Relationships of Vegetation and Environment in Buffalo Wallows

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ABSTRACT: Active and presently inactive buffalo wallows in central and southwestern Oklahoma were examined to determine the distribution and seasonal variation of herbaceous species in relation to environmental factors. Species cover values and soil data were collected from six areas along a transect which spanned the long axis of each wallow and included adjacent prairie at each end. Vegetation composition inside both active and inactive wallows was consistently different from that outside wallows. In each case, these vegetational differences corresponded to differences in soil texture, soil moisture, available phosphorus and *p*H along the topographic gradient from wallow bottom to prairie.

An ordination of samples from May, July and August revealed seasonal differences in the vegetation of areas inside and outside active and inactive wallows. Vegetation inside inactive wallows, though largely characterized by mesic species, displayed a seasonal sequence similar to that outside these wallows. These changes were due to a seasonal shift from cool-season species in May to warm-season species in August. Seasonal patterns inside active wallows were related to the intensity and frequency of disturbance by ungulates. Where disturbance was minimal, *Eleocharis* spp. remained dominant throughout the season. Vegetation changes resulted from the seasonal fluctuation of minor species. In highly disturbed wallows, cover of *Eleocharis* spp. and other species associated with inundated conditions in May declined and that of grasses increased with time.

INTRODUCTION

Buffalo wallows are small depressions in grasslands created when buffalo (*Bison bison*) trample the ground and roll in the exposed soil. Wallows are more or less oval in shape. They vary in depth from a few centimeters to a meter or more, and in diameter from a few meters to over 45 m when individual wallows merge (Barkley and Smith, 1934). Because of soil compaction by the buffalo, wallows often retain water for several weeks following rainy periods during the growing season (Barkley and Smith, 1934). Ephemeral standing water in wallows provides local habitats for prairie species adapted to mesic conditions. In addition, water can alter soil nutrient patterns (Patrick and Mikkelsen, 1971) so that edaphic factors may also contribute to differences in species composition between wallows and adjacent prairie.

Buffalo wallows were apparently a common feature of the pristine grasslands of central North America (England and DeVos, 1969). Until recently, however, only a single preliminary survey of their vegetation has been published (Barkley and Smith, 1934). With urbanization and the elimination of most buffalo herds, the number of buffalo wallows has rapidly diminished and their role in the dynamics of grassland vegetation is difficult to assess (Collins and Uno, 1983).

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This study was undertaken: (1) to compare the composition and seasonal changes of vegetation within and immediately surrounding buffalo wallows, and (2) to investigate relationships between variation in vegetation and changes in environmental factors along a gradient from prairie to wallow interior.

MATERIALS AND METHODS

Study area. — Ten active wallows were analyzed in the Wichita Mountains Wildlife Refuge, Comanche Co., southwestern Oklahoma (lat 34° 44′ N, long 98° 43′ W). This refuge contains a 23,885-ha mosaic of forest and grassland vegetation (Buck, 1964; Crockett, 1964). The vegetation of the Refuge has been protected from fire since 1901 and only recently has a prescribed policy of range burning been implemented. Since 1937, the area has been subjected to grazing by managed populations of approximately 300 longhorn cattle, 625 bison, 500 elk, 1200 deer and 400 wild turkeys.

All active wallows sampled were located in mixed-grass prairie areas underlain by soils classified as Mollisols (U.S. Dep. Agric., 1960). These soils of the Foard series consist of deep brown to reddish-brown loams to clay loams with appreciable amounts of scattered granite cobblestones (U.S. Dep. Agric., 1967). The 30-year (1951-1980) average annual precipitation is 714.7 mm (Wichita Mountains Wildlife Refuge Station). Of this amount, an average of 398.3 mm falls during the 5-month period from April through August. Total for the 5-month period in 1981 was 477.5 mm; total for the year was 861.6 mm. The 30-year average annual maximum and minimum temperatures are 23.5 and 8.6 C, respectively. The mean temperature of 16.1 C for 1981 represented an incease of 0.06 C over the norm (NOAA, 1980, 1981).

