

Twenty Years of Vegetational Change on a Southern Illinois Barren

Roger C. Anderson

Department of Biology
Illinois State University
Normal, Illinois 61761

John E. Schwegman

Division of Natural Heritage
Illinois Department of Conservation
Springfield, Illinois 62707

ABSTRACT: Vegetational change on a southern Illinois barren was studied for a 20-year period. A total of 212 vascular plants was sampled on the 0.2-ha site, which contained a mixture of prairie and woodland species. The site was subjected to four prescribed spring burns between 1969 and 1973 and the last sampling of the site occurred in 1988, fifteen years after the last burn. Annuals and perennial prairie species responded positively to burning as did two shrubs, prairie willow (*Salix humilis*) and silky dogwood (*Cornus amomum*). In the absence of fire, shade-tolerant to moderately shade-tolerant and mesophytic tree species—including sugar maple (*Acer saccharum*), paw paw (*Asimina triloba*), white ash (*Fraxinus americana*), and American elm (*Ulmus americana*)—and woodland herbs appeared on the site. Species diversity tended to be highest after cessation of burning, when species composition and abundance was in flux with decreasing abundance of fire-adapted species and increasing abundance of woodland plants. For woody stems ≤ 8.9 cm dbh, diversity was the lowest following burning, when two shrub species, prairie willow and silky dogwood, had a high density of stems as a result of resprouting. Irregular fire intervals act as stabilizing forces in barren vegetation, permitting species with different responses to fire to coexist on a single site.

INTRODUCTION

Various authors have used the term barren to describe a transitional vegetation type containing prairie grasses and forbs, a sparse growth of trees (the latter often maintained in a "scrub" growth form as a result of periodic fires), and various species of fire-resistant shrubs (Gleason 1922, Curtis 1959, Grimm 1984, Nuzzo 1986). In Illinois, barrens historically supported many of the herbaceous species associated with the tallgrass prairie, but they apparently contained more trees and shrubs than were found in prairies, and they may have lacked some characteristic prairie species (Vestal 1936). White and Madney (1978) viewed barrens as local inclusions in forested land of prairie flora mixed with forest.

Major tracts of Illinois tallgrass prairie were restricted to glaciated landscapes. Undoubtedly the broader ridges and stream valleys in the unglaciated portions of southern Illinois also occasionally supported barrens, as indicated by stands of prairie species in these locations (Anderson 1970, 1972; Anderson and Schwegman 1971). Barrens were recorded for some locations in extreme southeastern Illinois in the original land survey records, even though these areas now support closed forest.

Fire is thought to be necessary to maintain the prairie flora associated with barrens in this region; in the absence of fire, these

areas presumably would undergo succession to closed forest communities (Gleason 1922, Curtis 1959). Burning should enhance the prairie flora in a barren but it should not completely eliminate woody species, if the community as a whole is adapted to periodic fires.

In many portions of the Midwest, fire frequency declined as Europeans settled and displaced the aboriginal people (Curtis 1959; Pyne 1982, 1986; and others). In southern Illinois, however, European settlers continued the practice of burning the landscape until the arrival of the U.S. Forest Service and the creation of the Shawnee National Forest in the 1930s (Miller 1920, Anderson 1972). Thus it is likely that our study site had not been burned for at least 30 to 40 years when we initiated our research in 1968.

The purpose of this study was to document changes in barren vegetation in response to prescribed burning and in response to the absence of fire. The barren we studied had experienced major encroachment by the exotic Japanese honeysuckle (*Lonicera japonica*), so a further objective was to determine the effectiveness of fire in controlling honeysuckle.

The data also permitted us to examine some generalized models of succession that have been proposed by various workers (Egler 1954; Loucks 1970; Horn 1974,

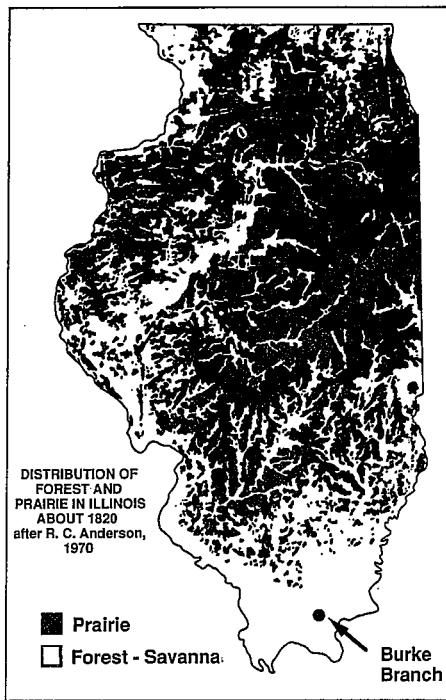


Figure 1. Location of the study site in Illinois.

1981; McIntosh 1980, 1981; Huston and Smith 1987). Specifically, we examined how species diversity, patterns of species replacement, and life history characteristics of the dominant plant species vary during succession, and how some of these are influenced by periodic prescribed burning.

The study site is about 0.2 ha in area on level terrain along the intermittent Burke Branch Creek, in Pope County, in extreme southeastern Illinois. The site, surrounded by forest, is located about 56 km south of the distribution of prairie in Illinois (Figure 1). There are, however, degraded barren remnants in scattered locations along Burke Branch Creek and on some of the uplands adjacent to the creek. Previously published papers reported on portions of the data from this site that were obtained after 3 (Anderson and Schwegman 1971) and 15 years (Schwegman and Anderson 1986) of a 20-year study. This paper summarizes data collected over the 20-year period.

