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RESTORING TALLGRASS PRAIRIE IN SOUTHERN MANITOBA, CANADA

BY

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THESIS ABSTRACT

Agriculture and urban development has reduced tallgrass prairie to less than 1% of its original land cover in southern Manitoba, Canada. Although much of the remaining tallgrass prairie in Manitoba is protected within a single Preserve, it continues to be degraded by the invasion of exotic and woody species, fire suppression, and overgrazing. My overall thesis objective was to assess the role of rehabilitation in tallgrass prairie restoration and more specifically to examine the relative effects of disturbance, soil fertility, and seeding. Two field studies were conducted within the St. Charles Rifle Range (SCRR) and Manitoba Tall Grass Prairie Preserve (MTGPP) to assess these objectives.

The impacts of burn-season were examined on a high quality tallgrass prairie located within the SCRR. This four-year study found burn-season to have a substantial impact on diversity and species composition. Fall-burn had the most desirable effect, increasing native graminoid and forb diversity, regardless of time-of-flowering. Summer-burn increased both native and exotic graminoid cover. Spring-burn had relatively no effect on species composition and was characterized by woody species. All burn-seasons, except fall-burn, became increasingly similar in species composition to the control over time. Spring-, summer-, and fall-burns had varied but desirable effects on diversity and species composition.

In 1999, a long-term experiment was initiated within the MTGPP to assess the role of disturbance (glyphosate, mowing, and fire), soil fertility (ammonium nitrate), and interseeding in rehabilitating degraded tallgrass prairie. Glyphosate had the greatest impact on diversity and species composition. Exotic and weedy native species increased and desirable native species (e.g. *Andropogon gerardii*) were adversely affected in glyphosate-treated plots. Mowing and fire had less of an effect, in large part because of long-term haying on this site. Fertilizer increased native forbs and graminoids, whereas exotic graminoids decreased. Interseeding with native tallgrass prairie species increased native graminoids and decreased exotic graminoids, but had no effect on forbs. Species composition of glyphosate-treated plots became more similar to the unsprayed and control plots over time, whereas effects of fertilizer and other disturbance factors showed little change.

Rehabilitation of tallgrass prairie shows great potential for southern Manitoba. Disturbance and fertilization can have desirable effects, but only when seedbank, above ground vegetation, and site-specific constraints have been identified. Effective techniques in rehabilitation are required if the degradation of remnant and restored tallgrass prairie is to be mitigated.

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CHAPTER 1: General introduction

Southeastern Manitoba was once dominated by tallgrass prairie. Much of this highly diverse ecosystem has been reduce to small relatively isolated fragments in an agriculture-dominated landscape. Less than 1% of the original 6000 km^2 (138 million ha) of tallgrass prairie in Manitoba remains, much of which is protected by a Preserve near the towns of Tolstoi and Gardenton (CWHP 1998). However, protection alone will not ensure the long-term survival of these prairie remnants, as they continue to be degraded by nutrient inputs, overgrazing, and woody and exotic species invasion.

Restoration can be used to slow or even reserve the degradation of natural habitat. Most restoration (i.e. reconstruction) involves changes in land-use and the creation of new habitat. However, rehabilitation of already existing, but degraded habitat often has greater potential for success (McDonald 2000). Regardless of which approach is used, the restoration of these sites to a desirable or even pre-existing state still can take many decades to occur (Knapp *et al.* 2003).

Much restoration (i.e. ecological restoration) is experience-based, whereby the processes of underlying vegetational change are not as important as the desired outcome (Bradshaw 1993). Despite its appeal to local communities and stewardship groups, interest is typically short-lived and consequently many of these projects fail as they become dominated by weedy or undesirable species. A complimentary approach to ecological restoration (i.e. restoration ecology) is experimental, and contains hypotheses, data collection, and analysis, but is relatively inaccessible and often deters involvement by the public (Higgs 1994). Ultimately, both approaches are necessary for restoration to succeed.

In human-dominated landscapes, prairie is often restored on post-agricultural land. Prairie restoration commonly encounters problems because these soils are generally high in fertility. While high levels of nitrogen increase primary productivity, they tend to decrease species diversity (Wilson & Tilman 1991). Native prairie species have evolved in nutrient-poor soils and are often out-competed by weedy species under these soil conditions. Thus, the proportion of exotic plant species tends to increase and can displace pre-existing native species (McLachlan 1997).

Historically, tallgrass prairies were naturally maintained by fire and grazing (Collins & Wallace 1990). Periodic low-intensity burns can prevent highly competitive species from dominating. The exposure of bare soil and competitive release provides an opportunity for early successional species to establish from the seed and propagule banks. However, burning is generally suppressed in human-dominated landscapes and without periodic burning, exotic species tend to dominate tallgrass prairies. Domestic cattle grazing has replaced native herbivores, such as bison and pronghorn antelope. However, much of the remaining tallgrass prairie is too small to support grazing and thus, overgrazing has greatly contributed to its decline. A number of alternative disturbance methods are being developed, these include mowing, herbicide application, tilling, and soil impoverishment, to manage prairie (Wilson & Gerry 1995).

Although most restoration focuses on the aboveground species composition, the seedbank can also have important ramifications for vegetation change, especially when dominated by exotic species (Sveinson & McLachlan 2003, Appendix 1). In the absence of an adequate seedbank, species reintroduction is often necessary. This can be achieved by broadcasting the seed onto the soil or, more successfully, by seed drilling into existing vegetation (Packard 1997) or tilled soil (Morgan 1997).

Despite much recent attention, there is a need to further research restoration techniques for northern tallgrass prairie, especially with respect to rehabilitation of existing but degraded prairies. The overall objective of this study was to examine the roles of disturbance, soil fertility, and seeding in restoring tallgrass prairie in southeastern Manitoba, Canada. Chapter objectives and specific question to be answered are as follows;

LIST OF OBJECTIVES

Objective one: To determine the relative effects of spring-, summer-, and fall-burns on high quality tallgrass prairie (Chapter 3). Specifically:

- What are the impacts of burn-season on species composition and diversity?
- What are the impacts of burn-season on functional guilds including origin, growth form, and flowering phenology.
- How do changes in species and guild composition and diversity varied over time?

Objective two: To determine the role of disturbance, soil fertility, and interseeding in rehabilitating degraded tallgrass prairie (Chapter 4). In particular:

- What are the differences in diversity and species composition for aboveground and seedbank components of degraded and neighbouring high quality prairie?

- How can fertilization and disturbance factors including fire, mowing, and herbicide might affect plant diversity and species composition?
- What are the effects of interseeding on species composition and diversity?
- How do these treatment-associated effects on vegetation change over time?

CHAPTER 2: Literature Review

INTRODUCTION

The conversion of natural habitat to agriculture and urban development has resulted in extensive disruptions to natural communities and ecosystems. These disruptions may result in the extinction of plant and animal species and the loss of important ecological processes (McCarty & Zedler 2002). Conservation of remnant natural habitat is extremely important, but difficult in a landscape surrounded by conflicting land-use and management practices. Of particular interest to this study, 1% of the original tallgrass prairie remains in Manitoba and it has become one of the most endangered ecosystems in North America (CWHP 1998). Although much of the remnant tallgrass prairie in Manitoba is protected within a single preserve, little research has been conducted in the northern range of the tallgrass prairie. It is important to study the effects of disturbance, this including nutrient inputs, overgrazing, exotic and woody species invasion, on species composition and diversity, in order to develop management techniques to protect and restore tallgrass prairie.

RESTORATION ECOLOGY PRINCIPLES

History of Restoration

Over the last decade, restoration used in combination with conservation has shown great promise as a method of slowing or even reversing the degradation of natural habitat (Geist & Galatowitsch 1999). Some have called it the new paradigm in conservation biology (Turner 1994; Young 2000), whereas others point out there are still many problems to overcome (Barrett 1994). Indeed, it has been criticized as simply gardening with native species and perhaps even, “an expensive self-indulgence for the upper class, a New Age substitute for psychiatry” (Kirby 1994).

As with many new disciplines, there is little agreement in terminology regarding restoration (Hobbs & Norton 1996). In general, it means returning some degraded portion of the landscape to an improved and “more natural” or pre-existing condition (Harker *et al.* 1999). It means re-establishing a healthy ecosystem, which Aldo Leopold (1949) defined as "the capacity of the land for self-renewal". More recently, Berger (1990) called restoration "an effort to imitate nature in all its artistry and complexity by taking a degraded system and making it more diverse and productive". Restoration combines the practice of art (i.e. things work for reasons unknown) and science (i.e. things work and we know why) (Harker *et al.* 1999). It is also defined by the Society for Ecological Restoration as the process of assisting the recovery of an ecosystem that has been degraded [subtle changes that reduce ecological integrity and heath], damaged [obvious changes in an ecosystem], or destroyed [removes all macroscopic life and commonly ruins the physical environment] (SER 2002).

Most high visibility restoration is associated with reconstruction (i.e. new habitat is created based, ideally, on historical data), to the degree that this term is used synonymously with restoration (Cairns 1993). However, the rehabilitation of existing but degraded natural habitat may have even greater potential for success (McDonald 2000). Regardless of which approach is used, the restoration of habitat to a desirable or even pre-degraded state still can take many decades, if not centuries, to occur (Knapp *et al.* 2003).

Much restoration is qualitative, experience based and non-experimental (i.e. ecological restoration). Data for monitoring are generally not collected and the processes underlying vegetational changes are not as important as the desired outcomes (Higgs 1994). A complimentary and more academic approach is generally experiment-based, contains hypotheses, data collection, monitoring, and analysis (i.e. restoration ecology), but is often restricted in time and space and deters involvement by non-experts (Bradshaw 1993). Ultimately, both approaches are necessary for restoration to succeed, and both are reflected in prairie restoration throughout North America.

Goals of Restoration

Restoration often attempts to establish a community that existed prior to human disturbance, in North America this most often being European settlement. However, information regarding original systems is often inadequate and should be used as a reference point rather than an end-point (Cairns 1988; Pickett & Parker 1994). Restoration should not attempt to preserve a static entity (Falk 1990), but rather emulate a healthy, ecologically robust, natural, self-regulating system that is integrated within the ecological landscape in which it is situated (Cairns 1991). In addition, the environment is extremely dynamic and conditions in a given area may no longer be appropriate for historic communities (McCarty & Zedler 2002). High quality existing reference sites (i.e. sites dominated by native species and few exotic species) have great potential to assess the direction, degree, and desirability of inevitable vegetational change associated with restoration (e.g. McLachlan & Bazely 2003). Restoration goals should be very site-specific and flexible, as ecological communities are complex and its behaviour depends to some degree upon their unique histories, specific spatial settings, and current influences (Pickett & Parker 1994).

Restoration vs. Conservation

Preservation or protection of biological diversity is one of the major goals of conservation biology. This was conventionally done in wilderness areas, with very little human influence or land-use that maintained high biological diversity, whereas today conservationists include altered habitats, such as rights-of-way, ditches, old fields, and wastelands (Meffe *et al.* 1997). Although conservation and restoration differ in their objectives and goals, ultimately both aim to maintain, manage, or restore ecological function that, in turn, protects endangered species and ecosystems. Furthermore, both studies utilize monitoring to determine change and future direction. Thereby the distinctions between these studies are often unclear. However, restoration should not rationalize damage to natural habitat, as many conservationists fear, and efforts should be focused on restoring past damage and protecting remaining natural habitats (Harker *et al.* 1999).

Monitoring

Monitoring has become an essential tool that can be used to evaluate the success of a restoration. Many agencies such as the Ecological Monitoring Assessment Network (EMAN) and Environmental Protection Agency (EPA) are developing standard protocols to make monitoring data useful, especially with regard to large-scale and long-term programs. Without standard protocols in study design, sampling procedure, data analysis, and reporting, it becomes difficult to assess the desirability of change over time and space (EMAN 2002).

The use of ecological indicators to measure components or processes of an ecosystem represents one aspect of monitoring. They are generally simplified to describe and communicate complex ecological processes to managers and policy makers. Regular data collection facilitates the assessment of changes systematically and whether these, often inevitable, management-associated changes in environment are desirable. Despite their importance, appropriate indicators are difficult to select and communicate to the general public or even experienced researchers (Schiller *et al.* 2001).

Restoration activities, especially in habitat reconstruction, are often outcome-oriented and not concerned with the actual processes underlying environmental change (McLachlan 1997). Outcomes are generally difficult to predict, in part because ecosystems are complex and poorly understood (Noss & Cooperrider 1994). Adaptive management (Holling 1978; Walters 1986) allows for the use of monitoring to modify management and restoration activities in an iterative and evolving manner (Grumbine 1994). Ideally, stakeholders would work together to determine the end points (Costanza 1992) or desired conditions (Christensen 1997) of the system being managed or restored. Restoration ecology combines theoretical and applied interests and is most successful when underlying ecological processes responsible for vegetational changes over time are considered.

SUCCESSION THEORY AND RESTORATION

Habitat-focused restoration activities can be considered succession-based, as they attempt to change or direct vegetation over time (McLachlan 1997). Succession is one of oldest, most basic, and yet most confounded ecological concepts (McIntosh 1980). Its past has been highly debated and is still unclear today.

History of the succession theory

Succession theory has played an important role in plant ecology throughout this century. It provided the first attempt to explain the distribution and abundance of plants on the landscape (Christensen 1988). Succession theory development has been considered to have occurred over four distinct time periods (Johnson 1979). Much of the theoretical framework was laid out between the years 1859 –1900 (Johnson 1979). During this period, Cowles (1899) provided the first detailed description of forest succession along the shores of Lake Michigan. His idea was based on the geographical cycle in which emphasis was placed on the orderly development of landforms (Davis 1899), this considered analogous to human development. The following period, between the years 1900 – 1930, was dominated by the works of Clements (1916; 1928; 1936). He viewed succession as a highly predictable process in which vegetation followed a predetermined, organism-like pathway from simple to climax community that is ultimately controlled by regional climate. The steps that this successional process followed were: i) nudation (the creation of a bare area by disturbance); ii) migration (the arrival of propogules); iii) ecesis (the establishment of plants); iv) competition (the interaction of plants); v) reaction (the modification of the site by established species thereby changing the ability of new species to establish); and vi) stabilization (the development of a climate-determined stable climax community).

During the years 1930 – 1947, Gleasonian views were favoured over those of the earlier phases (Johnson 1979). Gleason (1926) and his followers challenged the organismic or holistic concept of succession with more reductionistic approaches. Gleason argued that plant communities are highly integrated entities and stressed the unique, individualistic behaviour of plant species and chance events (Glenn-Lewin *et al.* 1992). He viewed plant communities as resulting from the chance overlap of species with similar environmental tolerances. However, it was argued that local differences, such as soil type and topography, would influence the successional pathway, resulting in different climax communities associated with the regional climate (Tansley 1935; Glenn-Lewin *et al.* 1992). Thus, leading to the combination of Clements' and Gleason's views to describe the climax community as varying continuously across a continuously changing landscape Whittaker (1953).

Although Clements and Gleason provided convincing theories, they were both highly criticized for suggesting disturbance was uncommon or non-essential component of the successional process (Cook 1996). Clements was also criticized for overlooking the importance of vegetation, propagules, and seedbank composition, in that no two patches contain identical composition and, thereby, develop differently (Miles 1982). In addition, the importance of facilitative changes in establishing later successional species, as most species were already present at the outset of succession, was questioned (Miles 1982). Following this period, less emphasis was place on Clements' classical succession model and several modern theories were developed (Johnson 1979).

Drury and Nisbet (1973) suggested that the autoecological or physiological level (i.e. not community) was the best scale for explaining succession. They also suggested that vegetation is constantly changing in response to disturbance and that succession theories should consider evolution (Cook 1996). Pickett (1976) further expanded on this idea and produced the first succession theory based on evolutionary strategies which are best suited to "environmental conditions along a successional gradient" (Cook 1996). He also suggested that disturbance was an important component of succession and operates at various spatial and temporal scales. In addition, life-history traits of individual species were considered important in determining successional pathways (Cook 1996).

Connell and Slayter (1977) summarized species' interactions during succession into three models: facilitation, inhibition, and tolerance. Each model incorporated the timing of species establishment, competition for space and resources, and autecological characteristics, such as species longevity and shade tolerance. The first model, facilitation, is where reactions of earlier species make the environment more suitable for later successional species (Clements 1916). However, stages of this model are rarely found (Miles 1982) and may only occur in primary succession and under extreme conditions, such as beaches and lava. The second model, tolerance, is where reactions of earlier species have little or no effect on the growth of later species. This model is further divided into passive and active tolerance. Passive tolerance follows Egler's (1954) initial floristic composition of old-field succession where all species are present in the seedbank prior to succession, succession merely representing changes in dominance over time. In contrast, active tolerance is based on individual plant species (Gleason 1926) and is mainly influenced by competition and underlying differences in structure, function, and resource use (Tilman 1985). The third, inhibition, is where reactions of earlier species make the environment less suitable for later species. For example, dense cover can prevent the colonization of later occurring species, until the inhibiting species is damaged or dies (Miles 1982).

Changing the view from vegetation or community level to species-level succession required a better understanding and description of species-level responses. From an evolutionary perspective species with similar vital attributes tend to occur together more often than by chance. Different traits are also advantageous in crowded versus uncrowded condition (MacArthur & Wilson 1967). When habitats are stable, species tend to stay at the carrying capacity or K. Harper (1977) identified two contrasting views that might increase the fitness of an organism in succession: i) reacts to the competitive selection pressures and evolves characteristics that enable it to persist longer in the succession (i.e. K-selection, life history which promotes a low reproductive rate) or ii) may develop more efficient mechanisms of escape from the succession and colonize suitable early stages of succession elsewhere (i.e. r-selection, life-history which promotes a high reproductive rate). Therefore, species that are good colonizers will tend to be poor competitors and vice versa (Brewer 1994; Begon *et al.* 1996). In general, r-selection species are good colonizers or primary succession species that are fast-growing, shade intolerant and short-lived herbs that produce a great number of seed which remain viable in the seedbank for many years. In contrast, K-selection species are slow-growing and shade tolerant, and can be considered climax or late successional species (Miles 1982).

