The Response of Understory Species Composition, Diversity, and Seedling Regeneration to Repeated Burning in Southern Appalachian Oak-Hickory Forests

Authors: Holzmueller, Eric J., Jose, Shibu, and Jenkins, Michael A.

Source: Natural Areas Journal, 29(3) : 255-262

Published By: Natural Areas Association

URL: https://doi.org/10.3375/043.029.0305

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Downloaded From: https://complete.bioone.org/journals/Natural-Areas-Journal on 16 Jan 2025
Terms of Use: https://complete.bioone.org/terms-of-use

RESEARCH ARTICLE

The Response of Understory Species Composition, Diversity, and Seedling Regeneration to Repeated Burning in Southern Appalachian Oak-hickory Forests

Eric J. Holzmueller[1]

Department of Forestry
Southern Illinois University
1205 Lincoln Dr.
Carbondale, IL 62901

Shibu Jose

School of Forest Resources and Conservation
University of Florida
PO Box 110410
Gainesville, FL 32611

Michael A. Jenkins[2]

National Park Service
Great Smoky Mountains National Park
Twin Creeks Natural Resources Center
1314 Cherokee Orchard Road
Gatlinburg, TN 37738

[1] Corresponding author: eholzmue@siu.edu; (618) 453-3708

[2] Current address: Department of Forestry and Natural Resources, Purdue University 715 West State Street, West Lafayette IN 47907

Natural Areas Journal 29:255–262

ABSTRACT: Understory plant composition and diversity levels in oak-hickory (*Quercus-Carya*) forests have historically been maintained by periodic low-intensity ground fires, but fire suppression has altered the structure and function of these communities. We examined burned and unburned oak-hickory stands to determine the influence of repeated burning on understory communities. We compared understory herbaceous, shrub, and tree species diversity and composition among four burn categories: unburned stands, and stands that had burned once, twice, and three times over a 20-year period (late 1960s to late 1980s). We hypothesized that stands that have received repeated burns will have greater understory diversity and reduced importance of shade-tolerant mesophytic species. We found that burned stands had greater species richness than unburned stands, regardless of burn frequency. Species composition was not drastically different among the four burn categories; however, individual species were indicative of particular burn categories. More forest herbs were associated with the single burn category, while more disturbance-dependent species (*Desmodium* spp. and *Solidago* spp.) were associated with the repeated burn categories. Burned stands contained greater densities of white oak (*Quercus alba* L.) and hickory species seedlings. Our results suggest that restoring and maintaining the historic fire return interval (10-15 years) will promote herbaceous species diversity and favor the regeneration of oak and hickory species. However, it has been 15-22 years since the stands we sampled last burned, and the similarity among burn categories suggests that additional burning is needed to prevent these stands from reverting to a suppressed condition.

Index terms: Carya, central hardwoods, fire, herbaceous, *Quercus*

INTRODUCTION

Oak-hickory (*Quercus-Carya*) forest is the most prevalent forest type in the eastern United States, comprising approximately 35% (54 million ha) of total forest cover, which is nearly 2.5 times greater than that of the next largest forest type, maple-beech-birch (*Acer-Fagus-Betula*; Smith et al. 2004). Historically, oak-hickory forests in eastern North America have been maintained by periodic low intensity fires (Harmon 1982; Abrams 1992; Shumway et al. 2001). These fires created open stand conditions favorable to shade-intolerant and mid-tolerant species, such as oak and hickory species, in the overstory and high herbaceous species diversity in the understory. Following massive wildfires during the late 1880s and early 1900s (Pyne 1982), the fire regime in these forests was drastically altered because of fire suppression (Harmon 1982; Abrams 1992; Ruffner and Groninger 2006). As a well-documented result of fire suppression, the regeneration layers of oak-dominated forests throughout eastern North America have become dominated by shade-tolerant species such as sugar maple (*Acer saccharum* Marsh.), red maple (*Acer rubrum* L.), American beech (*Fagus grandifolia* Ehrh.), and eastern hemlock (*Tsuga canadensis* L.) (Lorimer 1984; Abrams 1992; Jenkins and White 2002; Aldrich et al. 2003; Ozier et al. 2006; Holzmueller et al. 2008). Because of the ecological and economic importance of oak-hickory forests (Johnson et al. 2002), their perpetuation has been a high priority for forest management and restoration (Brose and Van Lear 1998; Crow 1988; Johnson et al. 2002; Boerner et al. 2008). Although members of the genus *Quercus* are generally thought to be early successional, overstory removal alone has proven inadequate to regenerate oak species on productive sites (Beck and Hooper 1986; Kellison 1993; Lorimer et al. 1994; Jenkins and Parker 1998). Furthermore, overstory manipulation is not a practical option for areas managed without intensive silviculture, such as state and national parks. Prescribed burning prior to harvest has been shown to provide adequate advanced regeneration of oak species on productive sites (Brose and Van Lear 1998). Therefore, understanding how repeated burning affects woody regeneration and herbaceous species composition in the absence of overstory manipulation is critical to successful management and restoration in these areas.

