BULLETIN OF THE TORREY BOTANICAL CLUB
VOL. 110, No. 4, pp. 474-481 OCTOBER-DECEMBER, 1983

# The effect of early spring burning on vegetation in buffalo wallows

**Scott L. Collins and Gordon E. Uno**[1]

Department of Botany and Microbiology, 770 Van Vleet Oval, University of Oklahoma, Norman, OK 73019

COLLINS, S. L. AND G. E. UNO (Dept. Botany and Microbiology, Univ. Oklahoma, Norman, OK 73019). The effect of fire on vegetation in buffalo wallows. Bull. Torrey Bot. Club 110: 474-481. 1983.—Buffalo wallows are patchily distributed disturbances in grassland vegetation initiated by male buffalo during the spring rutting season. During the rainy season in spring and early summer, wallows hold water resulting in greater soil moisture than in adjacent grasslands. We examined the effects of early spring burning on wallow vegetation in a wildlife refuge containing about 700 buffalo. Ordinations indicated two vegetation gradients. The first ordination axis was a moisture gradient separating vegetation located outside wallows from that within wallows. The second axis separated samples from the burned and unburned sites. Diversity and richness values were higher outside than inside the wallows. Evenness values, were greatest inside the wallows. Richness was significantly lower in burned than in unburned wallows. Ruderal species such as winter annuals were more abundant in unburned wallows. Overall, wallows contain vegetation different from that of surrounding prairie, which increases regional species diversity in southern mixed grasslands. Also, fire alters the composition of vegetation within wallows to a greater extent than adjacent vegetation. Finally, we suggest that wallows serve as safe-sites for ruderal species within mature grassland vegetation.

Key words: Buffalo wallow, disturbance, diversity, fire, grassland, Oklahoma.

There is increasing evidence that disturbance is a significant factor affecting climax vegetation (White 1979). In grasslands, fire is the most commonly studied natural disturbance (Daubenmire 1968, Vogl 1974, Kucera 1981), while studies on the impact of native herbivores are less common (c.f., McNaughton 1983, Coppock *et al.* 1983a,b). This is unfortunate because during the 1800's the Great Plains of central North America supported enormous populations of herbivores including buffalo (*Bison bison*), elk (*Cervus canadensis*), antelope (*Antilocapra americana*), and other ungulates (Mack and Thompson 1982). Reports by explorers suggested that these animals, especially buffalo, had a tremendous impact on vegetation composition and structure (England and Devos 1969). Larson (1940) maintained that buffalo populations of 20,000,000 to 60,000,000 animals imparted intense grazing pressure on prairie vegetation. An additional disturbance to grassland vegetation is the frequent wallowing behavior by buffalo, especially during the spring and summer rutting season. This behavior produces "wallows" which are concave disturbances formed as the animals paw the ground and roll in the exposed soil. Naturalist reports suggested that such wallows were widespread throughout the North American grassland (England and Devos 1969).

In grasslands where buffalo still occur, new wallows are created each year providing predictable habitats for colonization by ruderal plant species such as winter annuals (c.f., Grime 1979) within the mature grassland vegetation. Once wallows are formed, they may be re-visited by buffalo which continuously remove any vegetation. On fine-textured soils, a hard panned bottom forms in wallows from soil compaction by the animals (Polley 1983). This hardpan inhibits percolation of moisture into the soil, thus, at the end of the spring rainy season in Oklahoma, we have observed wallows filled with water for several weeks providing ephemeral pools in which wetland plants can grow.

In addition to the impacts of grazing

[1] We thank Susan Barber and Pat Collins for help with the field work. In addition, we thank Susan Barber, Wayne Polley, Paul Risser, and Linda Wallace for helpful comments on earlier versions of the manuscript.

Received for publication May 27, 1983 and in revised form September 10, 1983.

and wallowing by native herbivores, grassland vegetation undergoes frequent burning cycles (Daubenmire 1968, Vogl 1974). For some prairies, fire frequency has been estimated to occur once every three to five years (Wright and Bailey 1982). Fire provides many beneficial effects in grasslands, including removal of woody vegetation (Bragg and Hulbert 1976, Collins and Adams 1983) and increasing productivity via litter removal and soil heating (Rice and Parenti 1978).

