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Assessment of long-term tallgrass prairie restoration in Manitoba, Canada

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Abstract

Ecological restoration is important in mitigating degradation and habitat loss of tallgrass prairie in North America. In 2002, we assessed the progress of a long-term tallgrass prairie restoration initiated in 1987 in southern Manitoba (Canada). Nine restoration and three reference sites were examined, as was a neighbouring site of future restoration that is now used for agriculture. Vegetation diversity, species composition, and associated soil properties were compared among restoration and reference sites, and changes associated with restoration identified. Restoration had a substantial effect on diversity and species composition, although restoration sites had significantly lower native and higher exotic diversity than reference sites. Overall and native diversity decreased over time, as both exotic and seeded native species were lost from the restoration sites. Particularly vulnerable were native forb species, which represent much of the diversity of prairie habitats. Forb presence was negatively associated with that of warm season native grasses, especially *Andropogon gerardii* (big bluestem). Similarity of restoration and reference vegetation increased over time, particularly for seeded native graminoids. When species that had been seeded elsewhere and had colonized restorations were examined, similarity between restoration and reference also increased with time, suggesting that older sites may be self-propagating. No significant differences in soil properties variables were observed among restoration sites, indicating that changes in these factors are slow relative to vegetation changes. Although time-since-restoration had a substantial impact on diversity and species composition, this habitat will require ongoing restoration.

Keywords: Community structure; Diversity; Grassland; Restoration; Similarity; Tallgrass prairie

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1. Introduction

Urban development and agriculture have reduced tallgrass prairie to 1% of its historic landcover in North America (Samson and Knopf, 1994). What remains is highly fragmented by continued development and encroachment of woody vegetation (Heisler et al., 2003; Sveinson, 2003), resulting in increasing rates of species loss (Leach and Givnish, 1996) and invasion by exotic species. As such, protection of extant prairie may be complemented by restoration which constructs new, historically appropriate habitat. Active restoration thus contributes significantly to habitat conservation (Hobbs and Norton, 1996), by overcoming limitations in natural recruitment of native species and reducing dominance of undesirable species (Kindscher and Tieszen, 1998; McLachlan and Bazely, 2003).

Prairie, grassland, and heath restoration often aims to re-establish native vegetation on ex-arable lands (Kindscher and Tieszen, 1998; Pywell et al., 2002;

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Walker et al., 2004a). Under such conditions, exotic vegetation may limit diversity and seed banks of native species are often depleted (Sveinson and McLachlan, 2003). Restoration seeks to eliminate undesirable vegetation and seed banks by tillage and herbicide use (Wilson and Gerry, 1995; Choi and Pavlovic, 1998). Subsequently, native species are seeded to overcome dispersal and recruitment limitation (Kindscher and Tieszen, 1998; Wilson, 2002). Continued management, including prescribed burning (Howe, 1994, 1995; Heisler et al., 2003), mowing (Maron and Jefferies, 2001), and herbicide application (Grilz and Romo, 1995), is aimed at controlling exotic species and increasing persistence of native populations. Ultimately, it is hoped, self-sustaining native plant communities will develop (Hobbs and Norton, 1996).

Although prairie restoration is widely practiced across North America, it remains a long-term process. Most restorations are undertaken in the absence of an initial site description and without formal monitoring (Hobbs and Norton, 1996). In such cases, chronosequence studies, examining sites with relatively uniform environmental conditions, are often used to assess restoration progress (e.g., Kindscher and Tieszen, 1998; Baer et al., 2002; Sluis, 2002). While young restorations in North America are dominated by annual species, exotic and ruderal cover decreases over time (Baer et al., 2002) and perennial grasses including *Poa* spp. (bluegrass) and *Andropogon gerardii* (big bluestem) tend to increase (Sluis, 2002). The latter is facilitated by spring burning (Howe, 1994) as well as the use of grass-dominated seed mixes (Morgan, pers. com.; Sveinson, 2003), and, in turn, is likely associated with declines in seeded forb species (e.g., Kindscher and Tieszen, 1998; Baer et al., 2002; Wilson, 2002).

Soil characteristics may also be affected by restoration activities (Baer et al., 2002). Indeed, reduction of soil fertility is often an explicit goal of restoration (Walker et al., 2004b). However, such changes are generally slow to occur. Little change in edaphic factors was observed after 24 and 35 years of restoration in Wisconsin (Brye et al., 2002) and Kansas (Kindscher and Tieszen, 1998), while soil C and N increased over 12 years in Nebraska (Baer et al., 2002). Factors accompanying vegetation changes in prairie restorations continue to be poorly understood.

This study was conducted on a long-term tallgrass prairie restoration at Beaudry Provincial Park in southern Manitoba. The restoration was initiated by the provincial government in 1987 and, comprising over 120 ha of formerly cultivated land, is now the largest of its kind in Canada. The overall objective of this study was to assess the progress of long-term prairie restoration. More specifically, we examined differences in native and exotic plant diversity, species composition and similarity between reference and restored sites; changes in vegetation over time; and changes in soil properties associated with restoration.

2. Methods

2.1. Study area

Beaudry Provincial Park is 10 km west of Winnipeg, in southern Manitoba, on the Assiniboine River (lat. 49° 52′N, long. 97° 29′W). It is in the prairie ecozone, 94% of which is now used for agriculture (Wiken, 1996). Soils of the region are in the Red River association of blackearth soils, in the Scanterbury, St. Norbert, Osborne and Red River series. Prairie remnants and restoration sites within Beaudry Park occur on heavy clay soils overlying lacustrine deposits (Veldhuis, 1986). The region has a continental climate and the mean annual temperature is 2.6 °C, with a mean maximum of 25.8 °C in July and a mean minimum of −22.8 °C in January (Environment Canada, 2003). An average of 514 mm of precipitation occurs annually, with 416 mm as rain (Environment Canada, 2003).

Beaudry Provincial Park was created in 1975, and now comprises 950 ha of riparian forest and upland habitat. Lowland forest adjacent to the river is dominated by *Populus deltoides* (plains cottonwood), *Acer negundo* (Manitoba maple), *Ulmus americana* (American elm), and *Tilia americana* (basswood). Remnant tallgrass prairie and savannah in the park are characterized by *A. gerardii*, *Spartina pectinata* (prairie cord grass), *Dalea purpurea* (purple prairie clover), *Symphoricarpos occidentalis* (western snowberry), and *Quercus macrocarpa* (bur oak). Until 1986, approximately 225 ha of parkland were leased for agriculture. From 1987 to 2000, sections of three agricultural fields were sequentially removed from cultivation along a north-south gradient, tilled, summer fallowed, and seeded with prairie species (Fig. 1). Seed was collected from local prairie sites within a 180 km radius of Beaudry Park using a manual harvester. This was supplemented by commercial seed (Prairie Habitats, Argyle, Manitoba) and seed grown at the park. Mixes had high proportions (~85%) of grass seed by weight (Berg, 1992; Morgan, pers. com.). Reseeding of sites into standing vegetative cover has been infrequent, occurring twice at site 98 and once at site 99, where successful establishment of vegetation from a previous seeding was compromised by flooding (Friesen, pers. com.). These sites are also mowed repeatedly in the summer to control exotic species, including *Cirsium arvense* (Canada thistle), and *Sonchus arvensis* (perennial sow thistle). Commonly, patches within all restoration sites are mowed to control invasive exotics *Melilotus alba* (white sweet clover) and *Melilotus officinalis* (yellow sweet clover). Prescribed burning is conducted every 5 years and always in early spring.