METHODS

The study site was subjected to four prescribed burns in the springs of 1969, 1970, 1972, and 1973. The site was sampled six

times during the 20 years of the study: a preburn sample (1968), after the 1969 and 1970 spring burns, in 1971, and in 1983 and 1988 (10 and 15 years after the last prescribed burn, respectively).

Nested quadrats were placed at five permanent sampling points. At four of the points, trees (stems > 8.9 cm dbh [diameter at breast height, 1.4 m]) were measured in a 0.01-ha circular quadrat. Presence of woody plants, tree reproduction, shrubs, and vines was recorded in a 0.004-ha quadrat in five size classes: (1) > 15 cm tall but ≤ 1.4 m tall, (2) > 1.4 m tall but ≤ 1.2 cm dbh, (3) > 1.2 cm dbh but ≤ 3.8 cm dbh, (4) > 3.8 cm dbh but ≤ 6.4 cm dbh, and (5) > 6.4 cm dbh but ≤ 8.9 cm dbh. Frequency of herbaceous plants and woody plants ≤ 15 cm tall was determined using ten 1m² quadrats located within the 0.01-ha circular quadrat. The density of Japanese honeysuckle was so great that it would have had nearly 100% frequency in the 1m² quadrats. Consequently, it was recorded in a 5dm² quadrat nested within the 1m² quadrats. At the fifth sampling point, the area available to sample was too small to accommodate a 0.01-ha quadrat; the woody plants > 15 cm tall were sampled in a 0.004-ha quadrat and only four 1m² quadrats were used to sample herbaceous plants and woody plants ≤ 15 cm tall.

Tree (stems > 8.9 cm dbh) basal area (m²/ha) and density (stems/ha) were calculated by species for each year of the study. For woody plants (trees, shrubs, and vines) ≤ 8.9 cm dbh, density was calculated by size class. Species diversity was examined by computing species richness (number of

species) and the Shannon-Weiner index (H' , Shannon and Weaver 1949). Percent similarity (Gauch 1982) was calculated between samples using presence data for herbaceous species in the 1 m² quadrats.

Nomenclature follows Mohlenbrock (1986).

RESULTS

With a few exceptions, the highest similarity values were obtained for samples that were taken closest in time (usually 1–3 years) (Table 1). This suggests that there was a directional change in species composition over time and, perhaps, that fire had little effect on species composition. Nevertheless, similarity to the 1968 sample decreased from 1969 to 1970 after one and two burns, respectively, and then it increased slightly in 1971 after a one-year pause in burning. The 1983 and 1988 samples have the least similarity to the 1968 sample. This apparently resulted from the continued increasing dominance by forest species and a decline in the prairie flora that was only temporarily interrupted by the prescribed burns of the early 1970s.

Tree density decreased following the burn in 1969, varied between 157 to 180 trees/ha during the period 1970 to 1983, and then increased to 337 trees/ha by 1988 in the absence of fire (Table 2). Tree basal area increased slightly from 1968 through 1971 (4.9 to 5.5 m²/ha) because the larger trees were not killed by the fire and they continued to grow. Basal area increased to 7.9 m²/ha by 1983 and more than doubled between 1968 and 1988 (4.9 to 10.2 m²/ha). Based on

Table 1. Percent similarity based on presence in 1m² quadrats for herbaceous plants.

	1968	1969	1970	1971	1983
1969	55	X			
1970	51	66	X		
1971	57	68	68	X	
1983	41	44	39	40	X
1988	40	41	43	35	64

Table 2. Density (stems per ha) and basal area (m² per ha) of tree stems > 8.9 cm dbh.

Sample year	1968		1969		1970		1971		1983		1988	
	Basal Area	Density	Basal Area	Density	Basal Area	Density	Basal Area	Density	Basal Area	Density	Basal Area	Density
<i>Betula nigra</i>	1.47	44.9	1.44	44.9	1.51	44.9	1.8	44.9	1.4	22.4	3.0	45
<i>Juglans nigra</i>	0.32	44.9	0.16	22.4	0.32	44.9	0.4	44.9	1.2	67.4	1.5	68
<i>Platanus occidentalis</i>	2.84	67.4	2.84	67.4	3.01	67.4	3.3	67.4	3.7	44.9	3.7	45
<i>Prunus serotina</i>	0.14	22.4	—	—	—	—	—	—	0.2	22.4	0.8	90
<i>Ulmus alata</i>	0.16	22.4	0.16	22.4	0.16	22.4	—	—	—	—	—	—
<i>U. rubra</i>	—	—	—	—	—	—	—	—	—	—	0.4	22
<i>Quercus prinoides</i>	—	—	—	—	—	—	—	—	1.4	22.4	0.6	45
<i>Q. marilandica</i>	—	—	—	—	—	—	—	—	—	—	0.2	22
Total	4.93	202.0	4.60	157.1	5.0	179.6	5.5	157.2	7.9	179.5	10.2	337

basal area and density, sycamore (*Platanus occidentalis*), black walnut (*Juglans nigra*), and river birch (*Betula nigra*) were among the three leading species in the tree stratum throughout the study.