At a regional level, the combined effects of grazing, wallowing, and burning produce a heterogeneous environment resulting in a patchwork mosaic of denuded sites, microsuccessions, and mature vegetation. Overall, it is hypothesized that nonequilibrium conditions induced by disturbance would maintain a high regional plant species diversity (Huston 1979, Pickett 1980, Miller 1982). Therefore, the purposes of our study were to (1) compare wallow vegetation to immediately adjacent prairie moderately grazed by buffalo and other large herbivores, (2) determine the composition of vegetation in wallows in burned and unburned grasslands, and (3) estimate the effects of wallow vegetation on regional species diversity in southern mixed grass prairie.

**Materials and Methods.** STUDY AREA.— The Wichita Mountains Wildlife Refuge in southwestern Oklahoma contains an approximately 24000 ha mosaic of forest and grassland vegetation. The refuge receives approximately 70 cm of rain per year, most of which falls from April to June. General descriptions of the geology and plant communities can be found in Buck (1964) and Crockett (1964). Topography in the preserve includes small, talus-sloped mountains separated by gently rolling plains. The refuge supports herds of about 700 buffalo, 600 elk, 600 deer (*Odocoileus virginianis*), and 400 longhorn cattle (*Bos taurus*). Wallows created by the buffalo occur throughout the grasslands in the refuge. Until recently the management policy of the refuge was to control and eliminate wildfires. In 1978, a new management program was begun involving controlled burning of different grasslands at five year intervals. To date, most grasslands in the preserve have been burned at least once since 1978. Overall, we believe that the populations of native herbivores and the controlled burning program in the refuge provide a natural environment that generally reflects past conditions.

To determine the effect of early spring burning on vegetation in buffalo wallows, we sampled the vegetation in two groups of wallows from grasslands subjected to different fire treatments. The first site, Antelope Flat, was burned in early April 1979 and will be called the "unburned site" in this study. The second study site, Buffalo Spring, was burned in late February, 1982 and will be referred to as the "burned site." Charcoal on the soil indicated that the fire burned vegetation in and around the wallows. The two sites are about 2 km apart and both are on soils of the Lawton-Foard complex; slit-clay loams with a 3–5% slope (USDA 1967).

VEGETATION. Nomenclature follows Gould (1975) for grasses and Waterfall (1972) for other plants.

METHODS. A stratified sampling scheme was established by visually dividing each wallow into three zones: outer, edge and inner. All wallows sampled were approximately 3.0–5.0 m in diameter and 0.2 m deep. Aerial cover was estimated for all plants rooted within 0.1-$m^2$ quadrats located randomly in the inner zone, but one or two quadrats were placed in each of the four cardinal directions for the edge and outer zone samples. Eight wallows were sampled at the unburned site by a total of 50, 34, and 24 quadrats in the inner, edge, and outer zones, respectively. Six wallows were sampled at the burned site by a total of 40, 24, and 24 quadrats in the inner, edge, and outer zones, respectively. Inner and edge samples cover about 20–25% of this portion of the wallows. Exterior samples were placed adjacent to wallows for comparison of compositional differences between wallow and prairie vegetation, but exterior samples are too few in number to adequately represent the grassland as a whole. All sampling occurred between late June and early July, 1982. However, the wallows support populations of winter annuals which are only present as seeds during the summer. To determine density of winter annuals, the inner zones of wallows at the two sites were re-sampled in November, 1982. Six 16 cm × 16 cm quadrats were randomly located in each wallow. Density was determined by counting the number of plants rooted in each quadrat.

DATA ANALYSIS. A total of 37 species was recorded. Cover values were averaged by species in each zone. Species with fewer than three occurrences were deleted from the multivariate analyses (after Gauch 1982), but all species were included in calculations of diversity. Average cover values were transformed to the Domin scale to minimize heterogeneity in the data matrix, and the remaining rare species were downweighted in proportion to their frequency (Hill 1979). These data were then subjected to detrended correspondence analysis (DCA) (Hill and Gauch 1980) to reduce matrix complexity and elicit patterns of variation in the data.

