Fire and Understory Vegetation: A Large-scale Study in Ohio and a Search for General Response Patterns in Central Hardwood Forests

Todd F. Hutchinson[1] *and Steve Sutherland*[2]

Abstract

Oak-dominated ecosystems throughout the central hardwood region (CHR) are experiencing a shift in species composition toward more mesic and/or fire-sensitive species such as red maple (*Acer rubrum*), sugar maple (*Acer saccharum*), and blackgum (*Nyssa sylvatica*). Prescribed fire can enhance oak regeneration but few studies have examined the effects of fire on other ecosystem components, including understory vegetation. In 1994, a multi-disciplinary project was initiated to study the use of prescribed fire as a restoration tool in mixed oak ecosystems in southern Ohio. Here, I report on the response of understory vegetation after 3 years of early spring (dormant-season) fires. Each year, from 1995 to 1998, species' frequencies were recorded in 1,728 2m^2 quadrats in four 75 to 100 ha study areas. Each study area included a control, infrequently burned (1X), and frequently burned (3X) unit. In all, 428 vascular plant species were identified. Surface fires have altered the understory environment by greatly reducing the quantity of leaf litter on the forest floor, but light availability has increased only slightly as the tree canopy has remained closed. Several groups of species have responded consistently to fire, including seed bank increasers, tree seedlings, and spring monocots. On control plots, few species have increased or decreased in frequency by more than 5 percent. On 1X plots, 18 species have increased and 5 have decreased; on the 3X plots, 22 species have increased and 18 have decreased in frequency. From 1995 to 1998, species richness (nearly all native species) increased on the burned plots relative to the control plots. This was particularly true at the quadrat level, where richness has decreased slightly on the control plots but increased by 11.4 and 10.4 percent on 1X and 3X plots, respectively. From our research in Ohio and from other studies in the CHR, we conclude that dormant-season prescribed fire may be used to promote oak and pine regeneration while maintaining or increasing the diversity of native understory species.

Introduction

Fire has played an important role in shaping the structure and composition of vegetation in the central hardwoods region (CHR). Fire use by Native Americans is widely believed to have created and maintained many of the more open plant communities in the CHR, including savannas, barrens, and prairies (Baskin and others 1999, Fralish and others 1999, Heikens 1999). Fire history studies using dendrochronology methods support the hypothesis that frequent fire maintained savanna vegetation in the CHR (Guyette and Cutter 1991, Batek and others 1999). Currently, fire is being used in the CHR by land management agencies including the Nature Conservancy, state heritage programs, USDA Forest Service, and the National Park Service to restore and maintain these plant communities, many of which contain threatened and endangered species (e.g., Bender, this volume)

It is also hypothesized that frequent fire maintained the dominance of oak (Abrams 1992, Abrams, this volume) and pine (Waldrop, this volume) in the presettlement CHR landscape. The absence of fire has been implicated in the widespread abundance of shade-tolerant and fire-sensitive tree species in the regeneration layer of oak forests in the eastern United States (Lorimer 1984, Loftis and McGee 1993, Lorimer and others 1994). Prescribed fire has been used to regenerate oaks with varying degrees of success (Wendel and Smith 1986, Barnes and Van Lear 1998, Elliot and others 1999). However, shelterwood harvests followed by high intensity prescribed fires have improved oak regeneration on productive upland sites in Virginia (Brose and others 1999, Van Lear and Brose, this volume).

In addition to understanding the effects of fire on tree regeneration, managers need to understand the effects of fire on the nontree components within the CHR. In this paper I examine the effects of fire on the understory vegetation layer (herbaceous and woody species) in forests in and around the CHR by presenting data from previous studies and an ongoing study of prescribed fire in mixed-oak forests in southern Ohio.

Effects of Fire on Understory Vegetation in the Central Hardwood Region

The understory vegetation layer in central hardwood forests is composed of several major life forms: graminoids (grasses, sedges, and rushes), forbs (nongraminoid herbaceous plants), shrubs, woody vines, and seedlings of tree species. Herbaceous species, particularly perennial forbs, comprise the majority of the species pool in CHR forests (Hutchinson and others 1999). The cover and abundance of herbaceous species varies annually due to climatic conditions (Rogers 1983) and throughout the growing season as spring ephemerals, summergreen species, and late-summer species emerge and reach maximum biomass at different times (Bratton 1976, Goebel and others 1999).

Understory composition and richness are strongly related to topographic moisture and fertility gradients (Huebner and others 1995, Olivero and Hix 1998, Hutchinson and others

[1]Research Ecologist, USDA Forest Service, Northeastern Research Station, 359 Main Road, Delaware, OH 43015

[2]Ecologist, The Nature Conservancy, Ohio Chapter, 6375 Riverside Drive, Suite 50, Dublin, OH 43017
Current address: USDA Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory, P.O. Box 8089, Missoula, MT 59807

1999), soil parent material (Howell and Vankat 1981), and land-use history (Motzkin and others 1996), including fire history (Swan 1970). Mean species richness of 14.5 species per m^2 has been reported in mixed mesophytic forests in the southern Appalachians (Duffy and Meier 1992). In the study described here, mean richness per 2 m^2 ranged from 5.9 to 29.6 and averaged 16.7 (Hutchinson and others 1999).

Due to the limited number of fire studies in the CHR, it is useful to first examine the long-term effects of fire on understory vegetation from 2 field studies in southeastern coastal plain pine forests. After 43 years of fire treatments in loblolly pine (*Pinus taeda*) stands on the Santee Experimental Forest, which included control (no fire), and both periodic and annual winter and summer burns, the structure, composition, and diversity of understory vegetation varied primarily by fire treatment (Lewis and Harshbarger 1976, White and others 1991). There was a gradient from shrub and hardwood domination on control plots to herbaceous (forb and graminoid) dominance in the burned plots. Maximum abundance and diversity of native herbaceous species occurred in plots burned annually (White and others 1991). Brockway and Lewis (1997) reported that longleaf pine (*P. palustris*) stands burned frequently over 4 decades had a much more diverse and productive herbaceous understory than control stands, which developed a dense shrub layer of gallberry (*Ilex glabra*) that reduced diversity.

In a long-term study within the CHR, DeSelm and others (1973) and DeSelm and Clebsch (1991) documented the effects of annual and periodic fires on vegetation over a 25-year period (1965-89) in an oak barrens community in middle Tennessee by recording vegetation cover annually using the point-intercept method. The burned plots maintained high forb and graminoid cover; forb cover averaged 46.5 and 28.3 percent on annually and periodically burned plots, respectively, and graminoid cover averaged 59.6 and 48.3 percent on annual and periodic burn plots. In sharp contrast, the control plots rapidly lost herbaceous cover, which had decreased to less than 1 percent by 1976 as woody plants invaded and shaded the ground-layer vegetation.

