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The Seed Bank of a Reconstructed Prairie

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Abstract

Seed banks, the reserve of viable seeds dormant in the soil, function in several important roles in the population and community dynamics of plant communities. Identification of the seed bank can furnish information on the vegetation history of a habitat, predict the future composition of the plant community, and provide insight on the seed viability and biology of plant species. Although seed banks of prairie ecosystems have been well studied, very little information exists on seed banks of reconstructed prairie. Identification of seed bank populations of reconstructed prairie provides a means to evaluate the success of restorations and establishes baseline data to monitor the development of prairie over time. A seed bank study of reconstructed prairie in central Iowa was conducted from March 2000 to July 2002. Samples of the seed bank in the top 3 cm of soil were collected at 15 sites on the reconstruction at the beginning of its fifth growing season. A seedling assay was used to identify and count seeds. A total of 2,693 seedlings and 62 plant taxa were observed in the seed bank. Out of the 78 plant species seeded at the study sites, 15 species were observed in the seed bank. Three of these were non-native species seeded by mistake. Among the other 47 species observed, about half were native and half were exotic. The most abundant species in the seed bank included green carpetweed (*Mollugo verticillata*), common yellow oxalis (*Oxalis stricta*), witchgrass (*Panicum capillare*), hairy white oldfield aster (*Symphyotrichum pilosum*), and amaranth (*Amaranthus rudis*). Total seed densities ranged from 293 seeds/m^2/3 cm to 12,247 seeds/m^2/3 cm. An ordination of the seed bank samples with the vegetation in 1999 and 2000 clearly shows a high dissimilarity between vegetation and seed bank as well as much greater variation in the seed bank composition than in the vegetation.

Keywords: seed banks, prairie reconstruction, seedling assay, restoration, prairie succession

Introduction

Seed banks, the reserve of viable seeds present in or on top of soil, function in several important roles in temperate plant communities. Most importantly, the presence of a seed bank provides for regeneration of vegetation after disturbances (Harper 1977, Fenner 1985). The degree to which the new plant community represents the preceding community depends on the composition of the seed bank. Seed banks also provide population stability. Persistent seed banks (seed viability greater than 1 year) with moderate to long-lived seeds (more than 10 years) buffer the variance of population size and reduce the risk of population extinction (Levin 1990). Persistent seed banks may also buffer population gene pools from fluctuation in genetic composition, they bias selection towards traits favored in seasons of high seed production, and they may be a source of new genetic variation from mutations occurring in genetic material during seed aging (Levin 1990). The enrichment of genetic diversity and increase in population stability provided by seed banks is especially valuable in endemic species with small population sizes (Baskin and Baskin 1978).

An investigation of the seed bank of a plant community can furnish information on its vegetation history, offer predictions on the future composition of the community, and provide insight on the long-term viability, dormancy and seed dispersal of the resident plant species. A thorough assessment of the plant community needs to include the seed bank to fully represent the entire flora (Major and Pyott 1966).

In general, studies of seed banks and their associated vegetation have demonstrated a high dissimilarity between the composition of seed banks and the above-ground vegetation (Harper 1977, Thompson and Grime 1979). Plant species with prolonged seed dormancy and viability are the species that more readily form persistent seed banks and have the potential to accumulate in the seed bank, assuming at least occasional inputs from seed rain. Such species are typically early successional species that have adapted the strategy of dispersal in time, meaning that rather than seeking disturbed sites in space (long-distance seed dispersal), they wait for disturbances to come to them (Fenner 1985). The dissimilarity between seed bank and vegetation is generally a consequence of the seed bank containing a high abundance of r-selected, early succession, annual and biennial species and the vegetation composed of K-selected, later successional, perennial species. Therefore the similarity between seed bank and vegetation depends on the successional status of the vegetation. In frequently or recently disturbed habitats the composition of the seed bank and vegetation is similar (Fenner 1985) due to recruitment and establishment of plant species in the seed bank. Over time and in the absence of disturbance, the vegetation matures and the similarity between seed bank and vegetation decreases (Fenner 1985).

Although seed banks of prairie ecosystems have been fairly well studied (Lippert and Hopkins 1950, Rabinowitz 1981, Johnson and Anderson 1986, Abrams 1988, Coffin and Laurenroth 1989, Rosburg and others 1994, Romo and Bai 2004) very little information exists on seed banks of reconstructed prairie. A common observation in these prairie studies is the lack of similarity in the composition of seed bank and vegetation, suggesting the study sites represented mature, relatively undisturbed prairie. The current seed bank study of reconstructed prairie differs from these previous studies in two important ways. First, since the study site is a four-year-old reconstruction, wide-scale disturbance is relatively recent and the vegetation represents an earlier successional stage than in the previous work. Second, the site experienced a large, recent and unnatural seed rain event when the seed mixes were planted. Furthermore, the species composition of that seed rain event is completely known.

Measurement of the seed bank associated with a prairie reconstruction provides data useful in monitoring the development of the prairie over time (to evaluate success) and facilitates an assessment of the fate of seeded species. The success of any reconstruction can be evaluated in many different ways depending on the goals of the evaluation. Up to now success on the study site has been evaluated with three criteria: (1) the percentage of seeded species present in the vegetation, (2) the abundance of seeded species in the vegetation relative to resident (non-seeded) species, and (3) a comparison of the vegetation (species composition, diversity, exotic species) in the reconstruction with the vegetation in a local remnant with a similar moisture regime. If a quantitative measure of the seed bank is available, then these indices can be extended to the seed bank. The greater the percentage of seeded species (which have established in the vegetation) present in the seed bank, or the greater the relative abundance of seeded species in the seed bank, the more evidence there is for long-term establishment of those species and the more successful the reconstruction. The more the seed bank of the reconstruction looks and functions like the seed bank of a prairie remnant, the more successful the reconstruction.

Another way in which seed bank data can provide an assessment of prairie development and success in a reconstruction is with a similarity measure between seed bank and vegetation. Prairie reconstruction is inherently a successional process, beginning with disturbance and early successional vegetation. Because of the differences in r- and K-selected plant species' strategies for dispersal (affecting seed production, dormancy and viability), the compositional similarity between seed bank and vegetation should decrease as the prairie reconstruction ages. Finally, in the cases where seeded species have apparently not yet established in the vegetation, seed bank studies may be helpful in detecting whether those species are still present and viable in the seed bank.