Five inactive wallows were studied near Washington, McClain Co., central Oklahoma (lat 34° 44′ N, long 98° 43′ W). These wallows were located on slightly sloping Mollisols (U.S. Dep. Agric., 1960) in a mixed to tallgrass prairie that, though mowed, had never been plowed and had not been grazed for at least 5 years. Estimates place the last buffalo in the area ca. 100 years ago. The surface layer of these Granite series soils is reddish brown silt loam underlain by a reddish-brown silty-clay loam subsoil (U.S. Dep. Agric., 1969).

The 30-year (1951-1980) average annual precipitation (Purcell, Oklahoma station) for this area is 859.8 mm, of which an average of 467.4 mm falls from April through August. Total precipitation for the 5-month period in 1981 was 578.9 mm; total for the year was 983.5 mm. The 30-year average annual maximum and minimum temperatures are 23.1 and 9.0 C, respectively. The mean temperature of 16.9 C for 1981 matched the annual norm (NOAA, 1980,1981).

Field measurements. — Vegetation and soil variables were recorded along a belt transect which bisected the long axis of each wallow. Each transect was divided into six evenly spaced segments so that the segment at each end of the transect was located in the prairie. At three sample periods (7-13 May, 28 June-5 July and 17-22 August) in 1981, a single 32 x 32 cm quadrat was randomly located in each of the six areas of the transect. All species rooted in each quadrat were visually assigned cover values according to the methods of van der Valk and Bliss (1971): + for $<1.0\%$ cover, 1 for 1-5% cover, 2 for 6-15% cover, 3 for 16-25% cover, 4 for 26-50% cover, 5 for 51-75% cover, 6 for 76-95% cover and 7 for 96-100% cover.

During each of the three sample periods a 7.0-cm diam soil sample was taken from within each of the six transect sections at 5-15 and 15-25 cm depths. Samples were placed in a sealed container and returned to the laboratory for gravimetric determination of soil moisture. During the sample periods in May and August, composite soil samples were taken for nutrient and textural analysis from the 5-15 cm depth within each transect section.

Soil analyses. — Composite soil samples were air-dried and visible particulate organic matter was removed. Gravel was removed with a 2-mm sieve and the remaining soil was stored in airtight plastic bags until analysis. Percent gravel (>2 mm) was determined as the percentage of total sample dry weight. Soil *p*H was determined by glass electrode in a 1:1 soil:distilled water suspension.

Exchangeable ammonium-nitrogen was determined in 2N KCl (5 ml per g of soil) extracts of soil using the MgO steam-distillation procedure of Bremner (1965). Nitrate-nitrogen was determined by steam-distillation with the addition of Devarda alloy following removal of ammonium (Bremner, 1965). Available soil phosphorus was determined in ammonium fluoride-hydrochloric acid soil extracts (Bray and Kurtz, 1945), using the ascorbic acid procedure of John (1970).

Mechanical analysis was made once with the hydrometer method (Bouyoucos, 1936; Piper, 1942) on composite samples. All other soil parameters were analyzed for soils collected in May and August. All soil analyses were performed in duplicate.

Vegetational analysis. — Species encountered in fewer than 5% of sampled quadrats during each sample period were omitted from the analysis. Cover class values for the remaining species were converted to percentages by using the midpoints of cover classes. Species cover data from transect sections 1 and 6, 2 and 5, and 3 and 4 of each wallow were grouped to give an average cover value by species for inner (sections 3 and 4), marginal (2 and 5) and outside (1 and 6) areas of wallows. Results of the soil analyses were likewise grouped to give an average value corresponding to each of the three vegetational zones. Measurements of *p*H were transformed to the antilog before averaging.