In more closed-canopied oak and pine forests, studies on fire effects have generally consisted of 1 to several fires. The response of understory vegetation in and around the CHR is summarized in Table 1.

Species groups that have increased in frequency, abundance, or cover following fire include annual forbs such as fireweed (*Erechtites hieracifolia*) (Masters 1991, Dolan 1994, Sparks and others 1998), legumes (e.g., *Desmodium* spp., *Lespedeza* spp) (Ducey and others 1996, Sparks and others 1998), warm-season grasses, including *Panicum* spp. and little bluestem (*Schizachyrium scoparium*) (Dolan 1994, Sparks and others 1998, Elliot and others 1999), and late-summer forbs such as the asters (*Aster* spp.), goldenrods (*Solidago* spp.), and sunflowers (*Helianthus* spp.) (Swan 1970, Wilhelm and Masters 1994, Sparks and others 1998). The most consistent species group was the brambles (*Rubus* spp.), which increased via abundant germination in almost every study (e.g., Swan 1970, McGee and others1995, Nuzzo and others 1996). For all of these species, increased light availability following fire likely was the most important response factor, i.e., it increased seed germination (Pickett and Baskin 1973, Baskin and Baskin 1988) and/or growth and reproduction (Pitelka and others 1985).

Most species that decreased consistently were tree seedlings, including red maple (*Acer rubrum*) and black cherry (*Prunus serotina*) (Swan 1970, Cole and others 1990), and shrubs and vines, including Virginia creeper (*Parthenocissus quinquefolia*) and greenbriar (*Smilax rotundifolia*) (Wilhelm and Masters 1994, Nuzzo and others 1996; Arthur and others 1998). The cover of mountain laurel (*Kalmia latifolia*), an evergreen shrub, decreased in several studies, but resprouted prolifically (McGee and others 1995, Ducey and others 1996, Elliot and others 1999).

Herbaceous cover generally increased following fire (McGee and others 1995, Nuzzo and others 1996) while the cover (Nuzzo and others 1996; Elliot and others 1999) and density (Schwartz and Heim 1996) of woody vegetation decreased (Table 1). However, due to resprouting, understory woody cover also has exceeded pre-burn levels within several years (McGee and others 1995, Arthur and others 1998). When mixed oak-pine stands in eastern Oklahoma were thinned and burned, herbaceous biomass increased significantly (Masters and others 1993).

In nearly all of the fire studies in the CHR, species richness or diversity increased following fire, though the magnitude and duration of the responses were highly variable (Table 1). In a sand forest in Illinois, species richness increased from 6.2-7.0/ m^2 to 9.8-10.8/ m^2 following the first of 3 fires, due to an increase in herbaceous species, particularly annuals (Nuzzo and others 1996). However, the strong effects were short-lived as richness subsequently declined after the first fire-free year. In western Arkansas, species richness increased significantly following a single dormant-season fire in restored shortleaf pine (*Pinus echinata*) forests (Sparks and others 1998). The stands gained 14-16 species and more than 3 species were gained per m^2 (Sparks and others 1998). More than 8 years following 2 fires in a transition oak-northern hardwood forest, forb richness increased significantly over pre-burn levels in 2 stands, 26 to 44 and 23 to 27 species/4 m^2, respectively (McGee and others 1995). Other studies reported increased species richness following fire (Cole and others 1990, Wilhelm and Masters 1994, Taft and others 1995, Arthur and others 1998), though Dolan (1994) found no change in richness and Schwartz and Heim (1996) reported a decrease (Table 1).

Fire intensity and season are other important factors that influence the response of vegetation. Ducey and others (1996) and Elliot and others (1999) reported that species richness increased more following high-intensity fires than in areas that burned at lower intensities. In Arkansas, dormant-season burns in March and April increased the abundance of several *Panicum* species but a September fire reduced *Panicum* abundance (Sparks and others 1998). After an

Table 1.—Summary of fire studies examining the response of understory forest vegetation in and around the central hardwoods region

Overstory dominant	Location	Duration (pre-burn data)	Fire Treatments	Herbaceous response	Author(s)
Post oak Shortleaf pine	OK	5 years (yes)	1 or 3 fires Winter	richness +	Masters 1991 Masters and others 1993
Shortleaf pine	AR	2 years (yes)	1 or 2 fires Mar-Apr; Sep	richness + density + / -	Sparks and others 1998
Mixed: oak, pine, maple, hickory	NC	2 years (yes)	1 fire Apr	richness + cover +	Elliot and others 1999
Scarlet oak Chestnut oak	KY	4 years (no)	1 or 2 fires Mar	richness + cover +	Arthur and others 1998
Post oak	IN	7 years (yes)	1 fire Apr	Richness: No effect	Dolan 1994
Mixed oak	NY	1 year (no)	1 wildfire Apr-May	# increasers > # decreasers	Swan 1970
Red oak, white oak, white pine	CT	1 year (no)	1 fire Apr	richness + density +	Ducey and others 1996
Red oak, white oak	NY	12 years (yes)	1 or 2 fires Apr	richness + height +	McGee and others 1995
Black oak	IL	5 years (yes)	3 fires (dormant) autumn and spring	richness + cover +	Nuzzo and others 1996
White oak, red oak, black walnut	IL	4 years (yes)	1 fire Mar or May	richness - (May burn only)	Schwartz and Heim 1996
Mesic woodland	IL	5 years (no)	4 fires Spring	richness +	Wilhelm and Masters 1994

initial depression in species richness following both March (dormant season) and May (growing season) fires in Illinois, richness soon recovered following the March but not the May burns (Schwartz and Heim 1996).

Fire has not facilitated the invasion of exotic species in CHR, possibly because most of the areas that have been burned and studied quantitatively have been relatively xeric and undisturbed, and thus not highly invasible (Rejmanek 1989). In more mesic and disturbed forests where garlic mustard (*Alliaria petiolata*) has invaded, fire moderately reduced both its cover and abundance (Nuzzo and others 1996, Schwartz and Heim 1996).

Effects of Fire on Understory Vegetation in Ohio Oak Forests

Witness tree data from land surveys indicates that the unglaciated Allegheny Plateau region of southeastern Ohio was composed primarily of mixed oak forests just prior to European settlement (ca. 1800) (Gordon 1969). In the southern portion of this region, many of the oak forests were harvested repeatedly from 1850 to 1900 to supply charcoal for the numerous iron furnaces in the region (Stout 1933). In secondary forests dating to the end of the iron-producing period, oaks, primarily white (*Quercus alba*), chestnut (*Q. prinus*) and black (*Q. velutina*), continue to dominate the overstory but the midstory and understory layers are dominated by shade-tolerant species such as red maple (*Acer rubrum*), sugar maple (*Acer saccharum*), blackgum (*Nyssa sylvatica*), and beech (*Fagus grandifolia*) (Figure 1). Similar trends have been reported for numerous oak forests in the eastern United States (Abrams 1992). On the basis of these forest trends, a multidisciplinary study was established to examine prescribed fire as a tool to restore structure, composition, and function to oak forests in southern Ohio.

