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Effects of fire frequency on oak savanna in east-central Minnesota

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ABSTRACT

TESTER, J. R. (Department of Ecology and Behavioral Biology, University of Minnesota, Minneapolis, MN 55455). Effects of fire frequency on oak savanna in east-central Minnesota. Bull. Torrey Bot. Club 116: 134–144. 1989.—From 1964 to 1984, prescribed burning experiments were performed on oak (*Quercus* spp.) forest and oak savanna in east-central Minnesota, USA. Eighty-nine burns were carried out on 9 compartments ranging from 2.6 to 27.5 ha. Intervals between fires varied from 1 to 12 years. Soil pH increased significantly with frequency of burning. Total nitrogen was positively correlated ($P < 0.01$) with per cent organic matter. Species richness was highest in areas which were burned approximately every 2 years. Different plant functional groups responded differently to frequency of burning. Cover of true prairie grasses increased from less than 5 to about 15 per cent. True prairie forbs showed a significant increase in cover from less than 2 to about 8 per cent with increasing frequency of burning. Density of true prairie shrubs showed a tendency to increase whereas density of non-prairie shrubs and of trees showed tendencies to decrease with increased frequency of fire. Thus, the frequency of prescribed burning strongly influenced vegetative composition and physiognomy as well as soil characteristics.

Key words: oak savanna, prescribed burning, succession, prairie plants, nitrogen, species richness.

The structure, diversity and dynamics of vegetation is controlled by a variety of factors: climate, soils, herbivory, disturbance frequency and other selective forces. Fire has been a major, natural force in prairie and savanna ecosystems. Plants and animals in these ecosystems are often adapted to fire, whereas species from other, nearby ecosystems may not be fire adapted (Frost 1985). Gibson (1988) indicated that the impact of fire on prairie communities was a function of the scale of analysis. He found that biomass and cover of different life forms were strongly influenced by the frequency of fire, but that some components, such as total cover, reflected climatic fluctuations. Thus, it seems likely that fire frequency is an important determinant of savannas in terms of interrupting the successional sequence and as a natural regenerative agent.

Prescribed burning has been widely used throughout the world to manage grasslands and savannas, and indirectly to manage animal populations which live in them. Much of the available knowledge on the effects of fire on plant communities has been derived from studies following the occurrence of a wild or uncontrolled fire (Mooney 1981). By experimentally manipulating burns we can obtain new information on the impact of fire on natural communities.

In 1964 a management program using prescribed burning was implemented to restore a portion of Cedar Creek Natural History Area to oak savannah from oak forest. This paper reports on the effects of these burns on aspects of the soil and vegetation.

Study Area. Cedar Creek Natural History Area in east-central Minnesota, USA, lies between the tallgrass prairie biome to the west and the deciduous forest biome to the east. Prior to settlement the vegetation in this region was probably a mixture of tallgrass prairie with scattered bur oak (*Quercus macrocarpa*) and Hill's oak (*Q. ellipsoidalis*) (Pierce 1954) and large patches of oak scrub (Grimm 1984). Historical data

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Table 1. Dates of prescribed burns at Cedar Creek Natural History Area in east-central Minnesota.

	Compartment number								
Year	11	13	7	15	8	5	1	3	4
1964							4/23		
1965						5/07	4/28	4/07	5/07
1966			8/30			4/25	4/13	4/25	4/13
1967			9/06	4/27	4/10	5/05	4/27	4/14	5/05
1968		4/29		4/26	4/29			4/26	4/26
1969	5/14		4/23					5/12	5/12
1970							5/04		5/04
1971					5/12	4/29		4/21	4/29
1972				5/08	4/25	4/25	5/08	5/18	4/25
1973			5/16	4/26		5/16	4/26	5/16	4/26
1974								4/16	5/18
1975			5/12		5/12				5/05
1976		5/06		4/26			4/26	4/26	4/29
1977				4/25		4/26	4/25	4/25	4/26
1978					5/15	4/28	5/01	5/01	4/28
1979			5/16		5/16	5/09		5/09	5/09
1980			5/14	4/17				4/17	5/21
1981	5/18		5/20	5/06			5/12	5/12	5/07
1982					5/24		4/03		4/29
1983		5/25			5/11	5/05		5/05	4/25
1984						5/10		5/10	
No. of burns	2	3	8	8	9	11	12	17	19

examined by Grimm (1984) indicate that wild fires caused by lightning strikes or by humans occurred annually over large areas in southern Minnesota. The frequency of fires is believed to be responsible for preventing the spread of the deciduous forest westward into the savanna. Prairie grasses and forbs were adapted to frequent fires and the thick bark and sprouting capability of the oaks allowed them to persist (Curtis 1959).

