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EFFECTS OF BURNING REGIME ON BURIED SEED BANKS AND CANOPY COVERAGE IN A KANSAS TALLGRASS PRAIRIE

MARC D. ABRAMS

ABSTRACT—Vegetation cover and buried seeds were studied on three upland sites burned at different intervals (unburned, 4-year burn, and annual burn) in tallgrass prairie in northeastern Kansas. Vegetation of all sites (89 species total) was dominated by *Andropogon gerardii* (76 to 81% cover). *Schizachyrium scoparium* and *Sorghastrum nutans* cover was higher, whereas *Poa pratensis* and *Sporobolus heterolepis* cover was lower on more frequently than on less frequently burned sites. A total of 735 seedlings comprising 28 species were recorded in soil samples from the three treatments. Seed density was variable within and between treatments but was generally highest in unburned and lowest in annually burned prairie. Many *Sporobolus cryptandrus* were recorded in each treatment, whereas *P. pratensis* averaged 35 seedlings in the unburned and 1 in the annual burn treatment. The number of forb seedlings was not significantly different between treatments and was dominated by *Erigeron strigosus* and *Oxalis stricta*. Many species that germinated from buried seeds were not recorded as vegetation on the site, and much of the vegetation was not represented as seedlings. The scarcity of viable buried seeds of the dominant tallgrasses and forbs suggest that they are highly dependent on vegetative propagation.

Large and diverse populations of viable buried seed are common in many plant communities (Oostings and Humphreys, 1940; Chippindale and Milton, 1934; Granstrom, 1982), and they may be important in the revegetation of sites following disturbance (Thompson and Grime, 1979; Abrams and Dickmann, 1984). However, there is often very little correlation between seed populations and existing vegetation of a site. (Major and Pyott, 1966; Thompson and Grime, 1979).

Disturbances such as fire, drought, and grazing are recurring factors in most North American prairies dominated by perennial herbaceous species (Risser et al., 1981). Fire frequency, for example, is known to cause dramatic differences in prairie vegetation composition and productivity (Risser et al., 1981; Abrams, et al., 1986; Abrams and Hulbert, 1987). Although the vast majority of these perennial species perpetuate themselves vegetatively, little is known about buried seed populations in North American prairie (Weaver and Mueller, 1942; Rabinowitz, 1981; Johnson and Anderson, 1986). No studies have investigated the effects of disturbance frequency on species composition and dominance in the seed pool. The purpose of this study was to characterize the viable buried seed populations in an upland tallgrass prairie in northeast Kansas burned at different intervals and to compare the buried seed populations with existing vegetation.

MATERIALS AND METHODS—Sites were located on Konza Prairie (3,487 ha) in the Flint Hills of northeastern Kansas, which were dominated by *Andropogon*, *Schizachyrium*, *Sorghastrum*, and *Panicum* species. The Flint Hills are near the western border of the tallgrass province and include the only extensive area of unplowed tallgrass prairie in North America. Konza Prairie was grazed

by cattle since European settlement in the mid-1800's until its acquisition as a research natural area from 1972 to 1977. Prairies in the Flint Hills were thought to have burned every 2 to 3 years since the mid-1800's (Abrams, 1985).

Buried seed banks and existing vegetation were characterized in an upland soil on three watersheds: one unburned since 1973, one burned in 1979 and 1983 (4-year burn), and one burned annually since 1978. No data on seed banks or vegetation composition were available for the study sites prior to the onset of the different burn treatments. The prescribed burns were conducted in April of each year. Each watershed contains relatively broad, level upland areas of Florence soil (cherty silt loam or cherty silty clay loam), which were relatively thin and well-drained and had numerous chert fragments in the upper horizons (Jantz et al., 1975). The watersheds ranged from 23 to 55 ha.

The climate was characteristic of continental areas with hot summers, cold winters, moderately strong surface winds, and relatively low humidities. The average maximum and minimum temperatures for January were 8.6 and 3.2°C and for July were 33.2 and 20.0°C, respectively. Average precipitation was 835 mm with 72% occurring during the 6 warmest months. Annual precipitation varied greatly, and droughts occurred frequently. According to the Palmer index, droughts occurred during 38% of the months between 1931 and 1968 in northeastern Kansas; 11% were severe or extreme (Brown and Bark, 1971). During the 1984 growing season, precipitation was 21% greater than average from April to June (387 mm) and 34% lower than average from July to September (188 mm).