Over the past two decades, managers have sought to reintroduce the pre-suppression fire regime to restore the structure and composition of oak-dominated forests (Brose et al. 2001). Over this same time span, researchers have begun to unravel how the reintroduction of fire affects vegetation communities in historically suppressed

Downloaded From: https://complete.bioone.org/journals/Natural-Areas-Journal on 16 Jan 2025
Terms of Use: https://complete.bioone.org/terms-of-use

stands (Wendel and Smith 1986; McGee et al. 1995; Nuzzo et al. 1996; Elliot et al. 1999; Kuddes-Fischer and Arthur 2002; Hutchinson et al. 2005). This research has improved understanding of how woody species mortality and regeneration respond to fire (Wendel and Smith 1986; Ebinger 1988; Kruger and Reich 1997; Arthur et al. 1998; Blankenship and Arthur 2006) and how understory vegetation, including herbaceous species, respond to single (Elliot et al. 1999; Kuddes-Fischer and Arthur 2002) and repeated burns (McGee et al. 1995; Nuzzo et al. 1996; Franklin et al. 2003; Hutchinson et al. 2005). Generally, these studies have found that fire reduces understory density, produces a short-term increase in herbaceous cover, and reduces the importance of mesophytic species. However, these studies examined the effects of small, often experimental, burns (< 40 ha) conducted at a limited number of sites (maximum of four) distributed across a limited spatial range. While there is great value in studies that focus on repeated measurements from spatially-discrete burns, more information is needed about how understory vegetation responds to repeated burns of varying size distributed across large and variable geographic areas. Restoring fire to fire-suppressed ecosystems can have unpredicted effects (Varner et al. 2005), and understanding the potential variability at a landscape scale is critical to restoration success.

The objective of this study was to examine herbaceous, shrub, and tree seedling species composition in unburned and burned areas to determine how understory vegetation in oak-hickory forests responds to repeated burning. We collected vegetation data from a chronosequence of burned sites ranging in size from 10 to120 ha and in fire frequency from 1 to 3 burns in a 20-year period. Sampled burns were distributed across Great Smoky Mountains National Park (GSMNP). We hypothesized that stands that have received repeated burns will have greater understory diversity and reduced importance of shade-tolerant mesophytic species. We also hypothesized that repeated burning will increase the density of advanced regeneration of oak and hickory species.

METHODS

Study site

Established in 1934, GSMNP is a mostly forested reserve that encompasses over 2000 km^2 in eastern Tennessee and western North Carolina. Complex ecological gradients combine to create a diverse mosaic of plant communities comprised of over 1600 native species, including over 200 species of trees and shrubs. The Park is internationally renowned as a center of biological diversity within North America and was designated as an International Biosphere Reserve in 1976. Because of its biotic diversity, large size, and protected status, GSMNP plays an important role in biological conservation within the eastern United States. Biological communities of GSMNP often serve as benchmarks for other state and federal conservation lands.

Within GSMNP, oak-hickory forest comprises approximately 31% (64,600 ha) of total forest cover (Madden et al. 2004). Prior to Park establishment in 1934, these oak-hickory forests burned periodically, with an average fire return interval of 10-15 years (Harmon 1982). As observed throughout eastern North America, however, fires within GSMNP have been heavily suppressed since Park establishment (Harmon 1982).

Study site elevation ranged from 287 to 975 m, and plots were located on moderately steep to steep slopes (45% $\pm$ 1.8%; mean $\pm$ 1 SE) with aspects ranging clockwise from SE (135º) to NW (315º). Predominant soil series included Cataska-Sylco complex (Typic Dystrudepts), Ditney-Unicoi complex (Typic Dystrudepts and Lithic Dystrudepts), Junaluska-Tsali complex (Typic Hapludults), and Soco-Stecoah complex (Typic Dystrudepts). These soils are well-drained and are typical of ridges and sideslopes in the Southern Appalachian Mountain region (USDA-NRCS 2008).

All study sites were located in secondary forests that were logged prior to Park establishment (Pyle 1988). Overstory composition was dominated by chestnut oak (*Quercus prinus* L.), white oak (*Quercus alba* L.), black oak (*Quercus velutina* Lam.), red oak (*Quercus rubra* L.), scarlet oak (*Quercus coccinea* Munchh.), red maple, yellow poplar (*Liriodendron tulipifera* L.), mockernut hickory (*Carya alba* L.), and pignut hickory (*Carya glabra* Mill.). The midstory was primarily composed of red maple, striped maple (*Acer pensylvanicum* L.), flowering dogwood (*Cornus florida* L.), blackgum (*Nyssa sylvatica* Marsh.), and sourwood (*Oxydendrun arboreum* L.) saplings. Refer to Holzmueller et al. (2008) for a more detailed description of the study site.

Field Sampling

Areas of the Park that burned during the late 1960s to 1980s and contained oak-hickory forest types (White et al. 2003) were identified prior to plot establishment using a map of vegetation communities (Madden et al. 2004), historic disturbance maps, and fire history records. We sampled seventy-nine 0.04 ha (20-m x 20-m) plots within 20 burned and unburned areas during June-August of 2001-2004 (Holzmueller et al. 2008). Fifty-five plots were randomly established in 14 stands that had burned up to three times over a 20-year period (late 1960s to the late 1980s). In addition, 24 reference plots were randomly established in six nearby unburned stands that had similar slopes, aspects, topography, and vegetation associations to the burn plots. Sampled areas were divided into four burn categories: (1) unburned (six stands, 24 plots); (2) single burn (seven stands, 30 plots); (3) double burn (four stands, 16 plots); and (4) triple burn (three stands, nine plots). Four 3.16-m x 3.16-m nested subplots (10 m^2) were placed within the corners of each 20-m x 20-m plot. All understory (< 1.4 m tall) herbaceous, shrub/vine (hereafter shrub), and tree vegetation within these subplots was identified. Cover and stem density of each understory shrub and tree species and cover of each herbaceous species was estimated within each 10 m^2 subplot. Cover was estimated visually using a modified Daubenmire scale (1 = Few; 2 = Few-1%; 3 = 1-2%; 4 = 2-5%; 5 = 5-10%; 6 = 10-25%; 7 = 25-50%; 8 = 50-75%; 9 = 75-95%; 10 = 95-100%) (Daubenmire 1959; Peet et al. 1998).

