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Mary Bomberger Brown
University of Nebraska-Lincoln, mbrown9@unl.edu

Shelly L. Shields
University of Nebraska - Lincoln

A. Tyrone Harrsion
University of Nebraska - Lincoln

Kathleen H. Keeler
University of Nebraska - Lincoln, kkeeler1@unl.edu

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Comparison of Old Field Succession on a Tallgrass Prairie and a Nebraska Sandhills Prairie

Mary L. Bomberger, Shelly L. Shields,
A. Tyrone Harrison and Kathleen H. Keeler[1]
School of Life Sciences
University of Nebraska
Lincoln, Nebraska 68588

Long held to be reasonably well understood, the process of ecological succession has recently come under attack. The predictability of successional changes has been doubted (Walker 1970), the mechanism of species replacement has been questioned (Connell and Slatyer 1977), and the reality of steady-state (climax) challenged (Botkin and Sobel 1975, Connell and Slatyer 1977, Connell 1978). In particular, several communities are presently recognized as having "cyclic succession" (Ricklefs 1973), in which the process is continually repeating. Such communities include heaths (Watt 1947), prairie pot-hole marshes (Vander Valk and Davis 1978), spruce-fir forests (Sprugel 1976, Sprugel and Bormann 1981), and intertidal communities (Levin and Paine 1974).

Secondary succession on abandoned fields in North American prairies has received little recent attention (but see Clements 1916, Shantz 1917, Booth 1941, Weaver 1954, Roux and Warren 1963, Rice 1974). A typical progression from annual weeds through a series of grass communities to the original, stable, composition is expected to require a minimum of 30 years (Rice 1974, Glenn-Lewin 1980).

In this study, we compare the progress of succession in two different grassland communities in Nebraska to each other and to the proposed models.

SITES AND METHODS

In Nebraska, tallgrass prairies are found in the eastern third of the state, where rainfall is approximately 80 cm/year, chiefly on fine textured glacial or loess-derived silt loam soils (Steiger 1930, Fichter 1954). The dominants, reaching 1.5 m in height, are *Andropogon gerardi*, *A. scoparius*, and *Sorghastrum avenaceum* (= *S. nutans*). Tallgrass prairies are not normally affected by large-scale, intense, soil related disturbances; however, they were previously influenced by periodic bison grazing and extensive fires. Local burrowing mammals may be important in the demographics of the minor species (Platt 1975, Platt and Weis 1977).

The Nebraska Sandhills prairie, in contrast, is a "mixed" prairie with both "tall" and "short" grass dominant species which cover approximately 52,000 km^2 in the center of the state. The rainfall is approximately 40 cm/year and the soils

[1]Offprint requests to K.H.K.

are coarse sands with little profile development. The sand forms rolling hills with up to 100 m relief, and long, broad, flat interdunal valleys spaced approximately 1 km apart. The vegetation of these prairies is dominated by the grasses, *Calamovilfa longifolia*, *Stipa comata*, *Bouteloua gracilis* and *B. hirsuta*, all generally less than one meter in height. The Sandhills prairies experience severe soil erosion in the form of wind-driven "blowouts" of open sand, especially after drought, fire, or extensive grazing (Rydberg 1895, Pool 1914, Weaver 1954, Wolfe 1973, Bragg 1978).

The two study areas are approximately 500 km apart, both at approximately 41° N latitude. Both have strongly continental climates with annual temperature extremes ranging from 35°C to -20°C (Lawson et al. 1977). At each site, an old field was compared with the immediately adjacent undisturbed prairie.

The tallgrass prairie study area, Nine Mile Prairie, is located 14 km northwest of Lincoln, Nebraska, in Lancaster County (NE¼ T10N R5E). It is a 97 ha research area owned by the Lincoln Municipal Airport Authority, temporarily leased and managed for preservation by the Audubon Society and the University of Nebraska. The ecology of this tallgrass prairie remnant has been described by Steiger (1930) and Fichter (1954) and has a long history of research use and publication (see Fichter 1954 for citations). According to aerial photographs, the old field, 2-3 ha, has not been in cultivation since before 1940 (Harrison unpubl). Both prairie and old field have a history of mid-summer mowing for native hay. The soil of Nine Mile Prairie is a fine-textured Carrington silt loam of glacial origins (Steiger 1930, Fichter 1954). In the old field most of the A horizon was lost by erosion during the past cultivation history. The elevation is approximately 370 m above sea level with relief of 45 m.