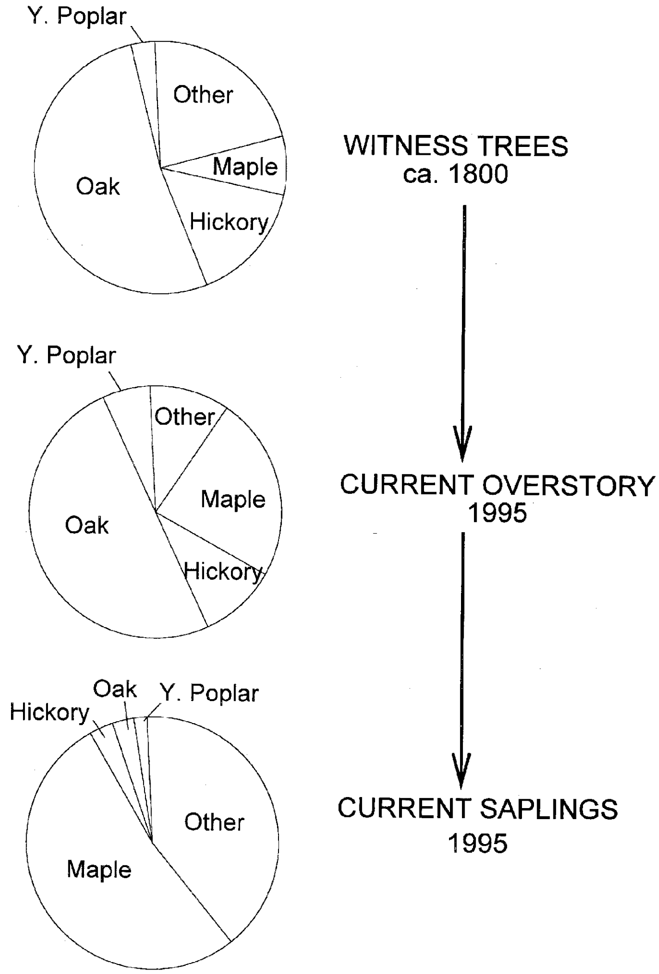

Figure 1.—Forest composition trends in southern Ohio. Witness tree data are from townships in and adjacent to the study areas. Data for the Vinton County areas are from Beatley (1959). Current overstory (trees > 10 cm dbh) and sapling (trees 1.37 m height to 9.9 cm dbh) data were collected from 108 vegetation plots The primary "other" species for the saplings are blackgum and beech.

Methods

Study Areas and Experimental Design

In 1994, four study areas (75 to 100 ha each) were established, two in Vinton County (Arch Rock, 39°12' N, 82°23' W; Watch Rock, 39°11" N, 82°22' W), and two in Lawrence County (Young's Branch (38°43' N, 82°31' W; Bluegrass Ridge (38°36' N, 82°31' W). The sites were dissected, underlain by sandstones and siltstones, and had moderately acidic siltloam alfisols with low water-holding capacity. The study areas have been relatively undisturbed since clearcutting 80 to 120 years ago, and were dominated by oak. Average tree basal area was 24 to 28 m^2/ha (Hutchinson and others 1999). Three fire treatment units were established within each area. Control units were not burned, infrequent units were burned once (1X) in March-April 1996, and frequent units were burned three times (3X) in March-April, 1996, 1997, and 1998. The surface fires generally were low intensity, with flame lengths less than 50 cm and temperatures averaging 89.6°C (193.2°F) at a height of 25 cm over the 3-year period (Hutchinson, unpublished data). In the uplands of each unit, nine 50 x 25m (0.125 ha) vegetation plots (N = 108 total plots) were stratified by a GIS-derived integrated moisture index based on a suite of landscape features (Iverson and others 1997).

Field Data Collection

The frequency of understory species was recorded in four 2 x 1 m quadrats along each of four transects spaced 5 m apart within a 25 x 25m portion of each plot (16 quadrats per plot). Each year, three quadrats per transect were located randomly and one quadrat was located permanently at the midpoint of each transect. Here, data from random and permanent quadrats were combined. Vegetation was sampled twice each year (May and September) from 1995 (pre-burn) to 1998. Herbaceous plants were recorded on a presence/absence basis in each quadrat to obtain frequency. For each species, the maximum frequency was recorded for the year. For understory individuals of tree species, we recorded the presence of each species in each of four size classes: < 30 cm height, 30 cm height to 2.99 cm diameter at breast height (dbh), 3.0 to 9.9 cm dbh, and $\geq$ 10 cm dbh.

Results and Discussion

Following the first fires, 37 percent of the small saplings (1.37 m height - 2.9 cm dbh), 9 percent of the medium saplings (3.0 - 5.9), and 4 percent of the large saplings (6.0 - 9.9) had been topkilled though most stems resprouted (Sutherland and others 1997). After three fires, nearly 95 percent of the small saplings had been topkilled (Sutherland and Hutchinson, unpublished). However, few trees greater than 10 cm dbh have been topkilled (D. Yaussy, USDA Forest Service, unpublished) and open sky remained below 6 percent after two fires on the 3X plots (Robison and McCarthy 1999). Leaf litter consumption ranged from 28.5 to 80.4 percent during the first fires in 1996 (Boerner and others, in press). Litter mass has continued to decrease on frequently burned plots, while increasing to pre-burn levels by 1998 on the 1X plots (Hutchinson, unpublished).

Over the 4-year period, we recorded 428 vascular plant species, composed of 254 perennial forbs, 59 graminoids, 45 trees, 30 shrubs, 24 annual forbs, 11 woody vines, and 5 monocarpic perennial forbs. While the frequency of most species did not change significantly following prescribed fire, the following groups exhibited distinctive patterns of change.

Seed Bank Increasers

Several species increased in frequency following abundant germination from the seed bank. Fireweed (*Erechtites hieracifolia*) and yellow-poplar (*Liriodendron tulipifera*) had the greatest increases in frequency on the burned plots (Figure 2). Prior to burning, fireweed had a mean frequency of less than 10 percent per plot; following the first fires in 1996, it increased to nearly 80 percent frequency Presumably, most of the germination was from the buried seed pool as fires would have consumed the previous autumn's small, wind-dispersed seeds. On the 1X plots, the frequency of fireweed returned to pre-burn levels following 2 years without fire; frequency remained high (> 55 percent) on 3X plots. Like many annuals, fireweed probably requires light for germination (Pickett and Baskin 1973, Baskin and Baskin 1988). Disturbances that remove litter and expose mineral soil are required to maintain fireweed at high frequencies in standing vegetation. Yellow-poplar, which produces seeds that are viable in the seed bank for 4 to 7 years (Burns and Honkala 1990), increased in seedling frequency from less than 25 percent prior to burning to nearly 80 percent on burned plots following the first fires. In contrast to fireweed, the frequency of yellow-poplar seedlings then decreased to approximately 50 percent on the 1X and 3X plots from 1996 to 1998. On the 1X plots, the decrease likely was caused by seedling mortality due to low light levels (Burns and Honkala 1990). On the 3X plots fire likely killed most of the seedlings that had germinated, though new germination maintained relatively high frequencies of seedlings.