Downloaded From: https://complete.bioone.org/journals/Natural-Areas-Journal on 16 Jan 2025
Terms of Use: https://complete.bioone.org/terms-of-use

Data analysis

Understory herbaceous, shrub, and tree species values from the four subplots were averaged for each main plot. Total shrub and tree seedling species density, density of selected tree seedling species, and herbaceous, shrub, and tree seedling cover were analyzed using ANOVA (mixed model procedure; SAS 2004). Species richness, evenness, and Shannon's diversity index were calculated for herbaceous, shrub, and tree seedling species with PC-ORD (McCune and Mefford 1999) and also analyzed with ANOVA (mixed model procedure; SAS 2004). The mixed model ANOVA was comprised of two factors; factor one (frequency of fire, hereafter referred to as "burn category") was fixed, and factor two (burn area, nested within burn category factor) was random. The sample size for the mixed model ANOVA was 20 (number of burned and unburned areas). When ANOVA revealed a significant difference between the four burn categories (unburned, single burn, double burn, and triple burn), we used the probability of difference (PDIFF) option for post-hoc pairwise comparisons (SAS 2004). Indicator species analysis was used to describe the relationship of species to categorical variables by combining species abundance in a specific category plus the faithfulness of occurrence of that species in that specific category (Dufrêne and Legendre 1997; Peterson and McCune 2001). The analysis produces a value (IndVal) of abundance for each species in each group and a test statistic produced from Monte Carlo tests (1000 iterations) to determine if occurrence in the maximum (indicator) group is greater than would be expected from chance.

RESULTS

Species diversity

Of the 138 taxa sampled and used in the species diversity analysis, sixty-eight (49%) of those taxa were herbaceous, twenty-six (19%) were shrubs, and forty-four (32%) were tree seedlings. Herbaceous species richness was similar among the four burn categories ($P = 0.40$); however, evenness and Shannon's diversity index was greatest in the single and triple burn categories and lowest in the double burn category (Figure 1). There was a significant difference in shrub species richness, evenness, and Shannon's diversity index between burn categories (Figure 1; $P < 0.05$), but there was no significant difference in tree seedling species richness, evenness, and Shannon's diversity index (Figure 1; $P > 0.18$). When herbaceous, shrub, and tree seedling species were combined, species richness was greater in burned stands (28 taxa) compared to unburned stands (22 taxa; $P = 0.03$). Combined evenness and Shannon's diversity index, however, did not differ among the four burn categories (Figure 1; $P = 0.50$).