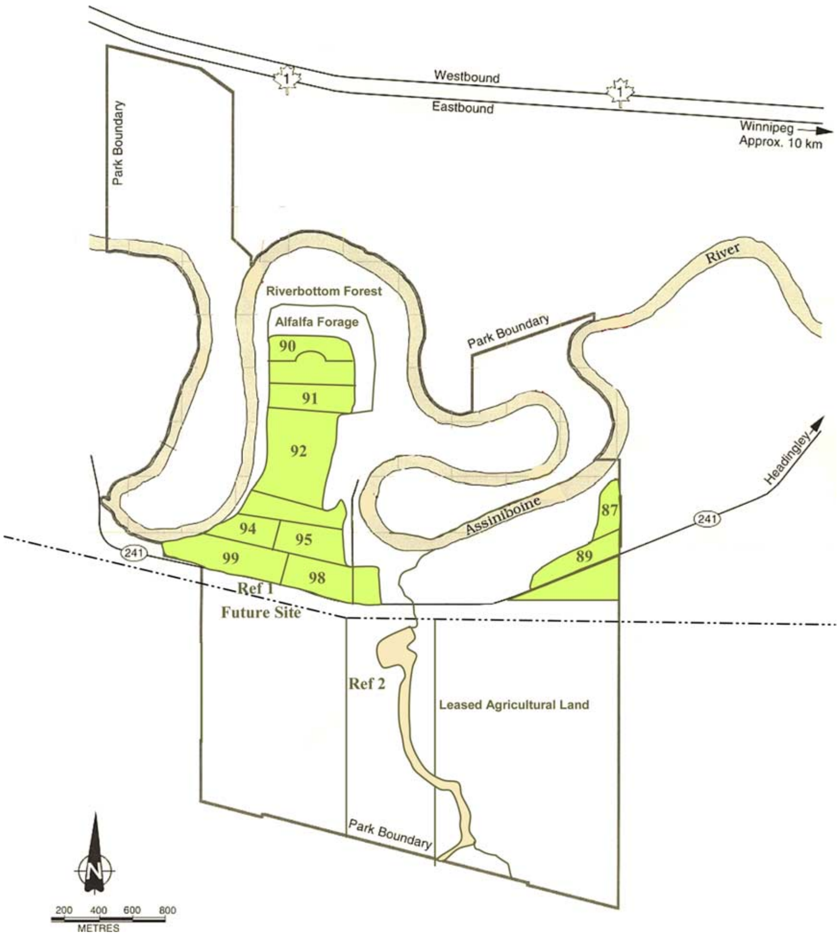

Fig. 1. Location of study sites at Beaudry Provincial Park. Restored sites are indicated by their initial year of seeding. (Ref 1, Reference site 1; Ref 2, Reference site 2; Future site, potential restoration site.)

2.2. Site selection

We categorized all restoration sites into three age classes to facilitate analysis where no prior knowledge of restoration composition was available. Though restoration progress is continual and gradual, we anticipated differences between young and old restorations. Three sites were randomly selected in each class: (i) those seeded in and between 1987 and 1990 (i.e., 87, 89, and 90); (ii) those seeded in and between 1991 and 1994 (i.e., 91, 92, and 94); and (iii) those seeded in and between 1995 and 1999 (i.e., 95, 98, and 99) (Fig. 1, Table 1). In addition, three unbroken remnant prairie sites were identified as target reference points (i.e., reference sites). Two of these remnants were located in Beaudry Provincial Park, along an abandoned rail line (Ref 1) and stream bank (Ref 2) (Fig. 1, Table 1). The third remnant (Ref 3) was located at the Living Prairie Museum (49° 54′N, 97° 17′W), 20 km east of Beaudry Park in the city of Winnipeg (Table 1). A future restoration site at Beaudry, which is still in agricultural use, was also examined, as it approximated site conditions prior to restoration (Fig. 1, Table 1).

To ensure the validity of the chronosequence approach, environmental and landscape characteristics were compared among all three restoration age classes and the reference class. Sites were described using area (ha), perimeter (km), and a shape index ($P/(2\sqrt{A} * \pi)$, where P, perimeter (m), and A, area (m^2) of the site), which measures the degree to which shape departs from a circle (Moffatt and McLachlan, 2003), to determine if edge effects may be greater in particular classes. As species composition may also be affected by adjacent land use, the proportion of site perimeter (%) adjacent to both forested and hayed lands and the distance to the nearest roadway (km) were calculated for each site. In addition, site elevation and a cumulative fire index, calculated as the number of times a site had been burned in the past 15 years, were compared among classes. One-way analysis of variance (ANOVA) (SAS, 1988) was used to determine if underlying differences among site classes may affect restoration progress (data not shown). Environmental and landscape variables did not differ significantly among age classes, with the exception of fire index, which was significantly lower ($P = 0.0056$) in young restoration sites. This initial assessment

Table 1
Descriptions of study sites at Beaudry Provincial Park, including common management practices

Site[a]	Adjacent land use	Soil series and texture[b]	Elevation (m)	Area (ha)	Perimeter (km)	Shape index[c]	Distance to road (km)	Perimeter forested (%)	Perimeter hayed (%)	Fire index[d]	Mowing
Ref 1	Abandoned rail line, road	Scanterbury (HC)	237.4	1.0	1.06	2.96	0	1.89	0	3	N/A
Ref 2	Stream, forest	St. Norbert/Osborne (HC)	237.3	0.4	0.32	1.41	0.25	53.13	0	0	N/A
Ref 3	Residential urban	Red River/Marquette (HC)	239.0	13.0	1.10	0.86	0.01	9.09	0	13	N/A
87	Forest, site 89	Scanterbury/St. Norbert (HC)	237.0	4.0	1.02	1.44	0.09	48.04	0	2	Selective
89	Forest, site 87, road	Scanterbury (HC)	237.8	2.8	1.00	1.64	0	31.00	0	2	Selective
90	Forest, forage, restoration	Scanterbury (HC)	238.3	14.2	1.79	1.34	1.35	16.76	41.34	3	Selective
91	Forest, forage, restoration	Scanterbury (HC)	238.5	16.6	1.77	1.23	0.96	15.25	18.08	3	Selective
92	Forest, restoration	Scanterbury (HC)	238.1	22.7	1.74	1.03	0.55	51.15	0	3	Selective
94	Forest, restoration	Scanterbury (HC)	237.3	13.8	1.06	0.81	0.28	20.75	0	1	Selective
95	Forest, restoration, road	Scanterbury (HC)	238.4	6.9	1.01	1.18	0.33	0.0	0	1	Selective
98	Restoration, road	Scanterbury (HC)	237.5	10.5	1.19	1.04	0	0.0	0	1	Complete
99	Forest, restoration, road	Scanterbury (HC)	237.3	13.0	1.86	1.46	0	15.05	0	1	Selective
Future site	Abandoned rail line	Osborne/Scanterbury (HC)	237.6	33.2	1.06	2.96	0.07	0.0	0	0	N/A

[a] Restored sites are identified by their initial year of seeding. Ref 1, Reference site 1; Ref 2, Reference site 2; Ref 3, Reference site 3; Future site, potential future restoration site.