The objectives of this research were: (1) to observe and characterize the species composition of the seed bank associated with a four year old prairie reconstruction, (2) compare the seed bank with the extant vegetation, and (3) use the seed bank to evaluate the success and progress of the restoration.

Methods

Study Site

The study was completed on a prairie reconstruction planned by the Iowa Department of Transportation and planted on the roadside of a section of Interstate 35 in Story County, Iowa (in central Iowa near Ames, or 35 miles north of Des Moines). The project area, which included both sides of the highway along a 9.6–km (6–mile) section, was seeded with 120 species in May of 1996. The pre-existing vegetation (exotic cool-season grassland and old-field forbs) was sprayed with glysophate in April 1996. After the vegetation died, seeding was accomplished by first using a no-till drill to plant the grasses followed by a dropseeder and cultipacker to seed the forbs and firm the seedbed. Prior to seeding, 15 study sites were established at locations representing the two most prevalent seed mixes—a mesic and dry-mesic mix. Together these two seed mixes contained 76 species.

Central Iowa has a temperate, continental climate with mean January high and low temperatures of –2.5°C (27.5°F) and –12.9°C (8.8°F) respectively, and mean July high and low temperatures of 29.2°C (84.5°F) and 17.2°C (63.2°F) respectively. Annual precipitation is 86.9 cm, most of which falls in May, June and July. The monthly mean percentages of sunshine ranges from 46% (December) to 72% (July). Annual snowfall averages about 83.5 cm (32.9 inches) (City-Data 2004). The growing season, defined as the number of days between last frost in spring and first frost in fall (0°C (32°F) or lower) averages 157 days (May 1 to October 6). The prevailing wind is from the northwest with average wind speed highest in the spring (DeWitt 1984)

Research Design and Vegetation Samples

Each of the 15 study sites contained four 3 x 6 m (9.8 x 19.7 ft) treatment plots where the effects of summer mowing, spring fire, and fall fire on species composition and prairie quality were studied between 1997 and 1999. Plant species inventories were conducted annually on each treatment plot from 1996 to 2002. The inventories used a stratified random sampling design to locate five quadrats 50 x 50 cm (19.7 x 19.7 in) within a 2 x 5 m (6.6 x 16.4 ft) sample area centered on a treatment plot (allowing a 0.5 m (19.6 in) buffer along the sides). Each of the 50 x 50 cm (19.7 x 19.7 in) quadrats was divided into four subquadrats each 25 x 25 cm (9.8 x 9.8 in). The density of stems, tillers, or caudices (for acaulescent species) was determined in these 20 subquadrats. See Rosburg (2001) for more details. For the purposes of this study, species composition data from all four plots representing a study site (80 subquadrats) was pooled to achieve a sample of the plant community at each study site.

Seed Bank Samples

The seed bank study was performed by sampling the soil of the reconstructed prairie, germinating the seeds, and identifying the seedlings to count and identify seeds of species in the seed bank (seedling assay). Seedling assays generally do not detect as many species nor as many seeds as do seed assays (Roberts1981, van der Valk and Rosburg 1997), but they are logistically easier to do and provide the best test for viability, and in this case the seedling assay was a better choice for an undergraduate project. Soil samples of the seed bank were collected on 26 and 27 March 2000, prior to any chance of natural germination. Each of the 15 study sites was sampled with 20 subsamples; five subsamples each were made in a stratified-random manner from each of the four treatment plots. A subsample consisted of the soil plug obtained with a bulb planter. Soil plugs were approximately 3 cm (1.2 in) deep and 6 cm (2.4 in) in diameter. The 20 subsamples obtained from each site were combined and mixed to distribute the seeds throughout the pooled sample (with a total volume of about 1,700 cm^3). Soil samples for each of the 15 sites were placed in cold storage in order to keep the seeds in dormancy until the seedling assay began in the fall of 2000. The seedling assay could not begin until fall due to the unavailability of personnel.

In October 2000, the 15 soil samples were removed from cold storage and individually sieved through a hardwire screen with mesh size approximately 6 x 6 mm (0.24 x 0.24 in) to remove large matter such as roots or gravel. From each of the 15 seed bank samples, three 500 cm^3 samples of seed bank soil were removed and layered 1.5 cm (0.6 in) deep into each of three 18 x 18 cm (7.1 x 7.1 in) trays half full of sterilized potting soil. The three trays thus prepared from each site created three pseudoreplicates for each study site (field replicate). Additionally, three control trays consisting only of the sterilized potting soil were used as a control for seeds that might be present in the potting soil mix. The samples were placed in a greenhouse under optimal light and moisture conditions to encourage germination. Trays were arranged in a block configuration, with the replicates from each site in one of three blocks that controlled for variation in temperature, light and air movement within the greenhouse.

Seedlings were allowed to grow until identification was possible and were then removed to allow room for additional seeds to germinate. If seedlings were not identifiable and needed to be removed due to crowding, several specimens were potted in separate containers and allowed to continue growth until they could be identified. By 1 March 2001, nearly all seed germination had occurred. To insure equal amounts of germination time for all trays and time for growth of seedlings for identification, all seedlings germinated after 1 March 2001 were pulled and counted as either unidentified dicot or monocot. By 15 May 2001, nearly all of the seedlings still present could be identified and counted. About 25 specimens that needed more time for growth were transplanted into an outdoor bed and labeled. Identification of these specimens was made by 2 July 2002, approximately 20 months after the seedling assay was started. Nomenclature follows the PLANTS Database (United State Department of Agriculture 2004).

Analytical Procedure

Data analysis focused on two types of information. One was a description of the seed bank composition and the representation of seeded prairie species. Raw seedling counts were converted to reflect seed density (seeds/m^2/3 cm (1.2 in) depth). A second goal was a comparison of the seed bank with the extant vegetation. This was done in two ways. One approach utilized Detrended Correspondence Analysis to ordinate the seed bank samples at each of the 15 study sites with the extant vegetation observed at the study sites in 1999 and 2000. Density of seeds in the seed bank and density of stems/caudices in the vegetation were used as measures of abundance, but because there was a large discrepancy in the magnitude of the data (some seed densities exceeded 5,000/m^2), all data were converted to relative density. A second approach in the comparison of the seed bank with the extant vegetation was to use Pearson Correlation to measure association between seed bank composition and vegetation at each site. To assure that the sample was limited in size and represented only the most relevant species, analysis was restricted to the 30 most abundant species in the seed bank and the 30 most abundant species in the vegetation.

