06		**0.00**
Galium					0.01	0.01	0.08	**0.07**	0.02	0.14	0.08	**0.06**	0.08	0.07	0.02	**-0.06**
Galium latifolium	1.05	0.79	1.52	**0.47**	0.52	0.25	0.47	**-0.05**	0.01	0.07	0.20	**0.19**	0.27	0.53	1.16	**0.89**
Gentiana					0.01	0.07	0.13	**0.12**	0.01	0.01	0.06	**0.06**				
Geranium maculatum		0.06	0.13	**0.13**	0.06	0.06	0.06	**0.00**	0.07	0.13	0.07	**0.01**	0.06	0.69	0.13	**0.06**
Geum virginianum					0.13	0.06	0.06	**-0.06**								
Goodyera pubescens	0.02	0.15	0.07	**0.06**			0.01	**0.01**	0.01	0.02	0.02	**0.01**	0.01	0.01	0.01	**0.00**
Helianthus decapetalus	0.06	0.38	0.06	**0.00**									0.07	0.50	0.45	**0.38**
Helianthus microcephalus							0.01	**0.01**	0.06	0.21	0.82	**0.76**	0.06	0.38	1.28	**1.22**
Helianthus strumosus	0.06			**-0.06**												
Heliopsis helianthoides													0.06	0.31		**-0.06**
Hieracium														0.01		**0.00**
Hieracium paniculatum	0.07	0.07		**-0.07**	0.08	0.07	0.07	**-0.01**			0.07	**0.07**	0.01	0.06	0.01	**0.01**
Houstonia purpurea	0.01	0.08	0.01	**0.01**	0.01	0.02	0.06	**0.05**	0.01	0.07	0.14	**0.13**	0.01	0.26	0.01	**-0.01**
Hydrophyllum canadense															0.06	**0.06**
Hypericum															0.01	**0.01**
Hypericum punctatum											0.06	**0.06**		0.01	0.06	**0.06**
Impatiens													0.01			**-0.01**
Impatiens pallida															0.06	**0.06**
Ipomoea pandurata					0.06	0.06		**-0.06**		0.01		**0.00**				
Lactuca														0.31	0.06	**0.06**
Laportea canadensis					1.63	1.39	1.82	**0.19**	0.07	0.32		**-0.07**	1.26	0.76	0.64	**-0.61**
Ligusticum canadense			0.01	**0.01**										0.69		**0.00**
Lilium michauxii		0.01		**0.00**	0.06	0.01	0.06	**0.00**		0.07		**0.00**		0.06		**0.00**
Lilium superbum	0.06			**-0.06**										0.06		**0.00**
Lysimachia quadrifolia	2.73	0.70	0.63	**-2.10**	0.31	0.19	0.09	**-0.22**	0.63	0.44	0.32	**-0.31**	0.28	0.94	0.69	**0.41**
Maianthemum racemosum	1.06	0.13	0.26	**-0.80**	0.57	1.06	1.38	**0.81**	1.76	1.95	1.70	**-0.06**	0.81	1.28	1.75	**0.94**
Medeola virginiana	0.69	0.26	0.81	**0.12**	0.44	0.44	0.13	**-0.31**	0.14	0.94	0.76	**0.62**	0.69	0.14	0.45	**-0.24**

Treatment/Year:	**Control**				**Oak Shelterwood**				**Repeated Fire**				**Shelterwood/Fire**			
Species	**Pre**	**1**	**9**	**Pre:9**	**Pre**	**1**	**9**	**Pre:9**	**Pre**	**1**	**9**	**Pre:9**	**Pre**	**1**	**9**	**Pre:9**
Melampyrum lineare					0.13			**-0.13**		0.14	0.07	**0.07**				**0.00**
Monotropa hypopithys							0.06	**0.06**								**0.00**
Monotropa uniflora							0.01	**0.01**	0.06	0.01		**-0.06**				**0.00**
Osmorhiza					0.06	0.06	0.01	**-0.05**	0.08	0.08	0.07	**-0.02**	0.06		0.06	**0.00**
Oxalis										0.01		**0.00**		0.13	0.07	**0.07**
Oxalis grandis					0.31	0.06	0.01	**-0.31**						0.13	0.01	**0.01**
Oxalis stricta														0.38		**0.00**
Packera anonyma														0.01		**0.00**