The Sandhills prairie study area, Arapaho Prairie, is located 16 km south of Arthur, Nebraska, in Arthur County (Sec. 31, 32 T18N R39W). It is a 526 ha research preserve managed by the University of Nebraska for The Nature Conservancy. The "Big Old Field" area, 27 ha on section 31, has not been under cultivation since approximately 1937 (Keeler et al. 1980, Harrison unpubl). The entire Arapaho Prairie area was summer-grazed throughout its history until acquisition for preservation in 1977 (Keeler et al. 1980). The soil is Valentine fine sand and elevation is approximately 1,100 m with relief of approximately 60 m.

On both old field and adjacent prairie sites, the plant communities were sampled during the first week of September, 1980. Voucher specimens of all plants are on deposit in the Nebraska State Museum Herbarium. The vegetation was visually estimated using the Daubenmire canopy coverage technique (Daubenmire 1959) in a modified baseline grid system with 25 0.1 m^2 sampling quadrats located by the intersection of the 8 m interval grid lines, superimposed on a 40 x 40 m quadrat.

Community composition was compared using a chi-square test for independence (Steel and Torrie 1960). The Shannon-Weaver Diversity Index ($H' = -\sum_{i}^{N} p_i \ln p_i$, where p_i is the proportion of each component species in the total sample of S species) was calculated and the values compared (Poole 1974).

RESULTS

The results of the vegetation analysis are given in Table 1. All four sites had approximately the same total number of plant species (12 to 18). All sites are dominated by grasses with forbs occasionally present. The tallgrass prairie had more litter cover than the Sandhills prairie (96.1% vs. 63.4%) and correspondingly less bare area (0.6% vs. 23.1%) (Table 1). Both of the undisturbed prairies had more litter cover and less bare area than did the corresponding old fields. On the tallgrass prairie there was 96.1% prairie litter cover vs. 88.0% old field litter cover, and 0.6% prairie bare area vs. 2.9% old field bare area. On the Sandhills prairie there was 63.4% prairie litter cover vs. 54.4% old field litter cover, with 23.1% prairie bare area vs. 29.7% old field bare area.

After approximately 40 years of succession, the tallgrass prairie old field plant community composition is still significantly different from the adjacent undisturbed prairie ($x^2 = 127$, $df = 8$, $p < .005$). This difference in species composition is especially marked for *Andropogon gerardi*. This is the most abundant plant species in the climax prairie (54.2% cover), but is quite rare in the old field (0.1% cover).

Similarly, the Sandhills prairie old field is significantly different in species richness from the prairie itself ($x^2 = 39$, $df = 10$, $p < .005$). *Calamovilfa longifolia*, a characteristic, rhizomatous Sandhills community dominant, accounting for 20.2% cover in the climax Sandhills prairie, was absent from the old field even after approximately 50 years. Interestingly, *Andropogon hallii*, a closely related species to *A. gerardi* (which was absent from the tallgrass prairie old field), was also absent from the Sandhills old field.

No significant difference in plant diversity was found between the tallgrass prairie ($H' \pm 2\ SE = 1.50 \pm 0.15$), and the corresponding old field (1.41 ± 0.13). Similarly, there was no difference in plant diversity between the Sandhills prairie (1.45 ± 0.12) and the Sandhills old field (1.27 ± 0.12).

DISCUSSION

Typically, old field succession in the tallgrass and mixed grass prairies of the central Great Plains is believed to take place in a series of discrete vegetational steps (Clements 1916, Shantz 1917, Booth 1941, Weaver 1954, Roux and Warren 1963, Rice 1974). These steps are as follows: ruderals and pioneer weeds, 1-2 years; annual grasses, 1-13 years; perennial bunchgrasses, 10-20 years; and, ultimately, a fully developed prairie characterized by the presence of mixed rhizomatous and bunchgrasses, associated forbs, and a few woody species (Weaver and Clements 1938, Booth 1941, Rice 1974). This progression is presumed to be highly predictable.

After at least 40 years, the plant communities of old fields at both sites in Nebraska are still significantly different from that of the immediately adjacent climax community. Both old fields could be considered to be beyond the "perennial bunchgrass" stage, but each is still lacking at least one of the climax dominants (*Andropogon gerardi* in tallgrass prairie, *Calamovilfa longifolia* in the Sandhills). The reasons for the missing dominant species at each of these

Table 1. Identity and percent cover of plant community members.