[b] Soil series from Veldhuis, 1986 and Ehrlich et al., 1953. Surface texture is indicated in brackets. HC, heavy clay.

[c] Shape index, calculated as $P/(2\sqrt{A*\pi})$, where P, perimeter, and A, area of the site, measures the degree to which shape departs from a circle.

[d] Cumulative fire index calculated as the number of times a site has been burned in the past 15 years.

suggests that starting conditions were similar throughout the restoration chronosequence.

2.3. Vegetation sampling

Vegetation was sampled between August 19 and August 26, 2002, during the peak growth period. Early-flowering plants were surveyed in late June to facilitate subsequent sampling. All sites were divided into three strata, and a 300-m transect was randomly located in each of these strata, running parallel to the long axis of the site. Fourteen 1 m × 1 m quadrats were established in each site along these transects, and percent cover of all vascular plant species recorded. In the reference sites and one of the old restorations, this sampling arrangement was modified to accommodate the small size and linear shape of the sites, while maintaining the same sampling intensity. All quadrats were located in undisturbed standing vegetation. Nomenclature follows Scoggan (1957).

2.4. Soil properties

Between May 27 and June 18, 2002, eight of the 14 quadrats in each site were selected, such that four were located at the edge of the site and four in the interior. In each quadrat, two soil cores (3 cm × 15 cm) were collected, and all edge and interior cores were homogenized. Homogenized samples were dried, ground, and sieved through a 2-mm screen to remove plant material and rock. Soil pH and electrical conductivity were measured on a 2:1 deionized water:soil slurry with a standard hydrogen electrode and an ohmmeter, respectively (McKeague, 1978). Soil organic matter was determined by loss on ignition at 500 °C in a muffle furnace, from samples dried at 105 °C. Soil sulphate was assessed by spectroscopy of 0.1 M $CaCl_2$ sample extracts (McKeague, 1978). Spectroscopy of KM extracts (0.015 M NH_4F, 1.0 M CH_3COONH_4 and 0.5 M CH_3COOH) was used to estimate water-soluble nitrate and available phosphate (modified Kelowna test; Ashworth and Mrazek, 1995).

2.5. Data analyses

We analysed data to assess effects of time-since-restoration on vegetation and soil properties. Native, exotic and overall species diversity was calculated using Hill's (1973) measures, including N_0 or species richness, which is the total number of species but is sensitive to rare species; N_2 or effective species richness, which is the reci-procal of Simpson's diversity index and emphasizes dominant species; and E_3 or evenness, which is calculated as N_2 divided by the total number of species. Differences in native, exotic and overall species diversity between restored and reference sites were examined using t tests

(SAS, 1988). Differences in native, exotic and overall species diversity, and individual species cover were compared among restoration classes (i.e., young, mid-age and old restoration and reference sites) using one-way analysis of variance (ANOVA) (SAS, 1988). Soil variables, expected to change less rapidly, were compared among reference, restored and future restoration sites. Post-hoc Student–Neuman–Keul (SNK) multiple comparison tests (α, 0.05) were used to separate means when overall ANOVA model statements were significant. All data were log + 1-transformed to meet the assumptions of normality (Sokal and Rohlf, 1981), and untransformed data are presented. In addition to detecting species significantly affected by time, we identified seeded and non-seeded native species present in at least two age classes and which showed no significant change in cover across the four restoration classes.

Effects of restoration on community composition were analysed for all sites using correspondence analysis (CA). The CA identifies relationships between species and individual sites along orthogonal axes of variation that are extracted in descending order of importance (Ter Braak, 1988). Species cover values were averaged within each site and log + 1-transformed. Rare species were downweighted in importance. Formal site groupings, identified using cluster analysis with minimum increase in error sum of squares and chord distance (Podani, 1994), were mapped on the CA output.

Relationships among restoration and reference sites, species, and soil properties were examined using canonical correspondence analysis (CCA) (Ter Braak, 1988). This direct gradient analysis constrains the results of the CA using associated edaphic variables. Species and edaphic data sets were averaged within each site and log + 1-transformed, and rare species downweighted. The redundancy value, which measures the proportion of the total variation in the species data explained by the constraining variables, was also assessed (Økland, 1999).

The resemblance between restoration and reference sites was determined using Sorenson's similarity index. This is calculated as $2a/(2a + b + c)$, where a is the number of species present in both sites, b is the number of species unique to one site, and c is the number of species unique to the other site (McLachlan and Bazely, 2003). Similarity was calculated between all restoration sites and all reference sites for all species, seeded native graminoids, seeded native forbs, non-seeded native species, and exotic species. To assess the degree to which restorations were being colonized by desirable species, we also calculated similarity between restoration and reference sites for species which, though present in a given restoration, had only been seeded in other sites. Regression was used to determine the relationship between average similarity with reference sites and time since restoration (Sokal and Rohlf, 1981). As Sorenson's similarity is based solely on presence/absence data, chord distance was also calculated between all restored and reference sites. This metric measure of dissimilarity considers proportional abundance of species. Changes in chord distance over time were compared to those exhibited in Sorenson's similarity.

3. Results

3.1. Community composition measures

Species diversity differed substantially between restored and reference sites. Overall effective species richness was significantly higher ($P = 0.0096$) in reference sites than restored sites, as were native species richness ($P < 0.0001$) and effective species richness (ESR) ($P < 0.0001$) (Table 2). In contrast, exotic species richness and ESR were significantly higher ($P < 0.0001$ and $P < 0.0001$, respectively) in restored sites.

Table 2
Native, exotic and overall richness, effective species richness and evenness for vegetation in reference and restored sites[*]

	Reference	Restored	P[**]
Species richness			
Native	6.95 ± 0.42^a	2.53 ± 0.16^b	<0.0001
Exotic	2.02 ± 0.17^b	5.21 ± 0.12^a	<0.0001
Overall	8.98 ± 0.49	7.75 ± 0.19	0.0637
Effective species richness			
Native	3.18 ± 0.21^a	1.54 ± 0.08^b	<0.0001
Exotic	1.41 ± 0.08^b	2.41 ± 0.08^a	<0.0001
Overall	3.91 ± 0.26^a	3.21 ± 0.12^b	0.0096
Evenness			
Native	0.50 ± 0.03^b	0.64 ± 0.03^b	0.0034
Exotic	0.81 ± 0.04^a	0.48 ± 0.02^b	<0.0001
Overall	0.46 ± 0.03	0.42 ± 0.01	0.1775

[*] Means followed by different letters are significantly different at $P < 0.05$ according to a Student's t-test of log-transformed data. Untransformed data are presented values ± standard error.

[**] P-value of overall model statement presented.