Untransformed vegetation cover data from the three stands per wallow were ordinated for each sample period with detrended correspondence analysis (DCA; Hill, 1979; Hill and Gauch, 1980). Separate ordination analyses were performed on data from each sample period in active and inactive wallows. Ordinations produce an arrangement of species and stands along axes that may correlate with environmental gradients (Gauch, 1982). An environmental interpretation of the first two ordination axes was sought by correlating (Pearson product-moment) the position of each stand on the two axes with each of the 10 environmental parameters measured.

Patterns of seasonal vegetational change inside active and inactive wallows were compared to seasonal changes in prairie vegetation outside wallows. Cover values from stands inside (transect sections 2,3,4,5) and outside (sections 1 and 6) wallows were averaged and ordinated for each of the three sample periods of May, July and August. The time trajectory of each site was traced through the species-space ordination to ascertain seasonal vegetational changes inside wallows relative to seasonal changes in prairie vegetation outside wallows. General trends in species composition may become evident if a majority of sites show parallel or similar patterns through time (Hopkins, 1968; Austin, 1977; Collins and Adams, 1983).

RESULTS

For May samples, the first axis (x-axis) of DCA distinguished, on the basis of species similarity, marginal and inner stands from outside stands of both active (Fig. 1A) and inactive (Fig. 1B) wallows. The pattern holds except for wallows D and I, both of which were largely denuded by buffalo trampling and wallowing at the May sampling period.

Pearson product-moment correlation of stand position on the first two axes with each of the 10 variables provided an environmental interpretation of the pattern in each ordination. First-axis positions of stands from both active and inactive wallows were negatively correlated with percent clay, available phosphorus and soil moisture (Table 1). Soils from marginal and inner transect sections at both the Wichita Refuge and Washington sites had a higher percent clay, possessed higher levels of available phosphorus and had significantly more moisture relativi to outside stands at the same location. Additionally, soil nitrate-nitrogen was higher outside active wallows.

The first axes (x-axes) of the DCA ordinations of August data clearly segregated marginal and inner from outside stands in active (Fig. 2A) and inactive (Fig. 2B) wallows. The pattern again differs only for wallows D and I which remained largely denuded by buffalo activity.

Correlation of stand coordinates from each ordination for August with environmental parameters (Table 1) again showed that soils of marginal and inner stands had less sand, higher percent clay and more available phosphorus than those of outside stands. Soil moisture at 5-15 and 15-25 cm depths was higher inside active and inactive wallows, though a complete complement of samples was not obtained for the latter group. In August, soil *p*H was higher outside than inside both inactive and active wallows.