Panax quinquefolius							0.13	**0.13**		0.01	0.06	**0.06**	0.07			**-0.07**
Phryma leptostachya			0.06	**0.06**			0.01	**0.01**			0.06	**0.06**	0.06	0.13		**-0.06**
Phytolacca americana														1.08	0.31	**0.31**
Podophyllum peltatum					0.06	0.06	0.06	**0.00**						0.31	0.78	**0.78**
Polygonatum biflorum	0.01	0.01	0.13	**0.12**	0.14	0.19	0.26	**0.12**	0.24	0.65	0.33	**0.09**	0.45	0.38	0.38	**-0.07**
Polygonatum pubescens					0.45	0.57	0.31	**-0.14**	0.07	0.13	0.01	**-0.06**	0.39	0.13		**-0.39**
Porteranthus trifoliatus			0.06	**0.06**												
Potentilla	0.26	0.56	0.27	**0.01**	0.44	0.13	0.01	**-0.43**	0.14	0.32	0.10	**-0.04**	0.13	0.51	0.13	**0.00**
Prenanthes	0.44	0.45	0.27	**-0.17**	0.08	0.33	0.39	**0.30**	0.06	0.14	0.14	**0.07**	0.13	1.81	0.59	**0.46**
Prosartes lanuginosa	1.38	0.88	1.07	**-0.31**	0.27	0.44	0.51	**0.24**	1.38	1.26	1.31	**-0.06**	1.88	0.31	0.81	**-1.07**
Pycnanthemum	0.56	0.76	0.25	**-0.31**	0.44	0.07	0.25	**-0.19**	0.13	0.13	0.50	**0.38**	0.69	1.26	0.52	**-0.17**
Ranunculus							0.06	**0.06**			0.01	**0.01**		0.15		**0.00**
Rudbeckia					0.01			**-0.01**								
Sanguinaria canadensis	0.31	0.38	0.45	**0.14**	0.89	1.07	0.59	**-0.30**	0.33	0.51	0.41	**0.08**	0.67	0.70	0.92	**0.26**
Sanicula	0.01	0.01		**-0.01**	0.20	0.26	0.52	**0.32**	0.13	0.07	0.14	**0.02**	0.52	1.65	0.67	**0.15**
Sanicula canadensis															0.06	**0.06**
Scutellaria										0.06		**0.00**				
Sedum ternatum					0.02	0.07	0.07	**0.05**			0.01	**0.01**				
Silene virginica									0.01			**-0.01**				
Smallanthus uvedalius						0.31	0.06	**0.06**								
Smilax biltmoreana		0.06	0.06	**0.06**					0.13	0.25	0.08	**-0.05**			0.01	**0.01**

Treatment/Year:	Control				Oak Shelterwood				Repeated Fire				Shelterwood/Fire			
Species	**Pre**	**1**	**9**	**Pre:9**	**Pre**	**1**	**9**	**Pre:9**	**Pre**	**1**	**9**	**Pre:9**	**Pre**	**1**	**9**	**Pre:9**
Smilax herbacea	0.44	0.25	0.06	**-0.38**	0.06			**-0.06**					0.13	0.19	0.38	**0.25**
Solanum															0.06	**0.06**
Solidago arguta	0.13	0.06	0.13	**-0.01**	0.13	0.06	0.07	**-0.06**	0.26	0.20	0.19	**-0.07**				
Solidago bicolor		0.06	0.06	**0.06**		0.06	0.07	**0.07**							0.06	**0.06**
Solidago curtisii	1.72	2.07	1.33	**-0.39**	1.71	0.94	1.57	**-0.14**	0.82	0.94	0.82	**0.00**	2.13	2.82	2.33	**0.20**
Solidago puberula	0.51	0.44	0.38	**-0.13**	0.06	0.13	0.01	**-0.05**	0.01	0.08	0.25	**0.24**				
Solidago roanensis					0.06	0.06		**-0.06**								
Stachys clingmanii														0.06		**0.00**
Stachys latidens														0.13	0.07	**0.07**
Stellaria pubera										0.01	0.01	**0.01**				
Symphyotrichum cordifolium	0.01	0.06	0.06	**0.06**	0.31	0.19	0.31	**0.00**		0.06		**0.00**		0.13	0.82	**0.82**
Symphyotrichum phlogifolium	0.06	0.06		**-0.06**			0.01	**0.01**								
Symphyotrichum pilosum														0.06		**0.00**