Results

There was no difference in germination rates among the three greenhouse blocks, thus potential variation in light and temperature due to location in the greenhouse was not a factor affecting germination (Friedman Repeated Measures ANOVA $P = 0.651$).

A total of 2,696 seedlings were observed in the study. Germination of seedlings was fairly immediate and rapid. Over the first three weeks of the seedling assay, nearly 125 seedlings germinated per day, resulting in over 96.5% of the total germination observed. Seed density among sites ranged from 293 to 2,247 seeds/m^2/3 cm depth. Typical densities observed on most sites were in the range from 1,500 to 4,500 seeds/m^2/3 cm depth.

A total of 65 taxa were observed, but 3 of these were accounted for by the potting soil controls, resulting in 62 taxa represented in the seed bank samples (Table 1). Of these 62 taxa, 47 (or 76%) were resident (non-seeded) species and 15 (or 24%) were seeded in the reconstruction. With respect to seed densities, the 47 resident species in the seed bank accounted for 83% of the seeds, thus resident species were more abundant on a species by species basis than were seeded species (which accounted for 17% of the seeds). Among the 15 seeded species, three were exotic species seeded by mistake, consequently only 12 seeded prairie species were observed in the seed bank. These 12 species represent 16% of the 76 species included in the seed mixes and 18% of the 66 seeded species that had been observed in the vegetation by 2000. Among the 12 seeded prairie species, there were a total of 399 seeds observed over all 15 sites, which comprises 14.8% of the relative seed density. Nine of the 12 seeded prairie species (or 15% of the 62 species observed in the seed bank) can be considered representative of mid to late-successional prairie (Table 1).

The most abundant species in the seed bank was green carpetweed (*Mollugo verticillata* L.), which accounted for about

27% of all seeds counted and attained a mean seed density five times greater than any other species (Table 1, means were calculated for only the sites where present). The most widespread species in terms of presence on the study sites was hairy white oldfield aster (*Symphyotrichum pilosum* (Willd.) Nesom), one of the seeded species and the only species that was present on all 15 sites. However, hairy white oldfield aster is a typical species of old-fields and successional grasslands and most likely was a resident species of the Interstate 35 roadside. It is likely that many of these seeds originate from a resident seed bank. The seeded prairie species with the highest abundance in the seed bank was black-eyed Susan (*Rudbeckia hirta* L.), which resides in the seed bank on 12 of the 15 sites and has the ninth highest mean seed density (Table 1).

Three species observed in the seed bank are exotic plants that were included in the seed mixes due to mistakes or accidents somewhere in the process of planning, seed collecting, or seed distribution. Absinthium (*Artemisia absinthium* L.) is the most widespread and dense of these, followed by claspingleaf doll's daisy (*Boltonia decurrens* (Torr. & Gray) Wood), which was present at 3 sites, and ashy sunflower (*Helianthus mollis* Lam.), which was present at 1 site.

Among the 47 resident species about half are native (25) and half are exotic (22). Among the native species, at least 21 (84%) of them are ruderal or early successional grassland and old-field species. Similarly among the exotic resident species, at least 18 (82%) of them are weedy. Altogether, about 46 of the 62 species (74%) observed in the I–35 reconstruction seed bank are ruderal or early successional species that are favored by disturbance.

The seeded prairie species present in the I–35 seed bank are represented by four families, the Asteraceae (seven

Table 1. Seed bank composition of study sites on I–35 prairie reconstruction. Status includes seeded prairie species (Seed-Pra) and seeded exotic species (Seed-Exo) both in boldface; native prairie species (NatPra), native successional grassland species (NatSG), native ruderal species (NatRud), native wetland species (NatWet), native prairie-wetland species (NatPW), and exotic species (Exotic). Mean seed density is calculated only for sites where species was present. Potting Soil indicates the number of seeds in potting soil controls.

Scientific Name	Common Name	Status	Mean Seed Density per Site Present (seed/m^2/3 cm)	Total Sites Present	Number of Seeds Counted	Potting Soil
Mollugo verticillata	Green carpetweed	Exotic	2808	5	702	
Oxalis stricta	Yellow wood sorrel	NatRud	512	12	307	
Panicum capillare	Witchgrass	NatRud	297	14	208	
Symphyotrichum pilosum	Frost aster	Seed-Pra	295	15	221	
Amaranthus rudis	Pigweed	NatRud	248	10	124	
Potentilla norvegica	Norwegian cinquefoil	NatRud	185	7	70	1
Carex species	Sedge	NatPW	180	2	30	4
Lotus corniculatus	Bird's foot trefoil	Exotic	176	5	44	
Rudbeckia hirta	Black eye susan	Seed-Pra	173	12	104	
Erigeron annuus	Daisy fleabane	NatRud	170	10	85	
Poa pratensis	Kentucky bluegrass	Exotic	163	8	65	
Setaria faberi	Giant foxtial	Exotic	156	9	70	
Dichanthelium oligosanthes	Scribner's panicgrass	NatPra	140	1	7	
Setaria pumila	Yellow foxtail	Exotic	131	9	59	
Artemisia absinthium	Common wormwood	Seed-Exo	118	9	53	
Verbascum thapsus	Mullein	Exotic	113	3	20	1
Bidens aristosa	Bur marigold	NatRud	111	9	50	
Echinochloa species	Barnyard grass	Exotic	100	1	5	
Solanum americanum	Black nightshade	NatRud	96	5	24	
Barbarea vulgaris	Yellow rocket	Exotic	80	2	8	
Boltonia decurrens	Decurrent false aster	Seed-Exo	67	3	10	
Trifolium pratense	Red clover	Exotic	67	3	10	
Oenothera biennis	Evening primrose	Seed-Pra	57	7	20	
Symphyotrichum nova-angliae	New England aster	Seed-Pra	57	6	17	
Symphyotrichum laeve	Smooth aster	Seed-Pra	56	5	14	
Monarda fistulosa	Wild bergamot	Seed-Pra	53	3	8	
Thlaspi arvense	Penny cress	Exotic	48	5	12	
Chamaesyce maculata	Carpet spurge	NatRud	42	10	21	
Chenopodium album	Lamb's quarter	Exotic	41	6	21	2
Eupatorium altissimum	Tall boneset	Seed-Pra	40	3	6	
Digitaria sanguinalis	Hairy crabgrass	Exotic	40	3	6	
Helianthus mollis	Ashy sunflower	Seed-Exo	40	1	2	

Table 1, continued.