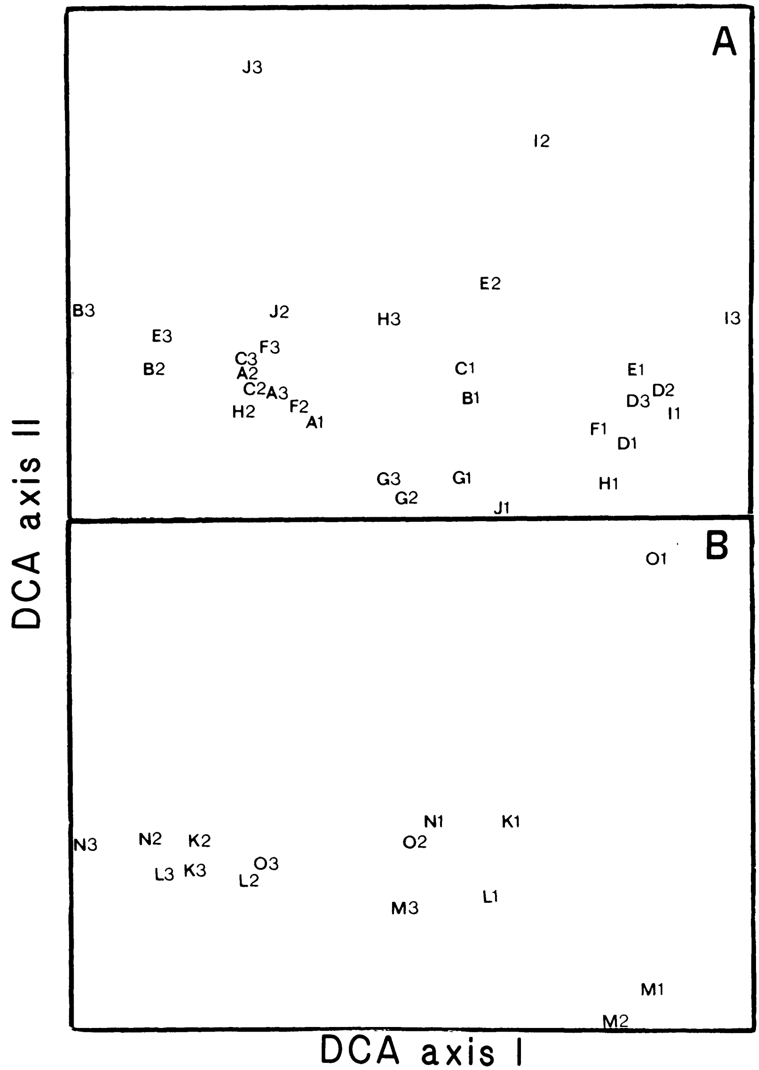

Fig. 1.—Two-dimensional ordination by detrended correspondence analysis of transect positions from (A) 10 active wallows, and (B) five inactive wallows in May 1981. Numerals correspond to transect positions: 1 = outside wallows, 2 = marginal, 3 = inside wallows. Wichita wallows = A-J, Washington wallows = K-O.

The trajectories of seasonal change for stands inside and outside inactive wallows show similar trends (Fig. 3A). The pattern is a seasonal shift from cool-season species in May to warm-season species in August.* Cool-season annuals like *Bromus japonicus* were dominant outside wallows in May, whereas warm-season species, such as *Sporobolus vaginaeflorus, Chloris verticillata* and *Eragrostis curtipedicellata,* were dominant in August. A similar seasonal pattern occurred inside inactive wallows. In May the vegetation was largely dominated by cool-season species like *Hordeum pusillum, Bromus japonicus* and *Cyperus acuminatus.* By August, subdominants included the warm-season species *Ambrosia psilostachya, Polygonum* sp., *Aristida oligantha, Buchloe dactyloides* and *Sporobolus vaginaeflorus.*