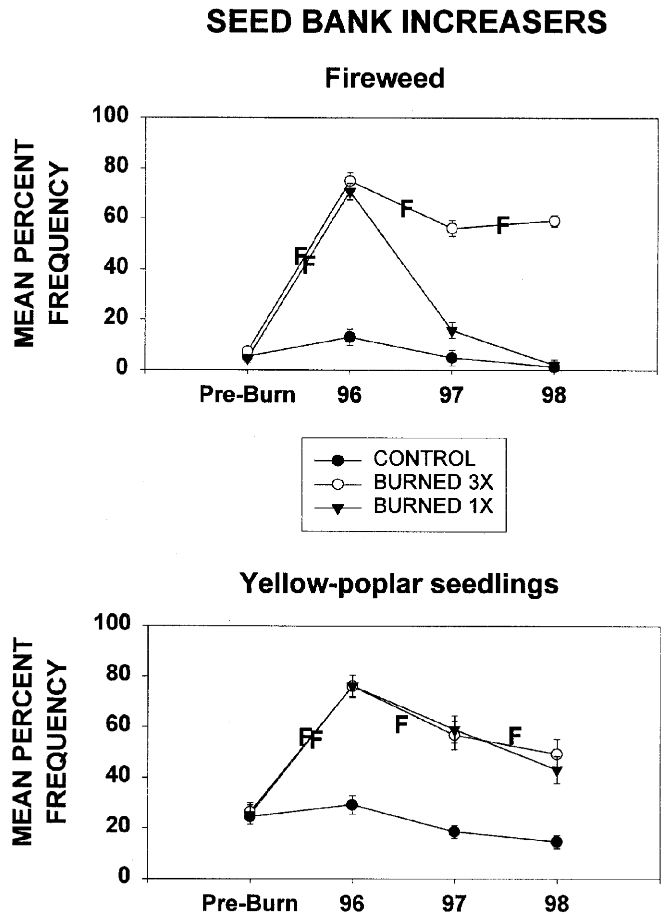

Figure 2.—Frequency data for fireweed and yellow-poplar seedlings. Mean frequencies were calculated as the mean number of quadrats per plot in which the species occurred for 36 plots per year in each of three fire treatments (fires are indicated with an F).

Other species in the pre-burn standing vegetation that increased in frequency by more than 10 percent on the burned plots included Virginia copperleaf (*Acalypha virginica*), sedges (*Carex* spp.), white snakeroot (*Eupatorium rugosum*), sweet-scented bedstraw (*Galium triflorum*), panic grasses (*Panicum boscii*, *P. latifolium*), brambles (*Rubus* spp.), sassafras (*Sassafras albidum*), violets (*Viola* spp.), and wild grapevine (*Vitis* spp.) Smooth sumac (*Rhus glabra*), which was absent from the pre-burn standing vegetation, increased in frequency to 11.3 percent on the 3X plots by 1998. Several species not recorded in the pre-burn standing vegetation germinated following fire, but remained at frequencies under 10 percent. These species included sensitive plant (*Chamaecrista nictitans*), horse-weed (*Conyza canadensis*), late eupatorium (*Eupatorium serotinum*), upland boneset (*E. sessilifolium*), cudweed (*Gnaphalium obtusifolium*), beggar's-lice (*Hackelia virginiana*), indian-tobacco (*Lobelia inflata*), pokeweed (*Phytolacca americana*), dwarf sumac (*Rhus copallina*), fire-pink (*Silene virginica*), and *Sphenopholis nitida,* a grass. Of several exotic species that appeared after the fires, only black bindweed (*Polygonum convolvulus*) was found in more than 1 percent of quadrats within burned treatments (2.4 percent in 1998).

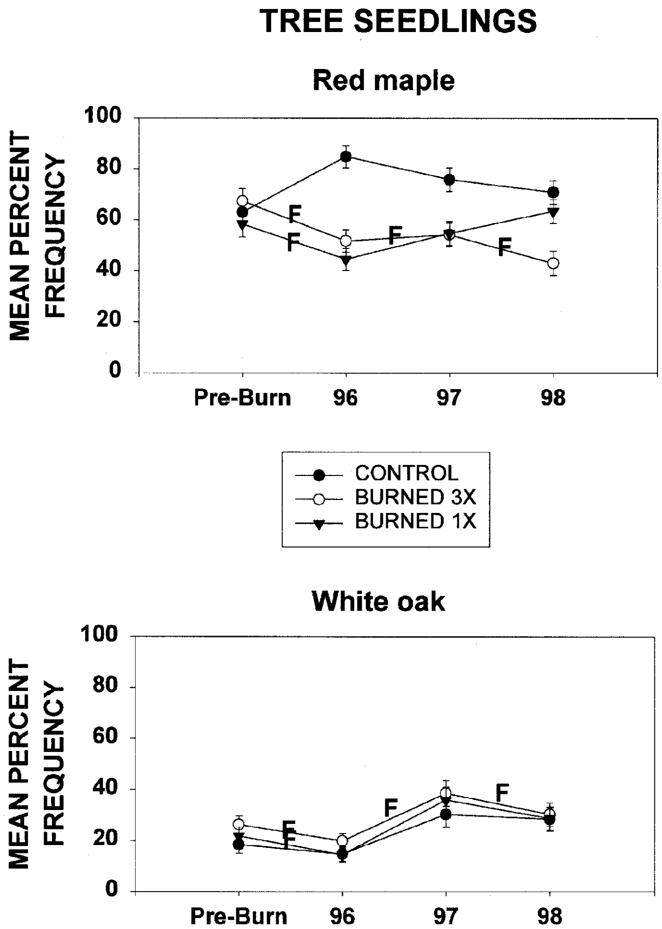

Figure 3.—Frequency data for red maple and white oak seedlings. Mean frequencies were calculated as the mean number of quadrats per plot in which the species occurred for 36 plots per year in each of three fire treatments (fires are indicated with an F).