Following prescribed burns in 1969 and 1970, the density of stems in the seedling stratum (includes seedlings and small resprouted stems [size classes 1 and 2]) increased; however, the density of woody stems in the sapling stratum (size classes 3, 4, and 5) decreased following burning (Figure 2). The increase in plant density in the seedling stratum in 1969 and 1970 was largely due to vigorous resprouting of two shrubs, prairie willow (*Salix humilus*) and silky dogwood (*Cornus amomum*), which largely increased stems in size class 1. In the absence of fire, stems in the seedling stratum decreased, whereas the stems in the sapling stratum increased (Figure 2). The decrease in stems in the seedling stratum was apparently due to suppression of prairie willow and silky dogwood caused by an increase in saplings of tree species and, perhaps, as the result of self-thinning of the vigorous growth of dogwood and willow shoots. In contrast, the shade-tolerant paw paw (*Asimina triloba*) showed a substantial increase in stems in size class 1 between 1983 and 1988 (Figure 3). Although the density of sassafras (*Sassafras albidum*)

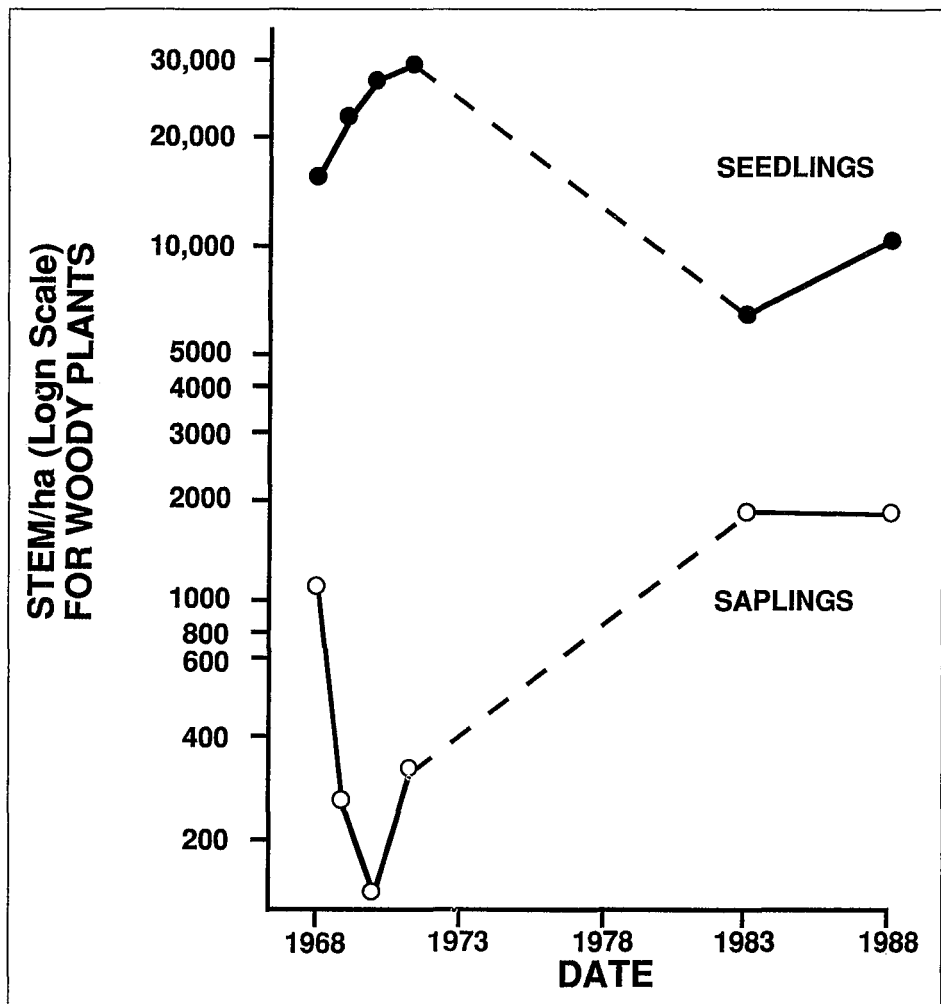


Figure 2. Changes in densities of woody plants in the seedling and sapling strata during the study.