Grime (1977) expanded on Pickett's idea of evolutionary strategies and further categorized herbaceous plant species according to two external factors which limit the amount of living and dead plant biomass. The first, stress, is the phenomenon that restricts photosynthetic production such as shortages of light, water, and mineral nutrients, or sub-optimal temperatures. The second, disturbance, is defined as the destruction of plant biomass caused by herbivores, pathogens, humans (e.g. trampling, mowing, and ploughing), wind, frost, drought, soil erosion, and fire. Both stress and disturbance vary enormously across the landscape. When the four extreme conditions of stress and disturbance are examined only three combinations are viable plant habitats. Grime (1979) has developed three plant strategies for these conditions: competitors, which exploit conditions of low stress and low disturbance; stress-tolerators, which exploit high stress and low disturbance; and ruderals, which exploit low stress and high disturbance.

Nobel and Slayter (1980) attempted to define vital attributes of species that would predict their performance during succession with recurrent disturbance. These attributes were based on methods of arrival or persistence after disturbance, abilities to enter or establish in an existing community and then grow to maturity, and the time required to reach critical stages in a species' life cycle, such as reproduction. In general, their model showed that attributes may be beneficial or detrimental under different disturbance regimes, and therefore, succession, just as restoration, may have multiple pathways and end-points (Cook 1996).

The investigation of competition and resource availability in succession lead to the development of the resource-ratio hypothesis (Tilman 1985). It emphasized that succession results from a gradient through time, this in turn affected by the relative availability of limiting resources, such as soil nutrients and sunlight, thereby changing competitive abilities of plant species and the successional pathway of a community. Furthermore, Tilman (1990) concluded that a three-way trade off between colonization, nutrient competition, and light competition is responsible for old-field succession. This hypothesis suggests that soil nutrients are lowest during early successional stages and over time, as biomass accumulates and decomposes, light availability decreases and soil nutrients become increasingly available.

Therefore, succession is tightly linked with environmental and competitive interactions as well as local influences. It is very complex, and cannot be simply described with one model for all situations and locations. Indeed, many researchers question the usefulness of "general" all-accommodating theories of succession.

Succession and management

Successional-based management can be used to direct ecosystems to a desired state (Luken 1990). For example, large blocks of forest in North America can be achieved by restoring forest on abandoned fields and other open areas. Similarly, succession theory can be used to restore prairie rapidly and efficiently on post-agricultural fields (Brewer 1994). In many cases, natural disturbance, such as fire or flooding, is needed for a system to regress to an earlier successional stage, which may, in turn, send it along the desired successional trajectory and eventually achieve complete recovery (Cairns 1989). However, this is not always the case since: i) early successional species may not be present for reinvasion, and ii) new species, including exotics, that are not part of early succession have since invaded (Harker *et al.* 1999).

Restoration can be used to reintroduce natural disturbances and native species as well as remove limiting factors that may help accelerate succession processes, thereby achieving desired outcomes. The earliest deliberate attempts at restoration concentrated on prairies, in particular tallgrass prairie. This, in part, is associated with its vulnerability, ease in restoration, association with important thinkers such as Aldo Leopold, and the operational similarity of prairie restoration to conventional agriculture (Packard & Mutel 1997).

NORTH AMERICAN PRAIRIES

Prairie development

Prairies began to develop in North American during the Miocene-Pliocene transition about 7 – 5 million years B.P., due to the rise of the Rocky Mountains and subsequent climatic changes (Robertson *et al.* 1997). These mountains created a rain shadow over central North America, resulting in a drier climate to the east (Axelrod 1985). These changes, in combination with frequent fire and grazing, provided favourable conditions for grasslands to become established as forests retreated.

Terminology and definitions

Early European explores were fascinated by the great extent and uniformity of the North American grasslands they encountered traveling from the eastern deciduous forest to the Great Plains (Risser *et al.* 1981). Charlevoix (1761) observed that "nothing to be seen in this course but immense prairies interspersed with small copses [or thickets] of wood, which seem have been planted by hand" (Curtis 1959). Similarly, Ruggles (1835) noted that "in some instances, prairies are found stretching for miles without a tree or shrub in site" (Risser *et al.* 1981). Early French explorers lacked the vocabulary to describe grasslands and called them prairie, French for meadow or grass-covered, treeless landscape. This term was later adopted by English settlers as they too lacked the terminology (Risser *et al.* 1981). Although the words prairie and grassland are used synonymously in the literature, they have different meanings. Prairie is generally defined as a large area devoid of trees and dominated by grass species but also containing forbs, whereas grasslands refer to large open area that is covered with both native and tame grasses used primarily for grazing and forage production (Risser *et al.* 1981).

The impact of early settlers on the prairies

Early settlers found the prairies unfavourable due to the swarms of insects, extreme summer heat and high humidity, cold winters, and periodic fires. Settlement, such as that of Winnipeg, initially followed forest along the rivers as a means of avoiding hostile prairie environments. Early settlers also had difficulties breaking prairie sod until the first steel-bladed plough was invented by John Deere in 1837. However, it was not until the development of the railroad system in the 1850s and 1860s that large tracts of American prairie were rapidly converted to agriculture (Robertson *et al.* 1997).

Conversion to agriculture eventually lead to suppression of landscape wildfires by settlers who predictably viewed them as a threat to their crops and homes, thereby further decreasing the ecological value of prairie. Over time, remaining prairie fragments inevitably succeeded into savannah and forest. Today, a few, small prairie remnants can be found on infrequently mowed or hayed cemeteries and railroads right-of-ways as well as old-fields that have escaped successful conversion to agriculture (Robertson *et al.* 1997). However, with large-scale abandonment of railroads and increases in herbicide use, many of these remnants have disappeared over the last 30 years. Changes in drainage patterns have also had significant impacts. Water once held by the prairie and slowly released throughout the season, now races off the surface agriculture fields, eroding the land as it runs into ditches, thus making irrigation necessary during dry periods (Robertson *et al.* 1997).

Prairie distribution and classification

Historically, prairies were one of the largest vegetation type in North America, covering approximately 20% of the total land area (Risser *et al.* 1981). Before European settlement, prairies occupied a triangular shaped area covering 3.6 million km^2 that extended from the Canadian provinces Alberta, Saskatchewan, and Manitoba southward through New Mexico into Texas. Habitat conversion for agriculture has lead to the deterioration of remnant prairies and replacement by sterile, brushy thickets, and disturbance-adapted non-native or exotic species (TNC 1995). Remnants are fragmented by human use and lack fundamental natural processes such as fire and grazing.

A number of schemes have been developed to categorize the great variety found in North American prairies. Prairies are generally divided into mesic eastern tallgrass prairie, intermediate mixed-grass prairie, and arid western short grass prairie (e.g. Coupland 1961; Risser *et al.* 1981) (Fig. 2.1). Similarly, Simms (1988) has separated prairies into tallgrass, mixed-grass, shortgrass, and palouse prairies as well as California grasslands. However, these classifications are American-based and tend to generalize Canadian prairies. Coupland (1992a) has classified North American prairies into mixed prairie, short-grass steppe, tall-grass prairie, coastal prairie, fescue prairie, Palouse prairie, California prairie, and desert grassland (Fig. 2.2). In this classification, Coupland (1961) provides a more accurate description of Canadian prairies: i) mixed-grass prairie; ii) tallgrass prairie; iii) palouse prairie; and iv) fescue prairie. Canadian mixed-grass, tallgrass, and palouse prairies are northern extensions of American prairies, whereas fescue prairie is only found in Canada. Palouse prairie is located west of the Rocky Mountains in British Columbia, while the other prairies occur to the east in the Prairie Provinces (Fig. 2.3) (Coupland 1961). Although there is little agreement on prairie regions, they can be described according geography, climate, and species composition.

Mixed-grass Prairie

Mixed-grass prairie is often considered an ecotone or transitional zone between the shortgrass and tallgrass prairie. Species composition is related to variability in precipitation. During years of drought, shortgrass species tend to be more prevalent, whereas mid and tallgrass species when conditions are more favourable (Coupland 1992b). Mixed-grass prairie accounts for 21% of North American prairies (Simms 1988) and is the largest Canadian prairie. In combination with fescue prairie, mixed-grass prairie accounts for much southern Saskatchewan as well as southeastern Alberta and southwestern Manitoba. Mixed-grass prairie also occurs in eastern Montana, western North Dakota, and western South Dakota; Wyoming and western Nebraska; and

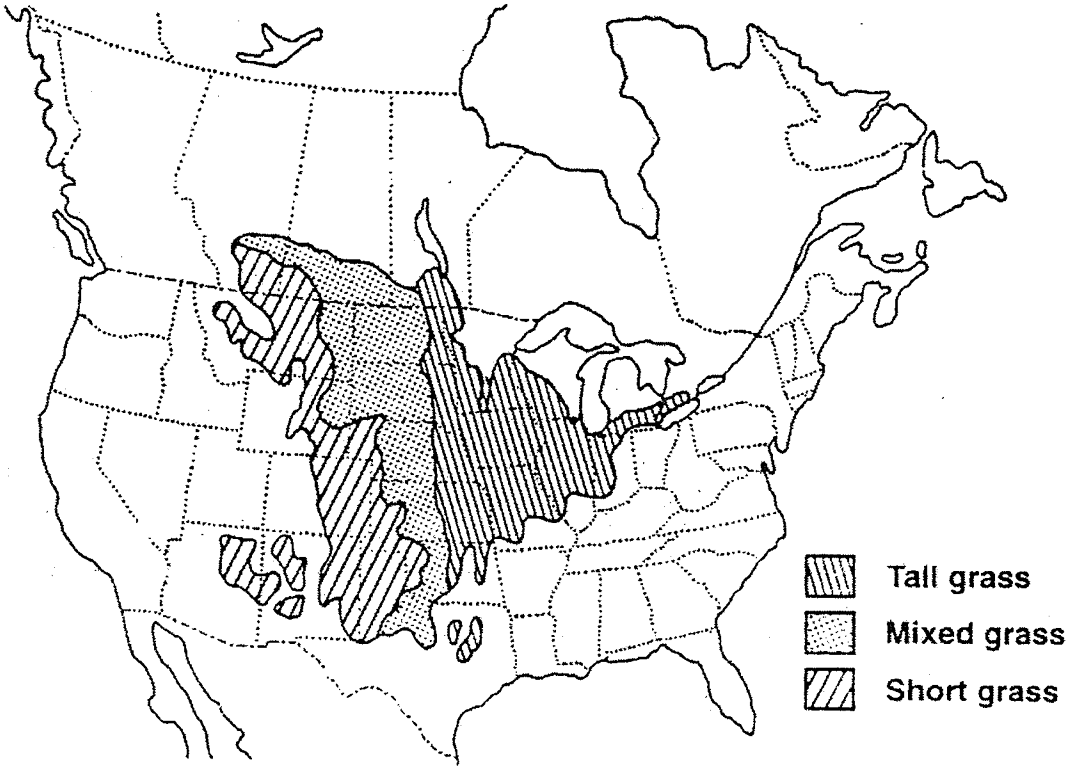


Fig. 2.1. Traditional classification of North American prairies (Adapted from Reaume 1993).

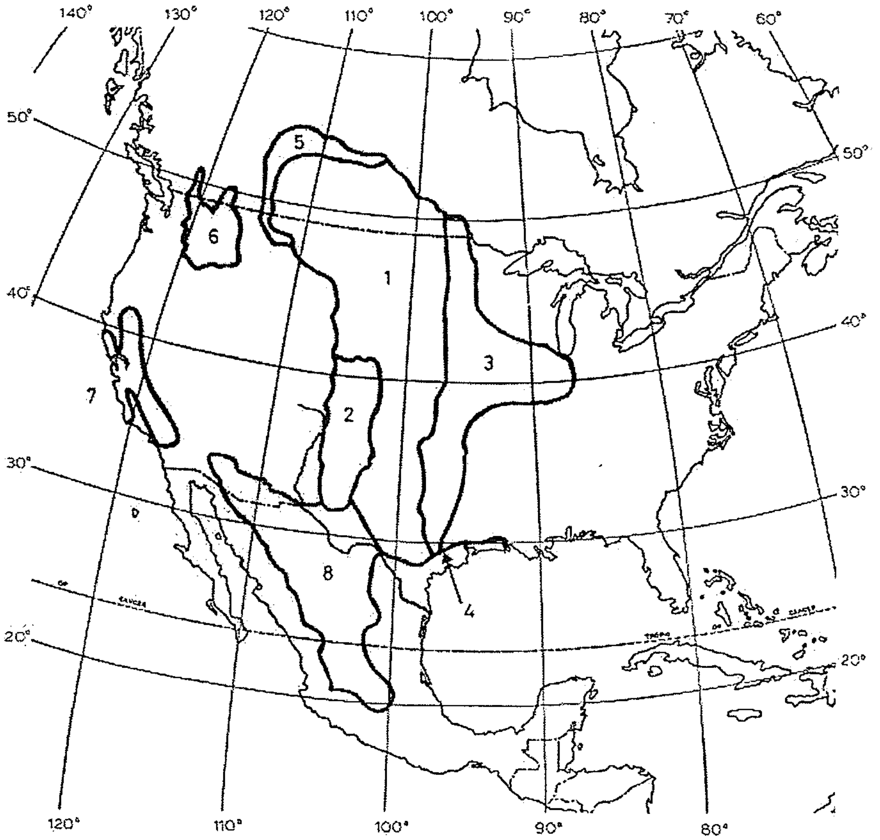


Fig. 2.2. North American prairie regions: 1 = mixed-grass prairie; 2 = short-grass steppe; 3 = tallgrass prairie; 4 = coastal prairie; 5 = fescue prairie; 6 = Palouse prairie; 7 = California prairie; and 8 = desert grassland (From Coupland 1992a).

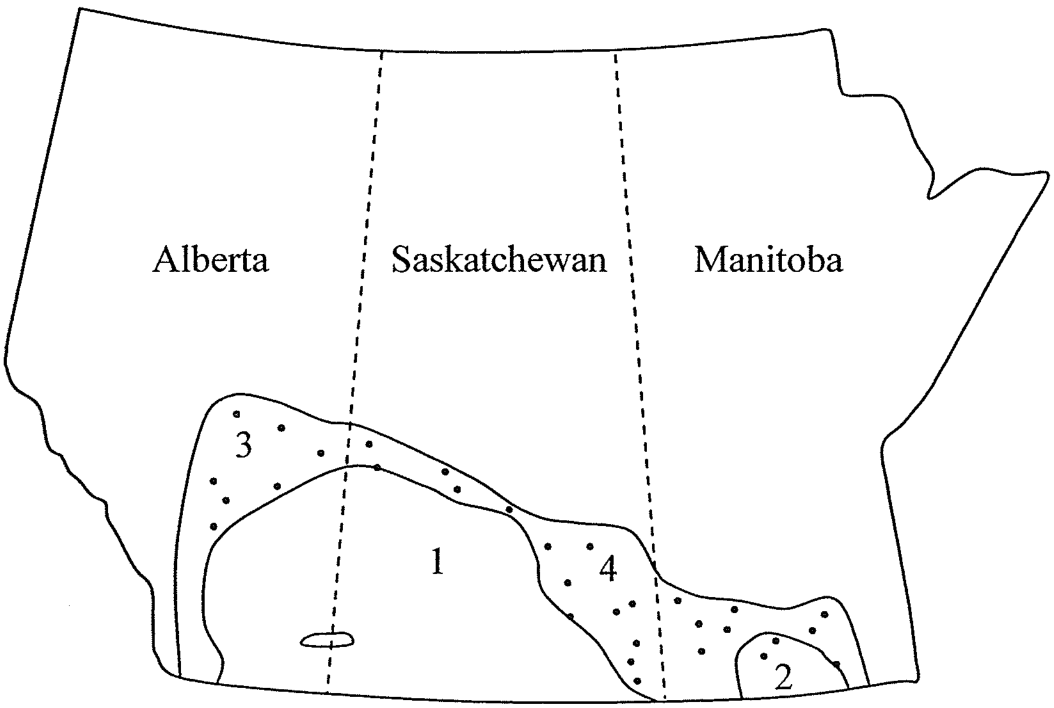


Fig. 2.3. Canadian prairie regions: 1= mixed-grass prairie; 2 = tallgrass or true prairie; 3 = fescue prairie; and 4 = combination of mixed-grass and fescue prairie. Dots represent *Populus* (Aspen) bluffs (Adapted from Coupland 1961).

southward through Kansas, Oklahoma and into Texas (Coupland 1992b).

Mixed-grass prairie climate is intermediate between that of tallgrass and shortgrass prairie, ranging from dry-subhumid to semi-arid (Coupland 1992b). Precipitation is highly variable and generally increases eastward from the mountains. Annual precipitation within the mixed-grass prairie ranges from approximately 30cm in the west to 60cm in the east (Braggs 1995). Mean temperatures also vary drastically, especially during the winter. In general, temperature increases southward from -18°C to 10°C in January and 18°C to 28°C in July. Similarly, length of growing season increases southward ranging from 100 to 200 frost-free days (Coupland 1992b).

Mixed-grass prairie is characterized by a combination of species from both shortgrass and tallgrass prairie. Coupland (1950) has identified five different types of mixed-grass prairie: *Stipa-Agropyron*; *Stipa-Bouteloua-Agropyron*; *Stipa-Bouteloua*; *Bouteloua-Agropyron*; and *Agropyron-Koeleria*. Important grass species in these faciations include *Stipa comata*, *Stipa spartea*, *Bouteloua gracilis*, *Agropyron dasystachyum*, *Agropyron smithii*, and *Koeleria cristata*. Forb species such as *Artemisia frigida*, *Artemisia cana*, *Phlox hoodii*, and *Antennaria micropylla* are less important in biomass, but contribute to overall species diversity of mixed-grass prairie (Coupland 1961).