Symphyotrichum undulatum	0.07	0.25	0.06	**-0.01**	0.01	0.01	0.13	**0.11**	0.06	0.06	0.01	**-0.06**				
Thalictrum dioicum					0.06		0.06	**0.00**	0.13	0.44	0.19	**0.06**	2.84	1.14	0.76	**-2.08**
Thaspium barbinode									0.01			**-0.01**	0.20	0.75	0.88	**0.68**
Tiarella cordifolia										0.01		**0.00**				
Tradescantia														0.06		**0.00**
Trifolium														0.13		**0.00**
Trillium					0.06	0.01	0.06	**0.00**	0.06	0.06		**-0.06**	0.01			**-0.01**
Trillium erectum					0.06			**-0.06**					0.01			**-0.01**
Unknown spp.	0.06		0.02	**-0.04**	0.13		0.01	**-0.12**	0.06	0.07	0.01	**-0.06**	0.07	0.07	0.02	**-0.05**
Uvularia grandiflora					0.13	0.07	0.38	**0.25**	0.13	0.38	0.38	**0.25**	1.19	0.44	0.76	**-0.43**
Uvularia perfoliata	0.26	0.31	0.26	**0.01**	0.45	0.19	0.26	**-0.19**	0.08	0.02	0.07	**-0.01**	1.24	0.38	1.26	**0.02**
Uvularia puberula	0.08	0.07	0.02	**-0.06**	0.38		0.44	**0.06**	0.15	0.52	0.22	**0.07**	0.07	0.06	0.07	**0.00**
Uvularia sessilifolia															0.14	**0.14**
Vernonia														0.06		**0.00**
Vicia caroliniana					0.06	0.06		**-0.06**		0.01		**0.00**				

Treatment/Year:	Control				Oak Shelterwood				Repeated Fire				Shelterwood/Fire			
Species	**Pre**	**1**	**9**	**Pre:9**	**Pre**	**1**	**9**	**Pre:9**	**Pre**	**1**	**9**	**Pre:9**	**Pre**	**1**	**9**	**Pre:9**
Viola							0.07	**0.07**	0.01	0.01	0.06	**0.06**	0.31			**-0.31**
Viola blanda					0.40	0.76	0.50	**0.10**		0.01	0.07	**0.07**	0.07	2.00	0.50	**0.43**
Viola canadensis						0.01	0.06	**0.06**	0.06	0.20	0.50	**0.44**	0.13	0.19	0.26	**0.13**
Viola hastata		0.13		**0.00**			0.01	**0.01**	0.01			**-0.01**			0.02	**0.02**
Viola pubescens					0.13	0.13	0.01	**-0.12**					0.06			**-0.06**
Viola rotundifolia	0.06	0.13	0.06	**0.00**	0.57	0.69	0.63	**0.06**	0.19	0.14	0.20	**0.01**	0.26	0.39	0.70	**0.44**
Viola sororia	0.49	0.60	0.33	**-0.17**	1.04	0.77	0.50	**-0.54**	0.42	0.85	0.66	**0.24**	0.68	3.22	1.15	**0.47**
Viola triloba							0.01	**0.01**			0.06	**0.06**				
Zizia trifoliata	0.08	0.09	0.20	**0.13**	0.07	0.07	0.01	**-0.07**	0.07	0.08	0.07	**0.01**	0.07	0.19	0.13	**0.06**
Shrubs																
Amorpha glabra			0.06	**0.06**	0.31		0.32	**0.01**								
Calycanthus floridus					1.00	0.63	0.31	**-0.69**					0.88	2.66	2.00	**1.12**
Ceanothus americanus										0.01		**0.00**				
Hydrangea arborescens			0.07	**0.07**			0.13	**0.13**					0.07	0.95	2.95	**2.89**
Ilex montana			0.01	**0.01**												
Kalmia latifolia	1.28	2.05	1.78	**0.50**					0.38	0.01		**-0.38**				
Lyonia ligustrina									0.13	0.13	0.13	**0.00**				
Malus	0.06	0.06		**-0.06**												
Pyrularia pubera	0.63	0.63	0.38	**-0.25**	0.44	0.19	0.69	**0.25**	1.32	1.75	4.26	**2.94**	0.50	0.07	0.19	**-0.31**
Rhododendron calendulaceum	0.32	0.31	0.19	**-0.13**	0.06	0.06	0.31	**0.25**	0.31	0.06	0.32	**0.01**				