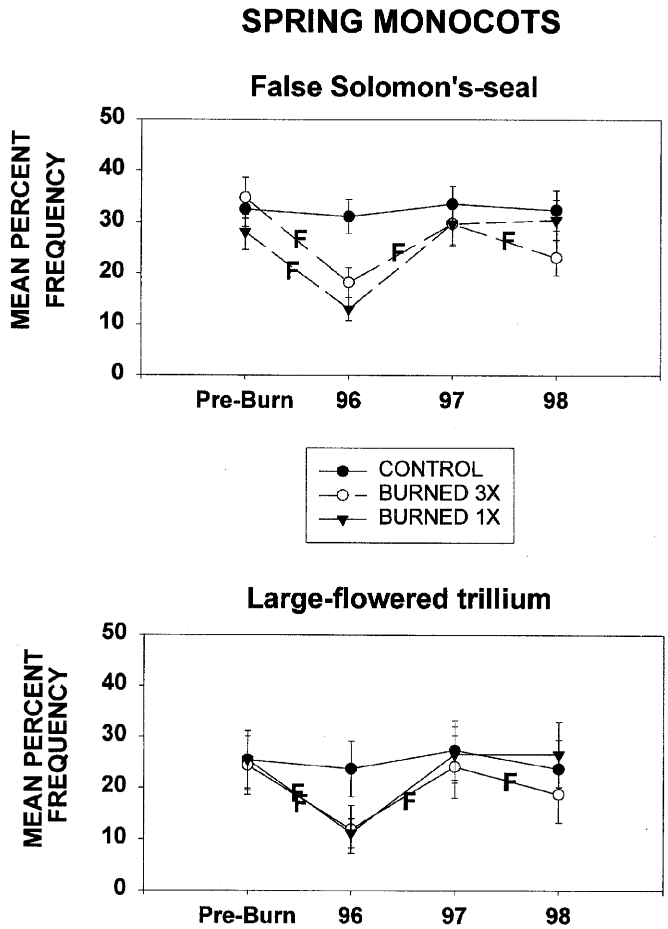

Figure 4.—Frequency data for false solomon's seal and large-flowered trillium. Mean frequencies were calculated as the mean number of quadrats per plot in which the species occurred for 36 plots per year in each of three fire treatments (fires are indicated with an F).

Tree Seedlings

The effects of fire on tree seedlings varied by species, as shown by the contrasting responses of red maple and white oak (Figure 3). From 1995 to 1998, the frequency of red maple seedlings increased from 63.0 to 70.8 percent on control plots, but decreased from 67.4 to 43.1 percent on the 3X plots. On the 1X plots, the frequency of red maple seedlings decreased from 58.4 to 44.6 percent following the fire but increased to 63.4 percent in 1998 after 2 years without fire. Although larger red maple seedlings sprout following topkill, three fires reduced frequencies substantially. By contrast, seedlings of white oak, which was the most abundant overstory species and the most frequent oak species in the seedling layer, exhibited a neutral response (< 5 percent frequency shift) to fire (Figure 3). White oak seedlings increased in frequency in all treatments following a mast year in 1996. In 1998, frequencies were nearly identical across treatments (28.3 to 30.2 percent). Other fire studies have shown similar responses of red maple and oaks (e.g., Kruger and Reich 1997).

Other tree species that decreased in seedling frequency by more than 5 percent from 1995 to 1998 on the 3X plots were flowering dogwood (*Cornus florida*, 17.0 percent), American ash (*Fraxinus americana*, 15.8), sugar maple (*Acer saccharum*, 10.4), slippery elm (*Ulmus rubra*, 8.2), hop-hornbeam (*Ostrya virginiana*, 7.5), and black cherry (*Prunus serotina* 6.9). In addition to white oak, common seedlings that showed a neutral response to fire on the burned plots included scarlet oak (*Quercus coccinea*), chestnut oak (*Q. prinus*), red oak (*Q. rubra*), black oak (*Q. velutina*), pignut hickory (*Carya glabra*), bitternut hickory *(C. cordiformis*), redbud (*Cercis canadensis*), hawthorn (*Crataegus spp.*), and blackgum (*Nyssa sylvatica*).

Spring Monocots

Several monocots that emerge early in the spring decreased in frequency on the burned plots, particularly in years when the fires were conducted later in the spring. Both false Solomon's seal (*Smilacina racemosa*) and large-flowered trillium (*Trillium grandiflorum*) decreased in frequency by

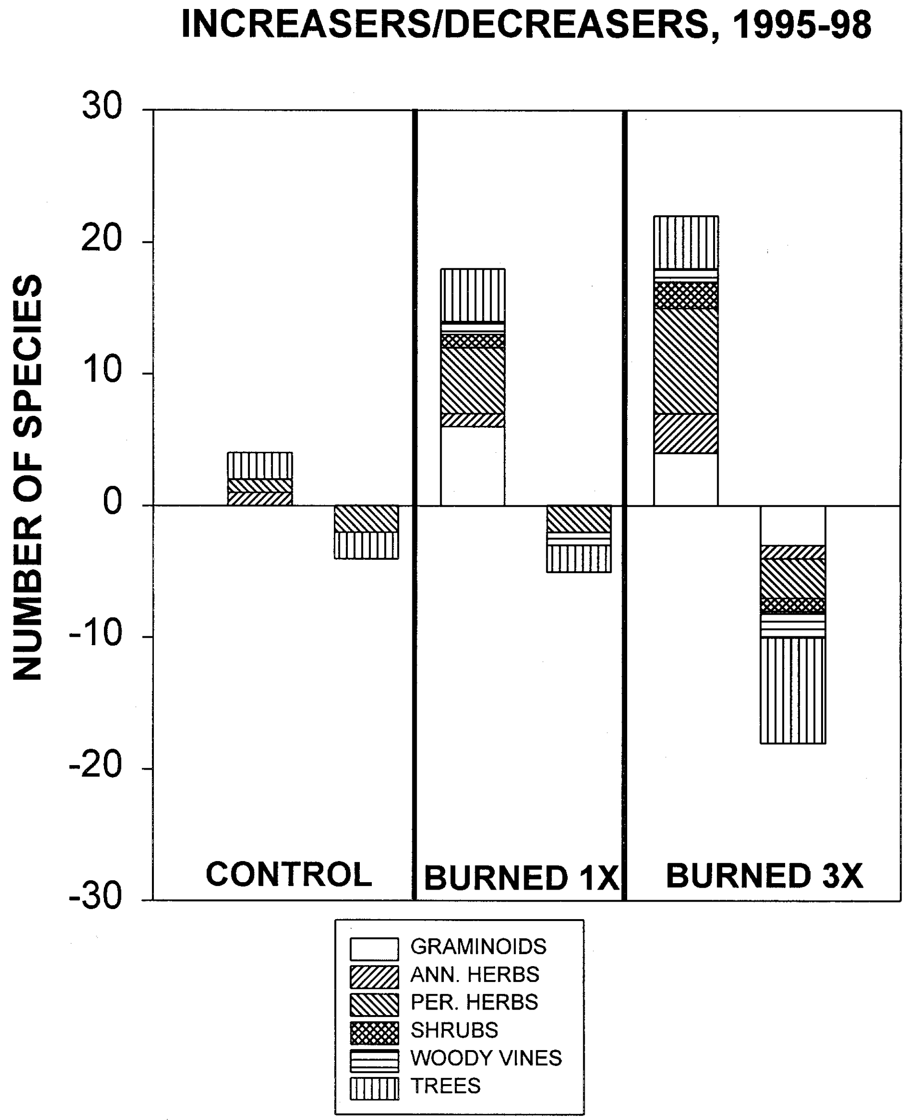

Figure 5.—Species that increased or decreased in mean frequency by more than 5 percent from 1995 to 1998 in three fire treatments.