Diversity in each zone was estimated by exp(H′) which is the number of equally common species necessary to produce the given diversity value (Peet 1974). This is based on the Shannon-Wiener formula:

$$H' = -\Sigma p_i \ln p_i,$$

where $p_i$ is relative average cover for species i. Evenness (E) was determined by (N2-1)/(N1-1), where N2 is the inverse of Simpson's index and N1 = exp(H′), as recommended by Alatalo (1981). This index is not based on species richness, thus minimizing errors caused by not sampling rare species. Statistical differences between diversity in equivalent zones from burned and unburned wallows were determined by the nonparametric Mann-Whitney U test.

**Results.** *Coreopsis tinctoria* was the most abundant species in all zones at the unburned site (Table 1). Common grasses were *Eragrostis intermedia* outside the wallows and *Bromus japonicus* at the wallow edge. Other than *C. tinctoria,* no species dominated the wallow interior. All wallows were filled with 5-10 cm of water when sampled, which may have limited growth of many grassland species. Common taxa in the wallows were *Juncus torreyi, Ammannia coccinea, Lythrum alatum,* and *Cyperus acuminatus,* all of which are species adapted to wet habitats.

At the burned site, *Ambrosia psilostachya* and *Eragrostis intermedia* were the dominant taxa, however, *A. psilostachya* only occurred outside the wallows (Table 1). Cover of *Coreopsis tinctoria* was substantially lower than at the unburned site. *Iva ciliata* and *Juncus torreyi* were abundant at the wallow edge while *Marsilea mucronata* dominated in the standing water of the wallow interior.

DCA produces species and stand ordinations simultaneously (Hill 1979). Because the species ordination is a weighted average of the stand ordination and vice versa, direct comparison of the two diagrams facilitates interpretation of each ordination. Beta diversity is moderate along each axis; about 3.9 and 2.8 half-changes along axis I and II, respectively (Figure 1), thus, differences along the axes result from shifts in species importance as well as changes in species composition. Two distinct compositional gradients appear in the ordinations (Figures 1A and B). Axis I of the stand ordination separated vegetation along a gradient from the exterior to the interior of the wallows (Figure 1A). This pattern reflected the occurrence of *Ambrosia psilostachya, Schizachyrium scoparium, Andropogon saccharoides,* and *Dicanthelium oligosanthes* outside wallows at either the burned or unburned site (Figure 1B). *Marsilea mucronata, Juncus torreyi, Lythrum alatum, Cyperus acuminatus,* and *Ammannia coccinea* characterized samples located inside the wallows.

The edge and interior samples from Antelope Flat were generally clustered together and were more similar to each other than were edge and interior samples from the burned site (Figure 1A). At the burned site, one interior sample, which had less *Iva ciliata* and more *Lythrum alatum* than the others, was more similar to the edge samples. Otherwise, samples from each zone of the burned site were distinctly separated along the first axis of the stand ordination.

The second axis of the stand ordination clearly separated samples from the burned and unburned sites (Figure 1A). Some overlap among exterior samples occurred because these samples were located in relatively mature mixed grass prairie on similar soils, with rapid regrowth of perennial grasses following fire. Compositional dif-

Table 1. Average cover for each species, diversity, evenness, and richness in three zones of buffalo wallows at the unburned (Antelope Flat) and burned (Buffalo Spring) sites.

