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The Soil Seed Pool of Huffman Prairie, a Degraded Ohio Prairie, and its Potential in Restoration

Scott J. Meiners
Eastern Illinois University, sjmeiners@eiu.edu

David L. Gorchov
Miami University - Oxford

The Soil Seed Pool of Huffman Prairie, a Degraded Ohio Prairie, and its Potential in Restoration[1]

Scott J. Meiners[2] and David L. Gorchov, Department of Botany, Miami University, Oxford, OH 45056

ABSTRACT. The germinable seeds in the soil of a relict Ohio prairie were investigated to determine the composition and density of dicots of potential value in restoration. Soil samples were collected from three areas of the prairie with distinctive species compositions: swale, north upland, and south upland. Seed density and species composition were based on seedling emergence over 90 days.

North upland and south upland samples yielded similar total seedling densities (5,902 and 5,109 m^{-2}) while that of the swale was greater (15,262 m^{-2}). Thirteen introduced and 18 native dicot species were present; seven of the latter were common in pre-settlement prairies. Sixty percent of the dicot seedlings were of native species. Swale samples contained fewer prairie species and were less diverse than those from the upland areas. Six species common in pre-settlement prairies had greater frequencies of germinable seeds than the vegetation; however, no seeds of prairie species were found that were not in the vegetation. This indicates that the seed pool may be useful in increasing densities of species already present but not in reestablishing species absent in the above-ground vegetation.

INTRODUCTION

Before European settlement, tallgrass prairie occupied a small but significant portion of the Ohio landscape (Nolin and Mutter 1988). Although some prairies were plowed after settlers realized the high fertility of the soil, unplowed prairies were often used for pasture, leading to the disappearance of many prairie species and to the introduction of invasive species (Gordon 1969). Some species of prairie plants have become common in successional habitats (i.e., *Oenothera biennis*) while others remain only in former prairie sites [i.e., *Liatris spicata* (Gordon 1969)].

Little remains of the original tallgrass prairie in the U.S. (Klopatek et al. 1979), and very few prairies remain in Ohio (Gordon 1969). Restoration of prairies, begun by Greene and Curtis at the University of Wisconsin Arboretum in 1936 (Anderson 1973), has been adopted by many conservation organizations and private landowners (Burton et al. 1988). While some of these restoration projects are initiated on unvegetated areas, others begin with degraded prairie (Green et al. 1981, Conover and Geiger 1989).

The species composition and abundance of seeds within the soil "seed pool" and on the soil surface may be quite different from that of the vegetation (Thompson and Grime 1979, Johnson and Anderson 1986). These seeds can yield information about the past and potential vegetation of an area. The presence of germinable seeds of a species not in the vegetation indicates that conditions have not been suitable for germination; a change in conditions could result in re-establishment of that species.

Most prairie species will not have germinable seeds present in the soil (Rabinowitz 1981, Johnson and Anderson 1986). However, those germinable seeds which are present are generally located near the surface and in small numbers (Rabinowitz 1981, Johnson and Anderson 1986). The seeds of most prairie species do not remain viable in the soil for long periods of time, however the seeds of forb species tend to be longer lived than those of grass species (Rabinowitz 1981, Thompson 1992). As Huffman Prairie has never been greatly altered by agriculture or other development (Nolin and Mutter 1988), the seeds of many forb species may remain dormant within the soil. If the seeds of prairie forbs are present, restoration of their populations by manipulation of germination conditions may be worthwhile.

The present study focuses on the species composition and abundance of dicot germinable seeds in the soil of a relict Ohio prairie. The objective of this study was to characterize the species composition of germinable seeds in three different areas of a degraded prairie and to assess the potential of manipulating germination conditions in prairie restoration.

MATERIALS AND METHODS

Study Site

The Huffman prairie ($\approx$32 ha) is one of the largest remaining tallgrass prairies in Ohio. It is contained within the Wright-Patterson Air Force Base, approximately 8 k northeast of Dayton (36° 45' N, 84° 15' W). The degenerate condition of the prairie is the result of a long history of human use. It was grazed for many years and a portion has been drained. Following drainage, the prairie was regularly mowed by the Air Force until 1984 (Nolin and Mutter 1988). Since then, portions of the prairie have been burned as part of the management program, and it has been designated a state natural landmark. The Ohio Chapter of The Nature Conservancy is now the steward of the prairie.