Fescue Prairie

Fescue prairie is the most northern type of prairie and is only found in Canada (Looman 1969). It is located around the western and northern perimeter of the mixed-grass prairie in Alberta and extends eastward into the transition region from open grassland to aspen (*Populus tremuloides*) forest in Saskatchewan and Manitoba (Coupland 1992c). Fescue prairie also occurs in an alternating fashion with mixed-grass prairie around the boundaries of the Canadian tallgrass prairie region (Looman 1969).

Climatic conditions of the fescue prairie vary, as it exists on a wide range in elevation. In the Cypress Hills, elevation reaches 1400m, whereas in central Saskatchewan elevation is approximately 500m. Mean annual precipitation and summer temperatures within the fescue prairie increase eastward as elevation decreases (Coupland 1992c).

Fescue prairie is dominated by species within the Poaceae genus *Festuca*. In general, *Festuca* spp. (e.g. *Festuca scabrella*) account for 50% or more of the vegetation cover in fescue prairies. Other important graminoid species include *Agropyron dasystachyum*, *Agropyron subsecundum*, *Agrostis scabra*, *Calamagrostis montanesis*, *Carex heliophila*, *Carex obtusata*, *Danthonia intermedia*, *Festuca idahoensis*, *Helictotrichon hookeri*, *Koeleria cristata*, *Poa canbyi*, *Poa interior*, *Stipa spartea*, and *Stipa viridula* (Coupland 1992c). Forb (e.g. Asteraceae spp.) and shrub (e.g. *Potentilla fruticosa* and Rosaceae spp.) species are also important and greatly contribute to fescue prairie species diversity (Looman 1969).

Tallgrass Prairie

Tallgrass prairie or true prairie is the most eastern and mesic prairie in North America. True (i.e. dominated by *Andropogon gerardii*, *Panicum virgatum*, and *Sorghastrum nutans*) or bluestem prairie (i.e. *Andropogon scoparius* is considered co-dominant) ranged from southern Manitoba along the Red and Missouri rivers through

North Dakota and western Minnesota southward into eastern Oklahoma and Texas (Simms & Risser 2000). The eastern extent of tallgrass prairie (i.e. dominated by *Elymus, Pseudorogneria*, *Pascopyrum*, *Andropogon*, and *Stipa* species) occurred from south-central Canada, through North and South Dakota and Nebraska to north-central Kansas with patches located as far east as Ohio and southern Ontario (Simms & Risser 2000; Kucera 1992). Tallgrass prairie also forms ecotones with aspen parkland and boreal forests to the north and deciduous or *Quercus* forests (i.e. Oak savannah) to the east and southeast (Risser *et* al. 1981; Kucera 1992). Collectively tallgrass prairie historically accounted for 22% of North American prairies.

Tallgrass prairie receives the greatest amount of precipitation of North American prairies. Mean annual precipitation ranges from 40 cm in the south to 100 cm in the north. Mean temperatures within the tallgrass prairie region vary greatly. In January temperatures range from -15°C in the north to 15°C in the south and in July temperatures from 20°C in the north and 30°C in south (Braggs 1995). Tallgrass prairie is the most productive North American prairie and also most threatened, as much of the original tallgrass prairie has been converted to agriculture.

Although tallgrass prairie was nearly continuous, it was by no means homogenous. Specialized communities such as fens, sedge meadows, marshes, ponds, savannahs, and prairie groves were embedded within a tallgrass prairie matrix. It was a shifting mosaic of prairie, forest, savannah, and wetland, controlled by variations in rainfall, climate, soil, and terrain as well as differences in fire and grazing frequency, and climatic conditions (Collins & Steinauer 1998). Important grass species include *Andropogon gerardii*, *Andropogon scoparius*, *Panicum virgatum*, *Sorghastrum nutans*, *Andropogon gerardii*, *Andropogon scoparius*, *Panicum virgatum*, *Sorghastrum nutans*, *Spartina pectinata*, and *Sporobolus heterolepis*. In general, grass species account for 80-90% of tallgrass prairie biomass, but only constitute 25-33% of species richness (Simms 1988). Forb species (e.g. *Asteraceae* spp. and *Fabaceae* spp.) are important in tallgrass prairies and tend to be associated with high species richness.

Three distinct tallgrass prairie associations have been identified based on soil moisture: true prairie or *Andropogon-Sorghastrum-Panicum*; *Agropyron-Andropogon-Stipa*; *Andropogon-Calamovilda-Stipa* (Simms 1988). The Nature Conservancy (TNC 1995) has further divided the North American tallgrass prairie region into six types: 1) wet prairies, sites in which soils are saturated through much of the growing season and are characterized by *Spartina pectinata*, *Carex* spp., and *Asclepias* spp.; 2) mesic prairies, sites in which soils are relatively well-drained, but have high moisture throughout the season and are characterized by *A. gerardii*, *Panicum virgatum*, and *Solidago* spp.; 3) dry prairies, sites on slopes and well-drained uplands that are characterized by *A. scoparius*, *B gracilis*, and *Aster* spp.; 4) hill prairies, a variation of dry prairies that occur on hills and ridges that are characterized by *Bouteloua curtipendula*, *Anemone patens*, and *Geum triflorum*; 5) sand prairies, sites of extensive sand deposits, that are characterized by *A.* scoparius, *Dalea* spp., and *Opuntia polyacantha*; and finally 6) savannas, sites that are scattered with trees (e.g. *Quercus* spp.) and are characterized by a well-developed ground cover of grasses and forbs.

DISTURBANCE DEPENDANT ECOSYSTEM

Fire

Fire played an important role in the development and maintenance of the North American prairie at the expense of forest cover (Daubenmire 1968; Collins and Wallace 1990; Pyne 1996). Prairies provide optimal environmental conditions for fire, in that vegetation becomes highly flammable during the dry season. They also have favourable terrain that facilitates the wide and quick spread of fire when winds are present (Axelrod 1985). Historically, they burned at varying times, intervals, and frequencies. It remains unclear whether the primary cause of fire was natural (i.e. lightning) or human in origin (Axelrod 1985; Vogl 1974). Widespread fire suppression combined with habitat loss and fragmentation has greatly contributed to the decline of the tallgrass prairie, and allowed for the invasion of woody and exotic species. Prairies now are generally burned by managers in the spring and, to a lesser extent, the fall. Summer-burns, regardless of origin, are rare and, in most cases, avoided or prevented because of the associated risk and questioned historic importance (Howe 1994). Spring is the most convenient time for prescribed burns, as it provides more flexibility, whereas fall conditions vary greatly from year-to-year, difficult to predict, and less safe (Janer & Zelder 2001).

Effects of fire on vegetation

Although highly variable and often site specific in effect, fire can have great impacts on prairie species composition and diversity (Collin & Wallace 1990). Fire damage will differ depending on phenology (i.e. early- or late-season flowering), origin (i.e. native and exotic), physiology (i.e. C_3 or C_4), life history (i.e. annual, biennial, or perennial), life-cycle (i.e. vegetative or reproductive), and growth form (i.e. graminoids, forbs, or woody). In general, they favour graminoids (i.e. grasses, rushes, and sedges) over forbs, shrubs, and trees. Graminoids have adapted to fire by producing growing points or apical meristems at or beneath the soil surface, and are, thus, protected from fire (Collins & Wallace 1990). These "quick surface" prairie fires result in highly variable soil surface temperatures, ranging from 83 to 680°C (Rice & Parenti 1978). Soil offers protection for underground root and rhizomes, resulting in minimal heat penetration, which is often less than 1 cm below the soil surface (Wright & Bailey 1982). In contrast, growing points of forbs, shrubs, and trees are located above the soil surface and are destroyed when exposed to fire. Furthermore, species are most susceptible to damage when they are flowering, developing seed, actively growing, or when carbohydrate reserves are relatively low (DeBano 1998).

Impacts of burn-season

Annual spring-burns are used to promote dominant C_4 grasses, such as *Andropogon gerardii* and *Sorgastrum nutans* for grazing (Benning & Bragg 1993), and late-season species, often at the expense of forbs, C_3 grasses, and early-season species (Howe 1994). Dormant-season, late fall or winter burns also favour native C_4 grasses by increasing the rate of soil warming, nutrient availability and soil moisture in the spring (Anderson 1997). Late fall-burns also are more effective than spring-burns for controlling exotic species, especially during a second fall growing season (Janer & Zedler 2001).

Summer-burns have recently gained interest in prairie management, but are still uncommon because of their debated historical importance and associated risks of dry-season burning (Higgins 1984; Howe 1994). They occur when warm-season plants are actively growing and thus, have different impacts on productivity, species composition, and diversity. Summer-burns generally decrease late-season flowering species and promote early-season species, especially forbs (e.g. Biondini 1989).

Plant responses to burn-season are highly variable and other factors other than phenology also may be involved (Engle & Bidwell 2001). These include differences in latitude, soil type, water and nutrient availability, burn interval, species composition, and grazing (Daubenmire 1968; Vogl 1974; Higgins *et al.* 1989). Drought is extremely important in determining the potential of burning, as they influence the amount of fuel available to carry fires and post-burn vegetational responses. Prairies are most susceptible to fire when dry, including active season burns (Anderson 1990). Generalizations regarding burn-season responses are often difficult to make and should be considered carefully before making management decisions.

Burn-frequency

Burn frequency is also important in prairie management (Morgan *et al.* 1995). In general, it is determined by local site conditions including the rate of woody species encroachment, presence of exotic species, litter accumulation, and the type of prairie (Packard & Mutel 1997). To maintain native species composition and diversity, highly productive wet prairies are burned every 2 to 5 years and dry prairies every 4 to 10 years (Janer & Zelder 2001). Burn-frequency in disturbed prairies is more variable than in remnant prairie management. In general, the former require more frequent burning than remnants for woody and exotic species control.

Grazing

In the past, grazing also played an important role in the maintenance of tallgrass prairies. Grass species may have evolved over time under the pressure of grazing and responded by producing relatively greater biomass under these conditions (Wallace & Collins 1990). Litter further accumulates in ungrazed tallgrass prairies, thereby decreasing diversity and increasing the presence of dominant species (Knapp & Seastedt 1986). Historically, tallgrass prairie was grazed by a wide variety of browsers including bison, elk, deer, rabbits, and grasshoppers (Riser *et al.* 1981). Bison, the dominant grazer on the prairie, selectively fed on grass and, since burning tends to favour grass production, they often preferentially grazed recently burned areas. Tallgrass prairie thus was historically managed by the complex interaction of grazing, in particular bison, and fire (Vinton *et al.* 1993). More recently, grazing has played a much less significant role, and though sometimes introduced on a small scale, has been largely replaced by management substitutes including herbicides and mowing.

Current Management Practices

The primary goals of tallgrass prairie management are to increase species diversity, decrease encroachment of woody species, and prevent the introduction of non-native species. These goals are generally accomplished by: 1) prescribed burning; 2) selective removal of woody or non-native species cover; and 3) habitat restoration. Burning is the dominant management practice in prairie conservation and restoration (Grace *et al.* 2002). It is used to suppress or kill exotic and woody species during their most vulnerable period of their life history. Supplementary methods include herbicides, mowing, girdling, cutting, and hand pulling undesirable species.

TALLGRASS PRAIRIE RESTORATION

Rationale

Tallgrass prairie as been highly fragmented by agriculture and urbanization and is considered one of the most endangered ecosystems in North America. Less than 1% of the original land cover in Manitoba remains, much of which is protected by a single preserve (CWHP 1998). Although these protection efforts are of fundamental importance, remnants continue to be degraded by nutrient inputs, fire suppression, overgrazing, and invasion by exotic and woody plants. Restoration, in the form of reconstruction and rehabilitation, can be used to increased land cover and quality of tallgrass prairie as well as its long-term persistence on the landscape.

Much of the restoration in Manitoba focuses on the reconstruction of new tallgrass prairie. In addition to increasing the amount of prairie habitat in the province, it provides an economical and ecologically sustainable long-term alternative to conventional high maintenance landscaping of public lands. In this province, this is reflected in the current move towards "greening" or "naturalizing" schoolyards, and the conversion of yards into prairie habitat by urban dwellers. Although these restoration projects are often smaller and more garden-like than most reconstructions, they too play an important role in increasing biodiversity and have become a priority for urban conservationists (McLachlan 1996). Despite their prominence, many of these projects are ultimately unsuccessful, in large part because of inadequate monitoring and maintenance.

Constraints

The invasion of prairies by exotic species has been facilitated by fire suppression and surrounding land-use. Native species are often out-competed by exotic cool-season grasses and woody species in the absence of fire. Properly timed burns can be used to control exotic species and enhance the growth of native species (Willson & Stubbendieck 2000). However, prairie management is often opportunistic and based on logistics rather than ecological information. Restoration can be used to re-introduce native species in order to displace exotics when seed is available. Although commercial suppliers and efficient collection techniques have somewhat alleviated this constraint (Wilson 2002), few species are available in large quantities and thus, prairie restorations are often simple in composition.

Restoration process

Four baseline site conditions for prairie restoration have been identified: 1) introduced perennials without native species; 2) introduced perennials with native species; 3) cultivated fields with a native species seedbank; and 4) cultivated fields without a native species seedbank (Wilson 2002). Under all these conditions, site preparation typically involves the use of prescribed burn, herbicides, and/or tillage to remove of existing aboveground vegetation and seedbank. Once exotic species have been removed or controlled, native species establishment or re-introduction can be accomplished by broadcasting, seed drilling, interseeding, seedlings, or sod (Wilson 2002; Morgan 1997; Packard 1997).

In general, degraded prairie remnants and reconstructions tend to have low native diversity, especially forb diversity. Sites are often isolated from other native habitat and opportunities for seed dispersal are limited. Seedbanks may be of limited function in prairies, especially when dominated by exotic species, and may require seeding to increase native diversity. Zero-till techniques for prairie restoration have gained interest (Daigle & Havinga 1996; Morgan *et al.* 1995) and primarily take the form of interseeding (Packard 1997), whereby seeds are sown into existing vegetation with minimal soil disturbance (Lanfond & Derksen 1996). Native species can also be established by low-intensity tillage, such as harrowing (Wilson 2002), no-till seed drilling (Derken *et al.* 1996) or reducing vegetation cover through the use of herbicides, burning, or mowing. Burning-associated nutrient flushes might further promote establishment, especially under nutrient poor conditions.

As tallgrass prairie is highly fragmented and very little remains, restoration provides as excellent opportunity to enhance existing remnants as well as increase patch size and connectivity. However, habitat conversion and conflicting land-use of neighbouring properties greatly threatens tallgrass prairie existence. Conservation efforts need to focus on protection and management practices that include restoration and mitigation.

STUDY AREA

This research was conducted on two remnant tallgrass prairies in southeastern Manitoba (Figs. 2.4 & 2.5). One study site was of high quality and located within the St. Charles Rifle Range (SCRR), immediately west of Winnipeg, whereas the other was a degraded tallgrass prairie located within the Manitoba Tall Grass Prairie Preserve (MTGPP), near the towns of Tolstoi and Gardenton. The study area is located at the northern edge of the tallgrass prairie region, where less than 1% (CWHP 1998) of the original land cover remains within a landscape dominated by agriculture and urban development. This tallgrass prairie ecosystem is characterized by dry-upland prairies and low lying sedge meadows, and marshes interspersed with aspen parkland and riparian forest along the waterways (Shay 1984).

Much of the tallgrass prairie has been converted to agriculture within the past century. In 1987, the Manitoba Naturalist Society initiated Manitoba's first systematic inventory of extant tallgrass prairie. The goal was to locate, protect, and manage tallgrass prairie as well as to educate landowners, resource managers, and the public (Joyce & Morgan 1989). Very few tracts of remnant tallgrass prairie were found, and many were less than a hectare in size (CWHP 1998). The largest tracts were found within what is now the MTGPP, which currently protects 2500 hectares of prairie habitat. This area was originally settled in 1896 and much of it escaped successful conversion to agriculture by early pioneers due to the presence of large boulders, aspen bluffs, and wetlands. Over 300 vascular plant species have been identified within the MTGPP. Low-lying areas are dominated by *Carex* spp. and drier uplands by *Andropogon gerardii* and *Sorghastrum nutans* (Borkowsky & Jones 1998).

Other notable tallgrass prairie remnants located within and near Winnipeg include the SCRR, Living Prairie Museum, Rotary Prairie, Oak Hammock Wildlife Management Area, and Lake Francis. Tallgrass prairie within SCRR was not discovered until 1993. Fire had been suppressed on this site for over 80 years and was then used to control woody species invasion onto the open prairie. Although military training and conservation activities differ in goals, SCRR prairie would not likely exist today without being designated as DND property. Some of SCRR (192 ha) had been cultivated in the 1930's and 48 hectares are considered to be high quality tallgrass prairie interspersed by aspen. It is the largest remaining "true" tallgrass prairie situated on Red River clay soil rather than the sandy Lake Agassiz beach ridge soils of the MTGPP.

SCRR prairie is surrounded by agricultural use, and is characterized by *Populus tremuloides*, mesic tallgrass prairie, and swales of *Salix* species. Dominant species include native graminoids *Andropogon gerardii*, *Sporobolus heterolepis*, *Spartina pectinata*, and *Carex* spp. and important native forbs include *Dalea purpurea*, *Artemisia ludoviciana* and *Helianthus maximiliani* (Morgan 1994a).

The site area climate is continental with a mean yearly daily temperature from 1971-2000 of 2.6°C (36.68°F) (Environment Canada 2002). The daily mean temperatures in July and January over this time period were 19.5°C (67.1°F) and -17.8°C (0.04°F), respectively. The average annual rainfall was 415.6mm, approximately 50% of this falling between June and August. The average annual snowfall was 110.6cm, the majority of it falling between November and January.