12.5 to 16.5 percent following the first fires (Figure 4). The 1996 fires were conducted later (through April 22) than in subsequent years due to a wet spring. However, in both fire treatments, these species returned to pre-burn frequencies in 1997 following another fire on the 3X plots and no fire on the 1X plots. The 1997 burns were completed by April 3, suggesting that dormant-season fires have a negative impact on these species only if conducted when they begin to emerge. Damage to the leaf tips of several monocot species has been observed frequently in the study areas (personal observation). From 1997 to 1998 the frequency of false solomon's seal and trillium decreased by 6.6 and 5.4 percent, respectively, suggesting that the fires occurred at a phenological stage intermediate to 1996 and 1997 (Figure 4). Solomon's seal (*Polygonatum biflorum*) and bellwort (*Uvularia perfoliata*) also decreased in frequency on burned plots.

Summary of Increasers and Decreasers

To examine the effects of fire on the entire species pool, we classified species as increasers or decreasers if their frequency shifted by more than 5 percent from 1995 (pre-burn) to 1998. On the controls, few species shifted in frequency by more than 5 percent (Figure 5). On the 1X plots, there were 18 increasers, of which 11 were graminoids and perennial forbs, and 5 decreasers. On the 3X plots, there were 22 increasers but also 18 decreasers, most of which were woody species (11), including 8 tree species. These results indicate that the composition of the 3X plots has changed more than the1X plots, primarily due to the reduced frequencies of several tree species. Despite the greater change on the 3X plots, most species have not shifted more than 5 percent following dormant-season prescribed fires. This suggests that perennial herbaceous species have not been damaged directly by fire, and have

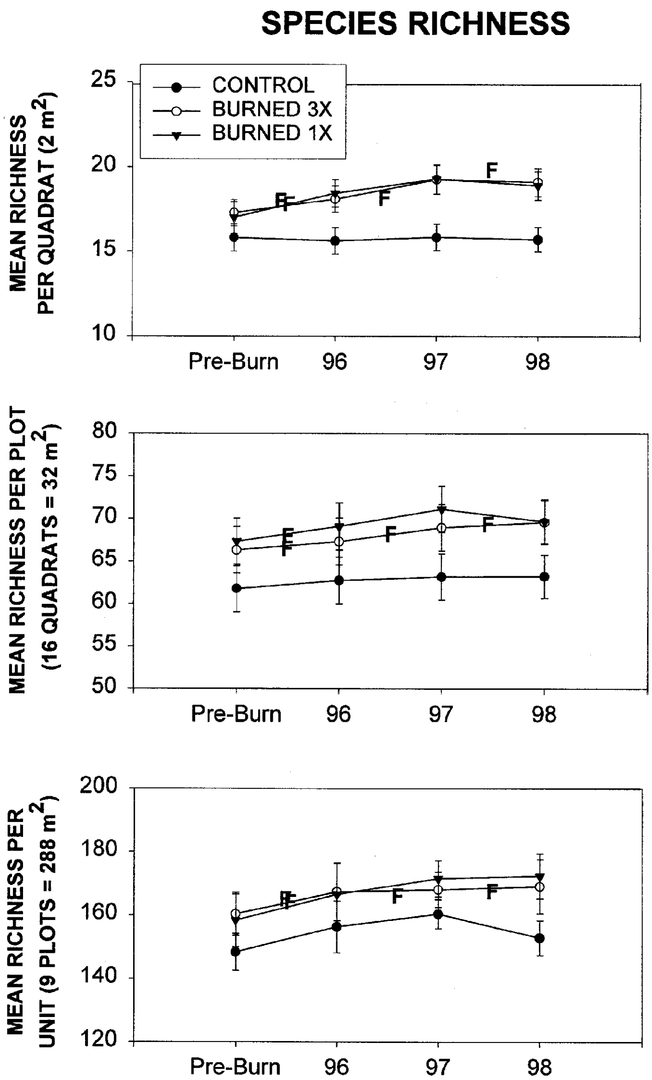

Figure 6.—Mean species richness values for the three fire treatments at three spatial scales of observation (fires are indicated with an F).

emerged in numbers similar to those on the controls. Also, most woody species that were topkilled by fire have resprouted. Although there have been several seed bank increasers, most species have not exhibited abundant germination following fires.

Species Richness

From 1995 to 1998, species richness per quadrat increased by 11.4 percent on 1X plots and 10.4 percent on 3X plots. Over the same period, richness decreased by less than 1 percent on the controls (Figure 6a). Species richness per plot (based on 16 quadrats) also increased more on the burned plots relative to the controls, but only by several species; richness increased by 2.4 percent on control plots, 3.4 percent on 1X plots and 5.0 percent on 3X plots (Figure 6b). When richness was summed for the nine plots in each unit, richness increased in all treatments from 1995-98, but to a greater degree on the burned plots. Richness per unit increased by 3.4 percent on control plots, 5.6 percent on 3X plots, and 8.9 percent on 1X plots. (Figure 6c).

The increases in species richness on the burned plots are subtle, but our results indicate that fire has not depressed richness in these oak forests over the initial 4-year period of this study. Our results also underscore the need for pre-treatment data when conducting fire studies. Our control units were less species rich prior to treatment at all three scales of observation. Had we examined only post-burn data, the presumed effects of fire on increased species richness would have been exaggerated.

Conclusions

Because trees dominate the structure of CHR forests and have high economic value, most research and discussion on fire effects in this region has focused on tree regeneration. However, plant diversity in the CHR region is concentrated in the understory layer, particularly among herbaceous species. It is these plants that also provide habitat and food for diverse assemblages of fauna. There is growing evidence that plant diversity directly affects the productivity and sustainability of ecosystems (Tilman and others 1996). From studies in the CHR it is clear that dormant season fire has no negative impact on plant diversity. In fact, most studies show small to moderate increases in diversity as fire creates an improved regeneration niche for some species (Table 1).

Our Ohio study showed that prescribed fire has both direct and indirect effects on undestory vegetation. Fire directly affects species composition by topkilling most of the smaller woody stems. The relative frequencies of woody species then shift due to variation in resprouting ability; we reported a decrease in the relative frequencies of maple, dogwood, ash, and elm seedlings to those of the oaks and hickories. Fire also directly damaged several herbaceous species (spring monocots), causing reduced frequencies.