Three different areas of the prairie were recognized: "north upland," "south upland," and "swale" (Fig. 1). The north upland area was dominated by native prairie grasses (*Andropogon gerardii* and *Sorghastrum nutans*) with little forb cover. The south upland area was also dominated by grasses, but had more forbs than the north
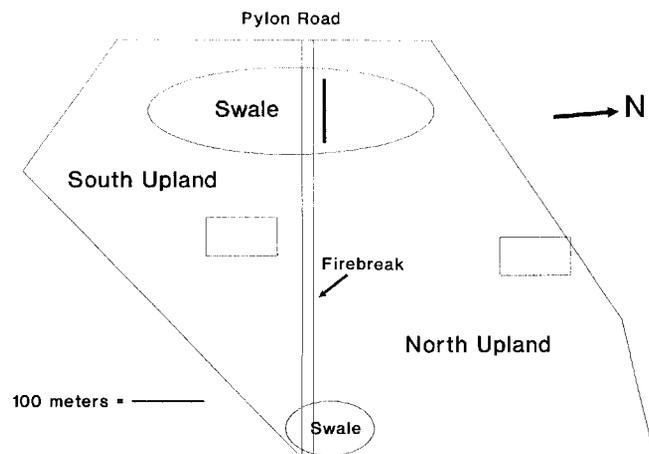
FIGURE 1. Map of the Huffman Prairie, located in the Wright-Patterson Air Force Base. Rectangles mark the upland sampling sites and the heavy line marks the sampling transect in the swale.

upland area with a high abundance of composites. The swale occupied two low lying areas of the prairie and was dominated by *Conium maculatum*. This area contained most of the weedy species found in the prairie (Minney 1990). The prairie has been invaded by many introduced species, especially the grass species *Bromus inermis*, *Agropyron repens*, and *Phleum pratense*.

Methods

All soil samples were collected on 24 January 1992. In both the north upland and south upland, one 100 x 50 m plot was delimited (Fig. 1). Within each plot, sample points ($n = 10$ for south upland and $n = 12$ for north upland) were selected using coordinates from a random number table. In the swale, 10 points were selected randomly along a 100 m transect (Fig. 1). At each point in each site, a sample 7.6 cm in diameter and 10 cm deep was collected. Samples were placed in plastic bags and kept cool and open to the air for five days. During this period each sample was sifted through a 5 mm mesh sieve to remove stones and plant fragments.

On 29 January 1992 the samples were spread onto flats (24 cm x 24 cm) filled with 3 cm of sterile greenhouse medium (Metromix®). Five control flats, consisting only of Metromix, were placed with the sample flats to detect contaminant seeds (Roberts and Vankat 1991). Flats were maintained in the Miami University greenhouse under natural light conditions and day/night temperatures averaging 24/18° C. The flats were watered and seedlings treated with pesticide to control aphids as needed.

Flats were inspected weekly until 9 March and bi-weekly until 29 April (92 days), when less than one seedling was emerging per flat per week. Positions of flats were rotated each time they were inspected.

All monocot seedlings were recorded and removed as they emerged. Dicot seedlings were marked with colored toothpicks (Johnson and Anderson 1986) and allowed to grow until they could be identified to species. Unidentified plants that became excessively large were removed from the flats and grown separately until they could be identified.

On 29 April, all remaining unidentified plants were removed and grown in pots until they could be identified. Voucher specimens are on deposit in the Miami University Herbarium (MU).

Determination of species common in pre-settlement Ohio prairies was based on Sears (1926), Gordon (1969), and Minney (1990). Nomenclature and determination of introduced status follows Gleason and Cronquist (1991).

Data Analysis

The densities of seedlings from the three areas of the prairie were compared using one-way ANOVA (SAS Institute Inc. 1985). Data were pooled by area for the calculation of species richness (number of species), diversity [Shannon-Wiener index (H'= $-\Sum (p_i)(\ln p_i)$), Shannon and Weaver 1949], and evenness (H'/H'$_{max}$). Cumulative species-area curves were generated for each area by randomly ordering the samples. The frequency of a species was the proportion of the 32 samples in which its seedlings emerged. Species frequencies in the vegetation were taken from The Nature Conservancy survey conducted August-September 1990 which sampled 340 0.5 m² quadrats placed at regular intervals along transects throughout the prairie (Minney 1990).