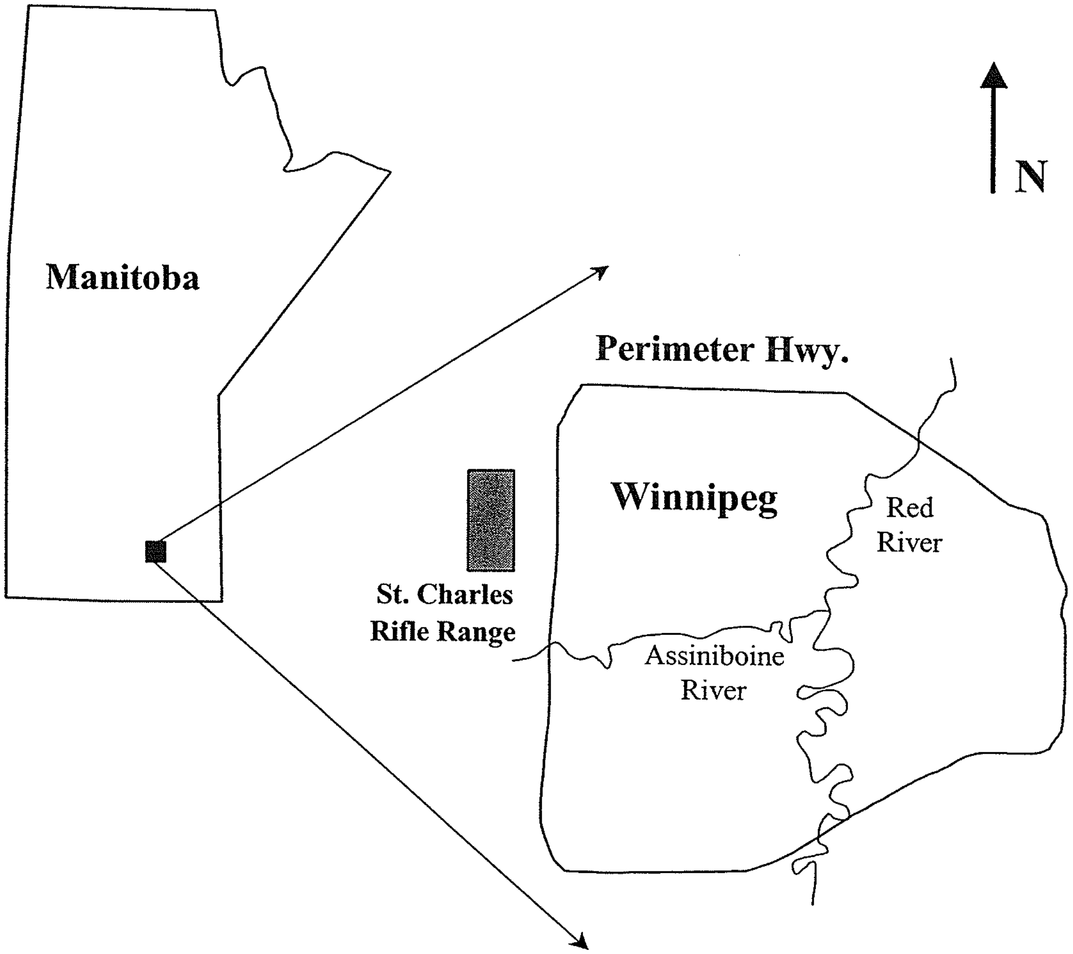


Fig. 2.4. Location of St. Charles Rifle Range study site relative to the City of Winnipeg (Adapted from Morgan 1994a).

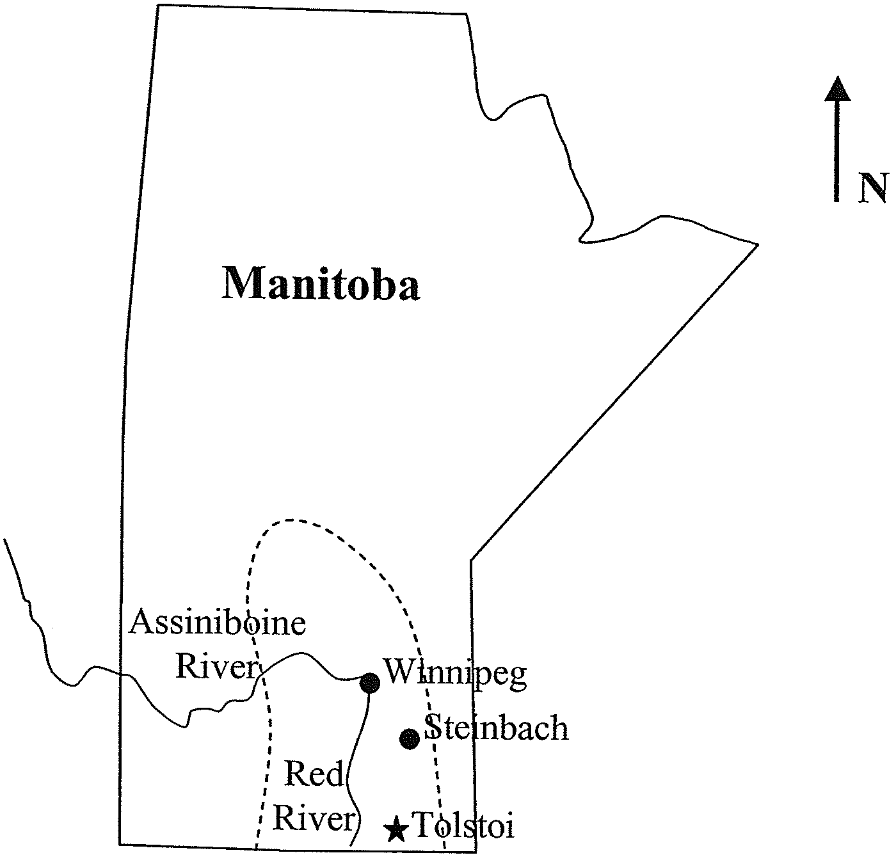


Fig. 2.5. The Manitoba Tall Grass Prairie Preserve study site, located near Tolstoi (star), and the historic range of tallgrass prairie in Manitoba indicated by the dashed line (Adapted from Reaume 1993).

CHAPTER 3: Impacts of fire-season on high quality northern tallgrass prairie

ABSTRACT

Tallgrass prairie has become one of the most endangered ecosystems in North America. Less than 1% of the original cover remains, as it has been highly fragmented and continues to be degraded by the invasion of exotic and woody species, and fire suppression. In 1997, a replicated experiment was initiated to determine the relative effects of spring-, summer-, and fall-burns on diversity and species composition of northern high quality tallgrass prairie. Burn-season had a substantial impact on diversity and species composition. Fall-burn had the most desirable effect, increasing native graminoid (e.g. *Andropogon gerardii* and *Panicum leibergii*) and forb (e.g. *Anemone canadensis* and *Aster ericoides*) diversity, regardless of time-of-flowering. Summer-burn increased both native (e.g. *Carex torreyi*. and *Juncus* spp.) and exotic (e.g. *Poa pratensis*) graminoid cover. The relatively late spring-burn decreased exotic graminoid diversity and cover, but had little effect on species composition and was characterized by woody species (e.g. *Rosa* spp. and *Symphoricarpos* spp.). All burn-treatments, except for the fall-burn, became increasingly similar in species composition to the control over time. Spring-, summer-, and fall-burns had varied but desirable effects. In the absence of clear management objectives and site-specific information for vegetation and seedbanks, burn-seasons should be rotated whenever feasible.

***Key-words*:** exotic, fire, flowering phenology, guild, tallgrass prairie, prescribed burn, restoration

3.1. INTRODUCTION

Less than 1% of the original tallgrass prairie remains and it has become one of the most endangered ecosystems in North America. Although southeastern Manitoba was once dominated by tallgrass prairie, it has been reduced to relatively small and isolated fragments by agriculture and urban development. Extant prairie is increasingly protected, but continues to be degraded by overgrazing, invasion by exotic and woody species, and, especially, by the suppression of fire.

Disturbance associated with fire has played an important role in the development and maintenance of tallgrass prairies (Riser *et al.* 1981; Collins & Wallace 1990), especially by increasing native diversity and reducing exotic diversity and woody encroachment (Hobbs & Huenneke 1992). Although the primary causes of fire were both natural and human in origin (Axelrod 1985; Vogl 1974), its widespread suppression, along with habitat loss and fragmentation, has greatly contributed to the decline of tallgrass prairie.

Most tallgrass prairie is burned in the spring and, to a lesser extent fall, as this provides the greatest flexibility and least risk for managers (Janer & Zelder 2001). Burn-season can have a great impact on prairie species composition and diversity, as plants are generally most susceptible when actively growing, flowering, and seeding, or when carbohydrates reserves are relatively low (DeBano 1998). Frequent spring burns are commonly used to promote dominant C_4 grasses, such as *Andropogon gerardii*, for grazing (Benning & Bragg 1993) and increased production (Collins & Steinauer 1998). But these late-season grasses increase at the expense of forbs, C_3 grasses, as well as early-season plants (Howe 1994) and overall diversity (McLachlan & Knispel 2003).

Dormant-season, late fall or winter, burns also favour native C_4 grasses by increasing the rate of soil warming, nutrient availability and soil moisture in the spring (Anderson 1997).

Although some recent reviews (e.g. Wilson 2002) question whether burning preferentially favours native prairie species, annual spring burns are often used to control exotic species (e.g. Smith & Knapp 2001). Fire effects on exotic species vary considerably due to site differences, burning regimes, and environmental conditions (Grace *et al.* 2000). Problematic species in the northern range of tallgrass prairie, including perennial exotic graminoids *Bromus inermis* (Blankespoor & May 1996) and *Poa pratensis* (White *et al.* 1993), have been effectively controlled by spring and fall burns during tiller elongation (Grilz & Romo 1995; Willson & Stubbendieck 1997; Smith & Knapp 1999). In contrast, burning at other pheonological stages has actually increased exotic graminoid productivity and decreased native species diversity (Willson & Stubbendieck 2000).

Encroachment by undesirable woody species is also mitigated by annual spring burns (e.g. Anderson & Bailey 1980). Long-term fire suppression has facilitated the expansion of woody species in tallgrass prairies (Briggs *et al.* 2002). Although fire has been successfully used to decrease new woody species recruitment, densities of well established species are relatively unaffected (Heisler *et al.* 2003). Indeed, when fire has been suppressed for long periods, burning tends to increase the density of woody species, and repeated burning (Morgan 1994a) at different burn seasons is often necessary.

Summer-burns are still rare in prairie management because of their debated historical importance (Higgins 1984; Howe 1994), increased risks of dry-season burning, and perception that living plant material and low litter accumulation compromise their effectiveness (Braggs 1982). They occur when warm-season plants are actively growing and thus, have differing impacts on productivity, species composition, and diversity. Summer-burns generally decrease late-season flowering species and promote early-season species, especially forbs. Recently, their role in controlling woody species (e.g. Engle *et al.* 1993), enhancing forb diversity (e.g. Biondini 1989), and simulating lightning fires (e.g. Ewing & Engle 1988; Howe 1995) has been explored. Summer-burns often burn a smaller area compared to dormant-season burns and are thought to increase landscape heterogeneity (e.g. Collins 1987), but landscape level research is lacking as remnant and restored prairies are small in size (e.g. Biodini 1989).

Relatively little is known about the role of fire in the northern range of the prairies. Most research that does exist has been conducted in the mixed-grass prairie region (e.g. Wilson & Shay 1990; Shay *et al.* 2001). Yet annual spring burns are routinely employed on both extant prairie and new restorations. The overall objective of this study is to determine the relative effects of spring, summer, and fall burns on high quality tallgrass prairie. Specifically I wanted to determine: 1) impacts of burn-season on species composition and diversity; 2) impacts of burn-season on functional guilds including origin, growth form and flowering phenology; and 3) how these changes in species and guild composition and diversity changed over time. I predicted that burning would increase native species diversity and suppress exotic and woody species. More specifically, spring-burning would promote dominant native late-season grasses at the expense of sub-dominant native forb species whereas fall-burning would promote early-season species.

3.2. METHODS

Study site

This four-year study was conducted at the St. Charles Rifle Range (SCRR), 1 km west of Winnipeg, Manitoba (49°55' N, 97°14'W) (Fig. 2.4). The SCRR was donated to the Department of National Defence (DND) in 1911 and has been primarily used as a military rifle range and land training facility. It is the largest remaining intact "true" tallgrass prairie situated on Lake Agassiz clay soil in Manitoba. Although a small portion of the prairie was plowed for agriculture until 1962, much of the 192 ha remnant is intact, and 48 ha are considered high in ecological integrity (Morgan 1994a).

This prairie is surrounded by agricultural use, and is characterized by *Populus tremuloides*, mesic tallgrass prairie, and swales of *Salix* species. Dominant native graminoid species include *Andropogon gerardii*, *Sporobolus heterolepis*, *Spartina pectinata*, and *Carex* spp. and important native forbs include *Dalea purpurea*, *Artemisia ludoviciana* and *Helianthus maximiliani* (Plate 3.1) Exotic species are relatively uncommon, except in disturbed soils along vehicle trails, and include *Bromus inermis* and *Poa pratensis*, both which were likely actively seeded in the past (Morgan 1994a). Prescribed spring burns were introduced by DND in 1994 to increase native tallgrass prairie species diversity, control woody species encroachment, and reduce the risk of wildfires caused by training activities.

From 1971-2000, the mean yearly daily temperature in Winnipeg was 2.6°C (36.68°F) (Environment Canada 2002). The daily mean temperatures in July and January over this time period were 19.5°C (67.1 F) and -17.8°C (0.04 F), respectively. The average annual rainfall was 415.6mm, approximately 50% of this falling between June

(R. Roughley)

Plate 3.1. High quality tallgrass prairie within the St. Charles Rifle Range.

and August. The average annual snowfall was 110.6cm, the majority of it falling between November and January.

Sampling design

A four-times replicated experimental design was used to examine the multi-year effect of burn-season on plant species diversity and composition. Three blocks were located in intact prairie (A, B, and C) and the other in a previously cultivated area (D). Each block contained four 50m x 50m treatment plots, these randomly located around a central refuge (Fig. 3.1). In 1997, spring-burn was conducted on June 6, summer-burn on August 5, fall-burn on September 9, and a control left unburned. A central refuge also was left unburned for an associated study on insect communities. Firebreaks were established around each of the treatment plots and then encircled with fire. Plots were only burned once and unburned vegetation was left intact (Roughley & Pollock 1999). Each burn treatment plot was divided into quarters and two 1m x 1m quadrats were randomly assigned to each quarter ($n = 8$). Percent cover of all plant species, litter, and bareground was recorded for each treatment using the Domin scale (Kent & Coker 1992) (Appendix 4). Vegetation was sampled in early July and, again, in late August for 1997, 1998, and 2000 for all treatments. In 1999, Blocks A, B, and C were only sampled in July, and Block D left unsampled, due to difficulties in accessing the site.

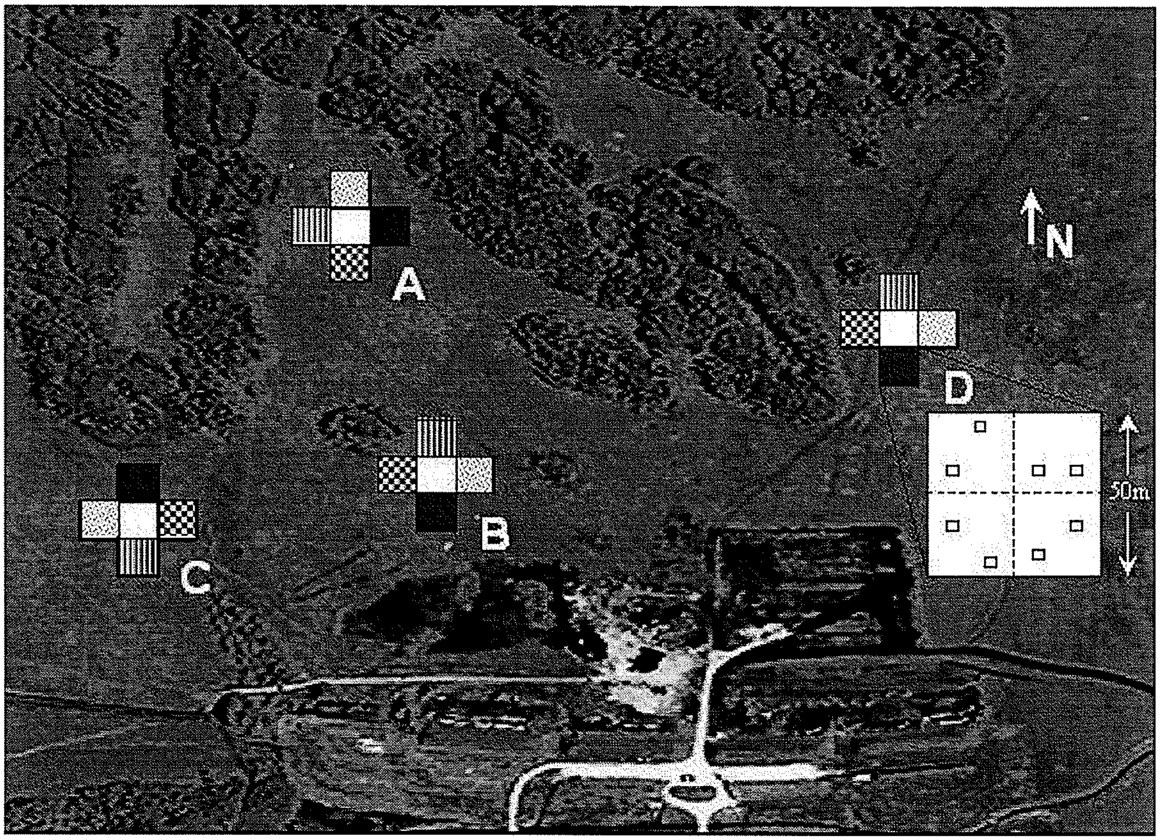


Fig. 3.1. Landscape layout and experimental design, including spring (vertical lines); summer (checkered board pattern); fall (solid); and control (dots) as treatments and the location of 1m x 1m vegetation sampling quadrats within each treatment plot (Adapted from Roughley & Pollock 1999).