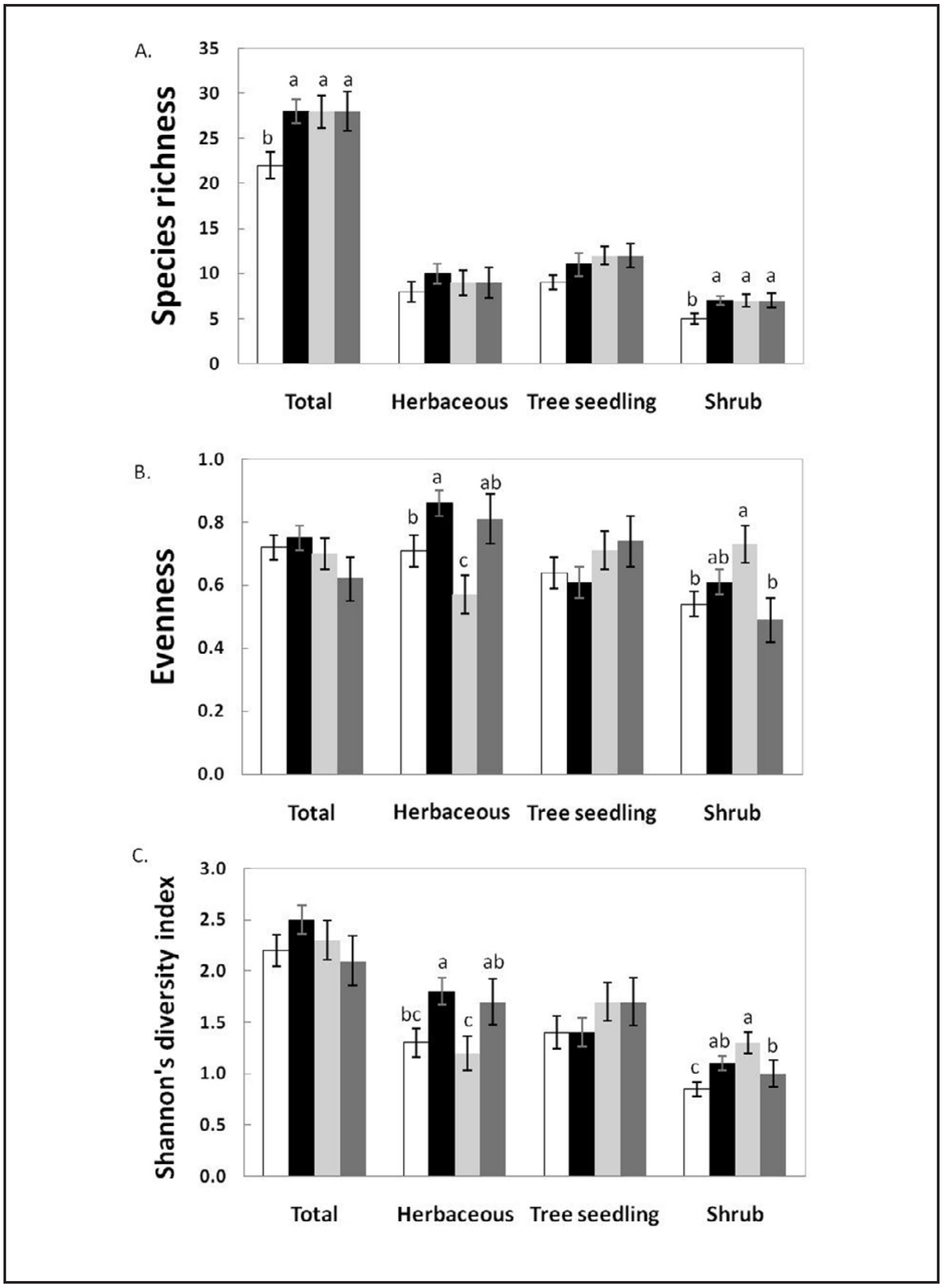

FIGURE 1. Measures (mean ± 1 SE) of (A) species richness, (B) evenness, and (C) Shannon's diversity index (McCune and Mefford 1999) among the four burn categories for four groups: all species (total), herbaceous species, tree seedling species, and shrub species. Different letters following means for each species group indicate a significant difference among the four burn categories (*P* < 0.05).

Downloaded From: https://complete.bioone.org/journals/Natural-Areas-Journal on 16 Jan 2025
Terms of Use: https://complete.bioone.org/terms-of-use

Indicator species analysis

The indicator species analysis revealed differences in herbaceous-layer taxa composition among the four burn categories (Table 1). Overall, there were 22 taxa identified as indicator species ($P < 0.05$). Eight herbaceous taxa were identified as indicator species, and a majority of those taxa identified occurred in the single burn category (Table 1). Beetleweed (*Galax urceolata* Poir.), however, was identified as an indicator species in the unburned category (IndVal 30.2, $P = 0.05$). Tick-trefoil species (*Desmodium* Desv. spp.) were indicative of the double burn category (IndVal 57.2, $P < 0.01$), while goldenrod species (*Solidago* L. spp.) were indicative of the triple burn category (IndVal 35.7, $P = 0.02$).

Seven shrub taxa were identified as indicator species (Table 1). All but one of these taxa, poison ivy (*Toxicodendron radicans* L.), were indicator species in the triple burn category. Plots in the triple burn category had the highest level of disturbance and taxa identified as indicator species, including Virginia creeper (*Parthenocissus quinquefolia* L.), winged sumac (*Rhus copallinum* L.), farkleberry (*Vaccinium arboretum* Marsh.), highbush blueberry (*Vaccinium corymbosum* L.), lowbush blueberry (*Vaccinium pallidum Alton*), and grape species (*Vitis* L. spp.) have been documented as responding well to disturbances, particularly fire (USDA Forest Service 2008).

Striped maple and eastern hemlock, shade tolerant species commonly found in undisturbed areas, were indicative of the unburned category (Table 1; $P < 0.04$). Species more tolerant of disturbance were indicative of burned stands, including red maple in the single burn category, white oak and red oak in the double burn category, and mockernut hickory and black locust (*Robinia pseudoacacia* L.) in the triple burn category (Table 1).

TABLE 1. Indicator values (percent of perfect indication) for understory vegetation (herbaceous, shrub/vines, and tree seedling species) and associated burn category. *P-value* **represents the proportion of randomized trials with an indicator value equal to or exceeding the observed indicator value.**

Species	Species type	Indicator group	Indicator value	*P*-value
Galax urceolata	Herbaceous	Unburned	30.2	0.05
Dioscorea quaternata	Herbaceous	Single burn	32.2	0.03
Houstonia species	Herbaceous	Single burn	16.7	0.04
Lysimachia quadrifolia	Herbaceous	Single burn	20.0	0.02
Maianthemum racemosum	Herbaceous	Single burn	50.1	<0.01
Polygonatum biflorum	Herbaceous	Single burn	20.7	0.04
Desmodium spp.	Herbaceous	Double burn	57.2	<0.01
Solidago spp.	Herbaceous	Triple burn	35.7	0.02
Toxicodendron radicans	Vine	Double burn	29.2	0.04
Rhus copallinum	Shrub	Triple burn	33.3	<0.01
Vaccinium arboreum	Shrub	Triple burn	20.5	0.02
Vaccinium corymbosum	Shrub	Triple burn	30.0	0.03
Vaccinium pallidum	Shrub	Triple burn	35.0	0.05
Parthenocissus quinquefolia	Shrub	Triple burn	63.4	<0.01
Vitis spp.	Vine	Triple burn	43.9	0.04
Acer pensylvanicum	Tree seedling	Unburned	31.9	0.04
Tsuga canadensis	Tree seedling	Unburned	37.6	0.03
Acer rubrum	Tree seedling	Single burn	41.0	0.03
Quercus rubra	Tree seedling	Double burn	35.7	0.03
Carya alba	Tree seedling	Triple burn	32.9	0.02
Robinia pseudoacacia	Tree seedling	Triple burn	28.8	0.05

Shrub and tree seedling density

Because of high plot variability, mean shrub and tree seedling density did not differ among burn categories (Table 2; $P > 0.15$). In addition, no significant difference was found among the burn categories when mean shrub and tree seedling densities were combined and analyzed together (Table

Downloaded From: https://complete.bioone.org/journals/Natural-Areas-Journal on 16 Jan 2025
Terms of Use: https://complete.bioone.org/terms-of-use

TABLE 2. Mean (± 1 SE) shrub and tree seedling density and mean herbaceous, shrub, and tree seedling cover among the four burn categories.