The similarity in seed species composition between pairs of areas was determined by Pielou's proportional similarity index (Pielou 1977) which ranges from 0 to 1.

$$PS = 2 \sum_{v=1}^{s} \min [x_{iv}/z, x_{jv}/z]$$

Where: i and j are the two samples
  x_{iv} is the number of individuals of species v in sample i
  z is the total number of individuals of all species in both samples

RESULTS

Emergence and Seedling Density

A total of 1,251 seedlings emerged, about 80% during the first three weeks of the experiment. Of these, 82% were dicots of which 73% (31 species) survived to be identified (Appendix).

Total seedling density (monocots + dicots) differed among the three areas ($F = 10.58$, $P = 0.0004$). Seedling densities in the samples from the swale were greater than in those from the upland areas ($P < 0.05$), which did not differ from each other (Table 1).

The density of monocot seedlings did not differ among the three sites [$F = 1.44$, $P = 0.25$ (Table 1)] while dicot seedling densities did differ ($F = 14.77$, $P = 0.0001$). Among the three areas, the swale area had a greater density of dicots than the other two ($P < 0.05$), which were not significantly different from each other (Table 1).

Dicot Diversity and Floristic Similarity

Sixteen dicot species were identified from the swale compared to 17 for each of the other two areas. Species area curves stabilized after 7-9 samples (Fig. 2). The south upland area had the greatest Shannon-Wiener diversity

TABLE 1

Seedling densities, species richness, Shannon-Wiener diversity, and evenness of the three prairie areas.

	Site in the prairie		
	South Upland	North Upland	Swale
Total seedling density (seedlings/m²)	5,109[A]	5,902[A]	15,262[B]
Monocot seedling density (seedlings/m²)	1,798[A]	1,864[A]	987[A]
Dicot seedling density (seedlings/m²)	3,311[A]	4,038[A]	14,275[B]
Species richness	17	17	16
Shannon-Wiener diversity	2.34	2.08	1.75
Evenness	0.51	0.41	0.28

Diversity and evenness measured as H' and H'/H'_{max} respectively. Values in a row with the same letter are not significantly different (P = 0.05) using Tukey's multiple test of means.

and the swale the lowest (Table 1).

Floristic similarity was highest between the north and south upland sites (PS = 0.40) but was still low. The swale was quite dissimilar to the other sites, with only a 0.14 similarity to the north upland and a 0.19 similarity to the south upland area.
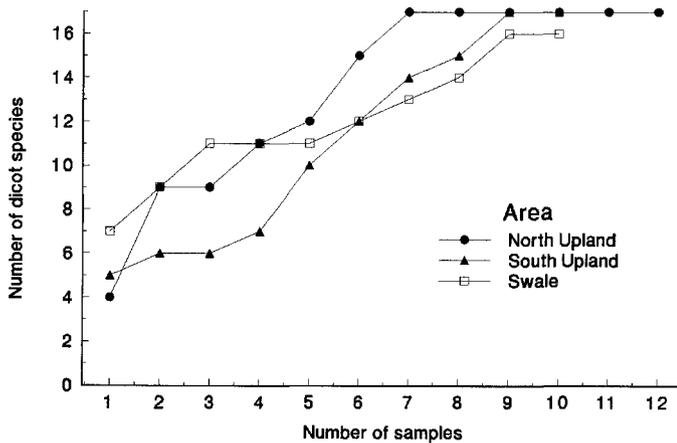
FIGURE 2. Cumulative species area curve for soil samples from the swale, north upland, and south upland areas.

Of the 31 dicot species present as seeds, seven were common to pre-settlement Ohio prairies, 11 were native non-prairie species, and 13 were introduced species. Native species accounted for 60% of the surviving dicot seedlings. Seedlings of native and introduced species were distributed unevenly among the different areas sampled (Fig. 3). Both upland sites had large proportions (greater than 60%) of seedlings of introduced species. The swale had the most seedlings of native species, but this