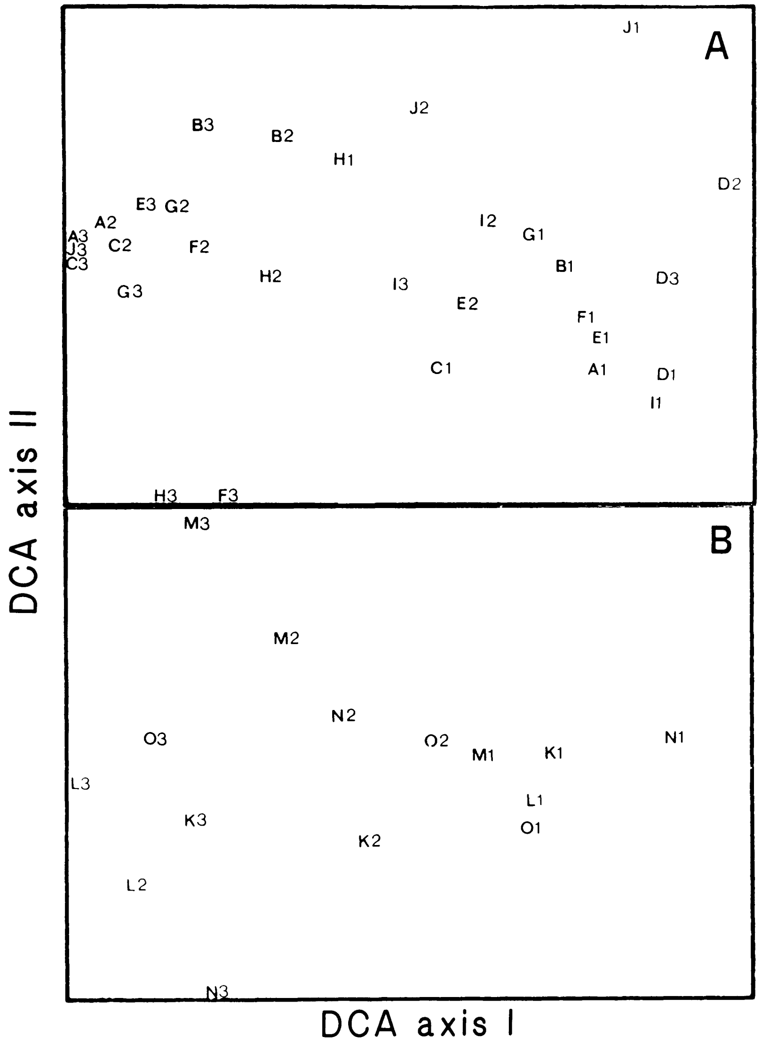

Fig. 2.—Two-dimensional ordination by detrended correspondence analysis of transect positions from (A) 10 active wallows, and (B) five inactive wallows in August 1981. Transect positions and wallow designations are noted as in Figure 1

* Plant nomenclature follows Waterfall (1979).

The trajectories of seasonal vegetation change inside active wallows are also clearly differentiated from those outside these wallows, although some convergence of July trajectories is evident (Fig. 3B). Convergence of outside stands in July reflects the increased importance of *Eleocharis* spp., a dominant inside the wallows throughout the growing season.

Vegetational change outside active wallows, like that outside inactive wallows, was largely a shift from cool-season annuals, including *Hordeum pusillum* and *Bromus japonicus* in May, to species characteristic of drier, late-season conditions in August. Variations in seasonal trends among outside stands primarily reflected differences in August dominants.

Owing to continued disturbance by buffalo, a general seasonal pattern is not evident inside active wallows (Fig. 3B). The orientations suggest that seasonal trends vary with the frequency and intensity of disturbance by buffalo. For simplicity, only representative examples of seasonal trajectories are shown in Figure 3B. Only slight seasonal change of vegetation occurred inside wallows A and C, where *Eleocharis* spp. contributed the majority of cover throughout the season. The trajectories for inside areas of wallows F, G and H follow a clear trend along the second axis. This pattern reflects the seasonal occurrence of generally minor species with *Eleocharis* spp. dominant throughout the sample period (Table 2). Trajectories for wallows E and J are oriented along the first axis. In these frequently disturbed wallows, *Eleocharis* spp., though abundant in May, were not as dominant as in other wallows. Vegetational changes from May to August resembled changes in the prairie. May dominants such as *Eleocharis* spp., *Juncus interior, Coreopsis tinctoria* and *Cyperus acuminatus* were replaced in August by the warm-season species *Sporobolus asper, Aristida oligantha* and *Buchloe dactyloides.* Total vegetation cover declined with time in these frequently disturbed wallows.

DISCUSSION

A clear compositional change exists along the prairie-to-wallow gradient in both active and inactive buffalo wallows. Wallow vegetation remained distinct from that of the immediately adjacent prairie throughout the season. Substantial changes in species composition were associated with a topographic gradient of only a few centimeters. The gradient included at least five different environmental parameters, chief of which were soil texture, moisture and available phosphorus.

Vegetation pattern was correlated with a moisture gradient associated with variations in soil texture. Soils from inside wallows contained considerably more clay than did soils of the surrounding prairie. Directly related to both the topographic depression of wallows and the higher clay content of their soils, moisture was higher in wallows than in the adjacent prairie throughout the growing season.