Potting Scientific Name	Common Name	Status	Mean Seed Density per Site Present (seed/m²/3 cm)	Total Sites Present	Number of Seeds Counted	Soil
Daucus carota	Wild carrot	Exotic	40	1	2	
Erigeron strigosus	Prairie fleabane	NatPra	33	3	5	
Conyza canadensis	Horseweed	NatRud	33	3	5	
Ambrosia artemisiifolia	Common ragweed	NatRud	30	6	9	
Lactuca serriola	Prickly lettuce	Exotic	30	6	9	
Rumex altissimus	Pale dock	NatGS	30	2	3	
Chamaesyce species	Spurge	NatRud	30	2	3	
Cirsium vulgare	Bull thistle	Exotic	30	2	3	
Digitaria ischaemum	Smooth crabgrass	Exotic	30	2	3	
Cardamine (parviflora)	Bitter cress	NatGS	29	7	10	
Schizachyrium scoparium	Little bluestem	Seed-Pra	27	3	4	
Acalypha virginica	Viginia copperleaf	NatRud	24	5	6	
Rumex crispus	Curly sour dock	Exotic	24	9	16	1
Melilotus species	Sweet clover	Exotic	20	4	4	
Cirsium arvense	Canada thistle	Exotic	20	3	3	
Eragrostis species	Lovegrass	NatRud	20	3	3	
Andropogon gerardii	Big bluestem	Seed-Pra	20	2	2	
Abutilon theophrasti	Velvet leaf	Exotic	20	2	2	
Symphyotrichum ericoides	Heath aster	Seed-Pra	20	1	1	
Symphyotrichum oolentangiense	Sky blue aster	Seed-Pra	20	1	1	
Sorghastrum nutans	Indian grass	Seed-Pra	20	1	1	
Descurainia pinnata	Tansy mustard	NatGS	20	1	1	
Cirsium altissimum/discolor	Tall/field thistle	NatGS	20	1	1	
Solidago gigantea	Giant goldenrod	NatPW	20	1	1	
Verbena stricta	Hoary vervain	NatGS	20	1	1	
Solidago canadensis	Canada goldenrod	NatGS	20	1	1	
Polygonum species	Smartweed	NatWet	20	1	1	
Medicago lupulina	Black medick	Exotic	20	1	1	
Phalaris arundinacea	Reed canary grass	Exotic	20	1	1	
Urtica dioica	Stinging nettle	NatRud	7	1	3	2
Unknown Dicots					149	12
Unknown Monocots					35	
Species observed only in potting soil controls						
Phleum pratense	Timothy				1	1
Ranunculus sceleratus	Buttercup				1	1
Veronica serpyllifolia	Speedwell				1	1
Total Seeds					2,696	

species), Poaceae (three species), Onagraceae (one species) and Lamiaceae (one species). All three of the principal grasses seeded—big bluestem (*Andropogon gerardii* Vitman), little bluestem (*Schizachyrium scoparium* (Michx.) Nash), and Indiangrass (*Sorghastrum nutans* (L.) Nash)—are present in the seed bank. Their occurrence is limited to three sites or less and their mean seed densities where present are less than 30 seeds/m^2/3 cm. Among the aster family, five are *Symphyotrichum* species and account for all but one of the asters seeded. New England aster (*Symphyotrichum novae-angliae* (L.) Nesom) and smooth blue aster (*Symphyotrichum laeve* (L.) A.& D. Löve) are present at about 35% of the sites and have mean seed density of nearly 60 seeds/m^2/3 cm, while skyblue aster (*Symphyotrichum oolentangiense* (Riddell) Nesom) and white heath aster (*Symphyotrichum ericoides* (L.) Nesom) were observed at one site. Blackeyed susan and tall thoroughwort (*Eupatorium altissimum* L.) are the other two aster family species in the seed bank. Common evening primrose (*Oenothera biennis* L.) and wild bergamot (*Monarda fistulosa* L.) represent the last two families. Both are have mean seed densities of at least 50 seeds/m^2/3 cm, but evening primrose is more widespread occurring at nearly 50% of the sites while wild bergamot was observed at only 20% of the sites (Table 1).

Nine of the 62 plant species observed in the seed bank were not observed in the vegetation at the sites in either 1999 or 2000. These included velvetleaf (*Abutilon theophrasti* Medik.), bitter cress (*Cardamine* species), western tansymus-

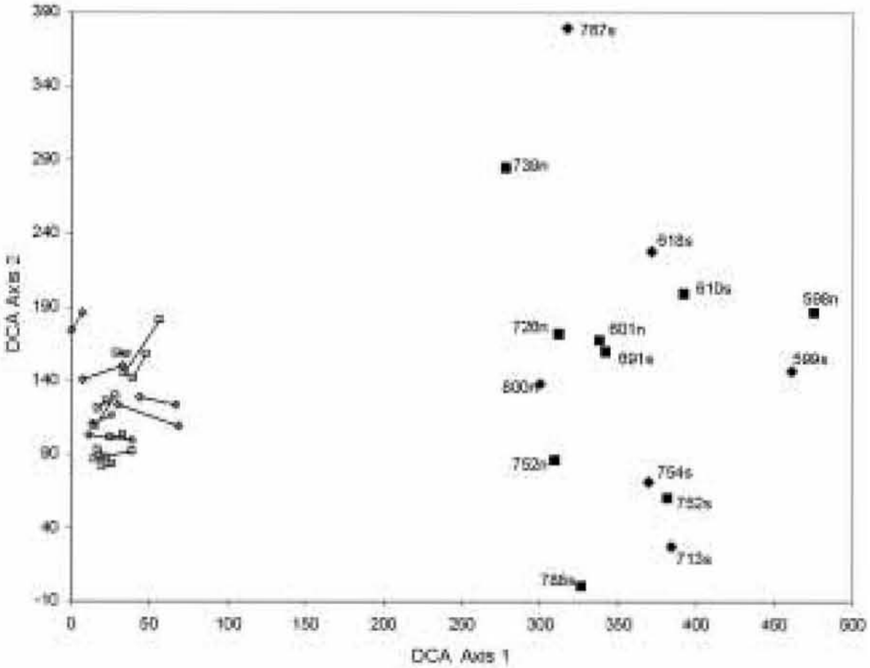

Figure 1. Detrended Correspondence Analysis of 1999 and 2000 vegetation samples (open symbols connected with a line) and 2000 seed bank samples (filled symbols) for the I-35 study sites. Dry-mesic sites (diamond symbols) and mesic sites (square symbols) are identified by a site number that identifies their location in the project area and occurrence on either the northbound or southbound right-of-way. Species space includes 158 species common to both the seed banks and the vegetation. See Figure 2 for an enlarged view of the vegetation samples.