Rhus glabra										0.01		**0.00**				
Vaccinium corymbosum											0.31	**0.31**				
Vaccinium pallidum	1.47	1.41	0.75	**-0.72**	0.07		0.94	**0.87**	0.94	0.45	1.25	**0.31**				
Vaccinium stamineum					0.31	0.31	0.31	**0.00**								
Vaccinium vacillans					0.31	0.06	0.31	**0.00**								
Viburnum acerifolium	0.07	0.07	0.44	**0.37**	0.01		0.06	**0.06**	0.50	0.81	1.53	**1.03**	0.06			**-0.06**
Vines																
Aristolochia macrophylla	0.40	0.72	0.82	**0.43**	1.08	1.90	2.99	**1.91**	0.20	2.19	1.83	**1.63**	0.89	0.45	0.07	**-0.82**

Treatment/Year:	**Control**				**Oak Shelterwood**				**Repeated Fire**				**Shelterwood/Fire**			
Species	**Pre**	**1**	**9**	**Pre:9**	**Pre**	**1**	**9**	**Pre:9**	**Pre**	**1**	**9**	**Pre:9**	**Pre**	**1**	**9**	**Pre:9**
Celastrus orbiculatus		0.06	0.06	**0.06**												
Euonymus americanus									0.01			**-0.01**				
Parthenocissus quinquefolia	0.44	0.44	0.51	**0.07**	2.67	3.64	4.15	**1.48**	0.19	0.19	0.13	**-0.07**	0.31	0.14	0.19	**-0.12**
Rubus allegheniensis	0.94	1.00	1.03	**0.09**	0.13	0.38	0.13	**0.00**		0.01	0.01	**0.01**	0.38	10.67	15.03	**14.65**
Rubus odoratus														0.31	1.94	**1.94**
Smilax glauca	0.28	0.44	0.70	**0.43**	0.52	0.38	0.39	**-0.13**	0.78	0.66	1.15	**0.37**		0.13	0.06	**0.06**
Smilax rotundifolia	2.27	2.03	2.45	**0.19**	0.64	0.51	2.76	**2.11**	2.13	2.14	3.19	**1.07**	1.01	0.51	0.83	**-0.18**
Toxicodendron radicans	0.06	0.31	0.06	**0.00**			0.13	**0.13**		0.01		**0.00**	0.06	0.31	0.06	**0.00**
Unknown spp.			0.01	**0.01**												
Vitis aestivalis	0.70	0.46	0.16	**-0.54**		0.33	0.16	**0.16**	0.31	0.67	0.46	**0.15**	0.26	6.56	4.85	**4.59**
Woody																
Acer pensylvanicum	0.31	0.31	0.04	**-0.28**	0.82	0.01	1.17	**0.35**	3.33	2.52	4.22	**0.90**	2.79	1.38	1.41	**-1.38**
Acer rubrum	2.80	1.97	1.51	**-1.29**	0.72	0.20	2.09	**1.37**	0.44	0.29	0.64	**0.20**	0.31	1.01	0.71	**0.40**
Acer saccharum	0.84	1.16	0.44	**-0.41**	1.56	1.63	1.94	**0.38**	0.25	0.19	0.19	**-0.06**	2.63	1.85	3.55	**0.92**
Aesculus flava													0.06	0.06	0.06	**0.00**
Amelanchier arborea		0.01		**0.00**	0.44	1.36	0.63	**0.19**		0.01	0.06	**0.06**				
Amelanchier laevis														0.06		**0.00**
Betula			0.01	**0.01**			0.01	**0.01**		0.01		**0.00**				
Betula lenta			0.01	**0.01**	0.01	0.01		**-0.01**		0.01	0.01	**0.01**	0.01	0.56	0.31	**0.31**
Carya	0.06		0.13	**0.06**			0.13	**0.13**	0.32		0.20	**-0.12**	0.01		0.07	**0.06**
Carya cordiformis			0.06	**0.06**	0.14	0.07	0.44	**0.30**		0.01	0.06	**0.06**	0.39	0.19	0.19	**-0.19**
Carya glabra	1.00	1.00	0.63	**-0.38**	0.25	0.13	1.00	**0.75**	0.07	0.13	0.13	**0.05**	0.44	1.72	0.38	**-0.06**
Carya ovalis	0.06	0.13	0.13	**0.06**	0.13	0.01		**-0.13**	0.19	0.25	0.69	**0.49**	0.07			**-0.07**
Carya tomentosa			0.31	**0.31**	0.31	0.31	0.31	**0.00**	0.38	0.38	0.63	**0.24**				