Other variables, including soil nutrients and *p*H, which were correlated with differences in plant composition, were apparently related to the soil moisture gradient.

TABLE 1. — Correlation coefficients of environmental parameters from May and August 1981 with stand position on the first axis of DCA ordination. Symbols: * P = 0.05, ** P = 0.01

	Wichita		Washington	
	May	August	May	August
gravel	0.04	-0.03	-0.22	-0.44*
sand	0.67**	0.76**	0.80**	0.79**
silt	-0.28	-0.25	-0.62**	-0.19
clay	-0.63**	-0.72**	-0.74**	-0.80**
*p*H	0.40*	0.30	0.57*	0.64**
NO_3(*Micrograms* $\mu g\ g^{-1}$)	0.42**	-0.04	-0.28	0.35
NH_4 (*Micrograms* $\mu g\ g^{-1}$)	0.18	0.27	0.27	0.14
P (*Micrograms* $\mu g\ g^{-1}$)	-0.37**	-0.42**	-0.71**	-0.74**
moisture (5-15 cm) (%)	-0.42**	-0.48**	-0.52*	----
moisture (15-25 cm) (%)	-0.31*	-0.63**	0.06	----

For active and inactive wallows, soil *p*H remained lower and available phosphorus remained higher inside than outside the wallows. Nitrate-nitrogen was lower inside than outside active wallows only in May.

These soil characteristics may be due to standing water in wallows and to processes such as leaching of nitrate (Patrick and Mikkelson, 1971), cation leaching and stimulated bacterial carbon dioxide production in submerged soils (Brady, 1974). Increased available phosphorus inside wallows could be due to either hydrolysis or reducing conditions or both (Shapiro, 1958).

Though seasonal trends differ somewhat with respect to species composition, areas outside both active and inactive wallows display a shift from cool-season annuals in