The first settlers arrived in the vicinity of Cedar Creek in the 1850's. Selective logging provided lumber for homes and other buildings. Pierce (1954) reported that the earliest record of clearing land for cultivation was 1855. By the early 1900's many farms existed in the vicinity of Cedar Creek. Most fires were controlled to prevent damage to buildings, crops, livestock, and the surrounding woodlands. As a result, the savanna characteristic of much of Cedar Creek changed to oak forest with a dense understory of shrubs. In some localities the change was very rapid, with openings becoming filled by saplings and shrubs within a decade (Curtis 1959). Based on increment core samples, the age of the oak forests at Cedar Creek is approximately 45 years (White 1983).

Cedar Creek (45°25'N, 93°10'W) comprises 2185 ha of the 220,000-ha Anoka Sand Plain, which was formed about 12,000 years ago by glacial outwash (Cooper 1935). The gently rolling topography varies from 175- to 288-m elevation. Soils are well-sorted fine and medium sands of the Sartell, Zimmerman and Nymore series, which are low in organic matter and poor in nitrogen (Grigal *et al.* 1974). Cedar Creek has a temperate, continental climate with a mean annual air temperature of 6°C and annual precipitation of 66 cm. Maximum monthly precipitation of 11.4 cm occurs in June, near the peak of the growing season.

Methods. BURNING. In 1964, nine forest sites, referred to as compartments, were established and randomly assigned for the application of different frequencies of prescribed burns (Irving 1970). These compartments, ranging in size from 2.6 to 27.5 ha, plus three unburned sites in adjacent oak forest, were chosen for the present study. The unburned sites were selected in stands believed to be typical of the entire study area. All 12 sites are within a 320-ha block in the southeast corner of Cedar Creek, and have similar topography.

A total of 87 spring and two fall burns were carried out on the nine compartments from 1964 through 1984 (Table 1). The number of burns in a given compartment ranged from 2 to 19. Although the actual dates of the spring burns on any given compartment might span a period of 2 months over the 20 years of the study, in each year the burn was conducted in "early spring" as soon as fuel and weather conditions were suitable.

Burning was done in late afternoon, using strip head-firing as the normal ignition pattern. In most years, fires moved at a forward speed of 4.1 to 7.6 cm/sec and fuel consumption ranged from 400 to 3100 g/m^2 (Axelrod and Irving 1978; White 1986). Fuel was primarily leaf litter and dried grasses present from the previous growing season. The burns produced flame heights from a few centimeters in sparse fuels to about 1 m in leaf litter and grass surface fuels. The depth of the flame front ranged from less than 30 cm in sparse grass to about 70 cm in heavy oak leaf litter.

SAMPLING. Vegetation was sampled in September 1984 in a 50-m × 75-m area near the center of each compartment. Basal area of all trees larger than 10 cm diameter breast height (dbh) was determined. Shrubs were sampled at 24 uniformly distributed points within the sample area using the point-centered quarter method (Cottam and Curtis 1956). Herbaceous vegetation was sampled in 24 1-m × 0.5-m quadrats, spaced uniformly in the sample area. Per cent cover of bare ground, litter and herbs by species was visually estimated on each quadrat, following Inouye *et al.* (1987).

All plant species were grouped based on life history, life form, and historical origin (Table 2). Each species present in the study area was designated as typically occurring in true prairie, as native to North America but not typically prairie, or being introduced from another continent. Although this grouping ignores patterns at the species level, it is useful in terms of projecting the effects of fire to communities in other parts of the world where species composition is different. Plants were categorized using data from Gleason and Cronquist (1963), Curtis (1959), and personal communications with E. Cushing, B. Delaney, and T. Morley.

Tree data were analyzed using density, basal area, and average dbh. Shrub data were examined using per cent cover and density and herb data using per cent cover. Species richness was calculated for each burn compartment by totaling tree and shrub species plus all species occurring in all 24 quadrats.

Soil cores 10 cm deep taken at the center of each of the 24 quadrats were analyzed individually. Organic matter content was determined by ashing 10 g of soil, and pH was measured using a 1:1 dilution of soil with deionized water that was allowed to equilibrate for 30 minutes. Total nitrogen was analyzed colorimetrically following persulfate digestion (Tilman 1984).

Regression analyses were performed using averages of per cent cover, soil nitrogen, pH, and organic matter for each compartment.

Results. SOIL FACTORS. In general, the impact of repeated fires on soil was to decrease nitrogen and organic matter and to increase pH. Increased frequency of burns correlated with a significant increase in soil pH ($r = +0.85$, $P < 0.01$) (Table 3). This result has also been reported by Viro (1974), Daubenmire (1968), and others who suggested that this change has little effect on vegetation.

Average total soil nitrogen in the top 10 cm showed no significant relationship to the frequency of fires (Table 3). The maximum value (1050.2 ppm) was found in a compartment which had been used as a pasture for domestic livestock in the 1940's. This is the only known instance of domestic grazing on the study area. Average per cent organic matter content also showed a nonsignificant negative trend with the frequency of burns ($r = -0.42$, $P = 0.14$) (Table 3). The correlation between nitrogen and per cent organic matter was highly significant ($r = +0.85$, $P < 0.01$).