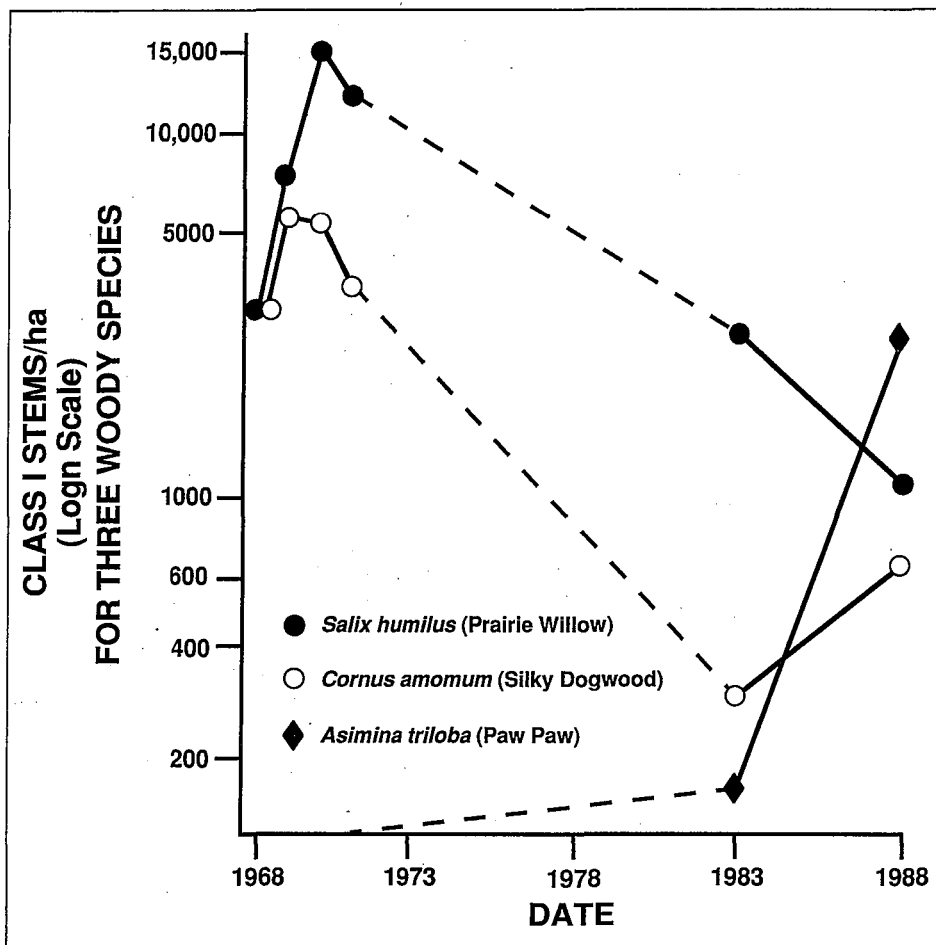


FIGURE 3. Variation in density in size class 1 (stems > 15 cm tall but \leq 1.5 m tall) for two fire-adapted shrub species and one tree species.

TABLE 3. Diversity of woody and herbaceous species.

	1968	1969	1970	1971	1983	1988
Species Richness ^a						
Herbs	51	69	73	53	65	84
Vines	2	4	2	4	4	5
Shrubs	11	10	9	9	8	12
Trees	11	10	12	14	20	23
All Species	75	93	86	80	97	124
H ^b						
Herbs	3.45	3.66	3.84	3.80	3.69	3.89
Woody Plants ^c	2.16	1.85	1.60	1.51	2.99	1.66

^a Number of species
^b Shannon-Weiner diversity index
^c Woody plants include shrubs, vines, and trees in the seedling and sapling strata

and black walnut in size classes 1 and 2 increased in response to burning, the decline in density in these classes in the absence of fire was less for these tree species than for the two shrubs. The sapling density of walnut decreased with fire but walnut and sassafras increased in sapling density after the cessation of burning (Figure 4).

A total of 212 species of vascular plants was sampled on the 0.2-ha site during the study: 5 vines, 17 shrubs, 31 trees, and 159 herbs. The smallest number of species (75) (Table 3) was found in the preburn data (1968). Species richness increased after the first two burns, but the largest number of species of herbs, shrubs, and trees (124) occurred in 1988. The number of species of shrubs (9–12) was relatively constant throughout the study; however, the number of herbaceous species (51–84) and trees (11–23) showed considerable variation.

Overall tree species richness in the seedling and sapling strata decreased with burning and then increased in the absence of fire. Tree species richness decreased from 9 to 6 (Table 4) after two fires and then increased to 18 and 20 after 10 and 15 years of fire exclusion, respectively. There was continuous flux in the tree species composition in the seedling and sapling strata (Table 4). Red cedar (*Juniperus virginiana*) was eliminated from the site after the first fire. Some species — including persimmon (*Diospyros virginiana*), black walnut, sassafras, and black cherry (*Prunus serotina*) — were on the site continuously, whereas other species — spanish oak (*Quercus falcata*), white oak (*Quercus alba*), black willow (*Salix nigra*), loblolly pine (*Pinus taeda*) and ironwood (*Ostrya virginiana*) — were recorded only once. In 1983 and 1988, several shade-tolerant to moderately shade-tolerant and mesophytic species were recorded on the site. These included sugar maple (*Acer saccharum*), paw paw, white ash (*Fraxinus americana*), American elm (*Ulmus americana*), and black gum (*Nyssa sylvatica*).

Diversity for herbaceous species, as measured by the Shannon-Weiner Index (H') (Shannon and Weaver 1949), varied little between years of the study, but it was lowest for the first year and highest for the last