Analysis

Effects of burn-season on diversity were evaluated using Hill's (1973) diversity measures, these consisting of N_0 (i.e. species richness), which is the total number of species and sensitive to rare species, and N_2 (i.e. effective species richness), which is the reciprocal of Simpson's index and emphasizes dominance. Differences in plant diversity and cover among burn-seasons were assessed using repeated measures analysis of variance (ANOVA) (SAS 1988) (Appendix 3). All data were log+1 transformed to meet the assumptions of ANOVA (Zar 1996) and original data are presented. Post-hoc multiple comparison Tukey's tests ($\alpha = 0.05$) were used to separate means when the overall ANOVA model was significant. Species also were categorized according to functional guilds, these including origin (native or exotic), growth form (graminoid, forb, or woody), and flowering phenology. The latter were classified as early- , late-, and all-season species, these flowering from May - June, July - September, and June - September, respectively (Peterson & McKenny 1996).

Changes in species composition over time were examined using canonical correspondence analysis (CCA). The CCA is a direct ordination technique that maximally separates samples according to differences in species composition and then constrains them to independent variables (ter Braak 1990). Data were log +1 transformed and rare species down-weighted. The CCA was initially conducted for all blocks and, to remove the dominant effects of past agriculture, only on Blocks A, B, and C.

All data analyses were conducted on the maximum midpoint percent cover value from July and August sampling for each species and year (i.e. 1997, 1998, and 2000). As the data for 1999 were incomplete, they were dropped from any subsequent analyses.

3.3. RESULTS

Native forb diversity and cover all had significant ($p<0.0001$) interactions between burn-season and year (Table 3.1a & 3.1b). For native forb species richness, burning had no effect in 1997, whereas in 1998, as might be expected, it was greater for all burn-seasons ($p<0.0001$) (Fig. 3.2a). However, by 2000, all treatments had recovered from burning and species richness was greatest in the control (Table 3.1a). Native forb effective species richness (ESR) and cover also had significant interactions between burn-season and year. However, no differences in native forb ESR occurred between burn-seasons in 1998 and 2000, suggesting that rare species were responding to the burning. Burn-season had no effect on native forb cover until 2000 where it was greatest in spring-burn and lowest in the control (Table 3.1a). By 2000, most native forb species, when examined individually, increased with burning and had the greatest cover in the fall-burn (Table 3.2).

Native graminoid diversity and cover also showed significant interactions between burn-season and year ($p<0.0001$) (Table 3.1a & 3.1b). In 1997, native graminoid species richness was decreased by summer-burn and greatest in the untreated fall-burn, whereas in 1998 it was increased by summer-burn and fall-burn and suppressed by spring-burn (Fig. 3.2b). By 2000, native graminoid species richness was greater ($p<0.0005$) in all burn-seasons than the control. As with forbs, burning had no effect on native graminoid ESR in 1997, whereas in 1998 it was greater in summer-burn and fall-burn and lowest in the spring-burn and the control. Although native graminoid ESR was greater summer-burn and fall-burn in 2000, no significant differences were found among burn-seasons. Native graminoid cover was greatest in spring-burn and lowest in summer-burn for 1997, whereas no differences were found in 1998 (Fig. 3.2c). However, in 2000 all burn-seasons increased native graminoid cover, this greatest in the spring and summer-burns ($p<0.01$). When individual graminoid species were examined, most species increased when burned, especially in the summer-burn and fall-burn (Table 3.2).

Native woody ESR ($p<0.01$) and cover ($p<0.0001$) showed a significant year effect (Table 3.1a & 3.1b). No differences in ESR were found between 1997 (mean ± S.E.) 1.59 ± 0.40) and 1998 (1.58 ± 0.04), whereas it had increased by 2000 (1.76 ± 0.05). Native woody cover doubled from 1997 (12.02 ± 1.21) to 1998 (24.51 ± 1.65), but, by 2000, it had declined to the original levels (12.29 ± 1.23). Native woody cover was also significantly ($p<0.0005$) affected by burn-season. As might be predicted, fall-burn (12.17 ± 1.29), summer-burn (13.97 ± 1.40), and spring-burn (14.88 ± 1.48) all decreased native woody cover compared to the control (24.06 ± 2.23). Individual species also responded in a similar way. By 2000, Rosa spp. and *Symphoricarpos* spp. (Fig. 3.3e) tended to be lower in all burn-treatments, and the latter was significantly ($p<0.01$) lower than the control in the fall burn (Table 3.2).

Exotic forbs showed a significant ($p<0.0001$) main effect with year (Table 3.1a & 3.1b). Surprisingly, both exotic forb species richness (1997 = 0.47 ± 0.05; 1998 = 0.70 ± 0.05; and 2000 = 0.80 ± 0.05) and ESR (1997 = 0.48 ± 0.05; 1998 = 0.70 ± 0.05; and 2000 = 0.83 ± 0.06) steadily increased over time (Table 3.1a & 3.1b). Exotic forb cover also increased approximately 5-fold from 1997 (0.29 ± 0.05) to 1998 (1.27 ± 0.16) and 2000 (1.30 ± 0.12). In contrast, burn-season had no significant effect on exotic forb diversity and cover. Similarly, when species were examined individually, none showed any significant changes, reflecting their relative infrequent occurrence (Table 3.2).

Exotic graminoid diversity and cover interacted significantly ($p<0.005$) with burn-season and year (Table 3.1a & 3.1b). In 1997, as might be expected, spring-burn suppressed exotic graminoid species richness and ESR compared to summer-burn and fall-burn, whereas in 1998 they were lowest in spring-burn, fall-burn, and control and highest in summer-burn (Fig. 3.2d). By 2000, exotic graminoid species richness and ESR had recovered, and no differences were found between the burn-seasons and control. For exotic graminoid cover, in 1997 all burn-seasons were lower than the control, whereas in 1998 it was greatest in summer-burn and lowest in fall-burn, spring-burn, and control (Fig. 3.2e). However, in 2000, exotic graminoid cover was significantly greater in the control than all burn-seasons, especially that of summer-burn and spring-burn. This might be associated with the increase in *Poa pratensis* (Fig. 3.3f) cover, which, by 2000, was significantly lower in the fall burn than either the control or the spring-burn (Table 3.2).

Flowering phenology affected diversity and cover responses to burn-season. Early-flowering and late-flowering species both showed significant interactions between burn-season and year (Table 3.1a & 3.1b). In 1997, early-flowering species richness was greatest in fall-burn (Fig. 3.2f) and late-flowering plants were lowest in the summer burn (Fig. 3.2h). In 1998, both early and late flowering plants were promoted by all burn treatments. However, by 2000, these flowering guilds were responding differently. Species richness for early-flowering species had decreased in all burn treatments compared to the control and for late-flowering species no significant differences were observed. ESR showed similar results except for 2000, where there were no significant differences observed, indicating that declines in total richness were driven by relatively infrequent species. In 1997, early-flowering cover was lower in all burn-seasons than the control (Fig. 3.2g) whereas for late-flowering cover, spring-burn was higher and summer-burn lower than the control (Fig. 3.2i). By 1998, early-flowering cover was lowest in the spring-burn whereas late-flowering cover was significantly greater for spring- and fall-burns. By 2000, early-flowering cover, like species richness, was significantly lower in all burn treatments than the control whereas, late-flowering cover was highest in spring-burn and lowest in the control.

Although burn-season effects were not as clear, all-season flowering species showed significant interactions between burn-season and year (Table 3.1a & 3.1b). In 1997, summer-burn decreased all-season flowering ESR (Fig. 3.2k) whereas species richness not effected (Fig. 3.2j). In 1998, all-season flowering species richness and ESR were promoted by both summer- and fall-burn and decreased by spring-burn. However, by 2000 no differences in diversity were found between the control and summer- and fall-burn, but spring-burn still remained lowest.

In contrast to functional guild diversity and cover measures, flowering phenology had little effect on individual species responses to burn-season, as forbs, regardless of time of flowering, responded positively to fall-burning. Thus, 4 of 5 early-flowering and 4 of 5 late-flowering species were most prevalent in the fall-burns (Table 3.2). Native forbs that had the greatest cover in this treatment included early-flowering *Anemone canadensis* ($p<0.0005$) (Fig. 3.3a), *Astragalus agrestis* ($p<0.0005$), *Lithospermum canescens* ($p<0.005$) as well as late-flowering *Aster ericoides* ($p<0.005$) (Fig. 3.3b), *Helianthus subrhomboideus* ($p<0.0001$), *Monarda fistulosa* ($p<0.001$), and *Solidago rigida* ($p<0.0001$) (Table 3.2). In contrast, *Glycyrrhiza lepidota* ($p<0.005$) and *Helianthus maximiliani* ($p<0.0001$) were significantly lower for summer- and fall-burns, while greater in spring-burn and *Solidago gigantea* ($p<0.005$) decreased in all burns relative to the control (Table 3.2). Similarly, flowering phenology had little bearing on graminoid responses to burn-season, as they increased in all burn-seasons compared to control (Table 3.2). Graminoids that were greater in all burn-seasons included late-flowering *Andropogon gerardii* ($p<0.01$) (Fig. 3.3d) and early-flowering *Panicum leibergii* ($p<0.0001$) (Fig. 3.3c) and *Stipa spartea* ($p<0.01$), whereas *Carex praegracilis* ($p<0.0005$) and *Carex tetanica* ($p<0.0005$) were greater in the fall-burns, but did poorly in the spring-burn and control and in summer-burn responses were mixed.

Results of canonical correspondence analysis (CCA) indicate that disturbance in the past had a substantial influence on species composition (Fig.3.4). Correspondence analysis (CA) axes 1 and 2 accounted for 11.3% and 7.9% of the variation, respectively, and represented 19.2% of the total variation within the species data. When constrained by burn treatments, blocks, and year in CCA, the species-environment correlation values were 0.921 and 0.880 for axes 1 and 2, respectively. Blocks separated along CCA axis 1 according to land-use history, suggesting a disturbance gradient. Blocks B and C were negatively correlated with CCA axis 1 (Fig. 3.4a) and characterized by native species including *Erigeron philadelphicum*, *Psoralea esculenta*, and *Psoralea argophylla* (Fig. 3.4b). Block D, located in the recently disturbed prairie, clearly separated from all other blocks. It was positively associated with CCA axis 1 and was characterized by woody and weedy native species and included *Carex lanuginosa*, *Salix lutea*, and *Lactuca pulchella*. Burn-season separated along CCA axis 2 and was negatively correlated with fall-burn and positively with the control. However, CCA results were dominated by differences in Block D, making burn-season responses unclear.

When block D and constraining variable "block" were excluded, CCA separated the plots according to burn-season and year (Fig. 3.5). CA axes 1 and 2 accounted for 9.3% and 8.4% of the variation, respectively, and represented 17.7% of the total variation within the species data. When constrained by burn treatments, blocks, and year in CCA, the species-environment correlation values were 0.829 and 0.909 for axes 1 and 2, respectively. Fall-burn distinctly separates from all other burn treatments on CCA axis 1 (Fig. 3.5a) and was characterized by graminoid and forb species, including *Andropogon scoparius*, *Erigeron philadelphicum*, and exotic forb *Sonchus arvensis* (Fig. 3.5b). Summer- and fall-burns separate from spring-burn and control on CCA axis 2. Summer-burns were characterized by native graminoids and included *Agropyron trachycaulum* var. *unilaterale*, *Carex torreyi*, and *Muhlenbergia richardsonis*. In contrast, spring-burn and control were characterized by woody species and included *Populus tremuloides*, *Salix bebbiana*, and *Spiraea alba*. Although individual species associated with burn treatments in CCA were different than species identified in ANOVA, over all functional guild trends are similar.

Changes in species composition over time also separate along CCA axis 2 (Fig. 3.5). All burn treatments, except fall-burn, increased in similarity as time since burning increased. Differences in species composition can also be attributed to increased moisture availability from 1997 to 2000 (Fig. 3.5a). Species present in 1997 preferred dry soil conditions and included *Andropogon scoparius*, *Elymus canadensis*, and *Gaillardia aristata*. In contrast, species in 2000 preferred wet soil conditions and included *Muhlenbergia richardsonis*, *Agropyron trachycaulum* var. *unilaterale*, and *Carex torreyi* (Fig. 3.5b).

Table 3.1a: Functional guild means (S.E.) for species richness, effective species richness (ESR), and cover in 1997, 1998, and 2000 for each burn-season. Means followed by different letters indicates significant differences in a single year at $p<0.005$ according to Tukey's Multiple Means Test.

	Year											
	1997				1998				2000			
	Spring	Summer	Fall	Control	Spring	Summer	Fall	Control	Spring	Summer	Fall	Control
Native												
Forbs												
Richness	8.16 (0.39) a	6.00 (0.35) b	9.31 (0.39) a	6.91 (0.43) b	9.09 (0.46) a	9.16 (0.40) a	10.47 (0.34) a	7.13 (0.44) b	9.13 (0.52) ab	8.81 (0.51) a	9.31 (0.49) ab	10.75 (0.63) b
ESR	3.68 (0.33) a	3.61 (0.24) a	5.18 (0.29) b	3.48 (0.24) a	3.60 (0.25) a	4.00 (0.29) a	4.35 (0.29) a	3.43 (0.24) a	6.07 (0.41) a	6.37 (0.41) a	5.60 (0.41) a	5.60 (0.44) a
Cover	0.73 (0.10) a	0.84 (0.24) a	0.62 (0.13) a	1.10 (0.25) a	1.89 (0.34) a	4.58 (0.94) a	3.86 (0.72) a	4.95 (1.27) a	4.61 (0.63) a	2.23 (0.24) bc	2.92 (0.43) b	1.66 (0.26) c
Graminoids												
Richness	2.41 (0.15) ab	1.88 (0.19) b	3.31 (0.30) a	2.44 (0.29) b	2.06 (0.16) a	3.47 (0.23) b	2.81 (0.21) bc	2.44 (0.26) ac	4.31 (0.33) a	4.88 (0.29) a	3.94 (0.32) a	2.72 (0.21) b
ESR	1.50 (0.09) a	1.31 (0.14) a	1.69 (0.13) a	1.60 (0.17) a	1.29 (0.07) bc	1.78 (0.10) a	1.63 (0.10) ab	1.30 (0.13) c	1.97 (0.18) a	2.41 (0.24) a	2.33 (0.21) a	1.93 (0.14) a
Cover	6.40 (1.22) a	1.84 (0.68) b	3.83 (0.47) ac	4.06 (1.10) c	23.48 (5.00) a	29.75 (4.18) a	24.69 (3.66) a	27.17 (4.69) a	27.91 (4.00) a	15.11 (2.99) ab	7.57 (1.32) bc	6.69 (1.40) c
Woody												
Richness	2.16 (0.07)	1.84 (0.12)	2.00 (0.06)	2.38 (0.12)	2.13 (0.09)	1.88 (0.11)	2.03 (0.07)	2.19 (0.13)	2.03 (0.14)	2.06 (0.12)	1.91 (0.08)	2.16 (0.09)
ESR	1.72 (0.06)	1.44 (0.09)	1.53 (0.06)	1.65 (0.10)	1.68 (0.07)	1.44 (0.07)	1.60 (0.06)	1.59 (0.09)	1.73 (0.12)	1.76 (0.10)	1.62 (0.08)	1.94 (0.08)
Cover	10.77 (2.02)	9.16 (2.08)	7.04 (0.88)	21.10 (3.33)	22.67 (3.10)	24.16 (2.69)	18.65 (2.83)	32.56 (4.07)	11.21 (1.87)	8.59 (0.90)	10.84 (2.05)	18.51 (3.81)
Exotic												
Forbs												
Richness	0.59 (0.10)	0.44 (0.12)	0.38 (0.09)	0.53 (0.11)	0.75 (0.11)	0.63 (0.09)	0.88 (0.09)	0.56 (0.09)	0.72 (0.12)	0.66 (0.09)	1.03 (0.12)	0.91 (0.10)
ESR	0.58 (0.09)	0.42 (0.11)	0.38 (0.09)	0.50 (0.10)	0.75 (0.11)	0.63 (0.09)	0.88 (0.09)	0.56 (0.09)	0.69 (0.11)	0.66 (0.09)	1.00 (0.11)	0.88 (0.10)
Cover	0.41 (0.11)	0.27 (0.10)	0.18 (0.04)	0.30 (0.10)	1.28 (0.23)	0.68 (0.15)	1.86 (0.40)	1.25 (0.37)	1.55 (0.32)	1.15 (0.20)	1.20 (0.19)	1.30 (0.22)