LITTER. While not statistically significant, bare ground tended to increase with the frequency of burns ($r = +0.46$, $P = 0.13$). On the other hand litter decreased ($r = -0.72$, $P < 0.01$) from a maximum of 85% on one unburned compartment to a minimum 29% in the compartment burned 11 times (Fig. 1A).

SPECIES RICHNESS. A total of 113 plant species occurred on the study area. The number of species ranged from 21 in one of the unburned compartments to 54 in the

Table 2. Life history, life form and origin of plant species.

Species	Life history[a]	Life form[b]	Origin[c]
Acer rubrum	P	TR	N
Achillea millefolium	P	F	T
Agropyron repens	P	G	I
Ambrosia coronopifolia	P	F	T
Amelanchier sp.	P	SH	N
Amorpha canescens	P	SH	T
Amphicarpa bracteata	P	F	I
Andropogon gerardi	P	G	T
Anemone cylindrica	P	F	T
Antennaria plantaginifolia	P	F	T
Apocynum cannabinum	P	SH	N
Arenaria lateriflora	P	F	N
Artemisia caudata	P	F	T
Artemisia ludoviciana	P	F	T
Asclepias syriaca	P	F	N
Asclepias tuberosa	P	F	T
Aster azureus	P	F	T
Bouteloua hirsuta	P	G	T
Bromus inermis	P	G	I
Calamagrostis canadensis	P	G	T
Calamovilfa longifolia	P	G	T
Campanula rotundifolia	P	F	T
Ceanothus americanus	P	SH	T
Celastrus scandens	P	SH	N
Chenopodium alba	A	F	I
Comandra richardsiana	P	F	T
Coreopsis palmata	P	F	N
Cornus racemosa	P	SH	N
Cornus stolonifera	P	SH	N
Corylus americana	P	SH	N
Crepis tectorum	A	F	I
Cyperus/Carex spp.	P	S	T
Desmodium canadense	P	F	N
Elymus canadensis	P	G	T
Equisetum laevigatum	P	N	T
Eragrostis spectabilis	P	G	T
Erigeron canadensis	A	F	I
Erigeron strigosus	A	F	I
Euphorbia corollata	P	F	T
Fragaria virginiana	P	F	T
Fraxinus pennsylvanica	P	TR	N
Galium aparine	A	F	T
Galium boreale	P	F	N
Galium triflorum	P	F	N
Helianthemum bicknellii	P	F	T
Helianthus laetiflorus	P	F	T
Juniperus communis	P	SH	T
Lactuca canadensis	A	F	T
Lathyrus venosus	P	F	N
Lechea stricta	P	F	T
Lespedeza capitata	P	F	T
Lithospermum canescens	P	F	T
Lithospermum carolinense	P	F	T
Lychnis alba	P	F	I
Lysimachia ciliata	P	F	N
Maianthemum canadense	P	F	N
Monarda fistulosa	P	F	N
Muhlenbergia racemosa	P	G	T
Oenothera biennis	B	F	T
Oxybaphus hirsutus	P	F	T
Panicum oligosanthes	P	G	T
Panicum perlongum	P	G	T
Panicum praecocius	P	G	T
Panicum virgatum	P	G	T
Parthenocissus inserta	P	SH	N
Parthenocissus vitacea	P	SH	N
Parthenocissus sp.	P	SH	N
Pedicularis sp.	P	F	T
Physalis virginiana	P	F	T
Poa pratensis	P	G	N
Polygala polygama	B	F	T
Polygonatum biflorum	P	F	N
Polygonum convolvulus	A	F	I
Potentilla simplex	P	F	N
Prunus americana	P	SH	N
Prunus serotina	P	TR	N
Prunus virginiana	P	SH	N
Quercus ellipsoidalis	P	TR	N
Quercus macrocarpa	P	TR	T
Ranunculus rhomboideus	P	F	T
Rhus glabra	P	SH	T
Rhus radicans	P	SH	T
Rosa arkansana	P	SH	T
Rosa blanda	P	SH	T
Rubus sp.	P	SH	N
Rudbeckia serotina	P	F	T
Rumex acetosella	P	F	I
Salix sp.	P	SH	T
Schizachyrium scoparius	P	G	T
Scutellaria parvula	P	F	T
Senecio pauperculus	P	F	T
Setaria lutescens	A	G	I
Sisyrinchium campestre	P	F	T
Smilacina racemosa	P	F	N
Smilacina stellata	P	F	T
Smilax herbacea	P	F	N
Solanum dulcamara	P	F	T
Solidago gigantea	P	F	T
Solidago graminifolia	P	F	T
Solidago missouriensis	P	F	T
Solidago nemoralis	P	F	T
Solidago rigida	P	F	T
Sorghastrum nutans	P	G	T
Stachys palustris	P	F	T
Stellaria longifolia	P	F	N
Stipa spartea	P	G	T
Trientalis borealis	P	P	N
Trifolium sp.	P	F	I
Uvularia sessilifolia	P	F	N
Vaccinium angustifolia	P	SH	N
Viola pedatifida	P	F	T
Viola sagittata	P	F	T
Vitis riparia	P	SH	N

[a] A—annual, B—biennial, P—perennial.