	Tallgrass	% cover Prairie	% cover Old Field	Sandhills	% cover Prairie	% cover Old Field
Plant Communities	*Andropogon gerardi*	54.2	0.1	*Andropogon hallii*	3.0	-
	Andropogon scoparius	15.4	13.5	*Bouteloua gracilis*	3.5	6.6
	Aristida oligantha	-	0.1	*Bouteloua hirsuta*	2.5	1.5
	Koeleria cristata	0.9	0.1	*Calamovilfa longifolia*	20.2	-
	Panicum scribnerianum	5.8	8.8	*Panicum virgatum*	-	0.1
	Poa pratensis	16.3	0.3	*Sporobolus cryptandrus*	2.0	13.6
	Sorgastrum avenaceum	5.1	3.1	*Stipa comata*	26.8	39.7
	Sporobolus aspera	-	37.9	*Ambrosia psilostachya*	0.0	0.8
	Sporobolus heterolepis	0.8	-	*Artemisia ludoviciana*	0.6	3.0
	Stipa spartea	1.2	-	*Aster ericoides*	0.2	-
	Achillea millefolium	0.4	-	*Astragalus canadensis*	-	0.1
	Ambrosia psilostachya	1.8	21.1	*Carex heliophila*	1.4	2.0
	Amorpha canescens	1.2	-	*Eriogonum annuum*	-	0.1
	Amphicarpa bracteata	-	0.1	*Lithospermum sp.*	0.1	-
	Aster ericoides	-	0.3	*Opuntia fragilis*	0.7	-
	Euphorbia sp.	0.1	0.1	*Petalostemon purpureum*	-	0.1
	Fragaria virginiana	-	0.2	*Ratibida columnifera*	0.1	-
	Oxalis stricta	-	0.1	*Sphaeralcea coccinea*	-	0.8
	Petalostemon purpureum	0.8	0.7	Litter	63.4	54.0
	Physalis glabra	0.1	-	Bare	23.1	29.7
	Rosa arkansana	-	0.6			
	Solidago rigida	-	0.7			
	Viola pedatifida	0.1	-			
	Bare	96.1	88.0			
	Litter	0.6	2.9			

sites are unknown. Allelopathy may be involved in the tallgrass prairie; at least one of the successional species, *Aristida oligantha* is known to be allelopathic (Rice 1974, 1979) and seed sources for *Andropogon gerardi* are close by (less than 100 m). The lack of *Calamovilfa longifolia* on the Sandhills old field is more problematic. Again seed sources are immediately available and yet the few, large clones of *Calamovilfa*, aged approximately 27 years, are very infrequent in the old field. Germination and seedling establishment characteristics or competitive interference with existing *Stipa comata* may be involved here.

Despite the differences in species composition, species diversity of the plant communities does not differ significantly between old field and prairie at either the tallgrass or Sandhills praire sites. This is in marked contrast to the findings of Murdoch et al. (1973) that three different 40-year old fields in Michigan all had distinct plant species diversities.

If one compares the chi-square values of plant community similarity between the two study areas, a larger chi-square value indicates greater dissimilarity between the sample areas. Thus, in the tallgrass prairie, the old field is not as close to climax community composition as is the similar aged Sandhills prairie old field (x^2 = 127 and 39, respectively). Therefore, old field succession in the two prairies appears to be proceeding more rapidly in the Sandhills prairie than in the tallgrass prairie.

The pattern of central North American prairie old field succession as described by Clements (1916), Shantz (1917), Booth (1941), Weaver (1954), Roux and Warren (1963), Rice (1974), and Glenn-Lewin (1980) was orderly, predictable, and biotically controlled. The tallgrass prairie presumably follows this lengthy successional sequence. We found succession on Nine Mile Prairie old field to be retarded relative to the literature predictions. Perhaps the process is delayed in old abandoned fields in tallgrass prairie by excessive soil erosion and aggravated by excessive grazing and burning, since the dominant species require fertile soil and stable conditions (Booth 1941, Rice 1974).

In contrast, the Sandhills community is in a constant state of natural disturbance due to erosion of the sandy soil as a result of historic large-scale fires and droughts. The Sandhills prairie communities must have evolved in such a context. Hence, the dominant species can withstand more disturbance and may enter the succession process earlier (Noble and Slatyer 1980). As a result, old field succession could be greatly condensed and one would expect old field succession in the Sandhills prairie to go to completion more rapidly than in tallgrass prairie. Certainly, we found the Sandhills old field to be more similar to the adjacent prairie than the tallgrass old field and its adjacent prairie. However, neither can be said to have reached "climax" composition since both old fields lack one or more of the typical dominant plant species, even after 40 years. Even though plant communities were dissimilar, species diversity was not distinguishable between climax and old field. Sandhills prairie may constitute an example of cyclic succession, where change is inherent in the community composition, so that stability is low but resilience high (Holling 1973).

We conclude that much more careful experimental analysis needs to be done with the process of grassland succession in old fields: return to "climax" appears to be slower and perhaps less predictable than was formerly thought.

CONCLUSIONS

Comparative patterns of old field succession were examined on a tallgrass prairie and a Sandhills prairie in Nebraska. After 40 years of succession in both prairies, the old field in the Sandhills prairie more closely resembles the undisturbed prairie in terms of plant community similarity and species diversity than does the old field located in the tallgrass prairie.

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