	Unburned	Single burn	Double burn	Triple burn	*P* -value
Density (seedlings^{-1} ha^{-1})					
Shrub	18200 (5200)	24200 (5100)	11000 (6900)	37000 (9000)	0.15
Tree seedlings	27200 (4600)*	37500 (6100)*	30000 (8200)*	22000 (10000)	0.53
Total density	45400 (9000)	61700 (8300)	41000 (11100)	59000 (14300)	0.34
Cover (%)					
Herbaceous	5.8 (1.7)	6.4 (1.6)	12.8 (2.2)	3.7 (2.8)	0.19
Shrub	9.9 (4.2)	16.0 (3.8)	5.1 (5.2)	16.9 (6.3)	0.22
Tree seedlings	6.6 (3.1)	11.0 (2.8)	6.1 (3.8)	6.1 (4.7)	0.89
Total cover	22.3 (6.0)	33.4 (5.5)	24.0 (7.5)	26.7 (9.2)	0.63

[1]Indicates a significant difference ($P < 0.05$) between tree and shrub density

2; P = 0.34). When mean tree seedling density was compared to mean shrub density within each burn category, mean tree seedling density was greater than mean shrub density for the unburned, single, and double burn categories (Table 2; P < 0.02); however, no difference was found between mean tree seedling and mean shrub density in the triple burn category (Table 2; P = 0.59).

The difference in seedling density of a select group of species (oak and hickory species) among the four burn categories was also tested (Figure 2). White oak density was greater in the double burn category compared to the single and unburned burn categories (Figure 2; P < 0.04); however, other oak species densities did not differ among the burn categories (Figure 2; P > 0.62). Mockernut hickory density was greatest in the double and triple burn categories compared to the single and unburned categories (P < 0.02), while pignut hickory was greater in the single burn category compared to the unburned category (Figure 2; P < 0.05).

Species cover

There was no significant difference found among the burn categories in herbaceous, shrub, or tree seedling cover (Table 2; P > 0.19). When shrub, tree seedling, and herbaceous cover values were combined, values ranged from 22.3% coverage (unburned) to 33.4% coverage (single burn). Significant difference among burn categories, however, was not observed (Table 2; P = 0.63).

DISCUSSION

The results of our study show that past burning has had a subtle, but clearly discernable, effect on understory vegetation composition. Although it has been 15-22 years since the stands we sampled last burned, we observed greater species richness in the burned stands. In addition, according to indicator species analysis, a greater number of taxa were indicative of past burning. However, the long interval since the stands last burned has likely allowed homogenization among burn categories. The slight differences in understory community composition despite differences in burn frequency are potentially explained by several factors. Hutchinson et al. (2005) attributed lack of community differences in understory vegetation in burned and unburned stands to dormant season burns (before the emergence of most perennial species) and low fire intensity in a mixed-oak forest in southern Ohio. In an oak-hardwood stand in New York, McGee et al. (1995) reported minor composition differences in understory vegetation 8-12 years following 0, 1, or 2 springtime prescribed fires. The authors attributed these changes to resprouting of the dominant species and lack of ruderal species persistence as the interval since the last burn increased. In our study, a majority of the species inventoried have the ability to resprout, and the amount of time since the last burn may have been long enough for understory species composition to return to pre-burn conditions.

Although differences in overall species composition were slight, burn frequency did appear to have a pronounced effect on the frequency and abundance of multiple taxa. For example, beetleweed, a shade tolerant herbaceous species that thrives in undisturbed oak-hickory forests, was indicative of unburned stands. The single burn-category had the greatest number of indicator species, including a mix of taxa that are typically associated with disturbance [wild yam (*Dioscorea quaternata* J.F. Gmel.), bluet species (*Houstonia* L. spp.), and whorled yellow loosestrife (*Lysimachia quadrifolia* L.)] and with shaded forest conditions [false Solomon's seal (*Maianthemum racemosum* L.) and Solomon's seal (*Polygonatum biflorum* Walter)] (White et al. 2003). Taxa from two genera that are often associated with disturbance and high light conditions, *Desmodium* and *Solidago*, were associated with double and triple burns, respectively (Reid 1964; Goldberg and Werner 1983), and prescribed burning may be used to

Downloaded From: https://complete.bioone.org/journals/Natural-Areas-Journal on 16 Jan 2025
Terms of Use: https://complete.bioone.org/terms-of-use

increase the abundance and persistence of these herbaceous taxa (Huang et al. 2007). Most shrub species were indicative of stands with a high burn frequency (triple burn plots). While repeated burning has been shown to reduce the density of shrubs and saplings (Blake and Schuette 2000), prolific sprouting occurs if regular burning ceases (Matlack et al. 1993; McGee et al. 1995; Blankenship and Arthur 2006). Seedlings of individual tree species were also indicative of burn categories. Shade tolerant species such as eastern hemlock and striped maple were indicator species of the unburned category, while fire tolerant species such as white oak, red oak, and mockernut hickory were indicative of multiple burn categories. In addition, black locust, a shade intolerant species commonly found on frequently disturbed sites, was indicative of the triple burn category.