Table 3.1a. Cont'd

	Year											
	1997				1998				2000			
	Spring	Summer	Fall	Control	Spring	Summer	Fall	Control	Spring	Summer	Fall	Control
Graminoids												
Richness	0.78 (0.12) a	1.06 (0.06) b	1.09 (0.09) b	0.84 (0.09) ab	0.94 (0.08) ab	1.06 (0.04) a	0.94 (0.11) ab	0.78 (0.10) b	1.00 (0.04) a	1.06 (0.04) a	1.19 (0.07) a	1.19 (0.07) a
ESR	0.69 (0.09) a	1.02 (0.05) b	1.02 (0.08) b	0.81 (0.08) ab	0.92 (0.07) ab	1.02 (0.02) a	0.87 (0.09) ab	0.75 (0.09) b	0.99 (0.04) a	1.05 (0.04) a	1.12 (0.05) a	1.09 (0.05) a
Cover	2.75 (0.58) a	6.67 (2.70) ab	3.93 (0.92) a	10.49 (2.86) b	16.64 (3.23) a	33.16 (3.76) b	14.16 (2.47) a	19.16 (4.11) a	6.87 (1.03) a	5.66 (0.69) a	10.76 (1.18) b	30.05 (5.25) c
Phenology												
Early												
Richness	5.09 (0.27) a	4.62 (0.32) a	6.47 (0.35) b	4.87 (0.37) a	5.75 (0.28) a	6.69 (0.39) a	6.56 (0.32) a	4.75 (0.36) b	7.09 (0.37) ab	6.81 (0.35) ab	6.09 (0.36) a	7.81 (0.57) b
ESR	2.93 (0.21) ab	2.61 (0.23) ab	3.06 (0.19) a	2.31 (0.19) b	2.87 (0.18) a	2.79 (0.16) a	3.28 (0.19) a	2.22 (0.16) b	4.64 (0.35) a	4.42 (0.25) a	3.64 (0.28) a	4.27 (0.45) a
Cover	12.20 (1.33) a	16.23 (3.75) a	13.13 (1.26) a	31.71 (5.25) b	40.56 (4.45) a	70.49 (6.51) b	44.59 (4.65) ac	55.70 (5.47) bc	25.24 (2.59) a	17.52 (1.25) a	24.41 (2.57) a	55.97 (6.87) b
Late												
Richness	7.28 (0.33) bc	5.16 (0.23) a	7.78 (0.25) b	6.38 (0.34) c	7.41 (0.37) ab	7.09 (0.29) ab	8.13 (0.28) a	6.69 (0.35) b	8.19 (0.44) a	8.09 (0.37) a	8.34 (0.30) a	7.31 (0.33) a
ESR	3.00 (0.27)	2.89 (0.21)	3.63 (0.26)	3.29 (0.22)	2.72 (0.17)	3.17 (0.20)	3.49 (0.21)	3.16 (0.21)	3.77 (0.32)	3.75 (0.35)	4.32 (0.32)	4.44 (0.31)
Cover	34.89 (3.00) a	15.00 (3.08) b	26.30 (2.89) ac	22.48 (3.06) c	105.91 (4.84) a	77.68 (4.95) b	105.92 (6.31) a	89.28 (7.17) b	52.24 (4.14) a	44.69 (3.82) ab	37.98 (3.46) ab	31.87 (3.01) b
All season												
Richness	1.72 (0.13) a	1.44 (0.15) a	1.84 (0.14) a	1.84 (0.17) a	1.81 (0.15) a	2.41 (0.20) b	2.44 (0.13) b	1.66 (0.12) a	1.90 (0.21) a	2.56 (0.19) b	2.94 (0.16) b	2.59 (0.17) b
ESR	1.30 (0.08) ab	1.08 (0.8) a	1.52 (0.10) b	1.38 (0.08) b	1.35 (0.11) b	1.55 (0.11) ab	1.66 (0.07) a	1.34 (0.09) b	1.65 (0.17) a	2.00 (0.14) ab	2.25 (0.11) b	1.90 (0.13) ab
Cover	5.45 (1.48) a	2.63 (0.37) ab	2.27 (0.31) b	4.02 (0.80) ab	9.23 (2.09) a	9.23 (1.15) a	8.47 (1.18) a	7.00 (1.04) a	3.55 (0.38) b	5.07 (0.52) ab	5.20 (0.33) a	8.92 (1.39) a

Table 3.1b. Functional guild repeated measures ANOVA relationship for species richness, effective species richness (ESR), and cover.

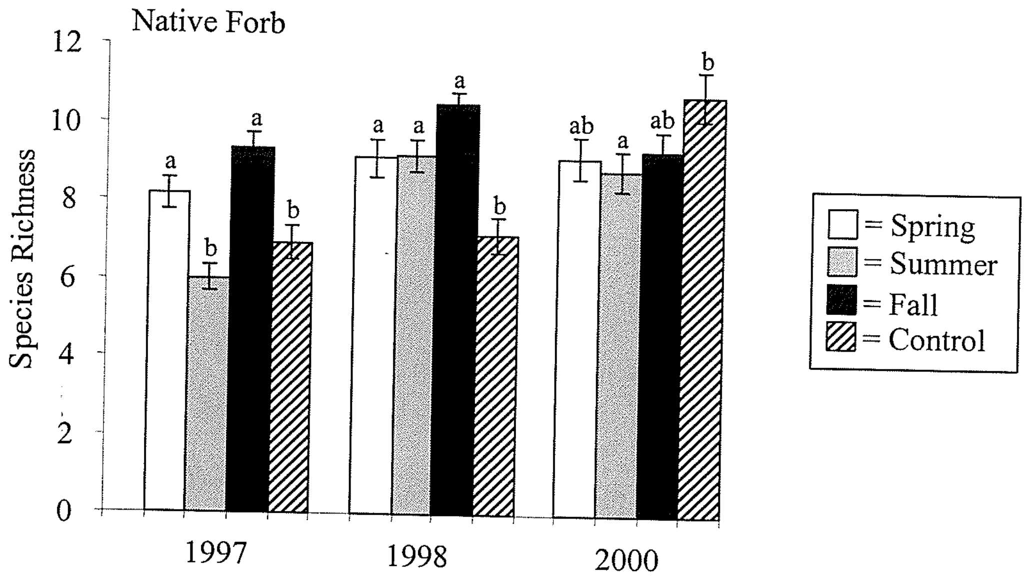
	ANOVA					
	Blk	Brn	Blk*Brn	Y	Y*Brn	Y*Blk
Native						
Forbs						
Richness	*	*****	*****	*****	*****	*****
ESR	*ns*	*ns*	*ns*	*****	***	*ns*
Cover	***	*ns*	****	*****	*****	**
Graminoids						
Richness	*****	****	**	*****	*****	*ns*
ESR	**	*ns*	*ns*	*****	**	*ns*
Cover	**	*	*****	*****	*****	*****
Woody						
Richness	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*
ESR	*ns*	*ns*	*ns*	**	*ns*	**
Cover	*ns*	***	*ns*	*****	*ns*	*****
Exotic						
Forbs						
Richness	*	*ns*	*	*****	*ns*	*ns*
ESR	*	*ns*	*ns*	*****	*ns*	*ns*
Cover	*ns*	*ns*	*ns*	*****	*ns*	*ns*
Graminoids						
Richness	*****	*ns*	*ns*	*****	**	****
ESR	*****	**	*ns*	*****	***	*****
Cover	*****	*****	*****	*****	*****	***
Flowering phenology						
Early						
Richness	*ns*	*ns*	*****	*****	*****	*****
Late						
Richness	*****	*****	****	*****	*****	*
ESR	*ns*	*ns*	*ns*	*****	*ns*	*ns*
Cover	*****	*****	***	*****	***	*****
All season						
Richness	*ns*	**	*ns*	*****	*****	*ns*
ESR	*	***	*ns*	*****	*	*
Cover	**	*ns*	*ns*	*****	*****	*****

*****$p<0.0001$; **** $p<0.0005$; ***$p<0.001$; **$p<0.005$; *$p<0.01$; and *ns>0.01*

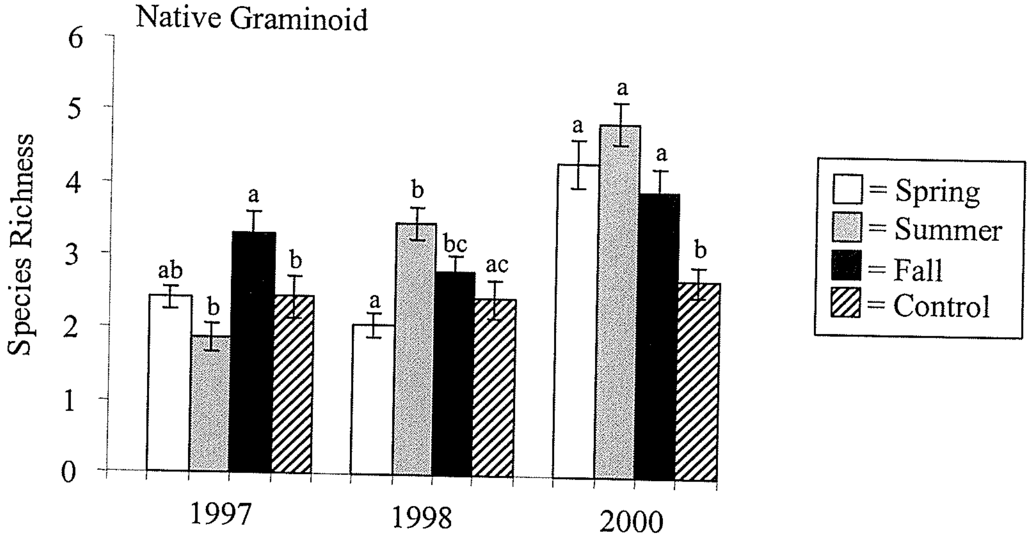
Blk = Block; Brn = Burn; and Y = Year

Fig. 3.2. Functional guild means and standard error (S.E.) for diversity (species richness and effective species richness) and percent cover in 1997, 1998, and 2000. Only significant Repeated Measures ANOVA results are shown and means followed by different letters indicates significant differences in a single year at $p<0.005$ according to Tukey's Multiple Means Test. Functional guilds include a) native forb species richness, b) native graminoid species richness, c) native graminoid cover, d) exotic graminoid effective species richness, e) exotic graminoid cover, f) early-flowering effective species richness, g) early-flowering cover, h) late-flowering species richness, i) late-flowering cover, j) all-season flowering species richness, and k) all-season flowering effective species richness.

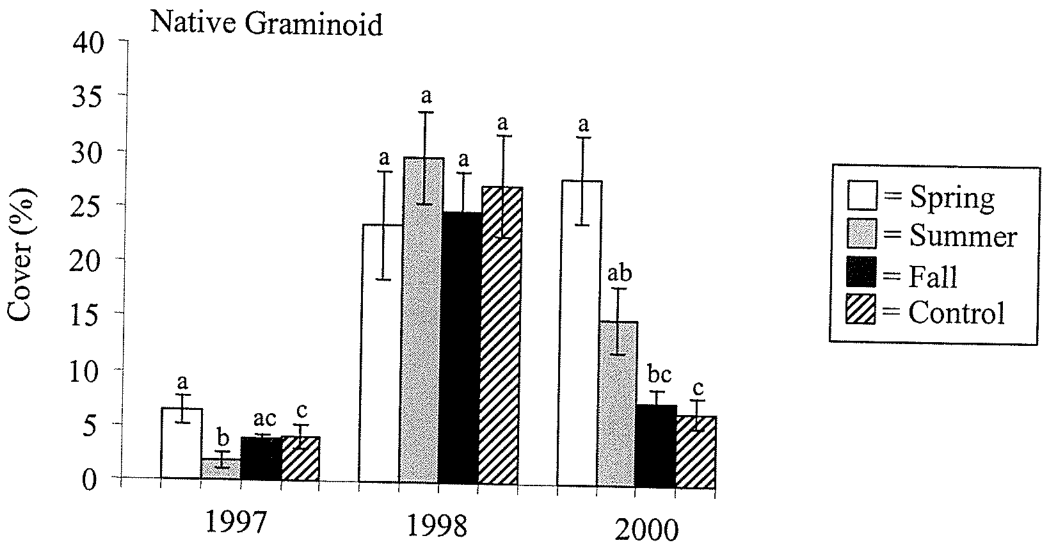
a)


Native Forb
Species Richness
12
10
8
6
4
2
0
1997
1998
2000
a
b
a
b
a
a
a
b
ab
a
ab
b
□ = Spring
▨ = Summer
■ = Fall
▨ = Control

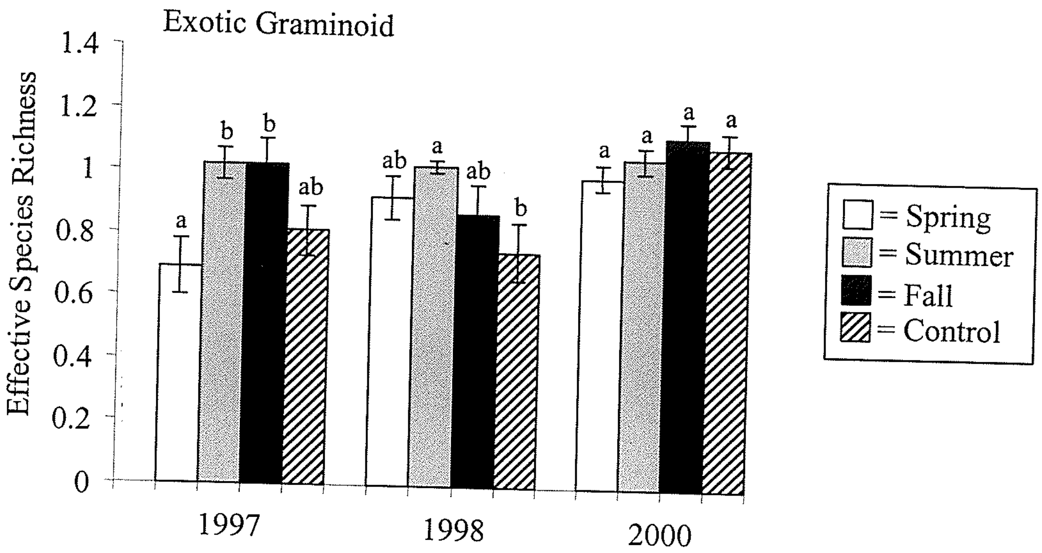
b)


Native Graminoid
Species Richness
6
5
4
3
2
1
0
1997
1998
2000
ab
b
a
b
a
b
bc
ac
a
a
a
b
□ = Spring
▨ = Summer
■ = Fall
▨ = Control

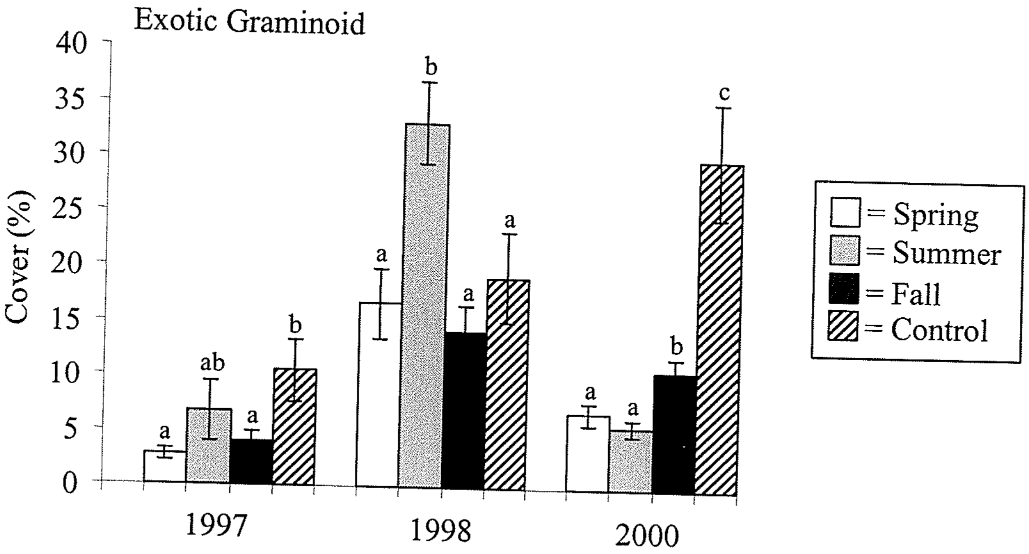
c)


Native Graminoid
Cover (%)
40
35
30
25
20
15
10
5
0
1997
1998
2000
a
b
ac
c
a
a
a
a
a
ab
bc
c
□ = Spring
▨ = Summer
■ = Fall
▨ = Control

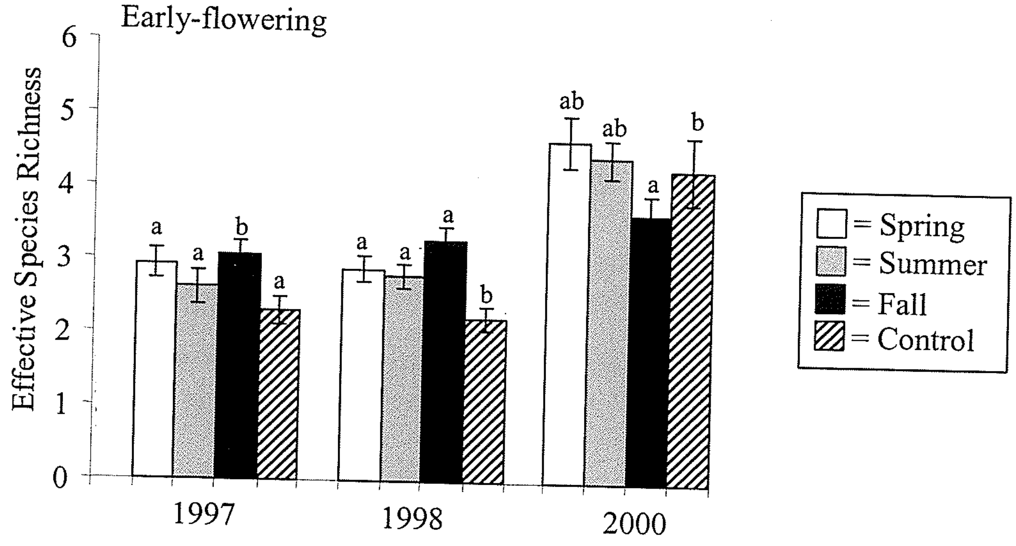
d)


Exotic Graminoid
Effective Species Richness
1.4
1.2
1
0.8
0.6
0.4
0.2
0
a
b
b
ab
ab
a
ab
b
a
a
a
a
1997
1998
2000
□ = Spring
▨ = Summer
■ = Fall
▨ = Control