Table 3
Native, exotic and overall richness, effective species richness and evenness of vegetation compared across the three restoration age classes and reference sites[*]

	Reference	87–90	91–94	95–99	P[**]
Species richness					
Native	6.95 ± 0.42^{a}	2.62 ± 0.26^{c}	3.55 ± 0.28^{b}	1.43 ± 0.19^{d}	<0.0001
Exotic	2.02 ± 0.17^{b}	4.95 ± 0.16^{a}	5.19 ± 0.19^{a}	5.50 ± 0.27^{a}	<0.0001
Overall	8.98 ± 0.49^{a}	7.57 ± 0.31^{b}	8.74 ± 0.37^{a}	6.93 ± 0.24^{b}	<0.0001
Effective species richness					
Native	3.18 ± 0.21^{a}	1.53 ± 0.10^{c}	2.04 ± 0.15^{b}	1.03 ± 0.12^{d}	<0.0001
Exotic	1.41 ± 0.08^{c}	2.09 ± 0.10^{b}	2.52 ± 0.15^{a}	2.64 ± 0.14^{a}	<0.0001
Overall	3.91 ± 0.26^{a}	2.96 ± 0.14^{b}	3.58 ± 0.25^{ab}	3.08 ± 0.19^{b}	0.0063
Evenness					
Native	0.497 ± 0.03^{b}	0.70 ± 0.04^{a}	0.60 ± 0.03^{ab}	0.62 ± 0.06^{ab}	0.0478
Exotic	0.81 ± 0.04^{a}	0.43 ± 0.02^{b}	0.49 ± 0.27^{b}	0.51 ± 0.03^{b}	<0.0001
Overall	0.46 ± 0.03	0.40 ± 0.02	0.41 ± 0.02	0.45 ± 0.03	0.1970

[*] Means followed by different letters are significantly different at $P < 0.05$ according to a post-hoc SNK test of log-transformed data. Untransformed data are presented values ± standard error.

[**] P-value of overall model statement presented.

Species diversity was also affected by time since restoration. Overall species richness and ESR were highest in reference sites and were significantly lower ($P < 0.0001$, and $P = 0.0063$, respectively) in old and new restored sites (Table 3). Interestingly, mid-aged restoration sites had significantly higher overall species richness than other restored sites (Table 3). Differences in vegetation response became more apparent when species origin was examined. Native species richness and ESR differed significantly ($P < 0.0001$ and $P < 0.0001$, respectively) across all four age classes, being highest in reference sites, lower in mid-age and old restorations, and lowest in young restorations (Table 3). In contrast, exotic richness and ESR predictably were highest in new and mid-age restorations and significantly lower ($P < 0.0001$ and $P < 0.0001$, respectively) in reference sites (Table 3). Native evenness was lowest in reference sites and highest in old restorations ($P = 0.0478$), whereas exotic evenness was significantly higher ($P < 0.0001$) in reference sites than in all restorations (Table 3).

3.2. Species composition

Species composition differed substantially between reference and restored sites, and also among restored sites, and further separated sites into distinct clusters (Fig. 2(a)). The first three axes extracted by correspondence analysis (CA) represented 61.5% of the variation in the data set. Axis 1 (24.5%) represented an effective habitat-quality gradient (Fig. 2(a)). Reference sites were negatively associated with axis 1, and were characterized by native *Bouteloua curtipendula* (side-oats grama), *Amorpha canescens* (lead plant), *S. pectinata*, *Galium boreale* (northern bedstraw) and *D. purpurea* (Fig. 2(b)). The future restoration site was positively associated with axis 1, and was characterized by exotic ruderals *Brassica kaber* (wild mustard) and *Malva rotundifolia* (round-leaved mallow) (Fig. 2(b)). Restored sites were grouped in the middle of axis 1, and characterized by natives *Schizachyrium scoparium* (little bluestem), *Anemone canadensis* (Canada anemone), and *Potentilla arguta* (tall cinquefoil) as well as exotics *Thlapsi arvense* (stinkweed), *Phleum pratense* (timothy), *Amaranthus retroflexus* (redroot pigweed), and *Pastinaca sativa* (wild parsnip) (Fig. 2(b)). Axis 2 (22.2% of variation; data not shown) separated the agricultural future restoration site from all other sites. Axis 3 (14.8% of variation) represented a time-since-restoration gradient, separating restorations according to age (Fig. 2(a)). Young restoration sites were characterized by exotics *Echinochloa crusgalli* (barnyard grass), *Chenopodium album* (lamb's-quarters), and *Sonchus asper* (annual sow thistle) and early successional natives *Elymus canadensis* (Canada wild rye), *S. scoparium*, and *Ratibida columnifera* (prairie coneflower) (Fig. 2(b)). Old and mid-age restorations were characterized by exotics *C. arvense*, *Alyssum alyssoides* (alyssum) and prairie natives *Agastache foeniculum* (giant blue hyssop), and *Rudbeckia hirta* (black-eyed susan) (Fig. 2(b)).

Species composition in restoration and reference sites was associated with corresponding changes in soil properties. Species–environment correlation values were 0.978, and 0.915, and the percent variance of the species–environment relations 40.8%, and 18.5%, for CCA axes 1 and 3, respectively. Axis 2 (species–environment correlation 0.838; 25.9% variance of species–environment relations; data not shown) separated the agricultural future restoration site from all other sites. The redundancy value was high at 55.36%. Organic matter was positively associated with axis 1 and reference sites (Fig. 3(a)), and characterized by natives *S. pectinata*, *D. purpurea*, *G. boreale* and *Carex* spp. (sedge), as well as woody species *Rosa* spp. (wild rose), *Glycyrrhiza lepidota* (wild licorice), *A. canescens* and *Elaeagnus commu-*

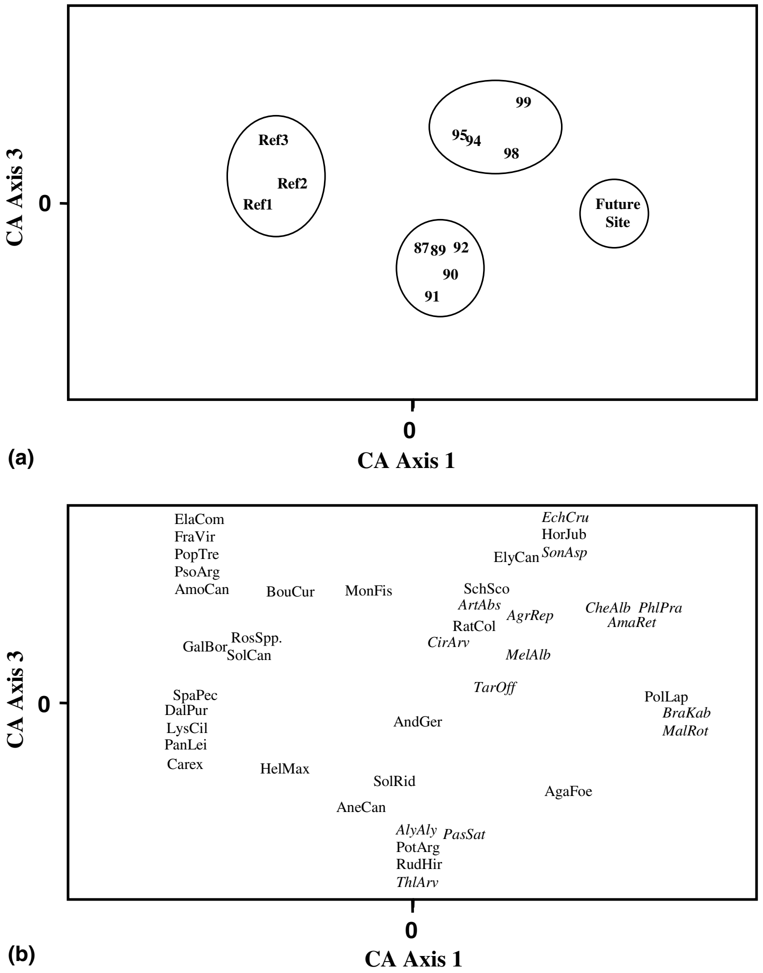

Fig. 2. Correspondence analysis (CA) of vegetation in restored, reference and future restoration sites (axes 1 and 3), showing (a) sites and groupings identified by cluster analysis, and (b) species associated with sites. Species are identified by first three letters of genus name and first three letters of specific epithet, and are available from corresponding author. Exotic species names are italicized. Restored sites are indicated by their initial year of seeding. (Ref 1, Reference site 1; Ref 2, Reference site 2; Ref 3, Reference site 3; Future site, potential restoration site.)