tard (*Descurainia pinnata* (Walt.) Britt.), stinging nettle (*Urtica dioica* L.), barnyard grass (*Echinochloa* species), lovegrass (*Eragrostis* species), green carpetweed, Norwegian cinquefoil (*Potentilla norvegica* L.), and common mullein (*Verbascum thapsus* L.). The last five species have been observed in the project area in inventories during other years, thus a seed source for them must exist in or near the project area. However, one of two options must exist for the other four species. Either they have an historic presence in the vegetation and have maintained presence only in the seed bank, or else they are dispersing seed rain into the reconstruction from adjacent areas. Velvetleaf and stinging nettle could easily be dispersing in from adjacent areas, whereas bitter cress and western tansy mustard are both small mustards that inhabit sandy areas and could have an historic presence on some of the sites.

The species compositions of the seed bank samples are very different from the extant vegetation (Figure 1). Axis 1 of the DCA ordination represents the most important gradient in the variation of vegetation and seed bank species composition. The seed bank samples all occur on the upper half of the first axis, while the vegetation samples for both 1999 and 2000 are tightly clustered at the low end of axis 1 (all scores less than 75). The second most important gradient in the variation of species composition is represented on DCA axis 2 (Figure 1). For the most part this variation only occurs in the seed bank samples and is most manifest in the difference in seed banks between site 767S (high axis 2) and 788S (low axis 2). The difference in variation in species composition between extant vegetation and seed banks is very clear. The area encompassed by the seed bank samples is 6 to 7 times greater than the area encompassed by the extant vegetation (Figure 1). The much larger variation in seed banks occurs despite a significantly lower average richness per site in the seed bank than in the extant vegetation (seed bank mean of 18.7 versus vegetation means of 47.8 for 1999 and 43.1 for 2000, One Way Repeated Measure ANOVA, $P < 0.001$). Likewise, the cumulative richness of the seed bank communities (62) is less than half of the cumulative richness of the vegetation samples (149).

The position of the vegetation samples in the DCA ordination (Figure 1) are somewhat aligned along axis 2 in a pattern that reflects the seed banks. Sites 767S and 739N have the highest axis 2 scores in the vegetation samples and site 788S has the lowest score, a pattern which is also reflected in the seed banks (Figures 1 and 2). In fact a significant correlation was found between a site's DCA axis 2 score of the vegetation (the mean for 1999 and 2000) and its DCA axis 2 score for the seed bank (Pearson Correlation, $r = 0.61$, $P = 0.016$). The same species composition gradient pulling the seed bank samples apart along axis 2 seems to be influencing the vegetation. It's not as apparent in the vegetation because the species do not have as high a relative density in the vegetation as in the seed bank due to the higher species richness in the vegetation. Therefore there is evidence for some association between the vegetation and the seed bank, at least at the level of community composition along a species compositional and environmental gradient. However, a correlation analyses between the seed bank and the two vegetation samples for each site demonstrated no association exists for any site (Table 2). Thus at the next lower level of organization (i.e., populations), the specific abundances of species in the vegetation and seed bank communities is not correlated.

Discussion

Seed Bank of a Reconstructed Prairie

The total seed densities observed in the I–35 prairie reconstruction (mostly 1,400 to 4,500 seeds/m^2/3 cm) are within the range of other grassland studies done with seedling assays: 880 to 3,240 seeds/m^2/2.5 cm (1 in) for variously grazed cool-season prairie in Alberta (Johnston and others 1981); 740 seeds/m^2/10 cm (3.9 in) for cool-season prairie in Saskatchewan (Archibold 1981); 6,470 seeds/m^2/12 cm (4.7

Table 2. Pearson correlation coefficients for species composition between seed banks and vegetation at individual sites. Only the overall top 30 species for the seed bank and top 30 species for the vegetation were used, resulting in a total of 50 shared species (n=50). None of the correlation coefficients were significant at P < 0.05.

Site	1999 vegetation	2000 vegetation
598N	–0.05	–0.04
599S	–0.07	–0.06
601N	0.11	–0.02
610S	–0.10	–0.11
618S	0.03	–0.05
691S	0.03	0.01
713S	–0.06	–0.11
726N	0.13	0.15
739N	0.16	–0.01
752N	0.17	0.19
752S	–0.02	–0.01
754S	–0.04	–0.06
767S	–0.02	–0.07
788S	0.15	0.16
800N	0.10	0.09

in) for tallgrass prairie in Missouri (Rabinowitz 1981); 2,020 seeds/m^2/10 cm (3.9 in) for tallgrass prairie in Illinois (Johnson and Anderson 1986); 1,450 to 2,890 seeds/ m^2/5 cm (2 in) for annually burned and unburned tallgrass prairie in northeast Kansas (Abrams 1988); and 740–980 seeds/m^2/3 cm (1.2 in) for dry tallgrass and midgrass prairie in western Iowa (Rosburg and others 1994).

The lowest mean seed density site in this study (293 seeds/m^2/3 cm at 767S) occurred on a dry, gravelly environment with relatively low productivity and diversity. It is one of a few sites to have supported prairie species such as prairie fleabane (*Erigeron strigosus* Muhl. ex Willd.) and switchgrass (*Panicum virgatum* L.) prior to reconstruction. Low productivity (and therefore seed production) is possibly one reason for the low seed density in the seed bank. Biomass data collected in 1999 indicates an annual net aboveground primary productivity of 330 g/m^2, the second lowest amount among the sites. The highest mean seed density site (12,247 seeds/m^2/3 cm (1.2 in) at 598N) was located on a broad sandy ridge, formed as an eolian sand dune associated with the nearby Skunk River valley. Slope is fairly level and the soil is a loamy sand. Net primary productivity is much higher than at the lower density site—about 500 g/m^2 was observed in the 1999 samples. It also supported some resident prairie species, for example Scribner's rosette grass (*Dichanthelium oligosanthes* (J.A. Schultes) Gould) and smooth horsetail (*Equisetum laevigatum* A.Braun). The main reason however, for the high seed density at 598N, is that most of the seeds (just over 80%) are from one species – green carpetweed – a sand loving species absent in the vegetation but apparently capable of forming a persistent seed bank via its high seed production and longevity. Thompson and Grime (1979) reported a similar observation in that persistent seed banks were detected for species scarce or absent in the vegetation for several habitats including woodland, hedge, grassland, wetland and a disturbed site with thin soil.