Castanea dentata	2.27	0.32	0.63	**-1.65**					0.31			**-0.31**				
Cornus alternifolia					0.06	0.06	0.78	**0.72**	0.31			**-0.31**	0.31	0.63	2.09	**1.78**
Cornus florida	0.14	0.44	0.69	**0.55**	0.38	0.13	0.69	**0.32**	0.83	0.19	0.88	**0.04**				
Fagus grandifolia							0.06	**0.06**								
Fraxinus americana	1.38	1.39	1.01	**-0.37**	1.67	1.52	1.82	**0.15**	0.77	0.83	1.48	**0.71**	4.17	3.78	2.04	**-2.14**

Treatment/Year:	**Control**				**Oak Shelterwood**				**Repeated Fire**				**Shelterwood/Fire**			
Species	**Pre**	**1**	**9**	**Pre:9**	**Pre**	**1**	**9**	**Pre:9**	**Pre**	**1**	**9**	**Pre:9**	**Pre**	**1**	**9**	**Pre:9**
Halesia tetraptera					2.56	0.84	1.47	**-1.09**	1.78	0.79	0.06	**-1.71**	0.31			**-0.31**
Lindera benzoin	0.31	0.31	0.13	**-0.19**			0.01	**0.01**		0.32	0.13	**0.13**				
Liriodendron tulipifera	2.09	1.79	1.02	**-1.07**	0.78	1.33	0.04	**-0.74**	0.31	0.54	0.79	**0.47**	0.31	3.17	1.88	**1.57**
Magnolia acuminata	0.63	0.31	0.01	**-0.61**	0.13	0.06		**-0.13**	0.06	0.06	0.07	**0.01**	0.13		0.07	**-0.06**
Nyssa sylvatica	0.39	0.13	0.13	**-0.26**	2.93	0.38	1.01	**-1.92**	0.32	0.33	1.22	**0.90**		0.32		**0.00**
Ostrya virginiana										0.01		**0.00**				
Oxydendrum arboreum	0.38	0.38	0.31	**-0.06**					1.83	0.01		**-1.83**				
Pinus strobus					0.01	0.01	0.07	**0.06**	0.01			**-0.01**				
Prunus serotina	0.20	0.57	0.28	**0.08**	0.29	0.08	0.60	**0.31**	0.05	0.17	0.20	**0.15**	0.11	0.59	1.00	**0.89**
Quercus alba	0.07	0.13	0.02	**-0.06**		0.01	0.13	**0.13**	0.22	0.28	0.75	**0.53**	0.06			**-0.06**
Quercus coccinea	0.01	0.06	0.26	**0.26**					0.88	0.64	1.78	**0.90**				
Quercus prinus	2.14	2.02	2.19	**0.05**	0.76	0.52	1.66	**0.91**	0.51	0.70	1.66	**1.15**	0.06	0.06	0.38	**0.31**
Quercus rubra	0.38	1.02	0.76	**0.38**	0.69	0.52	1.51	**0.81**	0.06	0.20	0.58	**0.52**	0.44	1.06	2.80	**2.35**
Quercus velutina	0.14	0.14	0.51	**0.38**	0.14	0.13	1.32	**1.18**	0.13	0.13	0.44	**0.31**		0.06		**0.00**
Robinia pseudoacacia		0.01		**0.00**		0.07	0.79	**0.79**	0.19	0.15	0.32	**0.13**	0.97	2.43	0.19	**-0.78**
Sassafras albidum	2.88	2.00	1.91	**-0.97**	0.50	0.13	0.75	**0.25**	0.88	0.40	0.56	**-0.32**	0.06	2.45	0.19	**0.13**
Tilia americana	0.13	0.31		**-0.13**	0.13	0.13	0.38	**0.25**					0.06			**-0.06**
Tsuga canadensis	1.30			**-1.30**					0.31			**-0.31**				
Unknown spp.			0.02	**0.02**			0.01	**0.01**								

Table A.3.8: USDA species codes with associated species and authority. Species present pre-treatment, year 1, and year 9 are listed.

USDA Code	**Species**	**Authority**
ACPA	*Actaea pachypoda*	Ell.
ACPE	*Acer pensylvanicum*	L.
ACRA7	*Actaea racemosa*	L.
ACRU	*Acer rubrum*	L.
ACSA3	*Acer saccharum*	Marsh.
ADPE	*Adiantum pedatum*	L.
AEFL	*Aesculus flava*	Aiton
AGAL5	*Ageratina altissima*	(L.) R.M. King & H. Rob.
AGRIM	*Agrimonia*	L.