tata (silverberry) (Fig. 3(b)). Electrical conductivity and soil sulphur also increased along CCA axis 1, though less significantly. Conversely, soil N and P were negatively associated with CCA axis 1 and positively associated with restorations (Fig. 3(a)), which were characterized by exotic legumes *Melilotus spp.*, and *Trifolium spp.* (clover) and by exotic *C. album*, *P. pratense,* and *Rumex crispus* (curled dock) (Fig. 3(b)). Soil S and P were negatively associated with CCA axis 2 (Fig. 3(a)), and positively associated with old restorations and reference site 1, these characterized by natives *P. arguta*, *Helianthus maximiliani* (narrow-leaved sunflower), *Lathyrus* spp. (wild peavine) and *A. canadensis* and exotics *P. sativa*, and *T. arvense* (Fig. 3(b)).

3.3. Individual species

Twenty-four species were significantly affected by time since restoration. Of these, 11 (45.8%) were seeded native species, four (16.7%) were non-seeded native species and nine (37.5%) were exotic species (Table 4). Ten native species were primarily associated with reference sites, including prairie natives *Artemesia ludoviciana* (white sage), *G. boreale*, *Solidago canadensis* (Canada goldenrod), *S. pectinata* and woody species *G. lepidota*, *Rosa spp*. and *S. occidentalis* (Table 4). Five exotic species were primarily associated with young restoration sites, including *C. arvense*, *M. alba*, *Polygonum convolvulus* (black bindweed), *S. arvensis* and *Taraxacum officinale* (dandelion) (Table 4). Species that dominated older restorations included natives *A. gerardii* and *Solidago rigida* (stiff-leaved goldenrod) as well as exotics *Bromus inermis* (smooth brome) and *Medicago sativa* (alfalfa) (Table 4). Importantly, 10 seeded native species were not significantly affected by time and remained present in at least two age classes. These species seem to have been successfully established and included *Achillea millefolium* (yarrow), *A. canadensis*, *E. canadensis*, *Erigeron lonchophyllus*

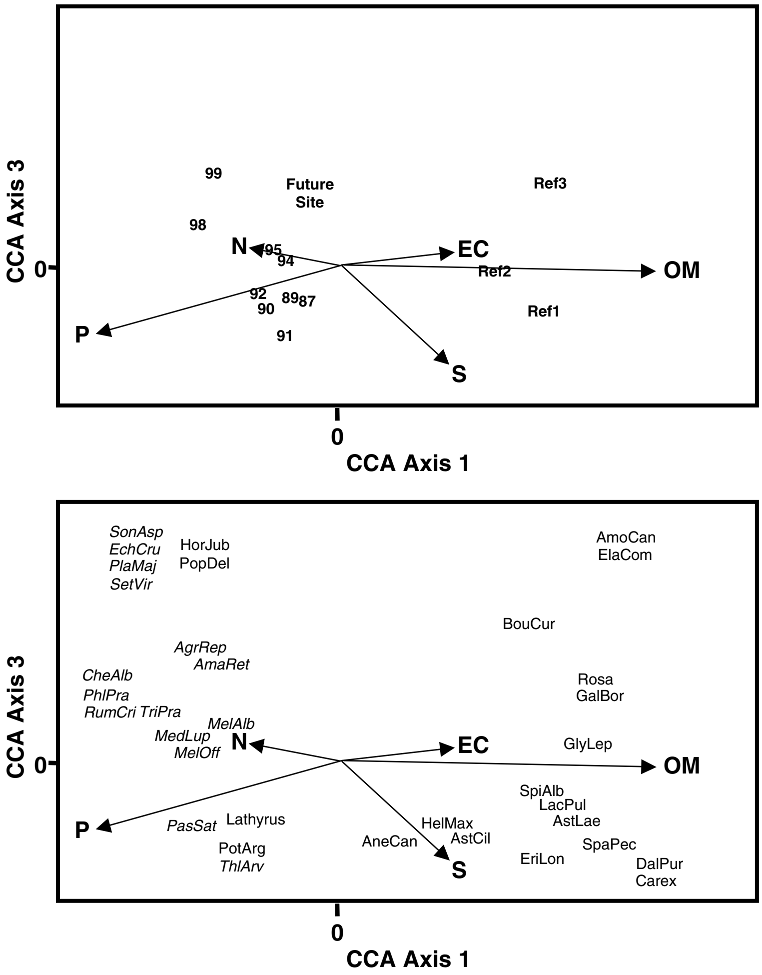

Fig. 3. Canonical correspondence analysis (CCA) of vegetation in restored and reference sites and constrained by edaphic variables (axes 1 and 3), showing (a) sites and variables on a 3× scale, and (b) species associated with variable vectors. Species are identified by first three letters of genus name and first three letters of specific epithet, and are available from the corresponding author. Exotic species names are italicized. Restored sites are indicated by their initial year of seeding. (Ref 1, Reference site 1; Ref 2, Reference site 2; Ref 3, Reference sites 3; N, soil nitrogen; P, soil phosphorus; S, soil sulphur; EC, electrical conductivity; OM, organic matter.)

(Fleabane), *H. maximiliani*, and *Monarda fistulosa* (wild bergamot) (data not shown). Two non-seeded native species, *Aster ciliolatus* (Lindley's aster) and *Convolvulus sepium* (hedge bindweed), also had become successfully established (data not shown).

3.4. Similarity

Similarity between restoration and reference sites generally increased with time. Overall similarity increased in the first 7 years since restoration initiation, but did not change thereafter ($P = 0.000088$) (Fig. 4(a)). When species origin and growth form were considered, similarity of native seeded graminoids and native species that had been seeded in some restoration sites and self-recruited in others increased linearly with time-since-seeding ($P = 0.008$; $P = 0.0014$, respectively) (Figs. 4(b), (d)). Similarity of native seeded forbs increased for the first 7 years, but decreased thereafter ($P = 0.009217$) (Fig. 4(c)). Exotic species showed no significant changes in similarity ($P = 0.991$) (Fig. 4(e)). Similar trends were observed when changes in chord distance, or dissimilarity, were examined over time (data not shown). Dissimilarity between restored and reference sites of native seeded graminoid species and native species seeded elsewhere decreased with time ($r^2 = 0.8084$, $P = 0.00097$; $r^2 = 0.8325$, $P = 0.0042$, respectively). Dissimilarity of native seeded forbs and exotic species showed no significant linear trends ($r^2 = 0.2458$, $P = 0.2578$; $r^2 = 0.3002$, $P = 0.1267$, respectively).