During the first couple years after the seeding in 1996, it became apparent that several plant species were in the seed mix which should not have been included for a reconstruction in central Iowa (they were not native to Story County). For example, absinthium and clasping leaf doll's daisy were widespread throughout the project area. Ashy sunflower, prairie goldenrod (*Oligoneuron album* (Nutt.) Nesom), and fire wheel (*Gaillardia pulchella* Foug.) occurred on a few sites (Rosburg and Severt 1999). After five years it seemed that these species were fading away; their abundance in the vegetation on the sites was decreasing. However the seed bank study has verified that at least three of these accidental species (absinthium, clasping leaf doll's daisy, and ashy sunflower) have not disappeared and in fact maintain a relatively high abundance in the seed bank. Knowing this is useful so that management of the reconstruction can avoid causing disturbances that would be favorable to their germination and establishment, and thereby circumvent a renewal of their seed bank through on-site seed production. The seed bank study has revealed the importance for avoiding accidental non-native species in prairie reconstructions; it clear that depending on the species, they can become well established in the seed bank and become a long-term problem. The surest way to prevent such mistakes is to use a locally derived seed source.

The relatively high abundance of resident mostly ruderal species in the seed bank (83% of the observed seeds) in contrast with the low occurrence of seeded prairie species corroborates the idea that seed banks constitute a memory of the previous vegetation (Templeton and Levin 1979). The cool-season grassland in the highway right-of-way prior to 1996 was present for decades. Frequent disturbance and perturbation (mowing, herbicides, highway salting, flooding, agricultural sedimentation) created opportunities for ruderal species to became established. Weedy ruderal species growing along the edges of the adjacent agricultural fields also contributed seed rain to the right-of-way (and still do). Ruderal species were able to form large and persistent seed banks in the cool-season grassland. Many of these species (at least 35) still occur, although for some only sporadically, in the vegetation of the reconstructed prairie (Rosburg 2004) and may continue to contribute to the seed rain. The "memory" of the previous vegetation can be quite long. Rosburg and others (1994) reported that seven of the ten most common species observed in the seed bank of prairie were species favored by grazing, despite the lack of grazing on the study area for over 20 years.

Table 3. The first 20 species (about 12% of the 158 analyzed) associated with low and high scores of axes 1 and 2 in the DCA ordination (Figure 1).

Low scores axis 1	High scores axis 1	Low scores axis 2	High scores axis 2
White goldenrod	Carpet weed	Norwegian cinquefoil	Prairie fleabane
Porcupine grass	Hoary vervain	Black medick	Black nightshade
Wild onion	Daisy fleabane	Hairy crabgrass	Curly sour dock
Rattlesnake master	Mullein	Smooth crabrass	Common ragweed
Virginia ground cherry	Spurge species	Common wormwood	Barnyard grass
Rough blazingstar	Bitter cress	Pigweed	Mullein
Switchgrass	Pigweed	Smartweed	Bird's foot trefoil
English plantain	Smartweed	Sweet clover	Common evening primrose
Grass leaf goldenrod	Carpet spurge	Red clover	Sedge
Sawtooth sunflower	Red clover	Yellow wood sorrel	Sky blue aster
Prairie coreopsis	Pale sour dock	Wild bergamot	Decurrent false aster
Canada milkvetch	Lovegrass	Wild carrot	Witchgrass
Gray goldenrod	Bull thistle	Lamb's quarter	Tall boneset
Rigid sunflower	Yellow wood sorrel	Giant foxtail	Canada bluegrass
Round-head bush clover	Witchgrass	Ashy sunflower	Black-eye susan
Wild rose	Stinging nettle	Bull thistle	Whorled milkweed
Sullivant's milkweed	Common wormwood	Tansy mustard	Squirrel tail barley
Prairie blazingstar	Penny cress	Smooth aster	Porcupine grass
Pepperweed	Black nightshade	English plantain	Rush species
False boneset	Curly sour dock	Penny cress	White goldenrod

Comparison of Seed Bank and Extant Vegetation

The variation and difference in species composition between the extant vegetation and their seed banks was clearly displayed in the ordination. The extant vegetation (with low axis 1 scores) is represented by greater abundance of perennial prairie species (Table 3). As axis 1 scores increase towards the seed bank samples, perennial prairie species decrease and are replaced by a greater abundance of ruderal, disturbance species (Table 3). The seed bank samples with the highest ruderal component are sites 598N and 599S (highest axis 1 scores), which both occur on sandy soil and also have the first and second highest total seed density in the seed bank due to very high densities of green carpetweed. The species composition gradient associated with axis 2 is not quite as obvious (Table 3). The best ecological explanation for the species gradient along axis 2 is that the high score species appear to be more tolerant of stressful environments (similar to a low level chronic disturbance) while the low score species tend to respond more to disturbances that open up space in crowded communities. Sites 767S, 739N, and 618S, which are located on the upper half of axis 2, can all be characterized as stressful environments. Low fertility, coarse textured soils occur at 767S, very steep and well-drained soils characterize 618S, while flooded conditions often occur at 739N. These three sites had the lowest productivity biomass samples collected in 1999 (all less than 360 g/m^2, mean of 328 g/m^2). At these sites space for colonization and establishment results from stressful abiotic conditions restraining growth. At sites 788S, 713S, 752S and 754S, which all have low scores on axis 2, fertility and productivity are high (mean biomass of 535 g/m^2 and highest productivity among all sites of 655 g/m^2 observed at 752S). Colonization and establishment require disturbance to open up the canopy and remove existing vegetation. The difference in the colonization and establishment environment—tolerance for stressful environments versus ability to quickly exploit canopy gaps—is reflected in the seed bank composition and to some extent in the extant vegetation since there was a significant correlation between axis 2 scores for vegetation and seed bank samples. Difference in life history and allocation of energy are seen as the principal factors affecting species composition along both axes in the ordination. Grime (1977) life history strategies, which asserts that there a three strategical options—ruderals (allocate energy to reproduction), competitors (allocate energy to growth) and stress-tolerators (allocate energy to maintenance), provide a good explanation for both of the compositional gradients. Axis 1 is a gradient of competitors (low scores) to ruderals (high scores) and axis 2 is a gradient of competitive ruderals (low scores) to stress tolerators (high scores).