Indirectly, fire caused a shift in species composition by greatly reducing leaf litter and exposing mineral soil, which facilitated the abundant germination of several species from the seed bank and the addition of species to the standing vegetation. Other indirect fire effects that may affect species composition include a subtle increase in light availability throughout the growing season, an increase in soil nutrients and pH from leaf litter ash (see Boerner, this volume), and a decrease in soil moisture through increased evaporation.

It is clear that fire suppression since the 1940's has resulted in significant changes in CHR forests. There is a need for long-term research on the effects of fire on the understory vegetation in these forests and for additional population-level studies of fire response by individual species. We also need to understand how the effects of fire and fire suppression on understory vegetation are linked to physical and biological patterns and processes (e.g., light availability and nutrient cycling) and to the population dynamics and behavior of animals, including herbivores, pollinators, and microbial communities.

Acknowledgments

We thank the many individuals and agencies whose assistance was invaluable in conducting this project. Marilyn Ortt provided the botanical expertise as well as 4 years of field work, Elaine Kennedy Sutherland provided project leadership, and Marty Jones, Ralph Boerner, and Louis Iverson reviewed an earlier draft of this manuscript. The following participated in either the collection of field data and/or assisted with data entry: Heather Bentsen, Rosemarie Boyle, James Buratti, Ginger Burnhold, Carolee Franklin, Rick Gardner, John Gire, Jennifer Gray, Meryl Hattenbach, Jennifer Hillmer, Erin Hines, David Hosack, Cindy Huebner, Louis Iverson, Julie Lapp, John Leach, Bob Long, Dave Minney, Anantha Prasad, Ava Rawn, Mary Ann Tate, and Jim Yerian. Mary Boda assisted with the graphical presentation of the data for the conference. We also thank Wayne Lashbrook, Steve Mathey, and Walt Smith, Mead Paper Corp., and Ralph Miller, Wayne National Forest, for supplying the study sites and logistical support. For conducting the prescribed fires, we thank personnel with the Wayne National Forest, particularly Art Martin, Terry Krasko, Tom Eaches, and Nelson Kruger who served as burn bosses. The following agencies and institutions also contributed personnel to conduct the fires: The Ohio Chapter of the Nature Conservancy, The Ohio Department of Natural Resources, Divisions of Forestry and Natural Areas and Preserves, Hocking Technical College, The Ohio State University, and Ohio University. Funding was provided by the Washington Office of the USDA Forest Service in a grant to Elaine Kennedy Sutherland for ecosystem management research.

Literature Cited

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

Arthur, M.A.; Paratley, R.D.; Blankenship, B.A. 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: 225-36.

Barnes, T.A.; Van Lear, D.H. 1998. **Prescribed fire effects on advanced regeneration in mixed hardwood stands.** Southern Journal of Applied Forestry. 22: 138-142.

Baskin, C.C.; Baskin, J.M. 1988. **Germination ecophysiology of herbaceous plant species in a temperate region.** American Journal of Botany. 75: 286-305.

Baskin, J.M.; Baskin, C.C.; Chester, E.W. 1999. **The big barrens region of Kentucky and Tennessee.** In: Anderson, R.C.; Fralish, J.S.; Baskin, J.M., eds. Savannas, barrens, and rock outcrop plant communities of North America. Cambridge University Press, Cambridge, UK: 190-205.

Batek, M.J.; Rebertus, A.J.; Schroeder, W.A.; Haithcoat, T.L.; Compas, E.; Guyette, R.P. 1999. **Reconstruction of early nineteenth-century vegetatiion and fire regimes in the Missouri Ozarks.** Journal of Biogeography. 26: 397-412.

Beatley, J.C. 1959. **The primeval forests of a periglacial area in the Allegheny Plateau (Vinton and Jackson Counties, Ohio).** Bulletin of the Ohio Biological Survey. 1: 1-166.

Boerner, R.E.J.; Sutherland, E.K.; Morris, S.J.; Hutchinson, T.F. [In press]. **Spatial variation in the effect of prescribed fire on N dynamics in a forested landscape.** Landscape Ecology.

Bratton, S.P. 1976. **Resource division in an understory herb community: responses to temporal and microtopographic gradients.** American Naturalist. 110: 679-693.

Brockway, D.G.; Lewis, C.E. 1997. **Long-term effects of dormant-season prescribed fire on plant community diversity, structure, and productivity in a longleaf pine wiregrass ecosystem.** Forest Ecology and Management. 96: 167-183.

Brose, P.; Van Lear, D.; Cooper, R. 1999. **Using shelterwood harvests and prescribed fire to regenerate oak stands on productive upland sites.** Forest Ecology and Management. 113: 125-141.

Burns R.M.; Honkala, B.H. 1990. **Silvics of North America, volume 2: Hardwoods.** USDA Agricultural Handbook 654. U.S. Department of Agriculture, Washington, DC. 877 p.

Cole, K.L.; Benjamin, P.K.; Klick, K.F. 1990. **The effects of prescribed burning on oak woods and prairies in the Indiana Dunes (Indiana).** Restoration and Management Notes. 8: 37-38.

DeSelm, H.R.; Clebsch, E.E.C.; Nichols, G.M.; Thor, E. 1973. **Response of herbs, shrubs and tree sprouts in prescribed-burn hardwoods in Tennessee.** In: Proceedings of the 13th Annual Tall Timbers Fire Ecology Conference. Tall Timbers Research Station, Tallahassee, FL: 331-344.

Deselm, H.R.; Clebsch, E.E.C. 1991. **Response types to prescribed fire in oak forest understory.** In: Nodvin, S.C.; Waldrop, T.A., eds. Fire and the environment: ecological and cultural perspectives: proceedings of an international symposium. Gen. Tech. Rep. SE-69. U.S. Department of Agriculture, Forest Service, Southeastern Forest Experiment Station, Asheville, NC: 22-33.

Dolan, R.W. 1994. **Effects of a prescribed burn on tree- and herb-layer vegetation in a post oak (*Quercus stellata*) dominated flatwoods.** Proceedings of the Indiana Academy of Sciences. 103: 25-32.

Ducey, M.J.; Moser, W.K.; Ashton, P.M.S. 1996. **Effect of fire intensity on understory composition and diversity in a *Kalmia*-dominated oak forest, New England, U.S.A.** Vegetatio. 123: 81-90.

Duffy, D.C.; Meier, A.J. 1992. **Do Appalachian herbaceous understories ever recover from clearcutting?** Conservation Biology. 6: 196-201.

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

Fralish, J.S.; Franklin, S.B.; Close, D.D. 1999. **Open woodland communities of southern Illinois, western Kentucky, and middle Tennessee.** In: Anderson, R.C.; Fralish, J.S.; Baskin, J.M., eds. Savannas, barrens, and rock outcrop plant communities of North America. Cambridge University Press, Cambridge, UK: 171-189.