3.5. Soil properties

To determine the effects of restoration on soil properties, reference, restoration, and future restoration sites were compared. Although affected by restoration, changes in these variables were much smaller than those of vegetation. Soil phosphorus was significantly higher

Table 4
Mean percent cover of native seeded, native non-seeded and exotic plant species significantly associated with restoration age classes[*]

	Reference	87–90	91–94	95–99	P[**]
Native seeded					
Reference sites					
Artemesia ludoviciana (white sage)	1.26 ± 0.30^{a}	0 ± 0^{b}	0 ± 0^{b}	0 ± 0^{b}	<0.0001
Galium boreale (northern bedstraw)	1.26 ± 0.52^{a}	0.001 ± 0.001^{b}	0 ± 0^{b}	0 ± 0^{b}	<0.0001
Helianthus laetiflorus (rhombic-leaved sunflower)	1.79 ± 0.64^{a}	0.55 ± 0.48^{b}	1.67 ± 0.73^{ab}	0.38 ± 0.36^{b}	0.0130
Lactuca pulchella (blue lettuce)	0.31 ± 0.17^{a}	0 ± 0^{b}	0 ± 0^{b}	0 ± 0^{b}	0.0034
Solidago canadensis (Canada goldenrod)	3.52 ± 0.89^{a}	0.05 ± 0.05^{b}	0 ± 0^{b}	0.14 ± 0.11^{b}	<0.0001
Spartina pectinata (prairie cord grass)	10.88 ± 3.70^{a}	0 ± 0^{b}	0 ± 0^{b}	0 ± 0^{b}	<0.0001
Thalictrum venulosum (veiny meadowrue)	0.22 ± 0.10^{a}	0 ± 0^{b}	0 ± 0^{b}	0 ± 0^{b}	0.0043
Old restorations					
Andropogon gerardii (big bluestem)	6.67 ± 2.04^{c}	33.10 ± 3.52^{a}	14.67 ± 2.78^{b}	9.79 ± 3.04^{c}	<0.0001
Solidago rigida (stiff-leaved goldenrod)	1.07 ± 0.50^{b}	5.12 ± 1.53^{a}	3.29 ± 1.16^{a}	0 ± 0^{b}	<0.0001
Mid-age restorations					
Aster ericoides (many-flowered aster)	0.72 ± 0.29^{bc}	1.91 ± 0.66^{ab}	2.60 ± 0.76^{a}	0.02 ± 0.02^{c}	<0.0001
Ratibida columnifera (prairie coneflower)	0 ± 0^{b}	0 ± 0^{b}	1.26 ± 0.58^{a}	1.10 ± 0.39^{a}	<0.0001
Native non-seeded					
Reference sites					
Glycyrrhiza lepidota (wild licorice)	6.21 ± 1.86^{a}	0 ± 0^{b}	0.05 ± 0.05^{b}	0 ± 0^{b}	<0.0001
Rosa spp. (wild rose)	8.74 ± 1.53^{a}	0 ± 0^{b}	0 ± 0^{b}	0.02 ± 0.02^{b}	<0.0001
Symphoricarpos occidentalis (western snowberry)	5.93 ± 1.13^{a}	0 ± 0^{b}	0.02 ± 0.02^{b}	0.05 ± 0.05^{b}	<0.0001
Old restorations					
Geranium bicknellii (Bicknell's geranium)	0.001 ± 0.001^{b}	0.005 ± 0.002^{a}	0.003 ± 0.001^{ab}	0 ± 0^{b}	<0.0001
Exotic					
Old restorations					
Bromus inermis (smooth brome)	3.72 ± 1.32^{b}	24.17 ± 3.20^{a}	23.45 ± 3.73^{a}	3.00 ± 0.83^{b}	<0.0001
Medicago sativa (alfalfa)	0.17 ± 0.12^{b}	3.34 ± 1.29^{a}	1.39 ± 0.37^{a}	0.41 ± 0.19^{b}	<0.0001
Mid-age restorations					
Euphorbia serpyllifolia (thyme-leaved spurge)	0 ± 0^{b}	0.001 ± 0.001^{b}	0.01 ± 0.002^{a}	0 ± 0^{b}	<0.0001
Vicia cracca (tufted vetch)	0.22 ± 0.13^{c}	4.45 ± 1.16^{b}	10.24 ± 2.34^{a}	0.22 ± 0.13^{c}	<0.0001
Young restorations					
Cirsium arvense (Canada thistle)	4.88 ± 1.61^{b}	0.84 ± 0.40^{c}	5.86 ± 1.51^{b}	9.57 ± 1.75^{a}	<0.0001
Melilotus alba (white sweet clover)	0.02 ± 0.02^{c}	0.36 ± 0.26^{c}	3.41 ± 1.47^{b}	10.64 ± 2.19^{a}	<0.0001
Polygonum convolvulus (black bindweed)	0 ± 0^{b}	0.003 ± 0.001^{b}	0.10 ± 0.05^{b}	0.41 ± 0.12^{a}	<0.0001
Sonchus arvensis (perennial sow thistle)	0.10 ± 0.06^{c}	0 ± 0^{c}	2.05 ± 0.75^{b}	5.98 ± 1.24^{a}	<0.0001
Taraxacum officinale (dandelion)	0 ± 0^{d}	6.24 ± 0.99^{c}	8.79 ± 0.71^{b}	31.74 ± 3.81^{a}	<0.0001

[*] Means followed by different letters are significantly different at $P < 0.05$ according to a post-hoc SNK test of log-transformed data. Untransformed data are presented values ± standard error.

[**] P-value of overall model statement presented.

($P = 0.0001$) in restoration and future restoration sites than in reference sites. Soil sulphate was also significantly higher ($P = 0.0006$), and soil nitrate tended to be higher, in the future restoration site than in restoration and reference sites (Table 5). In contrast, organic matter was significantly higher ($P < 0.0001$) in the reference sites than in other sites (Table 5).

4. Discussion

Tallgrass prairie is one of the most threatened ecosystems in North America (Noss et al., 1995). Remaining native habitat is highly fragmented: remnants examined in this and other studies rarely exceed 10 ha in size (Table 1; Leach and Givnish, 1996; Kindscher and Tieszen, 1998), and are often degraded by suppression of landscape scale disturbances (Leach and Givnish, 1996; Heisler et al., 2003). With little intact prairie remaining, opportunities for restoration are increasing on ex-arable land (Young, 2000). Such activities will necessarily play an important role in mitigating ongoing habitat loss and degradation in underrepresented conservation areas (Awimbo et al., 1996). Beaudry is one of the largest and longest standing tallgrass prairie restorations in Canada, and represents an important opportunity to examine the long-term impacts of prairie restoration on ex-arable land. Our results suggest that nearly 20 years of restoration have had desirable impacts on diversity and species composition at Beaudry, although this habitat will require ongoing restoration.