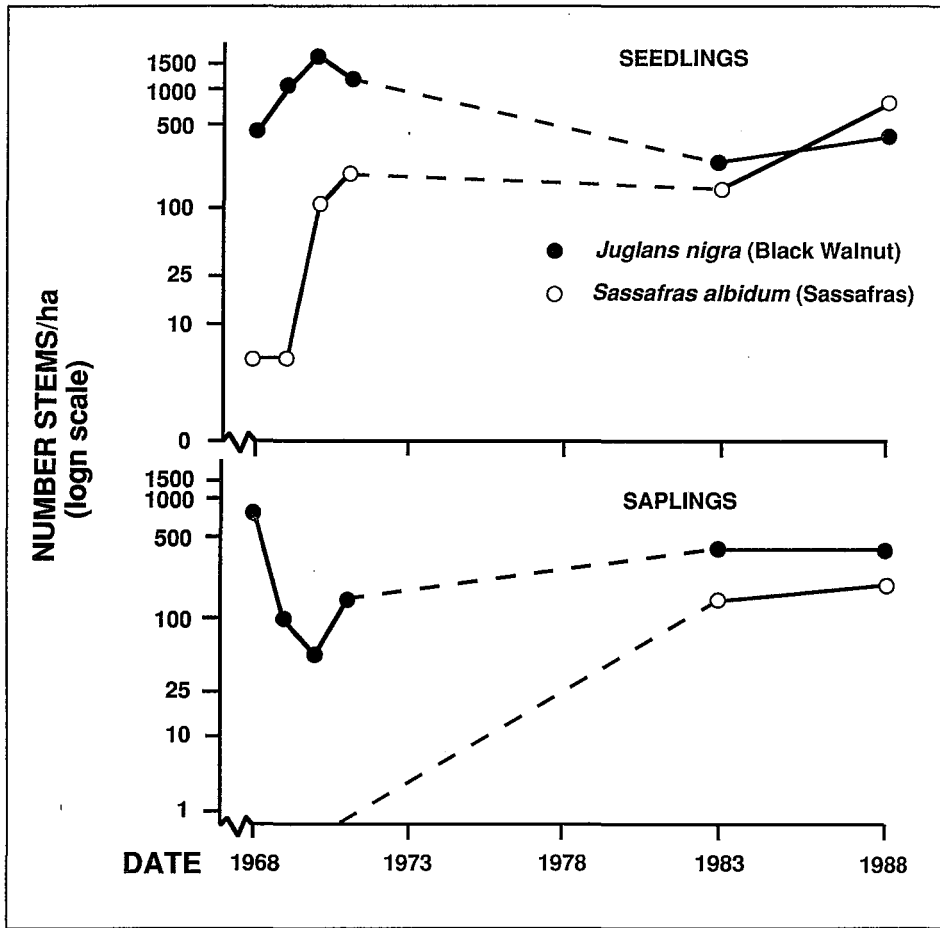


FIGURE 4. Changes in density for two tree species in the seedling and sapling strata during the study.

(Table 3). The density of woody stems in size classes 1–5 and the Shannon-Weiner Diversity Index were negatively correlated (Figure 5). Seedling and sapling density was high in growing seasons immediately after burns and in 1971, when a high degree of dominance (McNaughton and Wolf 1970) was expressed by prairie willow and silky dogwood, accounting for the decline in diversity. In the first year of the study (preburn) and in 1983, dominance was shared more evenly between the shrub and tree species (paw paw, sassafras, and black walnut). Nevertheless diversity as measured by the Shannon-Weiner index declined by 1988, even though total species richness (i.e., for all strata) was at its highest level (Table 3).

Prairie species such as big bluestem (*Andropogon gerardi*), partridge pea (*Cassia fasciculata*), little bluestem (*Schizachyrium scoparium*), tall tickseed

(*Coreopsis tripteris*), and Indian grass (*Sorghastrum nutans*) were prominent in the herbaceous layer after two fires (1970); however, their abundances decreased in the absence of fire, while woodland species such as *Chasmanthium latifolium*, skull cap (*Scutellaria incana*), and wood rush (*Luzula multiflora*), increased in importance (Table 5).

Several annual legumes experienced large increases in quadrat frequency following the first fire, and two annual legumes (*Cassia fasciculata* and *C. nictitans*) also had large increases in frequency after the second burn (Table 6). This immediate response to burning suggests that there were substantial quantities of seeds of these species in the soil seed bank. Annual legumes also showed rapid declines in frequency following fire cessation. Perennial species, including several prairie plants, also responded positively to burning, but their

increases in frequency in response to fire and their decreases in frequency following fire cessation were less rapid than that of the annual legumes. In the last two samples, woodland species such as *Chasmanthium latifolium*, Christmas fern (*Polystichum acrostichoides*), and skull cap increased in frequency.

The frequency of Japanese honeysuckle (Figure 6) did not decrease after the first burn but it was reduced by about one-half following the second burn. These results are somewhat misleading, however, because some of the honeysuckle that had climbed as a vine into the trees was killed back to ground level after the first burn (Anderson and Schwegman 1971). After the cessation of burning there was a marked increase in honeysuckle, suggesting that burning in fire-adapted communities may be an effective method of controlling, but perhaps not eradicating, Japanese honeysuckle (Faulkner et al. 1989).

DISCUSSION

Changes in the barren vegetation following the prescribed burns of 1969 and 1970 generally followed the pattern for secondary succession in deciduous forests proposed by several authors (Drury and Nisbet 1973, Horn 1974, and others). Herbaceous annual and perennial species increased with fire, and in the absence of fire, shade-

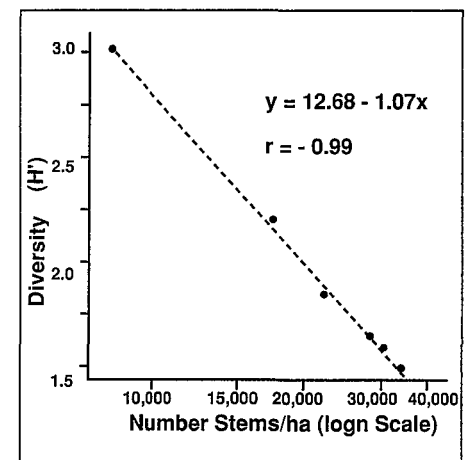


FIGURE 5. The relationship between the density of woody plants in size classes 1–5 and diversity as measured by the Shannon-Weiner Index (H').

tolerant trees species and woodland herbs increased in abundance. Nevertheless, vegetational changes are often more complex than those suggested by general models for secondary succession (McIntosh 1980, 1981; Horn 1981; Peet and Christensen 1980; McCune and Cottam 1985). Fire is a necessary component of the tallgrass prairie ecosystem; it ensures its long-term stability (Risser et al. 1981, Anderson 1982).