The density of white oak and hickory species seedlings was greater in burned stands, even though 15-22 years had passed since the stands we sampled had last burned. In a companion study that sampled the same stands, Holzmueller et al. (2008) reported greater frequency and abundance of multiple oak and hickory species in the overstory and midstory of multiple burn stands and a greater frequency and abundance of mesophytic, shade tolerant species in unburned stands. Holzmueller et al. (2008) reported decreased overstory stem density in burned stands, which potentially increased light availability on the forest floor. This suggests that past burning favored the successful reproduction of oak and hickory species by increasing light availability and reducing competition from fire-intolerant species. In a study of understory response to disturbance, Dolan and Parker (2004) reported greater photosynthetically active radiation levels reaching the forest floor on burned plots compared to unburned plots in a mesic oak-hickory forest in Indiana. Increased light availability would favor shade intolerant species, such as oak and hickory species. However, merely increasing light availability to the forest floor does not correspond to an increase in oak and hickory species regeneration. For example, silvicultural treatments can increase light availability, but research indicates that in order for oak and hickory advanced regeneration to succeed, competition must also be reduced with fire (Franklin et al. 2003; Albrecht and McCarthy 2006). Furthermore, multiple studies have recommended frequent use of prescribed fire to increase oak and hickory regeneration because, typically, single prescribed burns will not reduce competition enough for oak and hickory regeneration to succeed (Arthur et al. 1998; Holzmueller et al. 2008). While white oak and hickory species continue to have higher seedling densities in the burned stands we sampled, these seedlings are unlikely to advance above the seedling layer in the absence of additional burning.

CONCLUSION

Although it has been 15-22 years since the stands we sampled last burned, the results of our study suggest that repeated burning may have long-lasting effects on understory community composition and density of oak and hickory seedlings. Maintaining the historic fire regime interval (10-15 years) of oak-hickory forests is necessary to stop the shift of these forests towards more mixed-mesophytic, shade-tolerant composition. In addition, repeated burning may increase understory species richness and promote herbaceous species, such as naked tree tick-foil, as well as the abundance of desirable woody species, such as white oak and hickory species. Furthermore, the

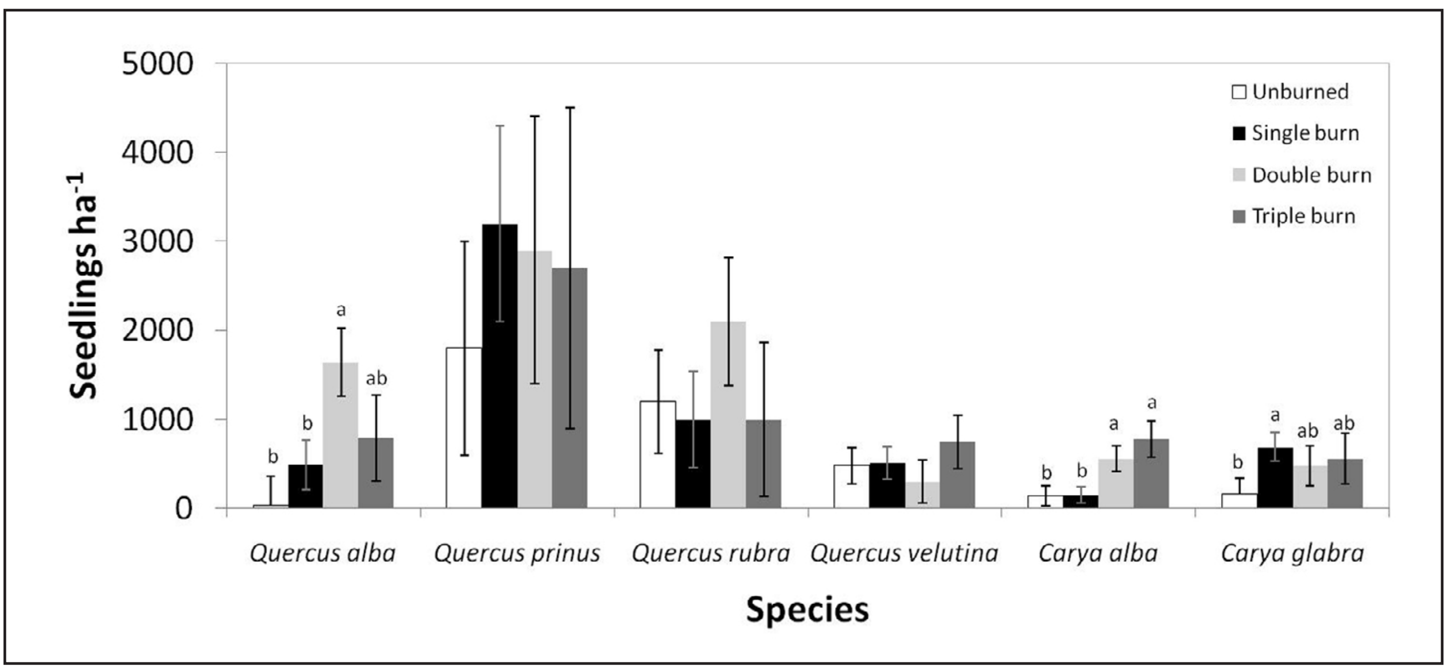

FIGURE 2. Mean (± 1 SE) seedling density of select oak and hickory species among the four burn categories. Different letters following means for each species indicate a significant difference among the four burn categories ($P < 0.05$).

Downloaded From: https://complete.bioone.org/journals/Natural-Areas-Journal on 16 Jan 2025
Terms of Use: https://complete.bioone.org/terms-of-use

results indicate that repeated burning can be used to restore and maintain the oak-hickory forest type in areas such as national parks, where intensive silviculture may not be an option for managers.