was mainly because of the dominance of *Urtica dioica* var. *procera* (Appendix), a non-prairie species. Seedlings of prairie species were represented fairly evenly throughout the areas.
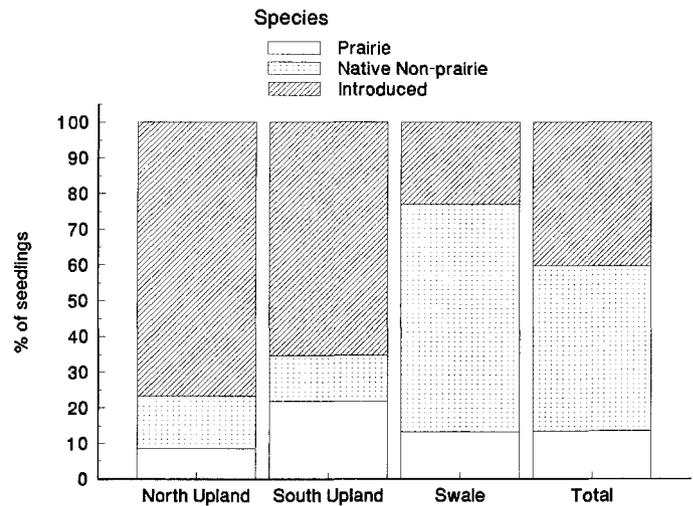
FIGURE 3. Relative abundance of seedlings of prairie, native non-prairie, and introduced species in soil samples from each of the three prairie areas. Data include only surviving dicot seedlings.

Comparison of the Vegetation and the Seed Pool

The frequency of a species in the seed pool could not be statistically compared to its frequency in the vegetation, because the soil sampling was stratified over the three areas of the prairie whereas the vegetation was sampled systematically over the entire prairie. Nevertheless, large and consistent differences in these frequencies are suggestive of significant differences. Of the seven prairie species found as seeds, six were more frequent as seeds than in the vegetation (Fig. 4). For example, only one *Liatris spicata* individual was found in the entire prairie (not located in the frequency plots) while we reported seedlings from samples in two different areas (6% frequency). Seeds of four of the prairie species were found in only one area, hence within this area their frequencies would be higher than the overall frequency reported here.

DISCUSSION

Sampling Rationale

Samples were taken during January because most seeds would be dispersed and would have received sufficient cold treatment to break dormancy (Rabinowitz 1981, Johnson and Anderson 1986). While this sampling cannot differentiate between the persistent seed bank and the transient seed bank (Thompson and Grime 1979), it reveals the seeds available for germination following natural or artificial soil disturbance during the dormant season. Sampling at this time also allows comparison with other studies such as Rabinowitz (1981). Because of the inability of the methods to differentiate between the persistent and transient seed banks and the probable high proportion of transient seeds, a more general term, seed pool, has been used in this paper.
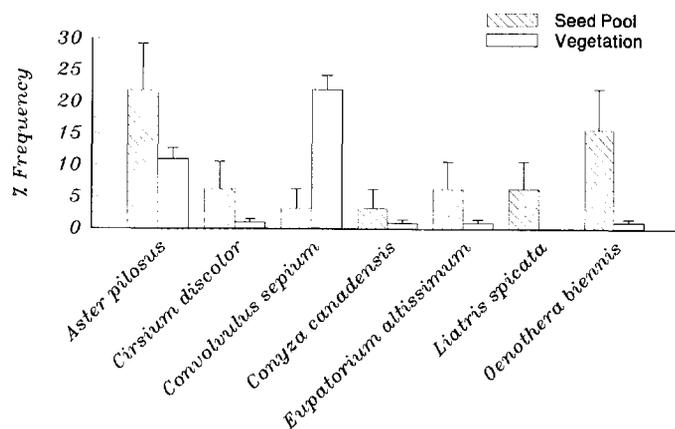
Figure 4. Frequencies of prairie species in the seed pool (this study) and vegetation (Minney 1990) of Huffman Prairie. Error bars represent one standard error.

Seedling Density

Seedling densities in the north upland and south upland samples are similar to the 6,470 seeds m^{-2} reported for a tall-grass prairie in Missouri (Rabinowitz 1981) which was also collected after fall seed dispersal. The greater density of seedlings in the swale area (15,262 seeds m^{-2}), is probably from the weedy nature of the species common there. Minney (1990) noted that swale vegetation contained the majority of non-native species. We found the higher dicot seedling density in the swale to be caused by *Oxalis corniculata* and *Conium maculatum* (non-native weeds); *Urtica dioica* var. *procera* (a native non-prairie species); and native composites. Many of the non-native dicot species present as seeds were considered to be degrading or potentially degrading to the prairie (Minney 1990).