| | | Unburned site | | | Burned site | | |
|---|---|---|---|---|---|---|---|
| Species | Abbreviation | outer | edge | inner | outer | edge | inner |
| *Acacia angustissima* | ACAN | 1.7 | 1.1 | | | | |
| *Ambrosia psilostachya* | AMPS | 3.8 | | | 42.0 | | |
| *Ammannia coccinea* | AMCO | | 7.1 | 5.2 | | | |
| *Andropogon saccharoides* | ANSA | | | | 4.0 | 0.8 | |
| *Bromus japonicus* | BRJA | 4.0 | 20.0 | 5.2 | 2.1 | 2.5 | |
| *Chenopodium album* | CHAL | 7.0 | 5.9 | 0.2 | 5.8 | 1.2 | |
| *Coreopsis tinctoria* | COTI | 37.6 | 35.4 | 22.4 | 4.9 | 1.5 | 0.8 |
| *Croton lindheimerianus* | CRLI | 1.1 | 0.4 | 1.0 | 0.2 | 0.1 | |
| *Cyperus acuminatus* | CYAC | 0.6 | 7.5 | 6.5 | 3.7 | 3.2 | 6.3 |
| *Dicanthelium oligosanthes* | DIOL | 1.9 | 2.8 | 0.4 | 7.4 | 6.6 | |
| *Eleocharis* spp. | ELEO | | 0.5 | 0.1 | 4.8 | | |
| *Eragrostis intermedia* | ERIN | 43.6 | | | 18.6 | 17.3 | 4.0 |
| *Euphorbia spathulata* | EUSP | | | | 0.4 | 0.1 | |
| *Haplopappus ciliatus* | HACI | 2.1 | | | 0.4 | 1.0 | 0.4 |
| *Hedeoma hispida* | HEHI | 0.1 | 1.8 | | | | |
| *Helenium amarum* | HEAM | 0.1 | 1.0 | 0.1 | | | |
| *Hordeum pusilum* | HOPU | | 0.4 | 1.0 | 0.8 | 0.1 | |
| *Iva ciliata* | IVCI | 1.1 | 1.6 | 2.2 | | 32.7 | 0.2 |
| *Juncus torreyi* | JUTO | | 7.8 | 4.7 | | 11.5 | 5.8 |
| *Lepedium virginicum* | LEVI | 0.1 | 0.3 | 0.6 | | 0.2 | |
| *Lythrum alatum* | LYAL | | 0.8 | 2.1 | 0.9 | 1.0 | 6.2 |
| *Marselia mucronata* | MAMU | | | | | 0.6 | 24.2 |
| *Oxalis stricta* | OXST | 1.0 | 2.7 | | 0.1 | | |
| *Plantago virginiana* | PLVI | 3.0 | 3.8 | 0.4 | | 0.4 | 0.1 |
| *Rudbeckia hirta* | RUHI | 2.6 | 0.8 | | | | |
| *Schizachyrium scoparium* | SCSC | 2.2 | 1.3 | | 3.6 | | 1.2 |
| *Solanum eleagnifolium* | SOEL | 1.2 | 1.7 | 0.1 | 1.8 | 0.4 | 0.7 |
| Diversity | | 5.74 | 5.49* | 3.92 | 5.86 | 4.26 | 3.51 |
| Evenness | | 0.61 | 0.68 | 0.81 | 0.73 | 0.76 | 0.80 |
| Richness | | 14.2 | 11.5* | 6.2* | 11.8 | 8.0 | 5.2 |

*$p = 0.05$. Values were significantly different for comparable zones at the burned versus unburned site based upon a Mann-Whitney U test.

ferences within wallows exist: *Iva ciliata, Haplopappus ciliatus* and *Eragrostis intermedia* characterized burned wallows at Buffalo Spring, while *Oxalis stricta, Hedeoma hispida, Helenium amarum,* and *Lepedium virginicum* characterized wallows at the unburned site (Figure 1B).

Ruderal species, based on classification by Slife (1960) and USDA (1971), comprise almost 60% of the total flora sampled. Most of these ruderals achieved highest cover values within the wallows (e.g., *Bromus japonicus, Hedeoma hispida*); however, some ruderals such as *Ambrosia psilostachya* were common outside the wallows on the burned site. Several species including *Marsilea mucronata, Ammannia coccina,* and *Iva ciliata* usually occur in mesic habitats. Most of the taxa were found only in or achieved greatest cover inside the wallows where moisture is often available for longer periods of time during the growing season. Thus, wallows appear to be important sites for ruderal and wetland species within the mixed grass prairie.

Average density of winter annuals was $1752/m^2$ (range 280-3400) in wallows at the unburned site and $108.7/m^2$ (range 20-250) in burned wallows at Buffalo Spring. *Hedeoma hispida* and *Lepedium virginicum* were the most abundant winter annual species. In some wallows at the unburned site, the density of basal rosettes (each only a few centimeters in diameter) covered nearly 100% of the ground. A survey of the grassland outside the wallows produced very few winter annuals.