AMAR3	*Amelanchier arborea*	(Michx. F.) Fernald
AMBR2	*Amphicarpaea bracteata*	(L.) Fern.
AMGL2	*Amorpha glabra*	Desf. ex Poir.
AMLA	*Amelanchier laevis*	Wieg.
ANPL	*Antennaria plantaginifolia*	(L.) Richards.
ARAT	*Arnoglossum atriplicifolium*	(L.) H. Rob.
ARDI8	*Aruncus dioicus*	(Walt.) Fern.
ARLA	*Arabis laevigata*	(Muel. ex Willd.) Poir.
ARMA7	*Aristolochia macrophylla*	Lam.
ARRA	*Aralia racemosa*	L.
ARSE3	*Aristolochia serpentaria*	L.
ARTR	*Arisaema triphyllum*	(L.) Schott
ASBI4	*Astilbe biternata*	(Vent.) Britt.
ASCA	*Asarum canadense*	L.
ASCLE	*Asclepias*	L.
ASDI	*Aster divaricatus*	L.
ASEX	*Asclepias exaltata*	L.
ASLO9	*Aster lowrieanus*	Porter
ASQU	*Asclepias quadrifolia*	Jaqu.
ASTER	*Aster*	L.
ATFI	*Athyrium filix-femina*	(L.) Roth
AULA	*Aureolaria laevigata*	(Raf.) Raf.
BELE	*Betula lenta*	L.
BETUL	*Betula*	L.
BIFR	*Bidens frondosa*	L.
BOBI	*Botrychium biternatum*	(Sav.) Underwood
BOVI	*Botrychium virginianum*	(L.) Sw.
BRER2	*Brachyelytrum erectum*	(Schreb. ex Spreng.) Beauv.
BROMU	*Bromus*	L.

USDA Code	Species	Authority
BRPU6	*Bromus pubescens*	Muhl. ex Willd.
CAAT	*Cacalia atriplicifolia*	L.
CABL	*Carex blanda*	Dewey
CACO15	*Carya cordiformis*	(Wangenh.) K. Koch
CACO7	*Carex communis*	Bailey
CADE12	*Castanea dentata*	(Marsh.) Borkh.
CADI3	*Campanula divaricata*	Michx.
CADI5	*Carex digitalis*	Willd.
CAFL22	*Calycanthus floridus*	L.
CAGL8	*Carya glabra*	(P. Mill.) Sweet
CAOV3	*Carya ovalis*	(Wangenh.) Sarg.
CAPE6	*Carex pensylvanica*	Lam.
CAREX	*Carex*	L.
CARYA	*Carya*	Nutt.
CATH2	*Caulophyllum thalictroides*	(L.) Michx.
CATO6	*Carya tomentosa*	(Lam.) Nutt.
CAVI4	*Carex virescens*	Muhl. ex Willd.
CEAM	*Ceanothus americanus L.*	
CEOR7	*Celastrus orbiculatus*	Thunb.
CHLY2	*Chelone lyonii*	Pursh
CHMA3	*Chimaphila maculata*	(L.) Pursh
CILUC	*Circaea lutetiana*	ssp. canadensis (L.) Aschers. & Magnus
CIVU	*Cirsium vulgare*	(Savi) Ten.
CLUM2	*Clintonia umbellulata*	(Michx.) Morong
COAL2	*Cornus alternifolia*	L. f.
COAM	*Conopholis americana*	(L.) Wallr. f.
COCA4	*Collinsonia canadensis*	L.
COFL2	*Cornus florida*	L.
COMA6	*Coreopsis major*	Walt.
CREPI	*Crepis*	L.
CUSCU	*Cuscuta*	L.
DACO	*Danthonia compressa*	Austin ex Peck
DANTH	*Danthonia*	DC.
DASP2	*Danthonia spicata*	(L.) Beauv. ex Roemer & J.A. Schultes
DEAC4	*Deparia acrostichoides*	(Sw.) M. Kato
DENU4	*Desmodium nudiflorum*	(L.) DC.
DERO3	*Desmodium rotundifolium*	DC.
DIBO2	*Dichanthelium boscii*	
DICHA2	*Dichanthelium*	(A.S. Hitchc. & Chase) Gould
DICO2	*Dichanthelium commutatum*	(J.A. Schultes) Gould
DIDI6	*Dichanthelium dichotomum*	(L.) Gould

USDA Code	Species	Authority
DIQU	*Dioscorea quaternata*	J.F. Gmel.