Four widely-spaced (ranging from 0.25 to 1.00 km apart), 50-m, permanent transects were established in 1982 in relatively level areas on upland soils in each of the three watersheds. At 10-m intervals on each transect five 10-m² plots were established to survey vegetation (20 plots/watershed). Canopy coverage of each species was surveyed at three times during the 1984 growing season (early to mid-May, late June to mid-July, and mid- to late September). Most species were surveyed in June and July after full stature was attained. May and September surveys were conducted for species that developed early or late in the season. If a species was surveyed more than once, its highest seasonal cover value was used to compute species coverage. Vegetation canopy coverage was recorded by categories described by Daubenmire (1959). An additional 0 to 1% category was added because of the large plot size. Canopy coverage was defined as the area within lines connecting edges of the plant canopy, and the midpoint of each category was used to compute species coverage. Nomenclature followed that of Great Plains Flora Association (1986).

In March 1985, 15 surface mineral soil samples were extracted along the four transects in each of the three watersheds. Three 98-cm³ soil cores (diameter = 5 cm) to a depth of 5 cm were taken at arbitrary points just outside each of the five plots per transect and were grouped into one sample per transect (four per treatment). Surface organic matter was excluded from the samples to minimize the inclusion of recently dispersed, unburied seeds (e.g., the transient seed bank; Thompson and Grime, 1979). Samples were air-dried and screened through a 5-mm sieve to remove large rocks, roots, and rhizomes.

In April 1985, a 1,352-cm³ subsample from each of the twelve samples were put in 26 by 52 by 6.5-cm plastic flats to form a 1-cm thick layer over a 1:1 mixture of perlite and vermiculite. Two flats containing a mixture of sterilized potting soil, perlite, and vermiculite were used as controls. The samples were placed in an environmentally controlled greenhouse, regularly watered, and periodically rotated to reduce possible positional effects. The daytime and nighttime temperature ranges in the greenhouse were 24 to 30 and 18 to 24°C, respectively, and the mid-day solar irradiance on a clear day was 730 $\mu\text{E m}^{-2}\text{s}^{-1}$. Seedlings were counted daily for the first 2 weeks of the experiment and two or three times a week until 1 August 1985. Flats were watered until 15 September 1985 to allow identification of as many species as possible. Statistical analysis of the vegetation cover (individual plot data for species were averaged by transect; cf., Abrams and Hulbert, 1987) and seed bank data were accomplished using a fixed model, one-way analysis of variance and multiple range tests at $P < 0.05$ (Steel and Torrie, 1960).

RESULTS—Eighty-nine species were recorded in the vegetation from which the buried seed samples were obtained. Only ten species had cover values exceeding 5% on one or more treatments. The dominant species on all sites was *Andropogon gerardii* (76 to 81%; Table 1). *Schizachyrium scoparium* and *Sorghastrum nutans* cover was higher ($P < 0.05$), whereas *Poa pratensis*

TABLE 1—Canopy coverage (%) in 1984 for those species exceeding 5% cover on upland soils in one or more of three watersheds in which buried seeds were studied on Konza Prairie in northeastern Kansas. Values represent transect means \pm SE ($n = 4$).

Species	Unburned	4-year burn	Annual burn
Grasses			
<i>Andropogon gerardii</i>	77.6 \pm 3.6	81.4 \pm 5.7	76.0 \pm 2.8
<i>Poa pratensis</i>	30.3 \pm 10.9	7.0 \pm 1.1	
<i>Schizachyrium scoparium</i>	7.9 \pm 2.4	8.7 \pm 3.0	36.9 \pm 2.6
<i>Sorghastrum nutans</i>	6.3 \pm 2.0	16.5 \pm 4.0	42.2 \pm 2.7
<i>Panicum virgatum</i>	5.3 \pm 1.6	8.2 \pm 1.5	8.0 \pm 3.6
<i>Sporobolus heterolepis</i>	6.3 \pm 2.9		0.9 \pm 0.7
Forbs			
<i>Aster ericoides</i>	6.7 \pm 2.2	5.7 \pm 2.6	0.9 \pm 0.6
<i>Aster oblongifolius</i>	4.5 \pm 3.4	14.4 \pm 2.0	
<i>Ambrosia psilostachya</i>	3.0 \pm 1.4	17.1 \pm 2.3	1.3 \pm 0.6
<i>Artemisia ludoviciana</i>	2.6 \pm 1.8	6.7 \pm 0.5	