Many of the annual species that occurred on our study site are part of the prairie flora (Curtis 1959, Mohlenbrock 1986). They are opportunistic species that increased in abundance in response to reduced competition from fire-susceptible species and the removal of litter, which provided open sites for their germination and growth. Repeated

burning may have decreased the abundance of the annuals because of increased competition from perennial herbaceous prairie species. Annual ragweed (*Ambrosia artemisiifolia*) showed this pattern: it increased in frequency after the first fire but it decreased after the second. Cessation of fire also decreased the abundance of annual species, apparently as the result of an increase in dominance of tree seedlings and saplings, which resulted in reduced light intensity beneath the seedling-sapling canopy. Many annual species, however, can retain viable seed in seed banks for long periods of time (Baker 1989), so that periodic fires are likely to stimulate increases in annuals. This pattern has been documented for annual legumes on other sites in southern Illinois (Anderson and Van

Valkenburg 1977). Also, Martin and co-workers (1975) showed that under laboratory conditions, moist heat simulating field burning conditions enhances germination of several annual legumes with hard seed coats. The response of the annuals in our study supports the generalization proposed by Rice (1989): that seed banks occur in annual, weedy species that are able to respond to canopy openings created through perturbations, especially under conditions where there is a rapid decline in weedy annuals as the sward vegetation recovers.

In the absence of fire, the study site would undoubtedly undergo succession to a closed forest community dominated by many of the moderately shade-tolerant to shade-tolerant, mesophytic tree species that have recently invaded the site. These tree species include white ash, tulip poplar (*Liriodendron tulipifera*), sugar maple, and others. The changes in species composition on the site, especially in the seedling and sapling strata, support the "relay floristics" model (Egler 1954) in which species constantly invade the site and some species

Table 4. Tree species in seedling and sapling strata.

	1968	1969	1970	1971	1983	1988
Number of species	9	8	6	12	18	20
Species						
<i>Juniperus virginiana</i>	X					
<i>Quercus prinoides</i>	X	X		X	X	
<i>Betula nigra</i>	X				X	X
<i>Cornus florida</i>	X			X	X	X
<i>Ulmus rubra</i>	X	X	X	X		X
<i>Diospyros virginiana</i>	X	X	X	X	X	X
<i>Juglans nigra</i>	X	X	X	X	X	X
<i>Sassafras albidum</i>	X	X	X	X	X	X
<i>Prunus serotina</i>	X	X	X	X	X	X
<i>Carya cordiformis</i>		X			X	X
<i>Quercus velutina</i>		X		X	X	
<i>Ulmus alata</i>			X			
<i>Quercus falcata</i>				X		
<i>Quercus alba</i>				X		
<i>Salix nigra</i>				X		
<i>Pinus taeda</i>					X	
<i>Ostrya virginiana</i>					X	
<i>Carya ovalis</i>				X		X
<i>Asimina triloba</i>					X	X
<i>Cercis canadensis</i>					X	X
<i>Acer rubrum</i>					X	X
<i>Carya tomentosa</i>					X	X
<i>Quercus rubra</i>					X	X
<i>Ulmus americana</i>					X	X
<i>Liriodendron tulipifera</i>					X	X
<i>Quercus marilandica</i>						X
<i>Fraxinus americana</i>						X
<i>Nyssa sylvatica</i>						X
<i>Acer saccharum</i>						X

Table 5. Comparison of quadrat frequency^a in 1m² quadrats for herbaceous plants after two fires (1970) and 15 years postburn (1988).

	1970	1988
Species		
<i>Andropogon gerardii</i>	77	32
<i>Cassia fasciculata</i>	64	2
<i>Schizachyrium scoparium</i>	61	7
<i>Cassia nictitans</i>	56	0
<i>Panicum anceps</i>	48	2
<i>Coreopsis tripteris</i>	39	18
<i>Acalypha gracilens</i>	36	11
<i>Solidago nemoralis</i>	34	0
<i>Ambrosia artemisiifolia</i>	32	4
<i>Potentilla simplex</i>	30	25
<i>Sorghastrum nutans</i>	23	9
<i>Euphorbia corollata</i>	23	27
<i>Chasmanthium latifolium</i>	23	41
<i>Scutellaria incana</i>	9	30
<i>Muhlenbergia sobolifera</i>	2	33
<i>Luzula multiflora</i>	0	81

^aFor species with quadrat frequencies $\geq 21\%$ in 1970 or 1988

disappear, presumably in response to changes in environmental conditions on the site. Why the shade-tolerant to moderately shade-tolerant tree species did not invade the site earlier is unknown. However, the forests surrounding our study site have only recently begun to change from an oak-dominated forest to one in which more mesophytic and shade-tolerant species have increased importance. Propagules of these species may have only recently arrived at the study site. Also, the cover of perennial prairie grasses and forbs may have been sufficiently dense to prevent tree seedling establishment.

The changes in diversity on the site follow those predicted by several workers (Bazzaz 1968, Loucks 1970, and others). Diversity of herbaceous and woody species is greatest when the vegetation is in a state of transition from one major vegetation type to another. Diversity as measured by species richness (number of species) was highest in the last year of our study, when the prairie flora was decreasing in importance and the woodland trees and herbs were increasing in importance. These results are similar to those reported by Tester (1989), who found that of various fire frequencies, two years of burning followed by two years without fire results in the highest species richness in a Minnesota oak savanna. This fire frequency maintained an intermediate vegetation type containing both prairie and oak forest species.

In the seedling and sapling strata, diversity of woody plants, as expressed by the Shannon-Weiner Index (H'), was lowest when prairie willow and silky dogwood became dominant in response to burning. In the absence of burning, diversity (H') initially increased in the seedling and sapling strata, as the density of the two shrubs declined and the abundance of tree seedlings and saplings increased. Then diversity declined in 1988 as tree seedlings and saplings continued to increase in abundance and, presumably, suppressed the shrubs. This change in diversity follows the model proposed by Huston and Smith (1987). Diversity declines when the abundance of one or a few species rapidly increases. This results in a decrease in the abundance of other species and a decline in the evenness of the distri-

bution of abundances among the species.