The seed bank samples realize a much higher level of uniqueness in species composition utilizing a much smaller pool of species than does the vegetation. Each site's vegetation is fairly similar to vegetation at the other sites, most likely because each site's vegetation has developed from very similar seed mixes over the last four years. Unlike the vegetation, each site's seed bank is generally more unique and specific to that site (exceptions would be the trio of 601N, 691S, and 726N and the pair 754S and 752S). Because seed banks represent a memory of the vegetation, the varied histories of the sites over the last 30 to 40 years could lead to greater uniqueness of the seed banks. Because a prerequisite of seed banks is that species presence requires adaptation for seed dormancy and longevity, there are fewer species capable of forming seed banks than there are species in the vegetation. A high ratio of heterogeneity (variation in species composition) for a given species richness pool seems to be an important ecological distinction between seed bank communities and their associated aboveground vegetation.

Evaluating the Success and Quality of the Reconstruction with Seed Banks

The goal of prairie reconstruction is to replace an existing (probably anthropogenic) community with a prairie community. When research on the I–35 prairie reconstruction was initiated in 1996, one of the goals was the development of tools to assess the success and quality of prairie reconstructions (Siefert and Rosburg 1997). Two indices were devised and implemented with the I–35 prairie vegetation—one measured the proportion of seeded species that establish (PSSP or the proportion of seeded species present) and the other measured how well the prairie vegetation is replacing the preexisting resident vegetation (RASS-relative abundance of seeded species). Both of these indices have increased from 1996 to 2002 on the dry mesic sites (mean PSSP increased from 21% to 46%; mean RASS increased from 30% to 50%). Mesic sites have exhibited improvement mainly in PSSP over the same time (mean PSSP increased from 25% to 49%; mean RASS increased slightly from 44% to 50%) (Rosburg 2004).

Unlike natural prairie, reconstructions are characterized by a large input of seed (desirable, late-successional species) at the beginning of a successional process. Assuming we know which of those species have successfully established in the vegetation, seed bank data provides further assessment on their success in producing seed and maintaining population stability. Theoretically there is no reason why the criteria applied to the vegetation cannot also be applied to the seed bank. Although we know that seed banks and vegetation are often dissimilar, it is still useful to know to what extent prairie species (planted in the seed mix) are either maintaining or establishing a seed bank. Seed banks provide for long-term population stability. Individuals of perennial K-selected species eventually die, either from senescence, herbivory, or disease and need replacement for population maintenance. Late-successional prairie species occur in prairie seed banks, just not with the same high densities as ruderal species. The high dissimilarity between seed bank and vegetation mainly arises from their quantitative differences. Rosburg and others (1994) observed 25 late-successional prairie species in a prairie seed bank (out of 87 species, or 29%), including forb species such as leadplant (*Amorpha canescens* Pursh), lotus milkvetch (*Astragalus lotiflorus* Hook.), smooth blue aster, and nine anther prairie clover (*Dalea enneandra* Nutt.). Similarly, 17 out of the 45 species (38%) observed in the seed bank of Illinois tallgrass prairie were late-successional prairie species (Johnson and Anderson 1986).

Mid- to late-successional prairie species account for 15% of the seed bank species in the I–35 prairie reconstruction. Clearly there is room for improvement in this four-year-old prairie when compared to the 30 to 40% observed in native prairies. The proportion of seeded species present for the seed bank for all sites combined is 16% (based on 76 species in the seed mixes). Perhaps more appropriate for the seed bank is the proportion of seeded and established species present, which is 18% (based on 66 seeded species that had been observed in the vegetation by 2000). Both of these are much lower than the PSSP for the vegetation over all sites, which was 77% in 2000. That is to be expected given the much greater difficulty in detecting species in seed bank compared to the vegetation. Nevertheless, the data provide a benchmark for comparison with other studies (which do not exist) or better yet with other years later in the succession (monitoring). In this study, RASS for the seed bank was 15%, which again is considerably lower than RASS in the vegetation (between 30 and 50%). The difference in ability to detect ruderals (residents) and prairie (seeded) species in the seed bank is much greater than in the vegetation. Because the ruderal's strategy is to disperse in time and space to find a disturbance, they are much more likely to germinate in seedling assays than are late-successional prairie species. Again, difficulties in "seeing" the seed bank limit the usefulness of the data, but if studies are done with the same methodology, reliable comparisons can be made. If the seed bank study was repeated five or ten years later, and either PSSP, RASS, or proportion of late-successional prairie species in the seed bank was twice as large, it could be interpreted as a sign of higher quality in the reconstruction.

Trends in success and quality need to be revealed with monitoring, and this study, being the first seed bank study for the project, can only provide baseline data. A four-year-old reconstructed prairie has not had enough time to significantly alter the seed bank composition in its favor. Prairie species need time to germinate, establish, and produce seed. Because they are primarily K-selected perennial species, growth is slower and seed production is offset by allocation of energy to maintenance and vegetative reproduction. Many species have just recently established and not yet flowered. Concurrent with the growth and establishment of prairie species is the replacement of resident species in the vegetation and the reduction of resident seed production. Over time, the elimination of resident seed rain and the loss of resident seed from the seed bank through senescence, predation, and germination will favor greater relative abundance of prairie species in the seed bank. Monitoring the seed bank over time will provide a good assessment tool of how well the reconstructed prairie replaces the resident community in both the extant vegetation and the potential vegetation dormant in the seed bank.