and *Sporobolus heterolepis* cover was lower ($P < 0.05$), on the more frequently than on the less frequently burned sites. The cover of most of the dominant forbs (e.g., *Ambrosia psilostachya* and *Aster oblongifolius*) was highest ($P < 0.05$) on the 4-year burn and lowest on the annual burn treatment.

From the three sites, a total of 735 seedlings comprising 28 species were identified (Table 2). The number of seedlings ranged from 23 to 145 per flat. Germination peaked during week 2, was moderate during weeks 3 to 6, and was infrequent thereafter.

There was considerable variation in the seedling density within and among treatments (Table 2). The unburned prairie samples produced 78 ± 21 ($X \pm SE$) seedlings, and the annually burned samples produced 39 ± 6 seedlings. This difference was due primarily to a significant decrease ($P < 0.05$) in *P. pratensis* (a cool-season species), which averaged 35 seedlings in the unburned and 0.2 in the annual burn treatment. *Sporobolus cryptandrus* was important in all three treatments and averaged 20 seedlings per sample. The number of forb seedlings (dominated by *Erigeron strigosus* and *Oxalis stricta*) was not significantly different among treatments.

Many species that germinated from buried seeds were not growing on the sites, and much of the vegetation present was not represented as seedlings (Tables 1 and 2). For example, 246 seedlings of *S. cryptandrus* were recorded, yet it was not found in the three studied watersheds. Similarly, *E. strigosus* and *O. stricta* were absent or rare in the vegetation. Other species appearing as seedlings but not surveyed as vegetation on the respective plots (although found elsewhere on Konza Prairie) were *Eleocharis compressa*, *Lepidium densiflorum*, *Rhus glabra*, *Oenothera speciosa*, *Plantago rhodisperma*, *Sisyrinchium campestre*, *Commandra umbellata*, *Antennaria neglecta*, *Cercis canadensis*, *Euphorbia missurica*, *Euphorbia strictospora* and *Salix* sp. Of the dominant vegetation surveyed on the sites, only *P. pratensis* produced seedlings in numbers consistent with its distribution on the prairie. Seedlings of *A. gerardii*, *S. scoparium*, *S. nutans*, *Panicum virgatum*, *A. psilostachya*, and *A. oblongifolius* were few or absent.

TABLE 2—Number of seedlings ($\bar{X} \pm SE$) from buried seeds recorded in 1,352-cm³ soil samples ($n = 4$) extracted in March 1985 from three watersheds burned at different intervals on Konza Prairie in northeastern Kansas.