[b] F—forb, G—grass, TR—tree, SE—sedge, N—nonvascular, SH—shrub.

[c] I—introduced, T—true prairie, N—native/not prairie.

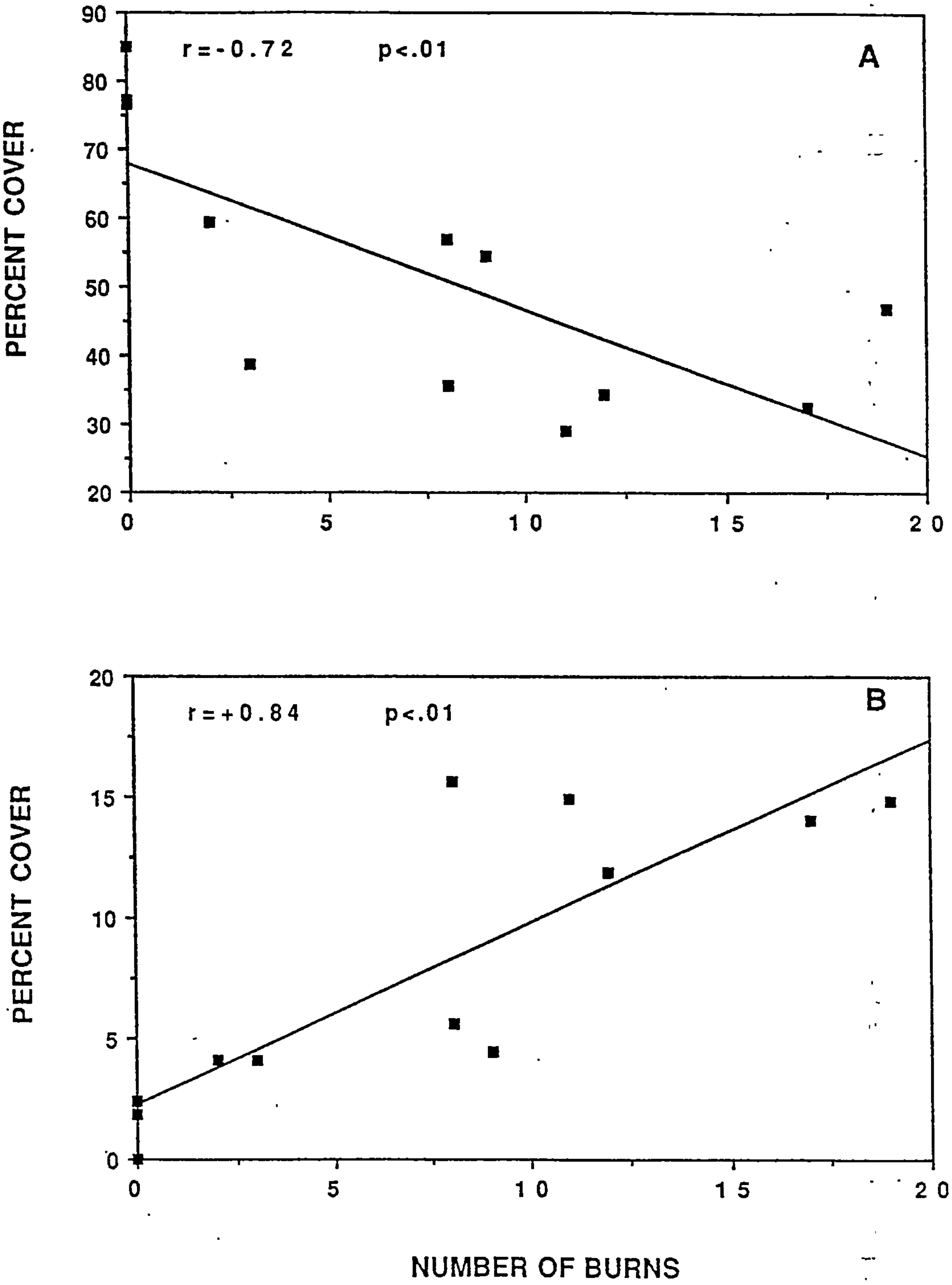

Fig. 1. Linear regressions showing effect of number of burns on litter (A) and grasses (B) (r = correlation coefficient).

Table 3. Effects of burn frequency on soil nitrogen, pH and organic matter.