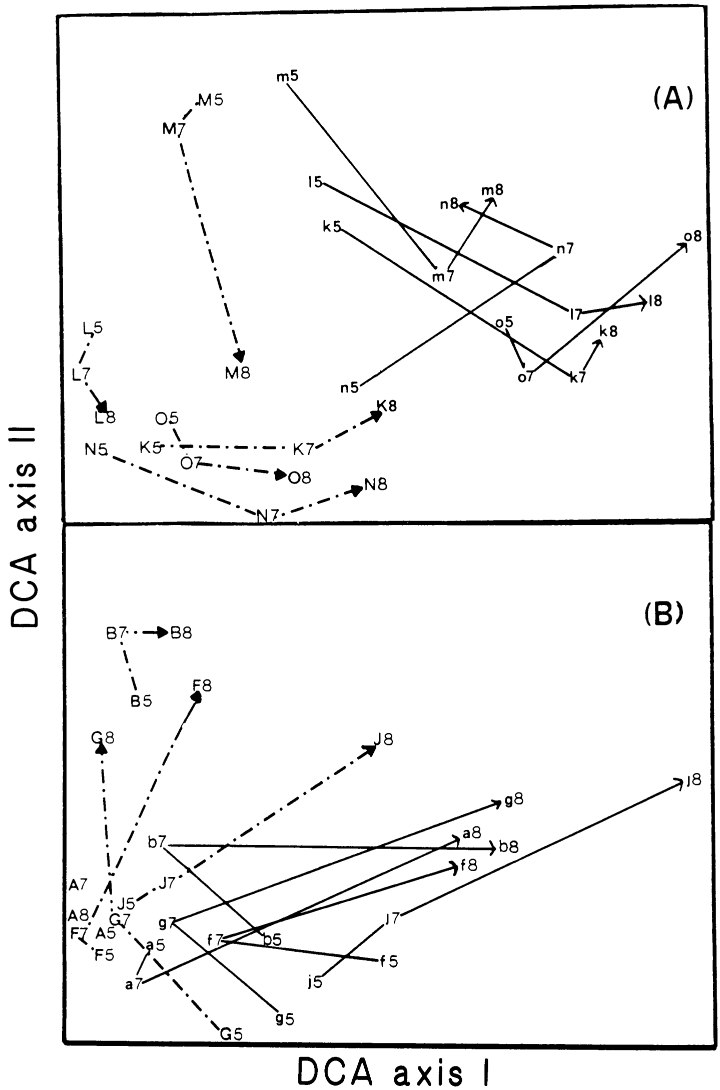

Fig. 3.—Two-dimensional ordination by detrended correspondence analysis of samples outside and inside (A) inactive wallows, and (B) active wallows during three sample periods. Numerals correspond to sample dates: 5 = May, 7 = July, 8 = August. Stands inside wallows are denoted by uppercase letters, those outside are lowercase

May to warm-season species in August (Fig. 3 A and B). Seasonal aspects of vegetation inside wallows differ markedly from those outside all sampled wallows. The primary factor influencing vegetation within all wallows is the moisture regime. Vascular plants occupying wallows are primarily mesic prairie species adapted to extremes of vernal moisture and desiccation.

The Washington wallows displayed a seasonal progression of composition similar to that observed in the prairie. Vegetational change was strongly influenced by shifts in dominants and subdominants, a number of which were ruderal species. Seasonal aspects inside active wallows were related to the intensity and frequency of disturbance. Cover of herbaceous plants was low inside highly disturbed wallows. Species dominant in inundated wallows declined and weedy grasses increased with time. In revegetated and infrequently disturbed wallows *Eleocharis* spp. were dominant. In some, *Eleocharis* spp. remained dominant throughout the season to the virtual exclusion of other species. In other wallows, temporal change was due to the seasonal occurrence mostly of minor species.

Grazing and fire are natural disturbances influencing species distribution in wetland areas (Holte, 1966; Dix and Smeins, 1967; Walker and Coupland, 1968; Collins and Uno, 1983). In addition to these disturbances, trampling by large ungulates such as cattle or buffalo affects species composition. Van der Valk (1975) reported that the microrelief created by cattle trampling altered Iowa fen vegetation, allowing certain weedy species to become established. Trampling in wallows leads to dominance by *Eleocharis* spp. These ungrazed sedges form dense rhizomatous mats well-adapted to trampling and seasonal fluctuations in standing water. Only during the drier latter part of the observation period, when these species became dormant, did other species gain prominence.

The Washington wallows, unused by ungulates for at least 5 years, retain a flora similar to that of active wallows. However, several species common to the adjacent prairie (*e.g.*, *Ambrosia psilostachya, Aristida oligantha, Sporobolus vaginaeflorus. Buchloe dactyloides* and *Andropogon saccharoides*) occurred as subdominants in these wallows. It appears that the absence of ungulate disturbance has allowed the establishment of prairie species in these wallows, producing a vegetation that is now a mixture of prairie and wallow taxa. As succession continues, prairie vegetation may eventually dominate these sites.

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TABLE 2.—Percent of total cover for transect segments 2,3,4,5 of Wichita wallows F,G and H

	May	July	August
Eleocharis spp.	32.6	26.4	3.0
Hordeum pusillum	19.7	0.8	0.1
Tridens albescens	2.0	2.5	1.6
Iva ciliata	1.3	2.8	2.1
Bromus japonicus	0.7	0.07	—
Coreopsis tinctoria	0.5	0.3	—
Geranium carolinianum	0.3	—	—
Oxalis stricta	0.07	—	—
Cyperus acuminatus	0.04	0.5	0.3
Polygonum sp.	0.04	0.09	1.3
Hedeoma hispida	0.03	—	—
Grindelia squarrosa	—	—	0.03
Aristida oligantha	—	—	0.07
Echinochloa crusgalli	—	—	0.07
Juncus interior	—	0.07	0.2
Panicum dichotomiflorum	—	—	1.2

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