Despite fewer samples, species richness and diversity were greater outside the wallows than inside the wallows; however,

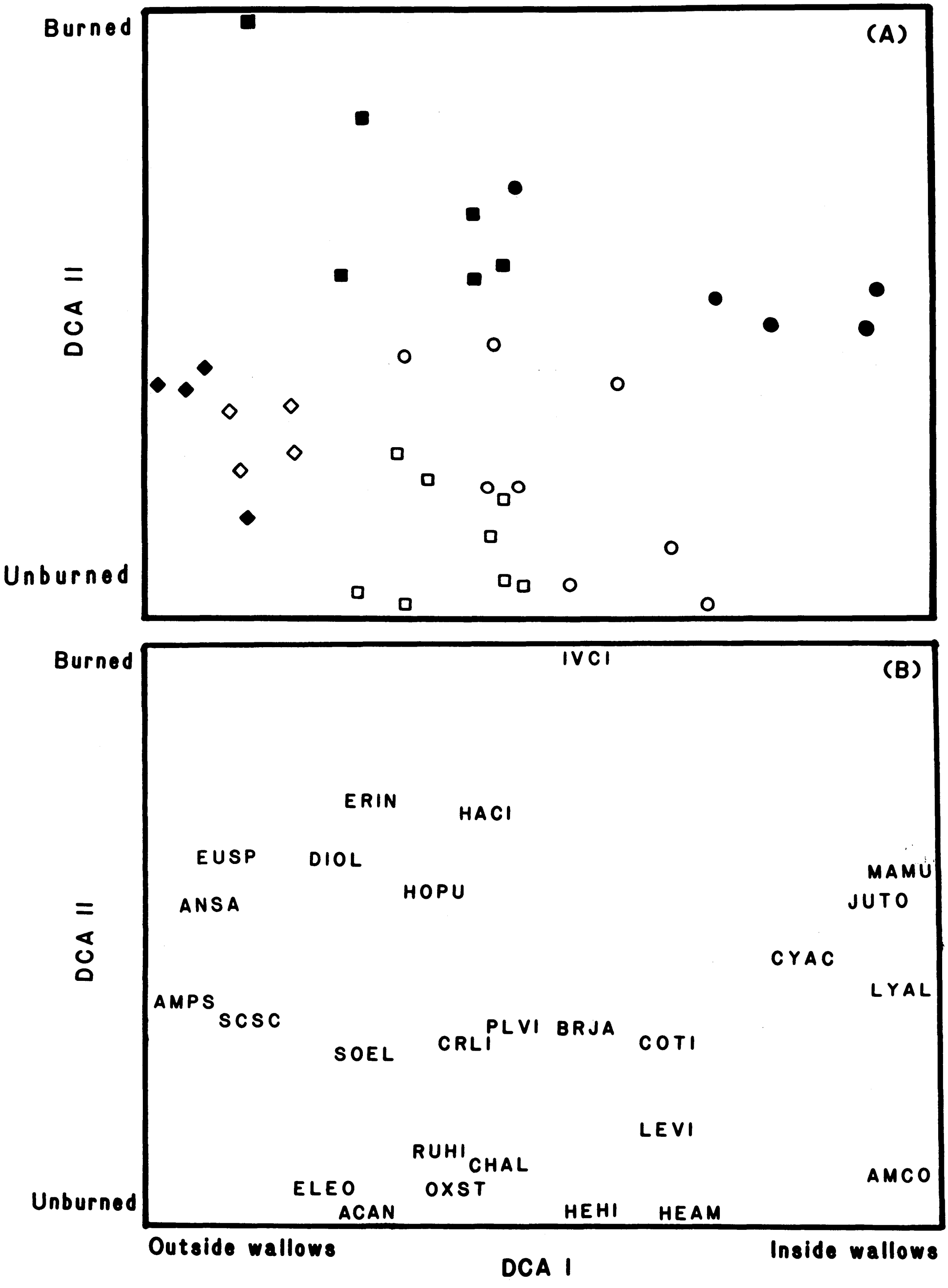


Fig. 1. A two-dimensional ordination by detrended correspondence analysis. Axis I is a moisture gradient separating vegetation from outside to inside the wallows. Axis II separated samples from burned and unburned sites. (◇) = unburned, outside; (□) = unburned, edge; (○) = unburned, inside; (◆) = burned, outside; (■) = burned, edge; (●) = burned, inside. A = stand ordination, B = species ordination. Species abbreviations are listed in Table 1.