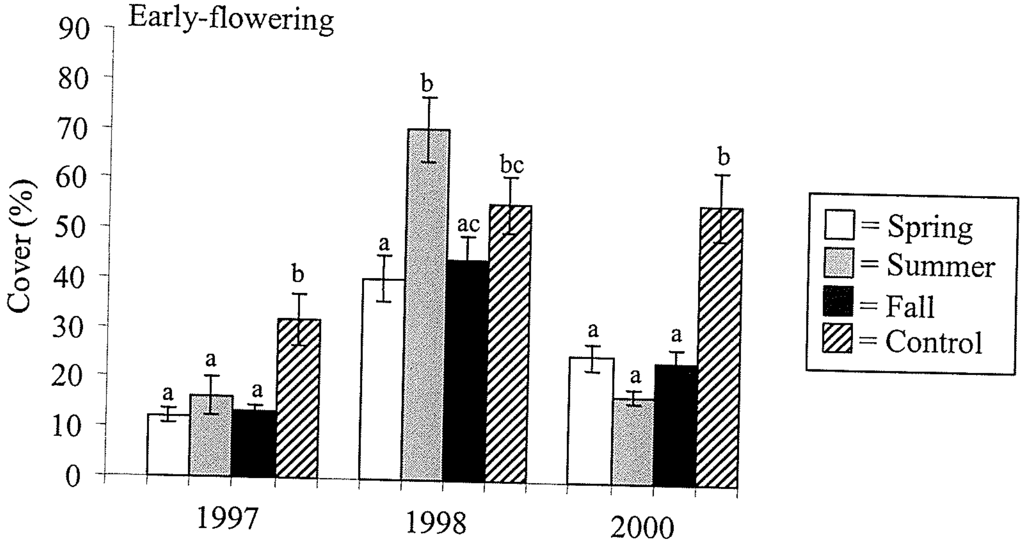
e)


Exotic Graminoid
Cover (%)
40
35
30
25
20
15
10
5
0
a
ab
a
b
a
b
a
a
a
a
b
c
1997
1998
2000
□ = Spring
▨ = Summer
■ = Fall
▨ = Control

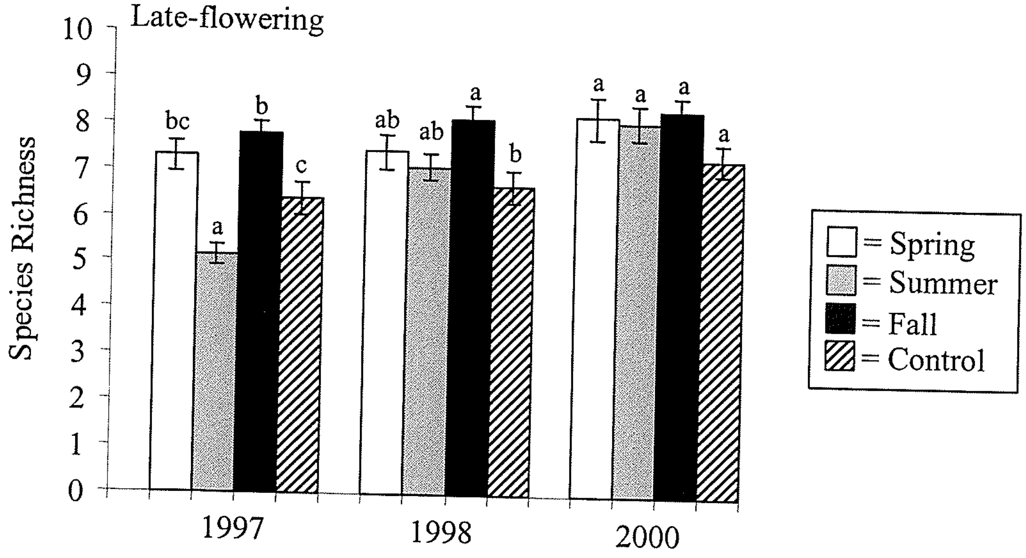
f)


Early-flowering
Effective Species Richness
0
1
2
3
4
5
6
a
a
b
a
a
a
a
b
ab
ab
a
b
1997
1998
2000
□ = Spring
▒ = Summer
■ = Fall
▨ = Control

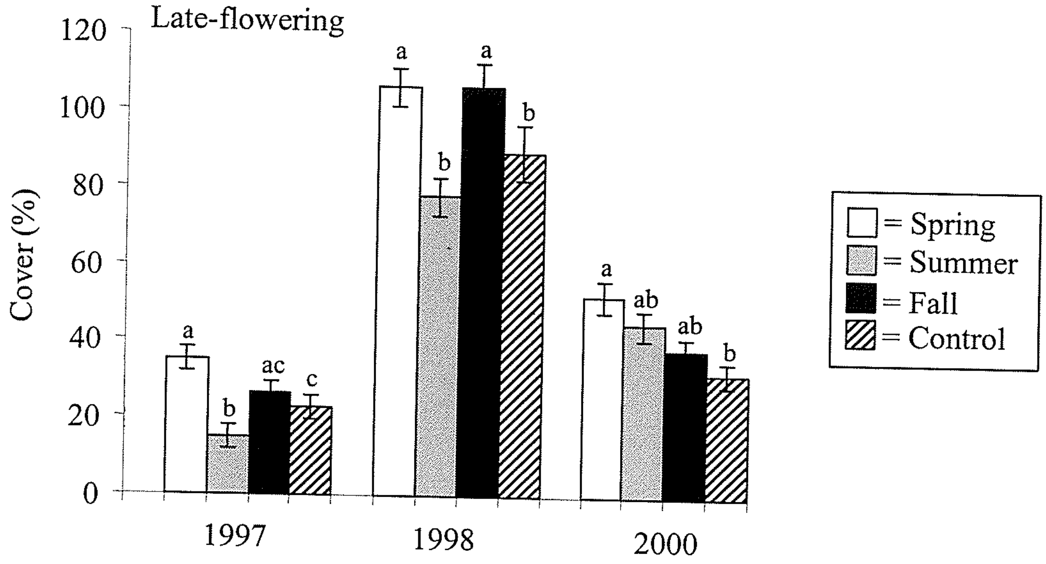
g)


Early-flowering
Cover (%)
0
10
20
30
40
50
60
70
80
90
a
a
a
b
a
b
ac
bc
a
a
a
b
1997
1998
2000
□ = Spring
▒ = Summer
■ = Fall
▨ = Control

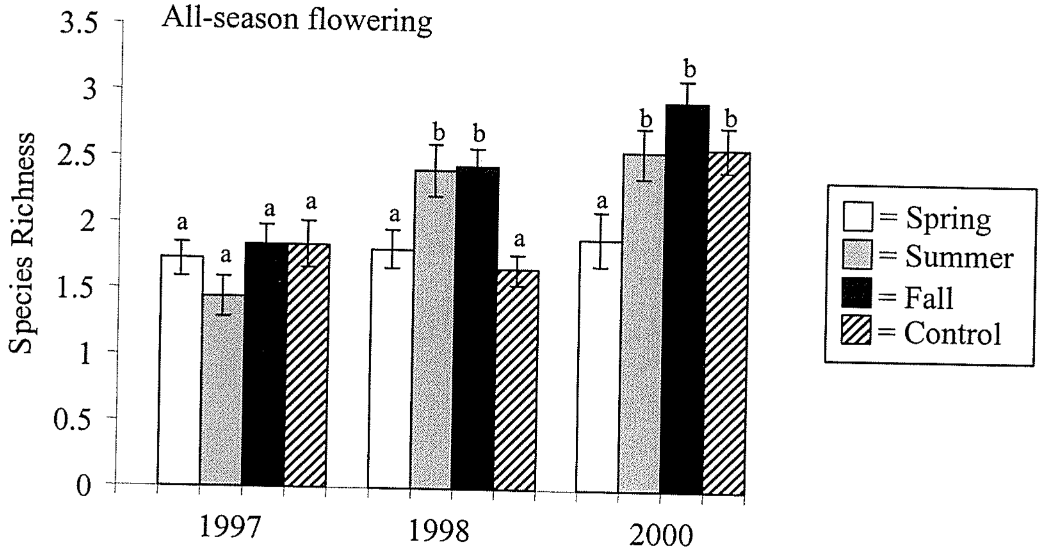
h)


Late-flowering
Species Richness
0
1
2
3
4
5
6
7
8
9
10
bc
a
b
c
ab
ab
a
b
a
a
a
a
1997
1998
2000
□ = Spring
▒ = Summer
■ = Fall
▨ = Control

i)


Late-flowering
Cover (%)
120
100
80
60
40
20
0
1997
1998
2000
a
b
ac
c
a
b
a
b
a
ab
ab
b
= Spring
= Summer
= Fall
= Control

j)


All-season flowering
Species Richness
3.5
3
2.5
2
1.5
1
0.5
0
1997
1998
2000
a
a
a
a
a
b
b
a
a
b
b
b
= Spring
= Summer
= Fall
= Control

k)

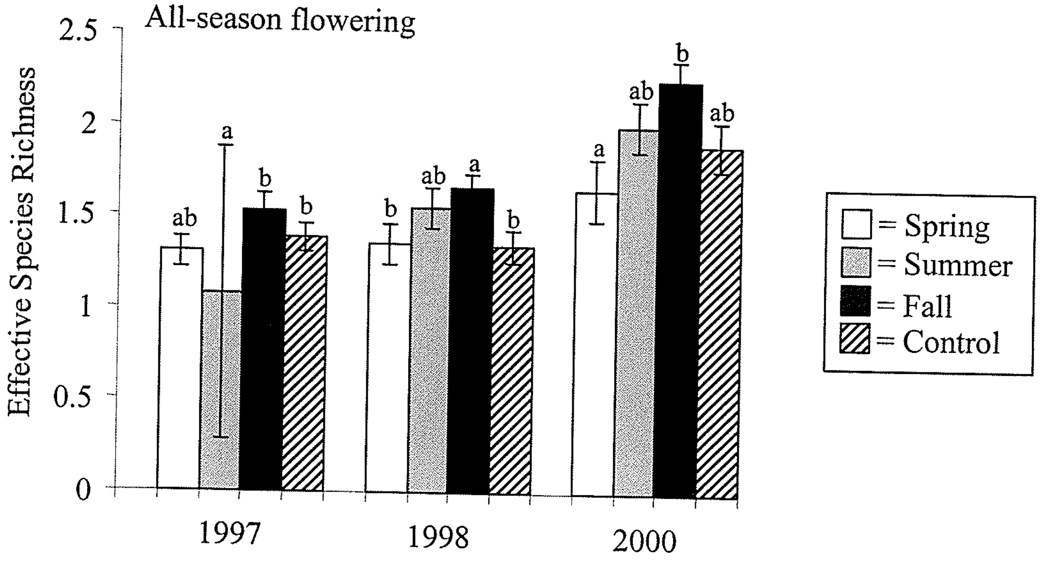

All-season flowering
Effective Species Richness
2.5
2
1.5
1
0.5
0
1997
1998
2000
ab
a
b
b
b
ab
a
b
a
ab
b
ab
= Spring
= Summer
= Fall
= Control

Table 3.2. Means (S.E.) individual species grouped according to origin (Org), growth form (Frm), and flowering phenology (Phen) in 1997, 1998, and 2000 for each burn-season and ANOVA results. Means followed by different letters indicates significant differences in a single year at $p<0.005$ according to Tukey's Multiple Means Test.

	Functional Guilds			Burn-season				ANOVA			
Species	Org[1]	Frm[2]	Phen[3]	Spring	Summer	Fall	Control	P-value	Blk[4]	Brn	Blk*Brn
Anemone canadensis	N	F	E	0.26 (0.13) bc	1.71 (0.65) a	0.95 (0.37) ab	0.08 (0.08) c	*****	*****	****	**
Astragalus agrestis	N	F	E	0.17 (0.09) a	0.65 (0.27) ab	1.09 (0.28) b	0.10 (0.08) a	***	*ns*	****	*ns*
Fragaria virginiana	N	F	E	0.70 (0.32)	0.15 (0.11)	0.17 (0.11)	0.08 (0.08)	*****	*****	*ns*	****
Glycyrrhiza lepidota	N	F	E	1.69 (0.65) a	0.13 (0.08) b	0.00 (0.00) b	1.70 (0.94) ab	***	*ns*	**	*ns*
Lithospermum canescens	N	F	E	0.08 (0.08) a	0.27 (0.11) ab	0.52 (0.16) b b	0.10 (0.08) a	*****	*ns*	**	****
Thalictrum venulosum	N	F	E	0.69 (0.15) a	2.91 (0.65) b	1.38 (0.18) ab	1.47 (0.33) a	*****	*****	****	**
Viola pedatifida	N	F	E	0.00 (0.00)	0.87 (0.19)	0.75 (0.16)	0.63 (0.16)	**	*	*ns*	*
Aster ericoides	N	F	L	1.46 (0.28) a	1.99 (0.43) a	5.12 (1.75) b	2.40 (0.81) a	*****	****	**	****
Aster laevis	N	F	L	1.95 (0.24) a	1.59 (0.27) ab	2.03 (0.24) a	1.11 (0.21) b	**	**	*	*ns*
Dalea purpurea	N	F	L	0.08 (0.08)	0.80 (0.32)	0.62 (0.32)	0.08 (0.08)	*	*ns*	*ns*	*ns*
Helianthus maximiliani	N	F	L	1.96 (0.83) a	0.22 (0.22) b	0.78 (0.78) b	1.74 (0.92) a	*****	*****	*****	*****
Helianthus subrhomboideus	N	F	L	2.22 (0.28) bc	3.18 (0.34) ab	4.58 (0.74) a	2.27 (0.62) c	***	*ns*	*****	*ns*
Monarda fistulosa	N	F	L	0.35 (0.13) a	0.65 (0.19) a	1.66 (0.37) b	0.64 (0.18) a	*****	*ns*	***	***
Psoralea esculenta	N	F	L	0.02 (0.02)	0.00 (0.00)	0.30 (0.23)	0.18 (0.11)	*	***	*ns*	*ns*
Solidago altissima	N	F	L	0.00 (0.00)	0.38 (0.24)	0.97 (0.89)	1.42 (0.80)	**	*ns*	*ns*	**
Solidago gigantea	N	F	L	0.23 (0.13) a	0.41 (0.16) ab	0.23 (0.13) a	2.23 (0.84) b	***	*ns*	**	*ns*
Solidago juncea	N	F	L	0.18 (0.11)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	*****	*ns*	*ns*	***

Table 3.2. Cont'd

	Functional Guilds			Burn-season				ANOVA			
Species	Org[1]	Frm[2]	Phen[3]	Spring	Summer	Fall	Control	P-value	Blk[4]	Brn	Blk*Brn
Solidago missouriensis	N	F	L	0.76 (0.27)	0.23 (0.11)	0.77 (0.20)	0.46 (0.16)	****	*ns*	*ns*	*****
Solidago rigida	N	F	L	1.92 (0.77) a	6.62 (1.90) b	6.16 (1.94) b	0.58 (0.25) a	*****	*****	*****	****
Allium stellatum	N	F	A	0.19 (0.09)	0.00 (0.00)	0.07 (0.04)	0.07 (0.04)	*	*ns*	*ns*	*ns*
Carex praticola	N	G	E	0.15 (0.09)	0.24 (0.09)	0.22 (0.09)	0.51 (0.16)	*	*ns*	*ns*	*ns*
Carex praegracilis	N	G	E	0.02 (0.02) c	0.40 (0.12) ab	0.55 (0.16) a	0.10 (0.08) bc	****	*ns*	****	*ns*
Carex tetanica	N	G	E	0.02 (0.02) a	0.00 (0.00) a	0.55 (0.26) b	0.02 (0.02) a	*****	**	****	*****
Panicum leibergii	N	G	E	1.85 (0.64) bc	2.37 (0.41) ab	2.53 (0.35) a	0.77 (0.20) c	*****	*****	*****	**
Stipa spartea	N	G	E	0.89 (0.57) ab	1.91 (0.89) ab	1.55 (0.36) a	0.58 (0.25) b	**	*ns*	*	*ns*
Andropogon gerardii	N	G	L	7.50 (2.50) ab	5.52 (1.88) ab	9.45 (2.19) a	4.19 (1.74) b	*****	*****	*	*ns*
Sporobolus heterolepis	N	G	L	7.83 (3.02)	9.07 (2.87)	8.45 (2.00)	7.85 (2.37)	*****	*****	*ns*	*ns*
Amelanchier alnifolia	N	W	E	0.23 (0.13)	0.00 (0.00)	0.31 (0.15)	0.16 (0.11)	**	*ns*	*ns*	**
Symphoricarpos spp.	N	W	E	6.22 (1.25) ab	9.11 (2.01) ab	4.13 (0.62) a	11.22 (2.34) b	**	*ns*	*	*ns*
Rosa spp.	N	W	A	3.61 (0.86)	3.09 (0.40)	2.44 (0.26)	4.94 (1.33)	**	*****	*ns*	*ns*
Cirsium arvense	E	F	L	0.50 (0.17)	0.40 (0.24)	0.00 (0.00)	0.46 (0.16)	*	*ns*	*ns*	*ns*
Bromus inermis	E	G	E	0.16 (0.11)	0.08 (0.08)	0.80 (0.32)	0.29 (0.22)	****	*ns*	*ns*	*ns*
Poa spp.	E	G	E	11.26 (2.54) ab	4.97 (0.84) bc	4.02 (0.87) c	22.82 (5.38) a	*****	*****	*****	*****

Org[1] N= Native; E = Exotic

Frm[2] F = Forb; G = Graminoid; W = Woody

Phen[3] E = Early-flowering; L = Late-flowering; and A = All season-flowering

[4] Blk = Block; Brn = Burn; and Y = Year

*****p <0.0001; ****p <0.0005; ***p <0.001; **p <0.005; *p <0.01; and *ns* >0.01

Fig. 3.3. Individual species means and standard error (S.E.) for percent cover in 2000. Only significant ANOVA results are shown and means followed by different letters indicates significant differences at $p<0.005$ according to Tukey's Multiple Means Test. Species include a) *Anemone canadensis*, b) *Aster ericoides*, c) *Panicum leibergii*, d) *Andropogon gerardii*, e) *Symphoricarpos* spp., and f) *Poa pratensis*.