4.1. Restoration-associated impacts on vegetation

When restorations were compared to reference sites, overall and native species diversity remained lower and species composition differed, reflecting results of other tallgrass restoration assessments (e.g., Kindscher and

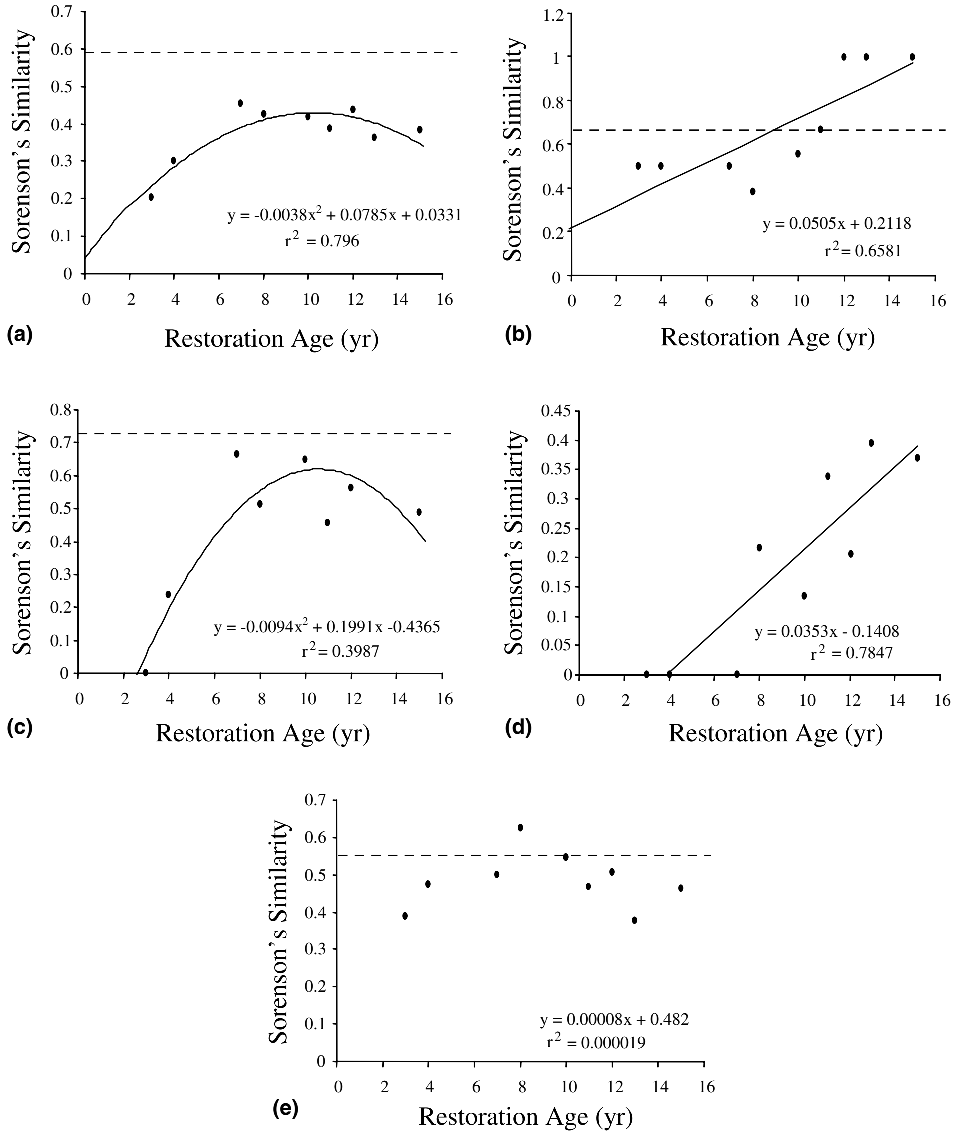

Fig. 4. Changes in Sorenson's similarity index over time, for (a) overall vegetation, (b) native seeded graminoids, (c) native seeded forbs, (d) native species seeded outside a particular site boundary, and (e) exotic species. Similarity values were calculated as the average similarity between restored sites and the three reference sites. Average similarity among the three reference sites is plotted as a reference line.

Table 5
Mean values of soil variables for reference, restored, and future restoration sites[*]

Soil property	Reference	Restoration	Future restoration	P^{**}
N (ppm)[a]	12.62 ± 2.97	14.62 ± 2.19	71.90 ± 13.10	0.0026
P (ppm)[b]	16.10 ± 6.32^{b}	37.36 ± 2.55^{a}	65.00 ± 0^{a}	0.0001
S (ppm)[c]	12.17 ± 2.94^{b}	9.22 ± 0.74^{b}	18.50 ± 6.50^{a}	0.0006
EC (ds/m)[d]	1.00 ± 0.03	0.84 ± 0.04	1.55 ± 0.46	0.0038
Organic matter (%)	15.25 ± 0.85^{a}	10.53 ± 0.24^{b}	11.50 ± 0.90^{b}	<0.0001
pH	7.23 ± 0.08	7.06 ± 0.06	6.85 ± 0.05	0.0484

[a] N, soil nitrate.

[b] P, soil phosphorus.

[c] S, soil sulphate.

[d] EC, electrical conductivity.

[*] Means followed by different letters are significantly different at $P < 0.05$ according to a post-hoc SNK test of log-transformed data. Untransformed data are presented values ± standard error.

[**] P-value of overall model statement presented.

Tieszen, 1998; Sluis, 2002). New restorations were dominated by exotic ruderals including *S. asper*, *T. officinale* and *M. alba*, as well as early-seral natives that were absent from older restorations, such as *E. canadensis* and *R. columnifera*. Older restorations tended to support later-seral native species, including *A. gerardii*, *S. rigida* and *A. foeniculum*. Species with clonal, rhizomatous growth forms generally were established more effectively in older restorations, whereas forbs that were seed-reliant were relatively vulnerable to extinction (McLachlan and Knispel, 2003). Though overall species composition of mid-age restorations was similar to that of old restoration sites (Fig. 2), important distinctions between these two restoration classes merit further exploration.

Not all time-associated changes were desirable. The high diversity of mid-age (8–11 years) restorations relative to both new (3–7 years) and old (12–15 years) restoration sites suggests that desirable species had not become established in new sites, whereas old restorations appear to have lost species. Similar results have been observed in other tallgrass prairie restorations (e.g., Kindscher and Tieszen, 1998; Baer et al., 2002; Sluis, 2002). At Beaudry, increases in similarity between restoration and reference sites only occurred for the first 7 years. Likewise, 41% of seeded species were observed in mid-age restorations, whereas only 26% remained in old restorations. These changes suggest that simple "sow-and-stop" revegetation will not likely recreate high-diversity natural habitat and that these sites will require ongoing maintenance if they are to continue recovering. Indeed, prairie may potentially require many decades to recover completely, far exceeding the duration of most restoration assessments (e.g., Baer et al., 2002; Brye et al., 2002; Pywell et al., 2002; Smith et al., 2003). Although restoration remains a long-term process, short-term changes in vegetation may be useful in assessing progress and directing subsequent management activities.

4.2. Restoration progress

Changes in similarity have been used as measures of restoration progress in grasslands (e.g., Pywell et al., 2002; Smith et al., 2003) and hardwood forests (e.g., McLachlan and Bazely, 2003). Increases in native species similarity between restoration and reference sites in our study suggest that observed vegetation changes were desirable, and that reference sites represented appropriate benchmarks for restoration. Increases were especially evident for native seeded graminoids, suggesting that grasses are most easily re-established. However, changes in similarity are calculated using presence/absence data, and may result from increases in evenness that can actually occur at the expense of diversity (Howe, 1999). For seeded graminoid composition, old restorations and reference sites were more similar than reference sites were to each other, indicating that, on average, old restorations have a more homogenous composition than reference sites. This homogeneity may have been associated with declines in graminoid diversity. However, changes in Sorenson's similarity corresponded with those in chord distance, which is calculated using proportional cover rather than presence/absence data. Thus, changes in similarity were not simply a function of changes in community homogeneity and represent a meaningful indicator of recovery in this study.