ACKNOWLEDGMENTS

We thank the National Park Service Southeast Region Natural Resources Preservation Program, Great Smoky Mountains Association, and the University of Florida College of Agriculture and Life Sciences for providing funding for this project. We also thank the faculty at the IFAS-Statistics Division for their help in data analyses. Huma Alverado, Kim Biedermann, Bethany Bins, Jennifer Griggs, Travis Martin, Hanni Muerdter, Playalina Nelson, Art vonLehe, Jeremy Volkening, and Mark Whited assisted with fieldwork.

Eric Holzmueller is an Assistant Professor of Forest Management and Ecology in the Department of Forestry at Southern Illinois University. His research focuses on the ecology of central hardwood forests and the effects of exotic pests and pathogens on forest communities.

Shibu Jose is a Professor of Forest Ecology in the School of Forest Resources and Conservation at the University of Florida. His research efforts focus on production ecology and ecophysiology of intensively managed pine and hardwood forests, restoration ecology of the longleaf pine ecosystem, invasive plant ecology and management, and ecological interactions in tree-crop mixed systems and mixed species forest plantations.

Mike Jenkins is an Assistant Professor of Forest Ecology in the Department of Forestry and Natural Resources at Purdue University. His research focuses on the interactions between disturbance and abiotic factors and their synergistic influence on ecosystem structure and function.

LITERATURE CITED

Abrams, M.D. 1992. Fire and the development of oak forests. BioScience 42:346-353.

Albrecht, M.A., and B.C. McCarthy. 2006. Effects of prescribed fire and thinning on tree recruitment patterns in central hardwood forests. Forest Ecology and Management 226: 88-103.

Aldrich, P.R., G.R. Parker, J.S. Ward, and C.H. Michler. 2003. Spatial dispersion of trees in an old-growth temperate hardwood forest over 60 years of succession. Forest Ecology and Management 180:475-491.

Arthur, M.A., R.D. Paratley, and B.A. Blankenship. 1998. Single and repeated fires affect survival and regeneration of woody and herbaceous species in an oak-pine forest. Journal of the Torrey Botanical Society 125:225-236.

Beck, D.E., and R.M. Hooper. 1986. Development of a southern Appalachian hardwood stand after clearcutting. Southern Journal of Applied Forestry 10:168-172.

Blake, J.G., and B. Schuette. 2000. Restoration of an oak forest in east-central Missouri: early effects of prescribed fire on woody vegetation. Forest Ecology and Management 139:109-126.

Blankenship, B.A., and M.A. Arthur. 2006. Stand structure over 9 years in burned and fire-excluded oak stands on the Cumberland Plateau, Kentucky. Forest Ecology and Management 225:134-145.

Boerner, R.E.J., A.T. Coates, D.A. Yaussy, and T.A. Waldrop. 2008. Assessing ecosystem restoration alternatives in eastern deciduous forests: the view from belowground. Restoration Ecology doi:10.1111/j.1526-100X.2007.00312.x.

Brose, P., T. Schuler, D. Van Lear, and J. Berst. 2001. Bring fire back: the changing regimes of the Appalachian mixed-oak forests. Journal of Forestry 99:30-35.

Brose, P.H., and D.H. Van Lear. 1998. Response of hardwood regeneration to seasonal prescribed fires in oak-dominated shelterwood stands. Canadian Journal of Forest Research 28:331-339.

Crow, T.R. 1988. Reproductive mode and mechanisms for self-replacement of northern red oak (*Quercus rubra*) – a review. Forest Science 34:19-40.

Daubenmire, R.F. 1959. Canopy coverage method of vegetation analysis. Northwest Scientist 33:43-64.

Dolan, B.J., and G.R. Parker. 2004. Regeneration response to disturbance in central hardwood forests. Pp. 285-291 *in* M.A. Spetich, ed., Proceedings of the upland oak ecology symposium: history, current conditions, and sustainability. General Technical Report SRS-73, United States Forest Service, Southern Research Station, Asheville, N.C.

Dufrêne, M., and P. Legendre. 1997 Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecological Monographs 67:345-366.

Ebinger, J.E. 1988. Woody understory after a spring burn at the Rocky Branch Nature Preserve, Clark County, Illinois. Transactions of the Illinois Academy of Science 81:25-30.

Elliott, K.J., R.L. Hendrick, A.E. Major, J.M. Vose, and W.T. Swank. 1999. Vegetation dynamics after a prescribed fire in the southern Appalachians. Forest Ecology and Management 114:199-213.

Franklin, S.B., P.A. Robertson, and J.S. Fralish. 2003. Prescribed burning effects on upland *Quercus* forest structure and function. Forest Ecology and Management 184:315-335.

Goldberg, D.E., and P.A. Werner. 1983. The effects of size of opening in vegetation and litter cover on seedling establishment of goldenrods (*Solidago* spp.). Oecologia 60:149-155.

Harmon, M.E. 1982. Fire history of the westernmost portion of Great Smoky Mountains National Park. Bulletin of the Torrey Botanical Club 109:74-79.

Holzmueller, E.J., S. Jose, and M.A. Jenkins. 2008. The relationship between fire history and an exotic fungal disease in a deciduous forest. Oecologia 155:215-403.

Huang, J., R.E.J. Boerner, and J. Rebbeck. 2007. Ecophysiological responses of two herbaceous species to prescribed burning, alone or in combination with overstory thinning. American Journal of Botany 94:755-763.

Hutchinson, T.F., R.E. Boerner, S. Sutherland, E.K. Sutherland, M. Ortt, and L.R. Iverson. 2005. Prescribed fire effects on the herbaceous layer of mixed-oak forests. Canadian Journal of Forest Research 35:877-890.

Jenkins, M.A., and G.R. Parker. 1998. Composition and diversity of woody vegetation in silvicultural openings of southern Indiana forests. Forest Ecology and Management 109:57-74.