Species	Unburned	4-year burn	Annual burn
Graminoids			
<i>Poa pratensis</i>	34.7 \pm 17.3	6.5 \pm 1.3	0.2 \pm 0.2
<i>Sporobolus cryptandrus</i>	19.5 \pm 3.3	26.7 \pm 3.9	15.3 \pm 2.5
<i>Andropogon gerardii</i>	2.5 \pm 0.4	1.0 \pm 0.3	1.0 \pm 0.8
<i>Sporobolus asper</i>	1.3 \pm 0.8	0.2 \pm 0.2	
<i>Cyperus lupulinus</i>	1.2 \pm 0.8	1.2 \pm 0.5	3.3 \pm 1.7
<i>Dichanthelium oligosanthos</i>	0.7 \pm 0.3	0.5 \pm 0.3	
<i>Carex</i> sp	0.2 \pm 0.2	1.3 \pm 0.1	
<i>Eleocharis compressa</i>	0.2 \pm 0.2		
Unidentified	1.0 \pm 0.2	4.0 \pm 1.2	1.5 \pm 0.6
Group total	61.3 \pm 19.9	41.4 \pm 3.9	21.3 \pm 3.6
Forbs and woody species			
<i>Erigeron strigosus</i>	4.5 \pm 1.1	14.0 \pm 4.1	10.8 \pm 3.8
<i>Oxalis stricta</i>	2.8 \pm 0.7	3.8 \pm 0.7	1.8 \pm 0.7
<i>Aster ericoides</i>	2.3 \pm 0.2	0.5 \pm 0.4	
<i>Lepidium densiflorum</i>	2.2 \pm 1.1	0.7 \pm 0.4	1.0 \pm 0.6
<i>Plantago rhodosperma</i>	0.8 \pm 0.3		
<i>Commandra umbellata</i>	0.5 \pm 0.4	0.5 \pm 0.2	0.2 \pm 0.2
<i>Rhus glabra</i>	0.2 \pm 0.2		
<i>Oenothera speciosa</i>	0.2 \pm 0.2	0.5 \pm 0.4	0.7 \pm 0.4
<i>Artemisia ludoviciana</i>	0.2 \pm 0.2	1.2 \pm 0.4	
<i>Sisyrinchium campestre</i>	0.2 \pm 0.2		
<i>Antennaria neglecta</i>		0.2 \pm 0.2	0.5 \pm 0.4
<i>Salvia pitcheri</i>		0.2 \pm 0.2	
<i>Tragia betonicifolia</i>		0.2 \pm 0.2	
<i>Lactuca canadensis</i>		0.2 \pm 0.2	
<i>Dalea purpurea</i>		0.5 \pm 0.4	
<i>Cercis canadensis</i>			0.5 \pm 0.4
<i>Euphorbia missurica</i>			0.2 \pm 0.2
<i>Euphorbia strictospora</i>			1.0 \pm 0.6
<i>Salix</i> sp.			0.2 \pm 0.2
<i>Ambrosia psilostachya</i>			0.2 \pm 0.2
Unidentified	3.0 \pm 0.8	1.8 \pm 0.6	1.2 \pm 0.3
Group total	16.9 \pm 1.5	24.3 \pm 5.6	18.3 \pm 3.1
Treatment total	78.2 \pm 21.2	65.7 \pm 7.6	39.3 \pm 6.4

DISCUSSION—The lack of correlation between the vegetation on a site and the buried seed populations seen in this study has also been reported in other grasslands (Lippert and Hopkins, 1950; Mayor and Pyott, 1966). The absence or scarcity of viable buried seed of the dominant tallgrasses reported here suggest a high dependence of vegetative propagation. Indeed, many dominant tallgrasses, such as *A. gerardii*, *S. scoparium*, *S. nutans*, and *P. virgatum* spread mainly by vegetative propagation and yield few viable seeds during drought years in many localities in the Central Plains (Weaver and Mueller, 1942; Risser et al., 1981).

Sporobolus cryptandrus was the main constituent of the seed pool in this study and in other studies of buried seeds in North American prairies. This has been attributed to dissemination by rabbits and the ability to produce large amounts of seed even during dry years (Weaver and Mueller, 1942; Lippert and Hopkins, 1950). *Sporobolus cryptandrus* is abundant in the

drier grasslands of western Kansas and occurs infrequently on Konza Prairie. It may have increased in past drought periods and produced many seeds that are still present in the soil. It is known that seeds of this species can remain viable in soil for many years (Goss, 1924).

The large amount of *S. cryptandrus* in the unburned plots contrasts with the findings of Lippert and Hopkins (1950) who reported a sixfold increase in its seedlings from burned compared with unburned mixed-prairie soil. The greatest effect of burning reported here involved *P. pratensis*, whose cover and viable seed density were much lower on more frequently burned sites. Smaller buried seed banks on burned compared to unburned areas were also reported following mid-summer burning in a sagebrush community in Utah, which were attributed to a decrease in cool season (C_3) grasses (Hassan and West, 1986). Low cover of *P. pratensis* and other cool-season grasses, relative to the warm-season (C_4) grasses, as a result of frequent burning in mid-spring is typical of Konza Prairie (Abrams and Hulbert, 1987) and other tallgrass prairies (Engle and Bultsma, 1984). This disparity probably results from differences in phenology of these grasses, in which cool-season species have extensive terminal growth destroyed by mid-spring burning, whereas most of the warm-season grasses are still dormant and, thus, lose little or no new growth.

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