Historically, barren vegetation may have fluctuated between a community dominated by herbaceous plants — primarily annual and perennial prairie species — to a community dominated by woody vegetation that suppressed the growth of the fire-dependent herbaceous species. In a region where barrens were a relatively common vegetation type, there may have been an array of sites that supported communities in various stages of transition from the herbaceous-dominated community to those where fire had been excluded for extended periods of time and woody species dominated. Also, many of the woody species associated with barrens, including various species of oaks and shrubs such as prairie willow and hazel (*Corylus* sp.), are adapted to fire and are not likely to be eliminated from a site by repeated burning, although their vigor and abundance might decline under a high-frequency fire regime. This may explain why it is so difficult to precisely define this vegetation type (Nuzzo 1986).

Fire is an important factor in the mainte-

nance of barren vegetation, but the role of fire in this community is complex. Fire did not eliminate the woody species from our study site, and several of the shrubs responded positively to burning. In the absence of fire, tree species increased in the

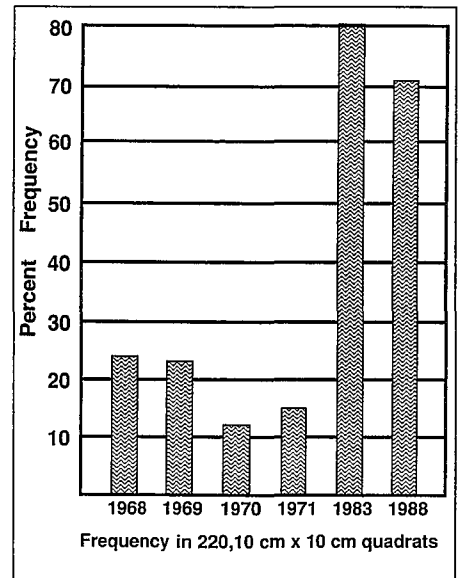


FIGURE 6. Changes in quadrat frequency for Japanese honeysuckle (*Lonicera japonica*) during the study.

Table 6. Changes in quadrat frequency of selected herbaceous species. The highest frequency value for each species is underlined.

	1968	1969	1970	1971	1983	1988
Annual Species						
<i>Ambrosia artemisiifolia</i>	7	<u>48</u>	32	9	0	4
<i>Strophostyles leiosperma</i>	0	<u>27</u>	11	4	0	0
<i>Cassia fasciculata</i>	16	43	<u>64</u>	27	9	2
<i>Cassia nictitans</i>	0	52	<u>57</u>	34	7	2
Perennial Species						
<i>Andropogon gerardii</i>	57	<u>84</u>	77	70	39	32
<i>Galium pilosum</i>	16	<u>18</u>	11	16	2	0
<i>Coreopsis tripteris</i>	23	32	<u>77</u>	50	39	19
<i>Rudbeckia hirta</i>	14	9	<u>20</u>	16	7	2
<i>Solidago canadensis</i>	4	6	<u>8</u>	7	4	2
<i>Tradescantia ohimensis</i>	2	4	<u>5</u>	4	2	4
<i>Potentilla simplex</i>	20	27	30	<u>45</u>	27	25
<i>Solidago nemoralis</i>	11	4	34	<u>41</u>	7	0
<i>Sorghastrum nutans</i>	18	21	23	<u>34</u>	21	9
<i>Chasmanthium latifolium</i>	23	9	11	11	39	<u>41</u>
<i>Scutellaria incana</i>	2	7	9	0	18	<u>30</u>
<i>Polystichum acrostichoides</i>	0	0	0	0	5	9

seedling and sapling strata, whereas the fire-adapted shrubs decreased in abundance, as did the herbaceous prairie species. Historically in southern Illinois, barrens may have burned at irregular intervals that tended to maintain a mixture of prairie and forest species. If fire is excluded from a barren for an extended period of time, there will be a complete loss of the prairie species and the forest will come to dominate.

Fire stabilizes barren vegetation if it occurs often enough to encourage the prairie species but not so often that forest species are eliminated. Thus fire frequency is the force in barrens that permits species with different responses to fire to coexist on a single site. Barren vegetation may have developed in areas with climatic, topographic, and edaphic features that encouraged fires to occur at irregular intervals and which were capable of supporting woody species tolerant of periodic fires (Curtis 1959, Anderson 1982, Grimm 1984, Anderson and Brown 1986).