Because successional mechanisms and processes comprise an important part of reconstruction ecology, monitoring the changes in seed bank composition and the similarity between seed bank and vegetation can provide information concerning the reconstruction's successional status. Studies of seed banks in association with successional vegetation have generally shown that species richness, species diversity, total seed

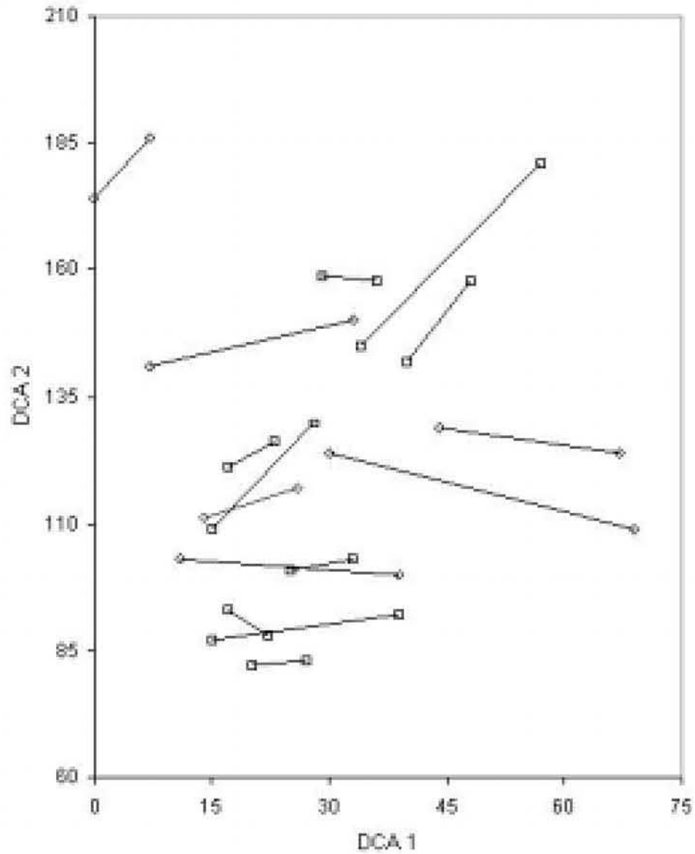

Figure 2. Enlarged view of Detrended Correspondence Analysis of 1999 and 2000 vegetation samples (open symbols connected with a line) from Figure 1. The symbols and site numbers are the same as in Figure 1.

density, and relative abundance of annuals and biennials (ruderals) decrease with time and the presence of later successional communities (Koniak and Everett 1982, Roberts and Vankat 1991). Likewise, similarity between seed bank and vegetation should decrease with time. Following disturbance, high recruitment and establishment from the seed bank fosters high similarity between the seed bank and vegetation. The longer a community is disturbance free allowing the seed bank and vegetation to diverge, the more dissimilar the seed bank and vegetation become. The dissimilarity in composition between seed bank and vegetation results from differences among species in seed production, dispersal and survival, and particularly the strategy of ruderal species to disperse in time as well as space.

However, although reconstructions are inherently successional and would be expected to exhibit similar successional patterns as natural vegetation, they are different in the occurrence of a large seed rain event (the seeding). The I–35 seeding mixes contained 76 mostly K-selected prairie species planted at an average density of 1,700 seeds/m^2. This large influx of seed has the potential to prolong the early-successional similarity between seed bank and vegetation. Recruitment of both resident seed and the seed mix seed after planting will foster a high initial similarity between seed bank and vegetation, but whereas a natural vegetation begins to diverge from the seed bank (due to the low presence of the establishing late-successional species in the seed bank), a reconstruction has the seed mix serving as a reservoir of late-successional species. The degree that the similarity between seed bank and vegetation is prolonged by the seed mix seed rain depends on three things: (1) to what extent does the seed mix dilute the resident seed bank, (2) to what extent does the seed mix germinate and establish, and (3) to what extent does non-germinated seed mix remain viable in the seed bank.

The lack of any association between vegetation and seed bank among all 15 sites on the I–35 reconstruction suggests that the prairie reconstruction is beyond the "early-successional" phase and that the seed mix seed rain has not extended the successional similarity between seed bank and vegetation. The apparent lack of a prolonging effect in similarity could be due to the fact that the seed mix did not effectively "swamp" the resident seed bank. Even with a fairly high seeding density of 1,700 seeds/m^2, the seed mix was still much below the median seed density (3,050 seeds/m^2/3 cm). There is simply too much ruderal seed in the seed bank compared to the seed mix seed rain. Another possible contributing factor is that there is little if any viable seed remaining from the seed mixes planted. As the planted seed is lost from the seed bank, either through recruitment or death, the seed bank would become more dominated by long-lived, ruderal resident species and lose similarity with the vegetation. It is impossible to know the source of the seed of the late-successional prairie species that were observed in the seed bank (seed mix seed vs. seed rain from established plants). Some of it may have originated on site from seed rain by established plants for the species that were quick to establish and which have already flowered (in this study the grasses big bluestem, little bluestem, and Indiangrass and the forbs wild bergamot, New England aster, black-eyed Susan, and common evening primrose). For slower to establish species that have not produced seed, the presence of their seed could indicate that viability in the planted seed has been maintained. Smooth aster, skyblue aster and white heath aster may be examples in this study. Unfortunately, we do not have data on the seed rain in the I–35 reconstruction since seeding and we know very little about the seed viability and longevity of late-successional prairie species. Nevertheless, the composition of seed bank indicates that most of the planted seed has either germinated (good) or has lost viability (not so good).

Since seed banks tend to be dominated by ruderal, disturbance-adapted species (and the I–35 sites are very good examples of that), another implication in the lack of association between the seed bank and vegetation is that the reconstructed prairie has developed without too much negative input from the seed bank. The necessity of reliance on seed germination to achieve results in prairie reconstruction does expose the area to the whole seed bank and potential problems with undesirable species. If there was a weedy stage, the lack of an association between the seed bank and vegetation is evidence that the prairie has matured beyond it. Careful inspection of the vegetation samples in the ordination (Figure 2) reveals that all but two of the sites exhibited vegetation change between 1999 and 2000 that made them less like the seed banks (movement along axis 1 from right to left, or decreasing axis 1 score). In fact there was a significant difference in the mean axis 1 scores for 1999 and 2000 (1999 = 36.1, 2000 = 21.9, paired t-test, P = 0.001). This is good evidence that the prairie is continuing to diverge from the seed bank. Since the reconstruction does not apparently contain a significant prairie component in the seed bank, the divergence is a positive sign of a maturing prairie. Eventually it would be ideal to see a greater representation of prairie species in the seed bank as assurance of some long-term stability in the community and its populations.

Acknowledgments

Funding for this research was provided by the Living Roadway Trust Fund in the Roadside Development Section of the Iowa Department of Transportation. Steve Holland, Coordinator of Iowa DOT's Living Roadway Trust Fund, has been instrumental in providing funds for research along Iowa's roadways. Comments from two anonymous reviewers were helpful in improving an earlier draft of this manuscript and were greatly appreciated.

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