this pattern was reversed for evenness values (Table 1). Dominance was more equitably distributed among species inside wallows where vegetative cover was reduced. High percent cover by *Coreopsis tinctoria, Bromus japonicus,* and *Eragrostis intermedia* contributed to the lowered evenness in the outer and edge zones. Total richness (gamma diversity) was at least double the richness from grassland samples outside the wallows. Richness values were significantly lower in the edge and inner zones at the burned site compared to the unburned site. Although diversity of wallow edge vegetation was also significantly lowered at the burned site, total number of species was nearly twice the number from grassland samples alone.

**Discussion.** The data suggest that (1) wallows contain vegetation different from that of surrounding prairie, which (2) increases regional species diversity on southern mixed grassland, and (3) fire alters the composition of vegetation within wallows to a greater extent than adjacent vegetation. For instance, *Coreopsis tinctoria* was abundant throughout the unburned site especially outside the wallows. *Ambrosia psilostachya,* a weedy annual, was dominant at the burned site, and many forbs including *C. tinctoria* produced less cover than at the unburned site, or were absent (Table 1). Hopkins *et al.* (1948) reported an increase in *A. psilostachya* following burning on a Kansas prairie.

The regrowth of plants after fire is affected by many factors including fire temperature, season during which burning occurs, and subsequent rainfall (Daubenmire 1968, Box and White 1969, Adams *et al.* 1982). Annual forbs that begin growth before a fire are usually killed while those developing after fire survive (Wright and Bailey 1982). Thus, the February fire at Buffalo Spring probably damaged or killed most winter annuals in these wallows. Subsequent precipitation created pools of water in the wallows at both sites. Therefore, although we did not sample wallows before the burn at Buffalo Spring, we attribute most of the compositional dissimilarities between the two study sites to the effects of burning. This is further supported by evidence from wallows in grassland several kilometers from our study site (Polley 1983). These wallows have not burned for several years and they contained vegetation similar to that in the wallows we studied at Antelope Flat.

In prehistoric times, fires were a common feature in prairie ecosystems. Wallows may have been especially abundant on burned sites because herbivores are attracted to graze in such areas after a fire (Vogl 1974). Because of the fire, grazing and wallowing activity may have been greater on the grasslands surrounding the wallows at Buffalo Spring. Thus, some of the differences between samples from burned and unburned sites may be due to increased herbivore activity as well as fire.

Total diversity at both sites was increased by vegetation in the wallows. This is not strictly a function of more samples in the wallows, but also because vegetation in the inner and outer zones is distinct at both sites (Figure 1A). Overall, the occurrence of wallows within a grassland produces a patchwork mosaic (Whittaker and Levin 1977, Pickett 1980) of local sites in different stages of succession. Gamma diversity would be expected to decrease as succession proceeds, however, the successional development of vegetation in wallows is unknown. Some wallows are repeatedly visited by buffalo which would prevent the establishment of perennial vegetation. Because all zones were somewhat similar at the unburned site, some vegetation changes probably result from encroachment by adjacent species. The broad distribution of the annual *Coreopsis tinctoria* suggests that seed dispersal may also be an important mechanism during succession. Whether or not succession always leads to the return of dominance by prairie species is not known. Wallows exist in central Oklahoma grasslands in unplowed pastures where buffalo have not occurred for at least 100 years. These wallows still hold water and support wetland plants and ruderals (Barkley and Smith 1934, Polley 1983).