LITERATURE CITED

- Anderson, R.C. 1970. Prairies in the prairie state. *Transactions of the Illinois Academy of Science* 63:214-221.
- Anderson, R.C. 1972. Prairie history, management, and restoration in southern Illinois. Pp. 15-20 in J. Zimmerman, ed., *Proceedings of the Second Midwest Prairie Conference*. University of Wisconsin, Madison.
- Anderson, R.C. 1982. An evolutionary model summarizing the roles of fire, climate, and grazing animals in the origin and maintenance of grasslands. Pp. 297-308 in J. Estes, R. Tyrl, and J. Brunken, eds., *Grasses and Grasslands*. University of Oklahoma Press, Norman.
- Anderson, R.C. and L.E. Brown. 1986. Stability and instability in plant communities following fire. *American Journal of Botany* 73:364-368.
- Anderson, R.C. and J.E. Schwegman. 1971. The response of southern Illinois barren vegetation to prescribed burning. *Transactions of the Illinois Academy of Science* 64:287-291.
- Anderson, R.C. and C. Van Valkenburg. 1977. Response of a southern Illinois grassland community to burning. *Transactions of the Illinois Academy of Science* 69:399-414.
- Baker, H.G. 1989. Some aspects of the natural history of seed banks. Pp. 9-21 in M. Leck, V. Parker, and R. Simpson, eds., *Ecology of soil seed banks*. Academic Press, New York.
- Bazzaz, F. 1968. Succession on abandoned fields in the Shawnee Hills, southern Illinois. *Ecology* 49:924-936.
- Curtis, J.T. 1959. *The vegetation of Wisconsin*. University of Wisconsin Press, Madison.
- Drury, W. and I. Nisbet. 1973. Succession. *Journal of the Arnold Arboretum* 54:331-368.
- Egler, F. 1954. Vegetation science concepts I. Initial floristic composition—a factor in old-field development. *Vegetatio* 4:412-417.
- Faulkner, J., E. Clebsch, and W. Sanders. 1989. Use of prescribed burning for managing natural and historic resources in Chickamauga and Chattanooga National Military Park, USA. *Environmental Management* 13:603-612.
- Gauch, H.G. 1982. *Multivariate analysis in community ecology*. Cambridge University Press, New York.
- Gleason, H.A. 1922. The vegetational history of the Middle West. *Annals of the Association of American Geographers* 12:39-85.
- Grimm, E.C. 1984. Fire and other factors controlling the big woods vegetation of Minnesota in the mid-nineteenth century. *Ecological Monographs* 53:291-311.
- Horn, H. 1974. The ecology of secondary succession. *Annual Review of Ecology and Systematics* 5:25-37.
- Horn, H. 1981. Some causes of variety in patterns of secondary succession. Pp. 24-35 in D. West, H. Shugart, and D. Botkin, eds., *Forest succession concepts and application*. Springer-Verlag, New York.
- Huston, M. and T. Smith. 1987. Plant succession: life history and competition. *The American Naturalist* 130:168-198.
- Loucks, O. 1970. Evolution of diversity, efficiency, and community stability. *American Zoologist* 10:17-25.
- Martin, R., R. Miller, and C. Cushwa. 1975. Germination response of legume seeds subjected to moist and dry heat. *Ecology* 56:1441-1445.
- McCune, B. and G. Cottam. 1985. The successional status of a southern Wisconsin oak woods. *Ecology* 64:1270-1278.
- McIntosh, R.P. 1980. The relationship between succession and the recovery process in ecosystems. Pp. 11-62 in J. Cairns, ed., *The recovery process in damaged ecosystems*. Ann Arbor Science Publications, Ann Arbor, Mich.
- McIntosh, R.P. 1981. Succession and ecological theory. Pp. 10-23 in D. West, H. Shugart, and D. Botkin, eds., *Forest succession concepts and application*. Springer-Verlag, New York.
- McNaughton, S.J. and L.L. Wolf. 1970. Dominance and the niche in ecological systems. *Science* 167:131-139.
- Miller, R.B. 1920. Fire prevention in Illinois. *Illinois Natural History Survey, Forestry Circular No. 2*.
- Mohlenbrock, R.H. 1986. *Guide to the vascular flora of Illinois*. Southern Illinois University Press, Carbondale.
- Nuzzo, V.A. 1986. Extent and status of midwest oak savanna: presettlement and 1985. *Natural Areas Journal* 6(2):6-36.
- Peet, R.K. and N.L. Christensen. 1980. Succession: a population process. *Vegetatio* 43:131-140.
- Pyne, S.J. 1982. *Fire in America: A cultural history of wildland and rural fire*. Princeton University Press, Princeton, N.J.
- Pyne, S.J. 1986. "These conflagrated prairies": a cultural fire history of grasslands. Pp. 131-137 in G. Clambey and R. Pemble, eds., *The prairie: past, present and future*. Proceedings of the Ninth North American Prairie Conference, North Dakota State University, Fargo.
- Rice, K.J. 1989. Impact of seed banks on grassland community structure and population dynamics. Pp. 211-230 in M. Leck, V. Parker, and R. Simpson, eds., *Ecology of soil seed banks*. Academic Press, New York.
- Risser, P., E. Birney, H. Blocker, S. May, W. Parton, and J. Weins. 1981. *The true prairie ecosystem*. Hutchinson Ross Publishing Company, Stroudsburg, Penn.
- Schwegman, J. and R. Anderson. 1986. Effect of eleven years of fire exclusion on the vegetation of a southern Illinois barren remnant. Pp. 146-148 in G. Clambey and R. Pemble, eds., *The prairie: past, present and future*. Proceedings of the Ninth North American Prairie Conference, North Dakota State University, Fargo.
- Shannon, C.E. and W. Weaver. 1949. *The mathematical theory of communication*. University of Illinois Press, Urbana.
- Tester, J.R. 1989. Effect of fire frequency on oak savannah in east-central Minnesota. *Bulletin of the Torrey Botanical Club* 116:134-144.
- Vestal, A.G. 1936. Barrens vegetation in Illinois. *Transactions of the Illinois Academy of Science* 29:29-80.
- White, J. and M. Madney. 1978. Classification of natural communities in Illinois. Pp. 309-405 in J. White, ed., *Illinois Natural Areas Inventory Technical Report. Vol. 2, Survey methods and results*. Illinois Natural Areas Inventory, Urbana.