Compartment number	Number of burns	Nitrogen ppm	pH	% Organic matter
10	0	794.2	4.8	3.0
16	0	650.6	4.7	2.6
17	0	969.0	4.6	3.8
11	2	628.5	5.0	2.6
13	3	818.9	5.1	2.8
7	8	631.4	5.2	2.2
15	8	1050.2	5.1	3.5
8	9	773.2	5.3	3.4
5	11	536.0	5.6	2.5
1	12	797.8	5.1	2.9
3	17	563.0	5.4	2.2
4	19	723.0	5.5	2.4
Correlation coefficient (*r*)		−0.299	0.852	−0.418
Probability		0.35	<0.001	0.14

compartment with nine burns (Fig. 2). When species richness was examined statistically with respect to the number of burns, a second order polynomial regression had a higher correlation coefficient but a lower probability than did a first order regression (second order: $r = +0.80$, $P = 0.010$; first order: $r = +0.75$, $P = 0.005$). From these results, it appears that species richness increases to a maximum with a burn frequency of about eight to nine fires over a 20-year period. This may be due to the persistence of typical forest trees and shrubs and the increase in prairie species occurring with this pattern of burning. As Fig. 2 reveals, more frequent burning reduces the number of woody species, and especially shrubs, whereas the number of true prairie species remains about the same. Nitrogen availability might also influence species richness in the burned compartments, as it does in old fields at Cedar Creek (Inouye *et al.* 1987).

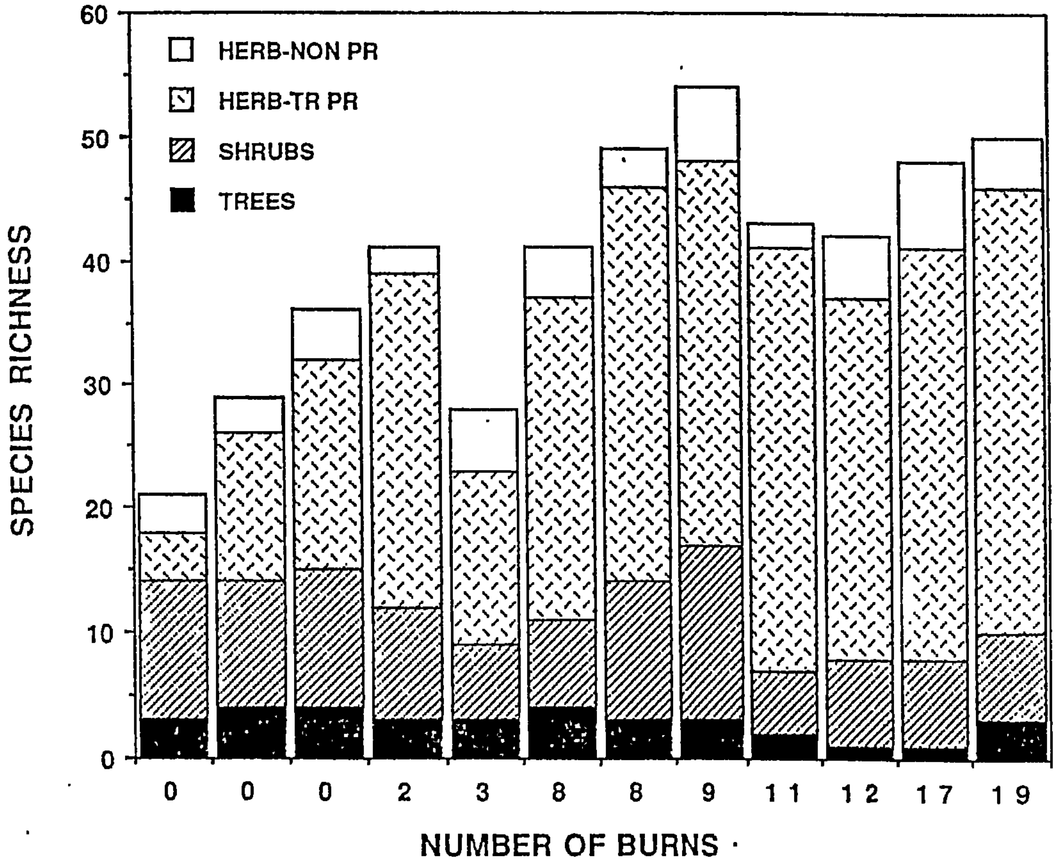

Fig. 2. Effect of number of burns on species richness of trees, shrubs and herbs. Herbs are divided into true prairie (TR PR) and non-prairie (NON-PR) categories.

However, multiple regression analysis testing the effects of both burn frequency and soil nitrogen on species richness indicated that only burn frequency was significant.

PLANT SPECIES COMPOSITION BASED ON ORIGIN. Of the 113 species in the study area, 65 were classified as true prairie, 36 as native non-prairie, and 12 as introduced (Table 2). Per cent cover of all categories of true prairie species, grasses, sedges, forbs and shrubs, tended to increase with the frequency of fire, with true prairie grasses (Fig. 3A) and forbs (Fig. 3B) showing significant positive correlations with fire frequency. The average per cent cover of native, non-prairie grasses (r = +0.17, P = 0.60) and forbs (r = +0.03, P = 0.93) did not show an obvious change with the frequency of fire. Per cent cover of shrubs tended to decrease with the frequency of fire, but not significantly (r = −0.32, P = 0.18). Neither introduced grasses (r = −0.43, P = 0.16) nor introduced forbs (r = +0.13, P = 0.70) showed a significant change in per cent cover with respect to number of burns. Only the pasture site had more than 1 per cent cover of introduced grasses. If *Bromus inermis* (5.23% cover) is removed from the analysis, the correlation coefficient increases to −0.43 (P = 0.16).