Although similarity generally increased over time, the large majority of seeded species failed to become established and older restorations had lower seeded forb diversity and similarity. These declines may be associated with the lower diversity of early seed mixes. However, they are also consistent observed species loss in older restorations, especially that of forbs. Proportionally more seeded species were lost from old restorations (74% vs. 59% in mid-age restorations) and forbs decreased in dominance over time (ratios of forb to grass cover decreased from approximately 1:1 in remnants and mid-age restorations, to 1:3 in old restorations).

Grass cover concomitantly increased as forb cover decreased, suggesting that dominance and diversity are inversely related. This is widely recognized for grasslands (Howe, 1999). Indeed, post-conversion management activities often focus on competitive warm season (C4) grasses (Howe, 1994). In particular, *A. gerardii* is commonly used as an indicator of recovery and eventually dominates restorations (e.g., Kindscher and Tieszen, 1998; Sluis, 2002). Though native prairies consist of large numbers of uncommon species and relatively few common species (Curtis, 1959), the high dominance observed in many restored habitats appears to occur at the expense of a large number of uncommon (forb) species (Sluis, 2002). The latter are susceptible to local extinction, such that at least one notable population of native *M. fistulosa* disappeared from an old restoration in our study (Berg, pers. com.).

Restoration progress also depends on controlling undesirable, largely exotic, components of the vegetation. At Beaudry, decreases in exotic diversity in older restorations suggest that many exotics will not persist (Baer et al., 2002). However, the mechanisms underlying these declines seem to vary. Restoration, especially reconstruction that effectively eliminates any existing vegetation cover and seed bank, represents an intense disturbance. Many of the exotics that declined (e.g., *T. officinale*, *S. arvensis* and *M. alba*) are ruderals that dominate seed banks, are normally associated with soil disturbance and reduced vegetative cover, and therefore are more likely to be found in newly restored sites. These exotic (and native) ruderals, may be adversely affected by the increased presence of graminoids in older sites, as exotic diversity tends to be inversely correlated with

C4 grass productivity (Smith and Knapp, 1999). As smaller plants reliant on seed production for regeneration, ruderals are likely out-competed by taller, vegetatively propagating grasses (Waddle, 2000; McLachlan and Knispel, 2003).

Although most exotics declined over time, both old and mid-age restorations were associated with a few important perennial exotic species, some of which, these including *B. inermis* and *Poa pratensis* (Kentucky bluegrass), even increased in dominance. Ubiquitous in rural landscapes in Manitoba (Moffatt et al., 2004), these species also dominated the propagule bank and were present in reference sites at Beaudry (McLachlan and Knispel, 2003). They, along with many dominant native grasses, reproduce vegetatively and disperse by wind, suggesting they will likely persist in restorations, especially if current management practices continue (McLachlan and Knispel, 2003).

4.3. Persistence

Limited natural seed dispersal and recruitment from adjacent habitats or propagule banks often constrain restoration success in both wetlands and post-agricultural grasslands (Galatowitsch and van der Valk, 1996; Kindscher and Tieszen, 1998; Sveinson and McLachlan, 2003; Bissels et al., 2004). Though active restoration, including seeding of native species, is meant to overcome these limitations, community persistence in the absence of repeated seed addition is an important goal of many restoration projects (Hobbs and Norton, 1996).

In our study, a number of desirable species became established in the restoration from seed sources outside individual site boundaries. These self-recruiting native species increased in similarity to reference site species composition over time, indicating that older restorations may eventually become self-propagating or persistent. Many of these colonizers were composites (e.g., *Aster ericoides* (many-flowered aster), *A. ciliolatus*, *H. maximiliani*, *Heliopsis helianthoides* (ox-eye)), and are dispersed effectively by wind (McLachlan and Knispel, 2003). Colonization may also have been facilitated by the close proximity and the relatively large size of these restorations, as well as repeated small-scale disturbance (e.g., burns, mowing, human passage, etc.). Functional attributes such as persistence might supplement the structural attributes (i.e., species richness and composition) that are the usual focus of restoration (Hobbs and Norton, 1996; Brye et al., 2002). Persistence is a meaningful indicator of recovery (Parker, 1997) and warrants further exploration.

4.4. Change in soil properties

High residual fertility is often a constraining factor in the restoration of natural communities on post-arable land (McLachlan and Bazely, 2003; Walker et al., 2004a). Relatively high soil phosphorus and nitrogen levels in all restorations and the future restoration site likely reflect past agricultural activities. High levels of soil phosphorus may compromise slow-growing, often forb species, favouring those that are competitive and dominant (Pywell et al., 2002). Thus, restored sites had much lower forb-to-grass species ratios than reference sites (3.5:1 vs. 5.4:1, respectively). Though nutrient reduction techniques have been employed in restoration projects (Walker et al., 2004b), reduction of soil fertility was not explicitly targeted at the Beaudry restoration. However, nitrogen and phosphorus levels of restoration sites are intermediate to those of reference and future restoration sites, suggesting that fertility may gradually approach natural levels with time.

High organic matter and moisture levels in reference soils are likely associated with the long-term presence of perennial vegetation, in contrast to restored sites which have been recently disturbed and used for agriculture (Kindscher and Tieszen, 1998). Lower organic matter may also be associated with more variable moisture conditions, which may favour rapidly growing, opportunistic species. Observed similarity in organic matter between the future restoration and restoration sites may have been due to our soil sampling methodology. These changes are expected to be greatest in the top 5 to 10 cm of soil, while we sampled the top 15 cm.

4.5. Conservation implications

Although restoration should not replace much-needed protection of extant tallgrass prairie, ongoing degradation of remnants suggests that restoration activities are increasingly valuable to conservation efforts (Young, 2000). Our results indicate that long-term restoration has effectively established native tallgrass vegetation and is facilitating further native seed dispersal among restorations.

It should be noted that many of the older sites are losing species, and that this restoration activity is better seen as an ongoing process that requires a long-term commitment. Many of the species in decline tended to be forbs, which may reflect the use of grass-dominated seed mixes. However, the use of such mixes is common in tallgrass prairie restorations, as these are generally cheaper and more accessible (Sveinson, 2003). The resemblance of mid-age restorations and reference sites in our study suggests such mixes may successfully be used in prairie restoration. However, increasing dominance of grasses over time should be addressed by modification of management practices subsequent to establishment. Frequently, limited resources and convenience lead to spatially and temporally uniform management practices and over-reliance on a few routine maintenance activities, regardless of age, location, or soil status of restoration sites. This may facilitate the expansion of competitive native and exotic grasses and decrease the importance of less common species (Sveinson, 2003). Reduction of the scale of maintenance activities may aid in increasing restoration heterogeneity.

Colonization might be enhanced by small-scale disturbance, including patch mowing or spraying of herbicides on dominant C4 grasses, minimally disturbing soils, and interseeding of native forbs. Use of vegetative propagules, such as *A. gerardii* rhizomes collected from mature sites, could also facilitate establishment in new restorations while reducing grass dominance in older sites. Vegetative propagules have been successfully used in marsh restoration, yielding over 90% survival and extensive vegetative spread after four growing seasons (Fraser and Kindscher, 2001). These and other small-scale post-seeding activities will likely increase structural complexity and native forb diversity, and thus warrant further exploration (e.g., Sveinson, 2003).

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