Goebel, P.C.; Hix, D.M.; Oivero, A.M. 1999. **Seasonal ground-flora patterns and site factor relationships of second-growth and old-growth south-facing forest ecosystems, southeastern Ohio.** Natural Areas Journal. 19: 12-29.

Gordon R.B. 1969. **The natural vegetation of Ohio in pioneer days.** Bulletin of the Ohio Biological Survey. 3: 1-109.

Guyette, R.P.; Cutter, B.E. 1991. **Tree-ring analysis of fire history of a post oak savanna in the Missouri Ozarks.** Natural Areas Journal. 11: 93-99.

Heikens, A.L. 1999. **Savanna, barrens, and glade communities of the Ozark Plateaus Province.** In: Anderson, R.C.; Fralish, J.S.; Baskin, J.M., eds. Savannas, barrens, and rock outcrop plant communities of North America. Cambridge University Press, Cambridge, UK: 220-230.

Howell, J.A.; Vankat, J.L. 1981. **An ordination of the forest herb stratum of Abner's Hollow, south-central Ohio.** Ohio Journal of Science. 81: 98-104.

Huebner, C.D.; Randolph, J.C. 1995. **Environmental factors affecting understory diversity n second-growth deciduous forests.** American Midland Naturalist. 134: 155-165.

Hutchinson, T.F.; Boerner, R.E.J.; Iverson, L.R.; Sutherland, S.; Sutherland, E.K. 1999. **Landscape patterns of understory composition and richness across a moisture and nitrogen mineralization gradient in Ohio (U.S.A.) *Quercus* forests.** Plant Ecology. 144: 177-189.

Iverson, L.R.; Dale, M.E.; Scott, C.T.; Prasad, A. 1997. **A GIS-derived integrated moisture index to predict forest composition and productivity of Ohio forests (U.S.A.).** Landscape Ecology. 12: 331-348.

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

Lewis, C.E.; Harshbarger, T.J. 1976. **Shrub and herbaceous vegetation after 20 years of prescribed burning in the South Carolina Coastal Plain.** Journal of Range Management. 29: 13-18.

Loftis, D.; McGee, C.E., eds. 1993. **Oak regeneration: serious problems, practical recommendations. Symposium proceedings**; September 8-10, 1992, Knoxville, TN. Gen. Tech. Rep. SE-84. U.S. Department of Agriculture, Forest Service, Southeastern Forest Experiment Station, Asheville, NC.

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

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

Masters, R.E. 1991. **Effects of fire and timber harvest on vegeation and cervid use on oak-pine sites in Oklahoma Ouachita mountains.** In: Nodvin, S.C.; Waldrop, T.A., eds. Fire and the environment: ecological and cultural perspectives: proceedings of an international symposium. Gen. Tech. Rep. SE-69. U.S. Department of Agriculture, Forest Service, Southeastern Forest Experiment Station, Asheville, NC: 168-176.

Masters, R.E.; Lochmiller, R.L.; Engle, D.M. 1993. **Effects of timber harvest and prescribed fire on white-tailed deer forage.** Wildlife Society Bulletin. 21: 401-411.

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

Motzkin, G.; Foster, D.; Allen, A.; Harrod, J.; Boone, R. 1996. **Controlling site to evaluate history: vegetation patterns of a New England sand plain.** Ecological Monographs. 66: 345-365.

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

Olivero, A.M.; Hix, D.M. 1998. **Influence of aspect and stage on ground flora of southeastern Ohio forest ecosystems.** Plant Ecology. 139: 177-187.

Pickett, S.T.A.; Baskin, J.M. 1973. **The role of temperature and light in the germination behavior of *Ambrosia artemisiifolia*.** Bulletin of the Torrey Botanical Club. 100: 165-170.

Pitelka, L.F.; Ashmun, J.W.; Brown, R.L. 1985. **The relationships between seasonal variation in light intesity, ramet size, and sexual reproduction in natural and experimental populations of *Aster Acuminatus* (Compositae).** American Journal of Botany. 72: 311-319.

Rejmanek, M. 1989. **Invasibility of plant communities.** In: Drake, J.A.; Mooney, H.A.; di Castri, F.; Groves, R.H.; Kruger, F.J.; Rejmanek, M.; Williamson, M., eds. Scope 37. Biological invasions: a global perspective. John Wiley and Sons, Chichester, UK: 369-388.

Robison, S.A.; McCarthy, B.C. 1999. **Potential factors affecting the estimation of light availability using hemispherical photography in oak forest understories.** Journal of the Torrey Botanical Society. 126: 344-349.

Rogers, R.S. 1983. **Annual variability in community organization of forest herbs: effect of an extremely warm and dry early spring.** Ecology. 64: 1086-1091.

Schwartz, M.W.; Heim, J.R. 1996. **Effects of a prescribed fire on degraded forest vegetation.** Natural Areas Journal. 16: 184-191.

Sparks, J.C.; Masters, R.E.; Engle, D.M.; Palmer, M.W.; Bukenhofer, G.A. 1998. **Effects of late growing-season and late dormant-season prescribed fire on herbaceous vegetation in restored pine-grassland communities.** Journal of Vegetation Science. 9: 133-142.

Stout, W. 1933. **The charcoal iron industry of the hanging rock iron district: its influence on the development of the Ohio Valley.** Ohio Archaeological and Historical Quarterly. 42: 72-104.

Sutherland, E.K.; Scott, C.T.; Hutchinson, T.F. 1997. **Sapling topkill patterns after prescribed fire in an Ohio *Quercus* forest.** Bulletin of the Ecological Society of America. 78: 193.

Swan, F.R. 1970. **Post-fire response of four plant communities in south-central New York state.** Ecology. 51: 1074-1082.

Taft, J.B.; Schwartz, M.W.; Loy, R.P. 1995. **Vegetation ecology of flatwoods on the Illinoian till plain.** Journal of Vegetation Science. 6: 647-666.

Tilman, D.; Wedin, D.; Knops, J. 1996. **Productivity and sustainability influenced by biodiversity in grassland ecosystems.** Nature. 379: 718-720.

Wendel, G.W.; Smith, H.C. 1986. **Effects of a prescribed fire in a central Appalachian oak-hickory stand.** Res. Pap. NE-594. U.S. Department of Agriculture, Forest Service, Norheastern Forest Experiment Station, Broomall, PA. 8 p.

White, D.L.; Waldrop, T.A.; Jones, S.M. 1991. **Forty years of prescribed burning on the Santee fire plots: effects on understory vegetation.** In: Nodvin, S.C.; Waldrop, T.A., eds. Fire and the environment: ecological and cultural perspectives: proceedings of an international symposium. Gen. Tech. Rep. SE-69. U.S. Department of Agriculture, Forest Service, Southeastern Forest Experiment Station, Asheville, NC: 51-59.

Wilhelm, G.; Masters, L. 1994. **Floristic changes after five growing seasons in burned and unburned woodland.** Erigenia. 13: 141-150.