TREES. Tree density and total basal area/ha decreased, although the changes were not significant. Tree density/ha averaged 636 in unburned compartments and was 165 in the most frequently burned area. Total basal area/ha ranged from 4.5 to 28.7 m^2/ha. Average dbh per tree ranged from 14.2 to 30.0 cm and showed little response. These results are consistent with White (1983, 1986) who found about a 50 per cent reduction in oak density and a slight reduction in basal area in Cedar Creek compartment No. 3 which was burned 13 springs between 1965 and 1979. Most of the reduction was in stems from 5 to 25 cm dbh. Larger trees have a higher fire tolerance, probably due to their thick bark which prevents girdling by surface fires (Irving and Aksamit 1983; White 1986).

SHRUBS. Per cent cover of true prairie shrubs tended to increase with the frequency of burns (r = +0.35, P = 0.19), whereas the per cent cover of native non-prairie shrubs tended to decrease (r = −0.32, P = 0.18), although the changes were not significant. Further analysis using shrub stems/ha did not indicate marked reduction in shrubs with more frequent fires (r = −0.10, P = 0.76). In analyzing data collected in 1972 from the same Cedar Creek compartments, Axelrod and Irving (1978) found that annual fires reduced stem biomass of *Corylus americana*, the dominant shrub of oak forests. They reported that stem density increased but stem height decreased. White (1983), however, found a significant decrease in per cent cover of *Corylus americana* in Cedar Creek compartment No. 3, burned 13 times in 15 years.

HERBS. Per cent cover of true prairie herbs (Fig. 4A) increased significantly with the number of burns (r = +0.81, P < 0.01), although non-prairie and introduced herbs did not change appreciably with the number of burns. Because 67 of the 113 species in the study area were categorized as true prairie, the high correlation between per cent cover and number of burns suggests that frequent fire can be extremely effective for restoration or establishment of prairie.

Examination of the 113 species revealed that 104 were perennials, 7 were annuals, and 2 were biennials. Cover of annuals plus biennials significantly increased with the number of burns (r = +0.60, P = 0.04) (Fig. 4B); although maximum cover of these plants was only 0.73%. This contribution is probably too small to be ecologically meaningful. Perennials showed a correlation of +0.52 (P = 0.08) with increasing frequency of burns, with cover ranging from 13.3 to 64.4 per cent.

Grasses are the most important floral element of most prairies and savannas, generally comprising a major proportion of the herbaceous vegetative cover. Fire frequency, soil moisture, and site characteristics all influence the effect of fire on grasses. True prairie grasses increased in response to frequency of burns, whereas the two introduced grasses decreased and four species of native non-prairie grasses increased slightly. Because the introduced grasses and native non-prairie grasses constituted less than 4 per cent of the total cover, it is again apparent that frequent fires can be very effec-