DISP2	*Dichanthelium sphaerocarpon*	(Ell.) Gould
DOIN2	*Doellingeria infirma*	(Michx.) Greene
DRMA4	*Dryopteris marginalis*	(L.) Gray
ERHI2	*Erechtites hieraciifolius*	(L.) Raf. ex DC.
ERPU	*Erigeron pulchellus*	Michx.
EUAM9	*Euonymus americanus*	L.
EUCH12	*Eurybia chlorolepis*	(Burgess) G.L. Nesom
EUCO10	*Euphorbia corollata*	L.
EUMA27	*Eurybia macrophylla*	(L.) Cass.
EUPU21	*Eupatorium purpureum*	L.
FAGR	*Fagus grandifolia*	Ehrh.
FRAM2	*Fraxinus americana*	L.
FRVI	*Fragaria virginiana*	Duchesne
GALA4	*Galium latifolium*	Michx.
GALIU	*Galium*	L.
GAQU	*Galinsoga quadriradiata*	Cav.
GASP5	*Galearis spectabilis*	(L.) Raf.
GAUR2	*Galax urceolata*	(Poir.) Brummitt
GEMA	*Geranium maculatum*	L.
GENTI	*Gentiana*	L.
GEVI4	*Geum virginianum*	L.
GOPU	*Goodyera pubescens*	(Willd.) R. Br. ex Ait. f.
HATE3	*Halesia tetraptera*	Ellis
HEDE	*Helianthus decapetalus*	L.
HEHE5	*Heliopsis helianthoides*	(L.) Sweet
HEMI3	*Helianthus microcephalus*	Torr. & Gray
HEST	*Helianthus strumosus*	L.
HIERA	*Hieracium*	L.
HIPA2	*Hieracium paniculatum*	L.
HOPUP3	*Houstonia purpurea*	var. purpurea L.
HYAR	*Hydrangea arborescens*	L.
HYCA3	*Hydrophyllum canadense*	L.
HYPER	*Hypericum*	L.
HYPU	*Hypericum punctatum*	Lam.
ILMO	*Ilex montana*	Torr. & Gray ex Gray
IMPA	*Impatiens pallida*	Nutt.
IMPAT	*Impatiens*	L.
IPPA	*Ipomoea pandurata*	(L.) G. Mey.
KALA	*Kalmia latifolia*	L.
LACA3	*Laportea canadensis*	(L.) Weddell

USDA Code	Species	Authority
LACTU	*Lactuca*	L.
LIBE3	*Lindera benzoin*	(L.) Blume
LICA16	*Ligusticum canadense*	(L.) Britt.
LIMI	*Lilium michauxii*	Poir.
LISU	*Lilium superbum*	L.
LITU	*Liriodendron tulipifera*	L.
LUEC	*Luzula echinata*	(Small) F.J. Herm.
LYLI	*Lyonia ligustrina*	(L.) DC.
LYQU2	*Lysimachia quadrifolia*	L.
MAAC	*Magnolia acuminata*	(L.) L.
MALUS	*Malus*	Mill.
MARA7	*Maianthemum racemosum*	(L.) Link
MELI2	*Melampyrum lineare*	Desr.
MEVI	*Medeola virginiana*	L.
MOHY3	*Monotropa hypopithys*	L.
MOUN3	*Monotropa uniflora*	L.
MUTE	*Muhlenbergia tenuiflora*	(Willd.) Britton, Sterns & Poggenb.
NYSY	*Nyssa sylvatica*	Marsh.
OSCI	*Osmunda cinnamomea*	L.
OSCL2	*Osmunda claytoniana*	L.
OSMOR	*Osmorhiza*	Raf.
OSVI	*Ostrya virginiana*	(P. Mill.) K. Koch
OXALI	*Oxalis*	L.
OXAR	*Oxydendrum arboreum*	(L.) DC.
OXGR	*Oxalis grandis*	Small
OXST	*Oxalis stricta*	L.
PAAN6	*Packera anonyma*	(Alph. Wood) W.A. Weber & Á. Löve
PAQU	*Panax quinquefolius*	L.
PAQU2	*Parthenocissus quinquefolia*	(L.) Planch.
PHAM4	*Phytolacca americana*	L.
PHHE11	*Phegopteris hexagonoptera*	(Michx.) Fee
PHLE5	*Phryma leptostachya*	L.
PIST	*Pinus strobus*	L.
POA	*Poa*	L.
POAC4	*Polystichum acrostichoides*	(Michx.) Schott
POBI2	*Polygonatum biflorum*	(Walt.) Ell.