Diversity and Floristic Similarity

Overall, the three areas were quite dissimilar in floristic composition, in part from the dominance of *Urtica dioica* var. *procera* in the swale. There were also several species which occurred in only one of the areas [e.g., *Eupatorium altissimum* and *Verbesina alternifolia* (Appendix)]. The low Shannon-Wiener diversity of each area is caused by the great abundance of seeds of a few species. Their abundance is most likely the result of seeds dispersed during the previous growing season (transient species).

Species with some types of dormancy, such as those with hard seed coats (e.g., *Convolvulus sepium*), would not have germinated in our study. Thus, there may be more species present in the seed pool than detected by our methods. However, species whose dormancy was not broken by the methods used in the present study would be unlikely to germinate after the soil disturbance of a management plan. The limited sampling of this study may have also missed specific microhabitats and the species located within them.

Comparison of Seed and Vegetation Compositions

Our results indicate that some important prairie species are present as seeds. While the samples did not yield any prairie species which were not found in the vegetation,

there were species that were more frequent as seeds than as established plants. Enhancing the germination of these seeds may be a faster or less expensive means of enhancing their abundance than current reintroduction practices. For those species not present in the vegetation, manipulation of germination conditions will not be productive.

Enhancing Seedling Recruitment

Active management could enhance the recruitment of seeds into the prairie vegetation. Natural seedling establishment in prairies may depend on some type of disturbance such as fire, burrowing, trampling, and grazing (Platt 1975, Rapp and Rabinowitz 1985, Collins 1987, Burton et al. 1988, Fahnestock and Knapp 1993). The incorporation of appropriate natural disturbance regimes may enhance populations of prairie species or maintain reintroduced species. These disturbances, especially fire, may also be used to control populations of invasive species with high seed densities.

Conclusion

The density and species composition of germinable seeds may prove to have some importance in the restoration of prairies, both as an indicator of weed problems and as a source of local genotypes. However, our results suggest that the potential of these seeds for species reintroductions may be limited, because species no longer present in the vegetation were not represented as seeds.

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APPENDIX

Number of seedlings of each species that emerged from the soil samples.

	South Upland	North Upland	Swale	Total
NATIVE DICOT SPECIES				
Acalypha rhomboidea Raf.	1	1	0	2
Aster pilosus Willd.	14	0	64	78
Cirsium discolor (Muhl.) Spreng.	0	2	0	2
Convolvulus sepium L.	0	0	1	1
Conyza canadensis (L.) Cronq.	1	0	0	1
Erigeron philadelphicus L.	0	0	5	5
Eupatorium altissimum L.	0	5	0	5
Leucospora multifida (Michx.) Nutt.	0	10	0	10
Liatris spicata (L.) Willd.	4	2	0	6
Oenothera biennis L.	3	5	0	8
Physalis longifolia Nutt.	7	0	0	7
Phytolacca americana L.	1	0	0	1
Potentilla norvegica L.	0	1	0	1
Solidago canadensis L.	3	12	40	55
Solidago sp.	0	1	0	1
Urtica dioica var. *procera* (Muhl.) Wedd.	0	0	235	235
Verbesina alternifolia (L.)Britton.	0	0	28	28
Viola papilionacea Pursh.	1	0	3	4
Subtotal	35	39	376	450
INTRODUCED DICOT SPECIES				
Conium maculatum L.	0	0	32	32
Daucus carota L.	15	71	7	93
Dipsacus sylvestris Hudson.	2	0	0	2
Leonurus cardiaca L.	0	0	2	2
Medicago/Melilotus spp.	13	12	6	31
Mollugo verticillata L.	8	0	0	8
Nepeta cataria L.	0	0	1	1
Oxalis corniculata L.	23	14	54	91
Pastinaca sativa L.	1	5	0	6
Petunia x *hybrida* Vilm.	0	2	0	2
Plantago lanceolata L.	0	12	2	14
Potentilla recta L.	2	3	1	6
Trifolium pratense L.	2	5	8	15
Subtotal	66	124	113	303
Unidentified Dicots	50	58	161	269
Monocots	82	102	45	229
Total	233	323	695	1251

*Species common in prairies.