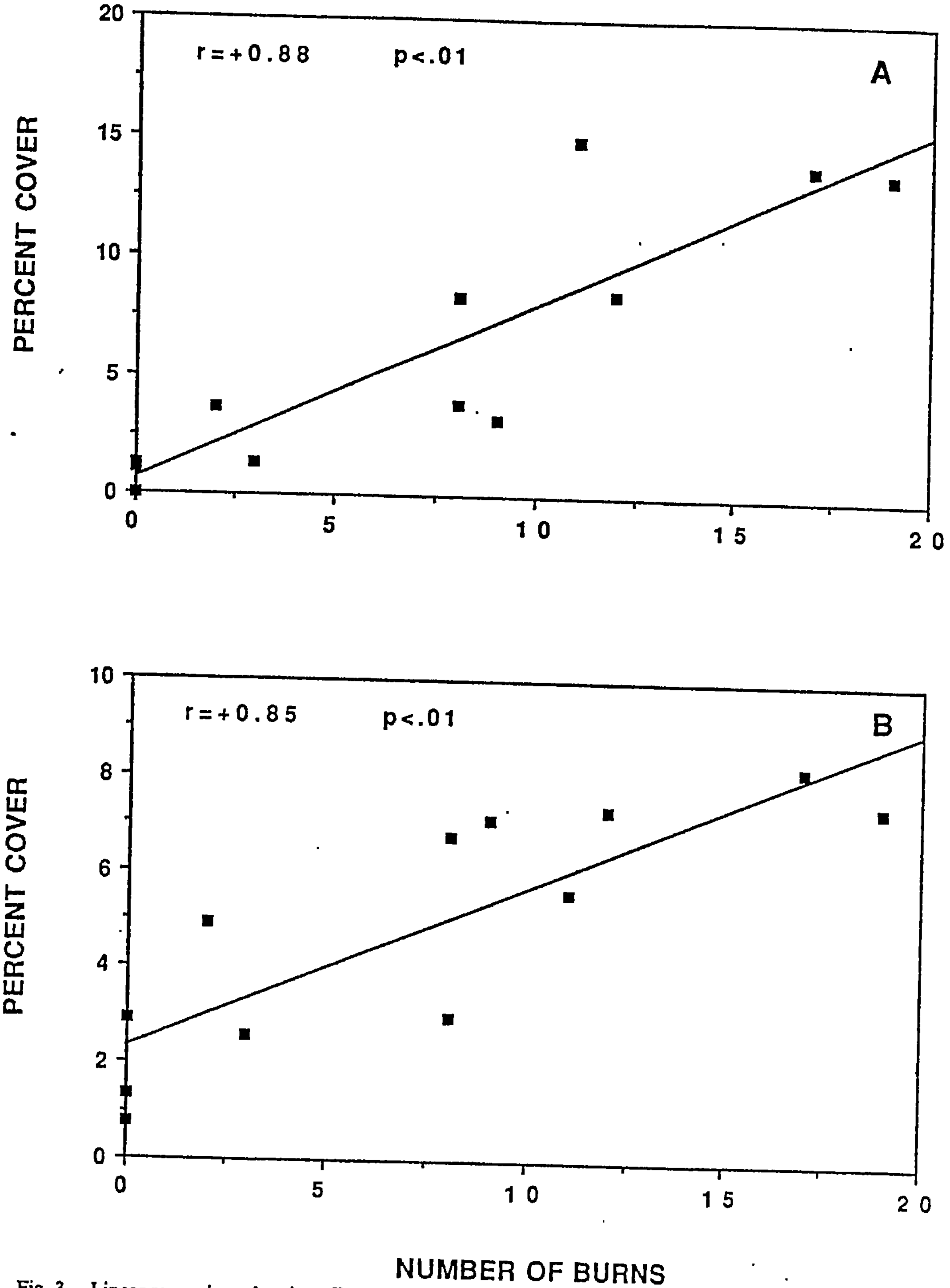

Fig. 3. Linear regressions showing effect of number of burns on true prairie grasses (A) and true prairie forbs (B).