Jenkins, M.A., and P.S. White. 2002. *Cornus florida* mortality and understory composition changes in western Great Smoky Mountains National Park. Journal of the Torrey Botanical Society 129:194-206.

Johnson, P.S, S.R. Shifley, and R. Rodgers. 2002. The ecology and silviculture of oaks. CABI Publishing International, New York.

Kellison, R.C. 1993. Oak regeneration - where do we go from here? Pp. 308-315 *in* D.L. Loftis and C.E. McGee, eds., Proceedings of oak regeneration: serious problems, practi-

Downloaded From: https://complete.bioone.org/journals/Natural-Areas-Journal on 16 Jan 2025
Terms of Use: https://complete.bioone.org/terms-of-use

cal recommendations. General Technical Report SE-48, United States Forest Service, Southeastern Forest Experiment Station, Asheville, N.C.

Kruger, E.L., and P.B. Reich. 1997. Responses of hardwood regeneration to fire in mesic forest openings. I. Post-fire community dynamics. Canadian Journal of Forest Research 27:1822-1831.

Kuddes-Fischer, L.M., and M.A. Arthur. 2002. Response of understory vegetation and tree regeneration to a single prescribed burn in oak-pine forests. Natural Areas Journal 22:43-52.

Lorimer, C.G. 1984. Development of the red maple understory in northeastern oak forests. Forest Science 30:3-22.

Lorimer, C.G., J.W. Chapman, and W.D. Lambert. 1994. Tall understory vegetation as a factor in the poor development of oak seedlings beneath mature stands. Journal of Ecology 82:227-237.

Madden, M., R. Welch, T. Jordan, and P. Jackson. 2004. Digital vegetation maps for Great Smoky Mountains National Park: final report. Center for Remote Sensing and Mapping Science, Department of Geography, University of Georgia, Athens.

Matlack, G.R., D.J. Gibson, and R.E. Good. 1993. Regeneration of the shrub *Gaylussacia baccata* and associated species after low-intensity fire in an Atlantic Coastal Plain forest. American Journal of Botany 80:119-126.

McCune, B., and M.J. Mefford. 1999. PC-ORD. Multivariate analysis of ecological data. Version 4.0. MjM Software, Gleneden Beach, Ore.

McGee, G.G., D.J. Leopold, and R.D. Nyland. 1995. Understory response to springtime prescribed fire in two New York transition oak forests. Forest Ecology and Management 76:149-168.

Nuzzo, V.A., W. McClain, and T. Strole. 1996. Fire impacts on groundlayer flora in a sand forest 1990-1994. American Midland Naturalist 136:207-221.

Ozier, T.B., J.W. Groninger, and C.M. Ruffner. 2006. Community composition and structural changes in a managed Illinois Ozark Hills Forest. American Midland Naturalist 155:253-269.

Peet, R.K., T.R. Wentworth, and P.S. White. 1998. A flexible, multipurpose method for recording vegetation composition and structure. Castanea 63:262-274.

Peterson, E.B., and B. McCune. 2001. Diversity and succession of epiphytic macrolichen communities in low-elevation managed conifer forests in western Oregon. Journal of Vegetation Science 12:511-524.

Pyle, C. 1988. The type and extent of anthropogenic vegetation disturbance in the Great Smoky Mountains before National Park Service acquisition. Castanea 53:183-196.

Pyne, S.J. 1982. Fire in America. University of Washington Press, Seattle.

Reid, A. 1964. Light intensity and herb growth in white oak forests. Ecology 45:396-398.

Ruffner, C.M., and J.W. Groninger. 2006. Making the case for fire in southern Illinois forests. Journal of Forestry 104:78-83.

SAS Institute. 2004. Version 9.1. SAS Institute, Cary, N.C.

Shumway, D.L., M.D. Abrams, and C.M. Ruffner. 2001. A 400-year history of fire and oak recruitment in an old-growth oak forest in western Maryland, U.S.A. Canadian Journal of Forest Research 31:1437-1443.

Smith, B.W., P.D. Miles, J.S. Vissage, and S.A. Pugh. 2004. Forest resources of the United States, 2002. General Technical Report NC-241, United States Forest Service, North Central Research Station, St. Paul, Minn.

[USDA Forest Service] U.S. Department of Agriculture, Forest Service. 2008. Fire Effects Information System, [Online]. United States Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory (Producer). Available online http://www.fs.fed.us/database/feis. Accessed 19 March 2008.

[USDA-NRCS] U.S. Department of Agriculture, Natural Resources Conservation Service. 2008. Soil survey geographic database for Great Smoky Mountains National Park, Tennessee and North Carolina. U.S. Department of Agriculture, Natural Resources Conservation Service, Fort Worth, Tex.

Varner, III, J.M., D.R. Gordon, F.E. Putz, and J.K. Hiers. 2005. Restoring fire to long-unburned *Pinus palustris* ecosystems: novel fire effects and consequences for long-unburned ecosystems. Restoration Ecology 13:536-544.

Wendel, G.W., and H.C. Smith. 1986. Effects of a prescribed fire on a central Appalachian oak-hickory stand. NE-RP-594, U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station, Broomall, Pa.

White, R.D., K.D. Patterson, A. Weakley, C.J. Ulrey, and J. Drake. 2003. Vegetation classification of Great Smoky Mountains National Park. Report submitted to BRD-NPS Vegetation Mapping Program. NatureServe, Durham, N.C.

Downloaded From: https://complete.bioone.org/journals/Natural-Areas-Journal on 16 Jan 2025
Terms of Use: https://complete.bioone.org/terms-of-use