POPE	*Podophyllum peltatum*	L.
POPU4	*Polygonatum pubescens*	(Willd.) Pursh
POTEN	*Potentilla*	L.
POTR11	*Porteranthus trifoliatus*	(L.) Britt.
PRENA	*Prenanthes*	L.

USDA Code	Species	Authority
PRLA9	*Prosartes lanuginosa*	(Michx.) D. Don
PRSE2	*Prunus serotina*	Ehrh.
PYCNA	*Pycnanthemum*	Michx.
PYPU	*Pyrularia pubera*	Michx.
QUAL	*Quercus alba*	L.
QUCO2	*Quercus coccinea*	Muenchh.
QUPR2	*Quercus prinus*	L.
QURU	*Quercus rubra*	L.
QUVE	*Quercus velutina*	Lam.
RANUN	*Ranunculus*	L.
RHCA4	*Rhododendron calendulaceum*	(Michx.) Torr.
RHGL	*Rhus glabra*	L.
ROPS	*Robinia pseudoacacia*	L.
RUAL	*Rubus allegheniensis*	Porter
RUDBE	*Rudbeckia*	L.
RUOD	*Rubus odoratus*	L.
SAAL5	*Sassafras albidum*	(Nutt.) Nees
SACA13	*Sanguinaria canadensis*	L.
SACA15	*Sanicula canadensis*	L.
SANIC	*Sanicula*	L.
SCUTE	*Scutellaria*	L.
SETE3	*Sedum ternatum*	Michx.
SIVI4	*Silene virginica*	L.
SMBI	*Smilax biltmoreana*	(Small) J.B.S. Norton ex Pennell
SMGL	*Smilax glauca*	Walt.
SMHE	*Smilax herbacea*	L.
SMRO	*Smilax rotundifolia*	L.
SMUV	*Smallanthus uvedalius*	(L.) MacKenzie ex Small
SOAR	*Solidago arguta*	Aiton
SOBI	*Solidago bicolor*	L.
SOCU	*Solidago curtisii*	Torr. & A. Gray
SOLAN	*Solanum*	L.
SOPU	*Solidago puberula*	Nutt.
SORO2	*Solidago roanensis*	Porter
STCL	*Stachys clingmanii*	Small
STLA5	*Stachys latidens*	Small ex Britton
STPU	*Stellaria pubera*	Michx.
SYCO4	*Symphyotrichum cordifolium*	(L.) G.L. Nesom
SYPH3	*Symphyotrichum phlogifolium*	(Muhl. ex Willd.) G.L. Nesom
SYPI2	*Symphyotrichum pilosum*	(Willd.) G.L. Nesom
SYUN	*Symphyotrichum undulatum*	(L.) G.L. Nesom

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THBA	*Thaspium barbinode*	(Michx.) Nutt.
THDI	*Thalictrum dioicum*	L.
THNO	*Thelypteris noveboracensis*	(L.) Nieuwl.
TIAM	*Tilia americana*	L.
TICO	*Tiarella cordifolia*	L.
TORA2	*Toxicodendron radicans*	(L.) Kuntze
TRADE	*Tradescantia*	L.
TRER3	*Trillium erectum*	L.
TRIFO	*Trifolium*	L.
TRILL	*Trillium*	L.
TSCA	*Tsuga canadensis*	(L.) Carr.
UNK	*Unknown spp.*	
UVGR	*Uvularia grandiflora*	Sm.
UVPE	*Uvularia perfoliata*	L.
UVPU2	*Uvularia puberula*	Michx.
UVSE	*Uvularia sessilifolia*	L.
VACO	*Vaccinium corymbosum*	L.
VAPA4	*Vaccinium pallidum*	Ait.
VAST	*Vaccinium stamineum*	L.
VAVA	*Vaccinium vacillans*	Kalm ex Torr.
VERNO	*Vernonia*	Schreb.
VIAC	*Viburnum acerifolium*	L.
VIAE	*Vitis aestivalis*	Michx.
VIBL	*Viola blanda*	Willd.
VICA2	*Vicia caroliniana*	Walter
VICA4	*Viola canadensis*	L.
VIHA2	*Viola hastata*	Michx.
VIOLA	*Viola*	L.
VIPU3	*Viola pubescens*	Aiton
VIRO2	*Viola rotundifolia*	Michx.
VISO	*Viola sororia*	Willd.
VITR2	*Viola triloba*	Schwein.
ZITR	*Zizia trifoliata*	(Michx.) Fern.