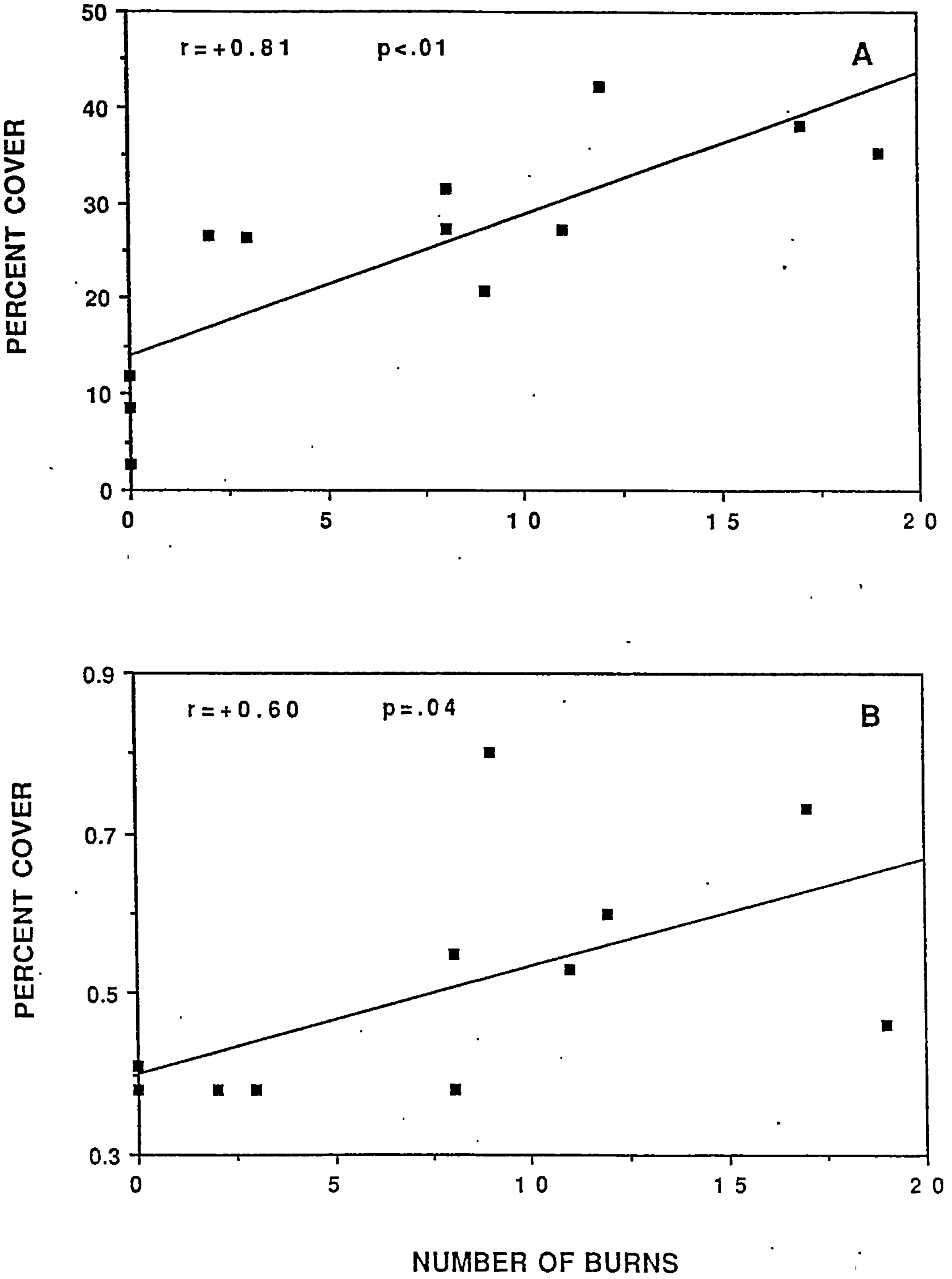

Fig. 4. Linear regressions showing effect of number of burns on true prairie herbs (A) and on annual and biennial herbs (B).

tive in the establishment and maintenance of prairie.

Discussion. Fire constitutes disturbance in any ecosystem, but should be recognized as a common natural event in grasslands, savannas, and in many temperate forests (see reviews in Mooney 1981 and Nuzzo 1986). Responses depend in part upon characteristics of the fire and occur in both physical and biological components of the ecosystem. Surface light, soil surface temperature and nitrogen are particularly important factors influencing these responses (Hulbert 1988).

The low per cent organic matter in the top 10 cm of the sandy soils of the 3 adjacent unburned compartments in oak forest at Cedar Creek (2.6 to 3.8 per cent by weight) suggests that, even though the area may have had savanna vegetation for hundreds or even thousands of years prior to settlement, total biomass was probably very low. If it had been otherwise, we would expect Cedar Creek to have the typical black loamy soils associated with tallgrass prairie in central North America.

Effects of fires on nitrogen in grasslands have received considerable discussion. Empirical data, however, are contradictory (Wright and Bailey 1982). Net loss of nitrogen due to volatilization during burning has been reported in some grasslands, but not in others. In some localities volatized nitrogen loss is balanced by precipitation input (see review by Daubenmire 1968), although this input is dependent upon the abundance of detritus and microbes (Seastedt 1985). Increases in abundance of nitrogen-fixing species and in microbial activity would also add nitrogen to the ecosystem. Although variation in soil nitrogen is high at Cedar Creek, Table 2 shows a slight tendency for nitrogen to decrease with the frequency of burns. In a detailed simulation of the effects of fire on prairie, Risser *et al.* (1981) reported that, while annual fires have the positive effect of increased utilization of such nutrients as phosphorus, they also result in a net loss of nitrogen to the system. This loss was greater with simulation of annual burns than with simulation using one burn every 3 years. The Cedar Creek data (Table 3) tend to support these results.

Species richness increased significantly as fire frequency increased to 8 to 10 burns in 20 years. The actual burning pattern for the two compartments showing the highest value for species richness (compartments 8 and 15) was 2 consecutive years of burning followed by 2 years with no fire (Table 1). If maximum species richness is a major objective, a similar burning regime is recommended. Two years with no fire allows for a build-up of fuel so that the subsequent burn is likely to be hotter and, therefore, more effective in controlling forest species (Anderson and Brown 1986). The second fire probably serves to further deplete food reserves stored in root systems which would lead to decreased vigor or death in these species.

Frequent burning at Cedar Creek leads to an increase in true prairie species, as also suggested by Vogl (1974), and a decrease in forest species (Fig. 2). Kucera and Koelling (1964) also reported that burning every other year in a Missouri prairie controlled invasion of woody species, yet resulted in higher overall species richness. This maximum value in species richness at the intermediate levels of fire frequency appears somewhat similar to certain successional patterns which indicate that diversity is highest at intermediate stages (Horn 1974; Shafi and Yarranton 1973) and to Connell's (1978) finding that diversity is highest at intermediate disturbance rates. However, Walker and Peet (1983) found that annual burning resulted in maximum species richness in coastal plain savannas in southeastern United States. It seems likely that the relation between diversity and frequency of burns is primarily dependent upon the type of community.

Responses of annual plants to burning are probably related to the time of each fire relative to the growing season (Gilliam and Christensen 1986). Vogl's (1974) review indicates that fires occurring prior to the growing season stimulate germination, growth, and seed production, whereas burning after annuals have initiated growth is usually detrimental. Perennials, on the other hand, are generally favored by fire at any time, primarily because of their ability to reproduce vegetatively. Some prescribed burns at Cedar Creek occurred prior to growth and some following, depending mostly on spring weather conditions. It appears that, regardless of timing or intensity, fire frequency has a direct impact on the composition of the communities at Cedar Creek, and favors species that are adapted to fire through their prairie evolutionary history.

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