The past significance of these gaps created by buffalo in the grassland vegetation is difficult to assess. Natural disturbances repeatedly generated by animals such as prairie dogs (*Cynomys ludovicianus*) (Bonham and Lerwick 1976), badgers

(*Taxidea taxus*) (Platt 1975) and buffalo would induce numerous microsuccessions within the mature grassland matrix. Perhaps ruderal taxa were restricted to such sites prior to the widespread disturbance of vegetation by humans (c.f., Marks 1983). Ruderals, especially winter annuals, were common in wallows on grasslands unburned for only a few years (Table 1). Native ruderal plants may have been restricted to wallows and other disturbance sites until a large scale perturbation such as fire disrupted the climax vegetation. Natural fires may occur throughout the year (Vogl 1974), however, some records indicate that most lightening-caused fires occur in the late summer and early fall (Bragg 1982). Therefore, winter annuals may have had a greater probability of survival under natural fire regimes. They could set seed prior to fires and seed germination would take place after fires removed canopy species.

The composition and dynamics of vegetation in the wallows can be explained by a model similar to that for wetlands proposed by van der Valk (1981) in which water level fluctuations governed species composition. The same would be true for vegetation in wallows since pronounced fluctuations in precipitation typify grassland environments (Risser *et al.* 1981). Thus, importance of wetland species would vary from year to year. Frequency and season of fires are additional factors affecting the composition of vegetation in wallows. Spring fires may reduce cover of annuals whereas summer and fall fires may increase the importance of winter annuals. Finally, animal visitation rates also impose controls; frequent visitation by buffalo would produce limited vegetation cover, primarily by annual weeds. Together these factors will produce highly heterogeneous plant communities within wallows. However, with a knowledge of the type and frequency of disturbance, general aspects about the vegetation in wallows (such as presence of ruderals or wetland taxa) is predictable.

## Literature Cited

ADAMS, D. E., R. C. ANDERSON, AND S. L. COLLINS. 1982. Differential response of woody and herbaceous species to summer and winter burning in an Oklahoma grassland. Southwest Nat. 27:55-61.

ALATALO, R. V. 1981. Problems in the measurement of evenness in ecology. Oikos 37:199-204.

BARKLEY, F. A. AND C. C. SMITH. 1934. A preliminary study of buffalo wallows in the vicinity of Norman, Oklahoma. Proc. Oklahoma Acad. Sci. 14:47-52.

BONHAM, C. D. AND A. LERWICK. 1976. Vegetation changes induced by prairie dogs on shortgrass range. J. Range Manage. 29:221-225.

BOX, T. W. AND R. S. WHITE. 1969. Fall and winter burning of south Texas brush ranges. J. Range Manage. 22:373-376.

BRAGG, T. B. 1982. Seasonal variations in fuel and fuel consumption by fires in a bluestem prairie. Ecology 63:7-11.

———— AND L. C. HULBERT. 1976. Woody plant invasion of unburned Kansas bluestem prairie. J. Range Manage. 29:19-24.

BUCK, P. 1964. Relationships of the woody vegetation of the Whichita Mountains Wildlife Refuge to geological formations and soil types. Ecology 45:336-344.

COLLINS, S. L. AND D. E. ADAMS. 1983. Succession in grasslands: thirty-two years of change in a central Oklahoma tallgrass prairie. Vegetatio 51:181-190.

COPPOCK, D. L., J. K. DETLING, J. E. ELLIS, AND M. I. DYER. 1983a. Plant-herbivore interactions in a North American mixed-grass prairie. I. Effects of black-tailed prairie dogs on intraseasonal aboveground biomass and nutrient dynamics and plant species diversity. Oecologia 56:1-9.

————, J. E. ELLIS, J. K. DETLING, AND M. I. DYER. 1983b. Plant-herbivore interactions in a North American mixed-grass prairie. II. responses of bison to modification of vegetation by prairie dogs. Oecologia 56:10-15.

CROCKETT, J. J. 1964. Influence of soils and parent materials on grasslands of the Wichita Mountains Wildlife Refuge, Oklahoma. Ecology 45:326-335.

DAUBENMIRE, R. 1968. Ecology of fire in grasslands. Adv. Ecol. Res. 5:209-266.

ENGLAND, R. E. AND A. DEVOS. 1969. Influence of animals on pristine conditions on the Canadian grasslands. J. Range Manage. 22:87-94.

GAUCH, H. G. JR. 1982. Multivariate analysis in community ecology. Cambridge Univ. Press, London. 298 p.

GOULD, F. W. 1975. The grasses of Texas. Texas A and M Univ. Press, College Station, Tx. 653 p.

GRIME, J. P. 1979. Plant strategies and vegetation processes. John Wiley and Sons, New York, NY 222 p.

HILL, M. O. 1979. DECORANA—A FORTRAN program for detrended correspondence analysis and reciprocal averaging. Cornell Univ., Ithaca, NY.

———— AND H. G. GAUCH, JR. 1980. Detrended correspondence analysis: an improved ordination technique. Vegetatio 42:47-58.

HOPKINS, H., F. W. ALBERTSON, AND A. RIEGEL. 1948. Some effects of burning upon a prairie in west-central Kansas. Trans. Kansas Acad. Sci. 57:131-141.

HUSTON, M. 1979. A general hypothesis of species diversity. Am. Nat. 113:81-101.

KUCERA, C. L. 1981. Grasslands and fire, p. 90-111. *In:* H. A. Mooney *et al.*, [eds.]. Fire regimes and ecosystem properties. U.S.D.A. For. Serv. Gen. Tech. Rept. WO-26. 596 p.

LARSON, F. 1940. The role of the bison in maintaining the short grass plains. Ecology 21:113-121.

MACK, R. N. AND J. N. THOMPSON. 1982. Evolution in steppe with few large, hooved mammals. Am. Nat. 119:757-773.

MARKS, P. L. 1983. On the origin of the field plants of the northeastern United States. Am. Nat. 122:210-228.

MCNAUGHTON, S. J. 1983. Compensatory plant growth as a response to herbivory. Oikos 40:329-336.

MILLER, T. E. 1982. Community diversity and interactions between the size and frequency of disturbance. Am. Nat. 120:533-536.

PEET, R. K. 1974. The measurement of species diversity. Ann. Rev. Ecol. Syst. 5:285-308.

PICKETT, S. T. A. 1980. Non-equilibrium coexistence of plants. Bull. Torrey Bot. Club 107:238-248.

PLATT, W. J. 1975. The colonization and formation of equilibrium plant species associations on badger disturbances in a tall-grass prairie. Ecol. Monogr. 45:285-305.

POLLEY, H. W. 1983. An analysis of the vegetation of buffalo wallows in relation to environmental gradients. M.S. Thesis, University of Oklahoma, Norman, OK.

RICE, E. L. AND R. L. PARENTI. 1978. Causes of decreases in productivity in undisturbed tall grass prairie. Am. J. Bot. 65:1091-1097.

RISSER, P. G., E. C. BIRNEY, H. D. BLOCKER, S. W. MAY, W. J. PARTON, AND J. A. WIENS. 1981. The true prairie ecosystem. Hutchinson Ross Publ. Co., Stoudsburg, PA. 557 p.

SLIFE, F. W., [ed.]. 1960. Weeds of the north central states. Univ. Illinois Press, Urbana, IL. 262 p.

USDA. 1967. Soil Survey Comanche County, Oklahoma. 58 p.

USDA. 1971. Common weeds of the United States. Dover Publ., New York, NY. 463 p.

VALK, A. G. VAN DER. 1981. Succession in wetlands: a Gleasonian approach. Ecology 62:688-696.

VOGL, R. J. 1974. Effects of fire on grasslands, p. 139-194. *In:* T. T. Kozlowski and C. E. Ahlgren, [ed.]. Fire and ecosystems. Academic Press, New York, NY. 542 p.

WATERFALL, U. T. 1972. Keys to the flora of Oklahoma. 5th Ed. Oklahoma State Univ., Stillwater, OK. 246 p.

WHITE, P. S. 1979. Pattern, process, and natural disturbance in vegetation. Bot. Rev. 45:229-299.

WHITTAKER, R. H. AND S. A. LEVIN. 1977. The role of mosaic phenomena in natural communities. Theor. Popul. Biol. 12:117-139.

WRIGHT, H. A. AND A. W. BAILEY. 1982. Fire ecology. John Wiley and Sons, New York, NY. 501 p.