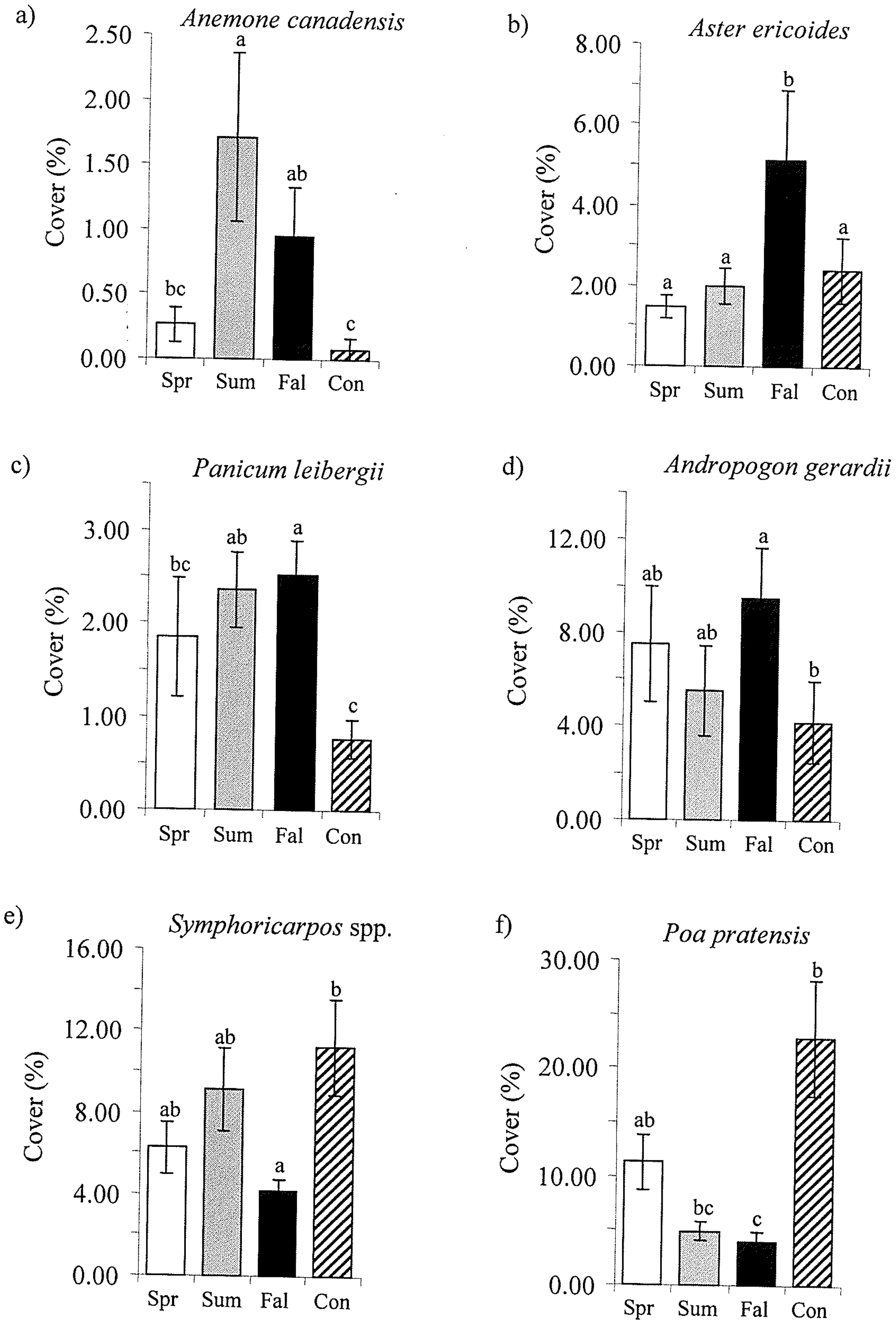
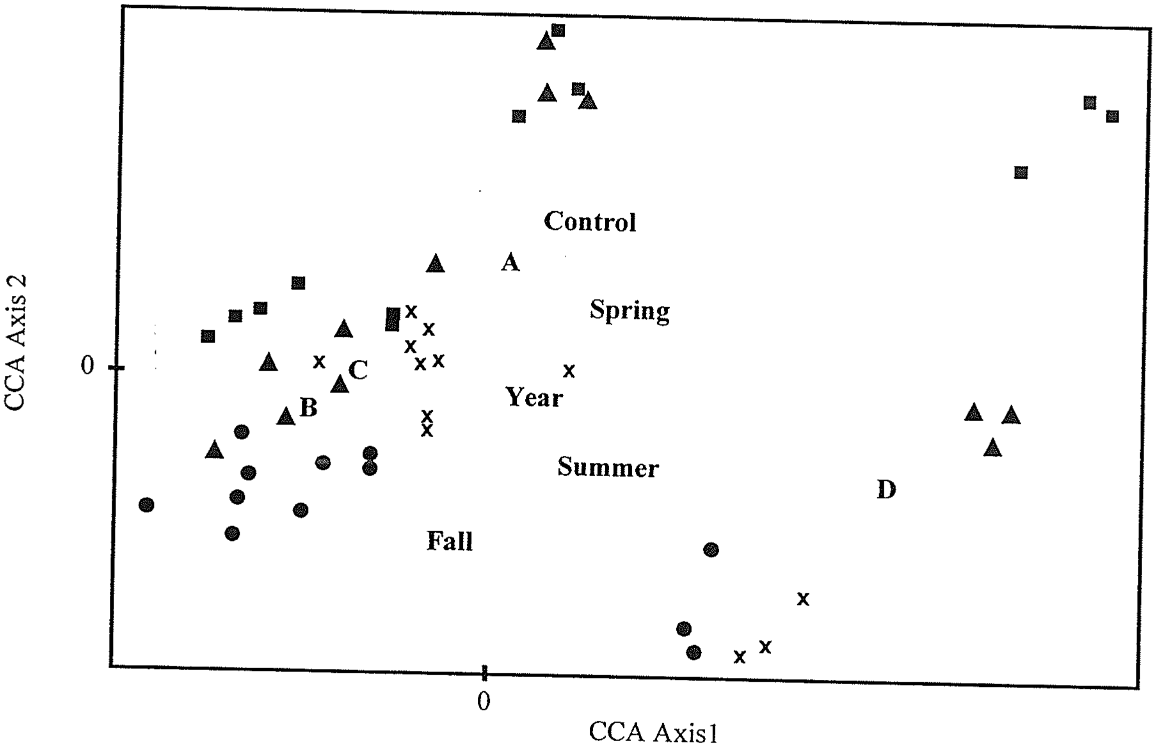

a)
Anemone canadensis
Cover (%)
2.50
2.00
1.50
1.00
0.50
0.00
bc
a
ab
c
Spr
Sum
Fal
Con
b)
Aster ericoides
Cover (%)
8.00
6.00
4.00
2.00
0.00
a
a
b
a
Spr
Sum
Fal
Con
c)
Panicum leibergii
Cover (%)
3.00
2.00
1.00
0.00
bc
ab
a
c
Spr
Sum
Fal
Con
d)
Andropogon gerardii
Cover (%)
12.00
8.00
4.00
0.00
ab
ab
a
b
Spr
Sum
Fal
Con
e)
Symphoricarpos spp.
Cover (%)
16.00
12.00
8.00
4.00
0.00
ab
ab
a
b
Spr
Sum
Fal
Con
f)
Poa pratensis
Cover (%)
30.00
20.00
10.00
0.00
ab
bc
c
b
Spr
Sum
Fal
Con

Fig. 3.4. Canonical correspondence analysis (CCA) ordination of a) treatment plots (n = 48) for all blocks (A, B, C, and D) and years (1997, 1998, and 2000) and b) associated aboveground species codes (Appendix 2), where spring-burn (triangle); summer-burn (letter x); fall-burn (circle) and; control (square). Species composition (p = 97) has been removed from the centre of the ordination.

a)


Control
A
Spring
C
B
Year
Summer
D
Fall
0
CCA Axis 2
0
CCA Axis1

b)

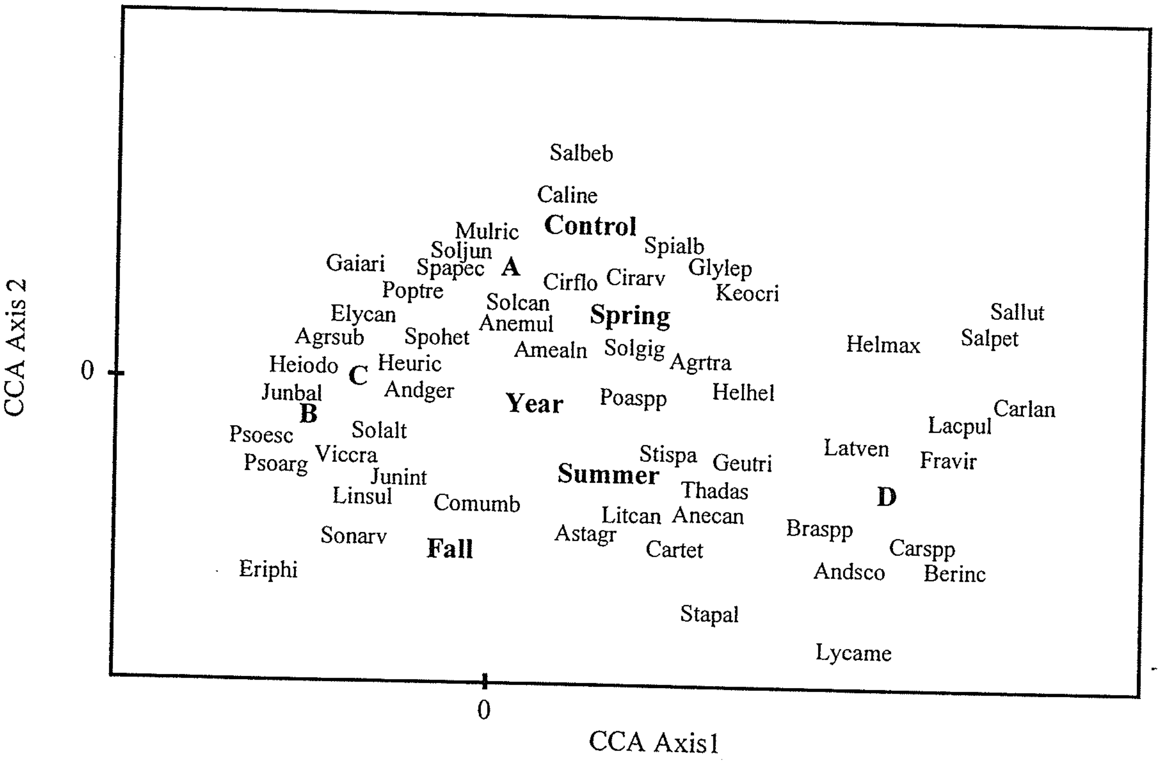
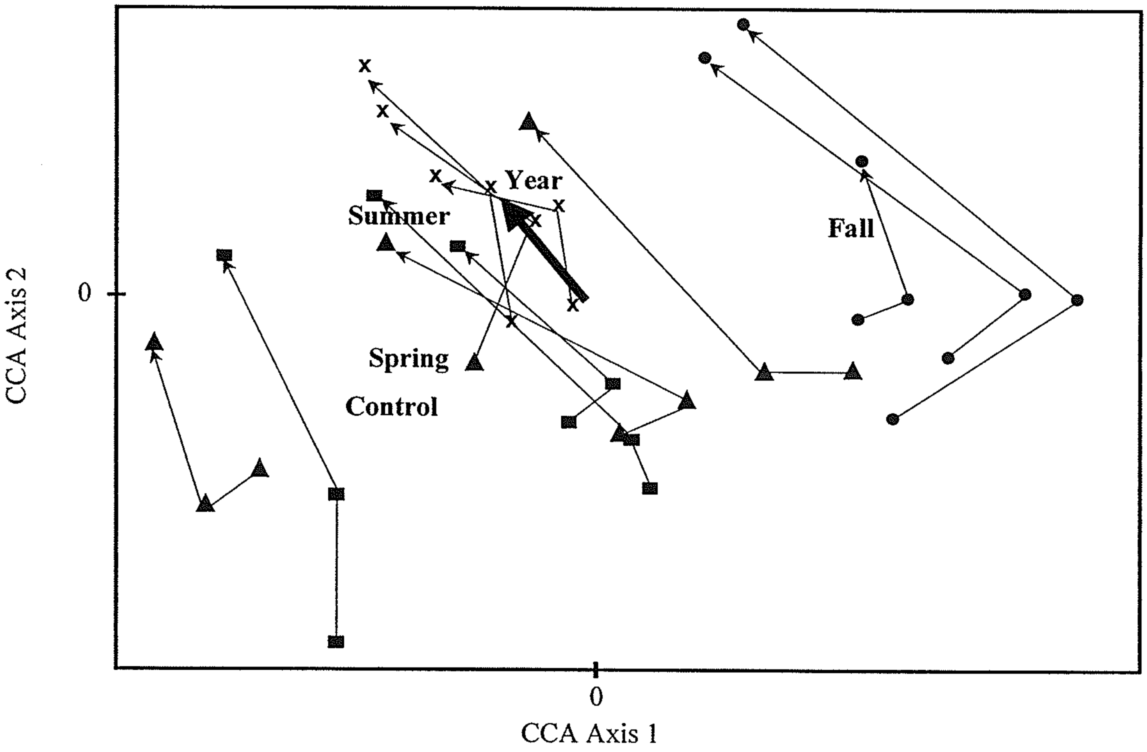
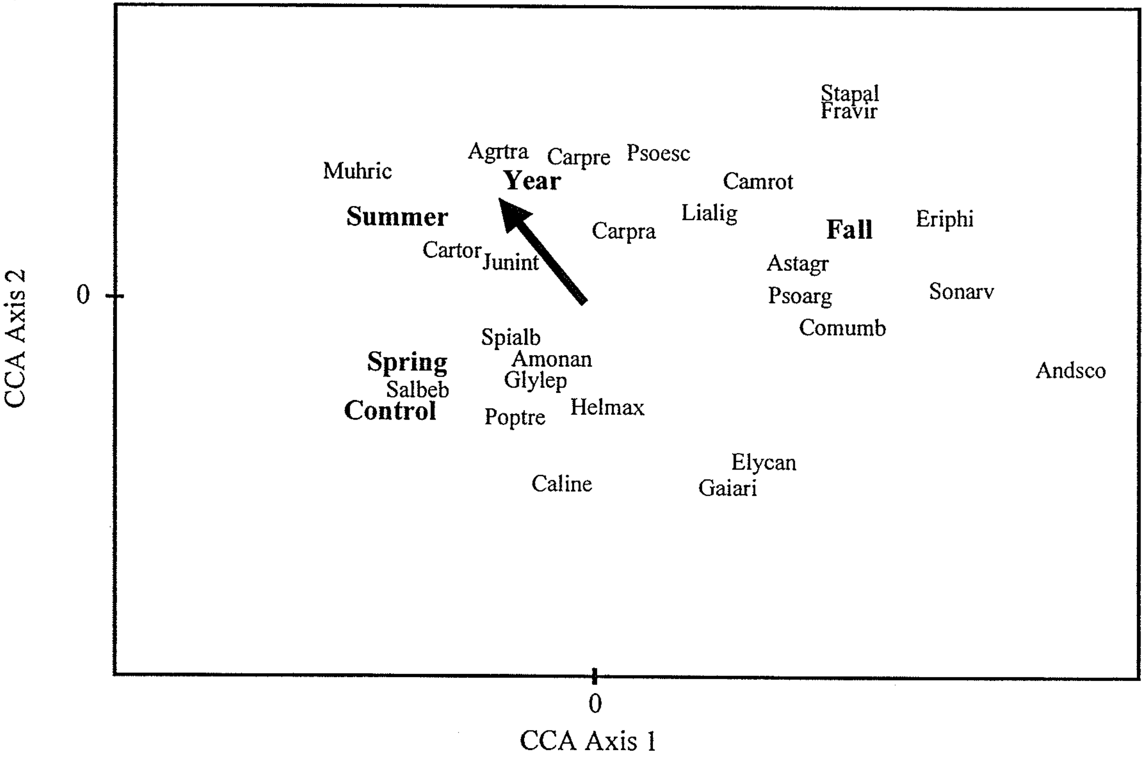

Salbeb
Caline
Mulric
Control
Soljun
Spialb
Gaiari
Spapec
A
Glylep
Cirflo
Cirarv
Poptre
Keocri
Solcan
Elycan
Anemul
Spring
Sallut
Agrsub
Spohet
Helmax
Salpet
Amealn
Solgig
Heiodo
C
Heuric
Agrtra
Junbal
Andger
Year
Poaspp
Helhel
Carlan
B
Lacpul
Psoesc
Solalt
Latven
Stispa
Geutri
Fravir
Psoarg
Viccra
Junint
Summer
Thadas
Linsul
Comumb
D
Litcan
Anecan
Sonarv
Astagr
Braspp
Fall
Carspp
Cartet
Eriphi
Andsco
Berinc
Stapal
Lycame
0
CCA Axis 2
0
CCA Axis1

Fig. 3.5. Canonical correspondence analysis (CCA) ordination of a) treatment plots (*n* = 36) for block A, B, and C and years (1997, 1998, and 2000) and b) associated aboveground species codes (Appendix 2), where spring-burn (triangle); summer-burn (letter x); fall-burn (circle) and; control (square). Species composition (*p* = 90) has been removed from the centre of the ordination.

a)


Year
Summer
Fall
Spring
Control
0
CCA Axis 2
0
CCA Axis 1

b)


Stapal
Fravir
Agrtra
Carpre
Psoesc
Muhric
Year
Camrot
Summer
Lialig
Carpra
Fall
Eriphi
Cartor
Junint
Astagr
Psoarg
Sonarv
Comumb
Spialb
Spring
Amonan
Glylep
Salbeb
Andsco
Control
Poptre
Helmax
Elycan
Caline
Gaiari
0
CCA Axis 2
0
CCA Axis 1

3.4. DISCUSSION

Burning is the dominant management practice in prairie conservation and restoration (Grace *et al.* 2002). When appropriately timed, it can be used to increase and maintain tallgrass prairie species diversity and suppress woody and exotic species invasion. Species dominance and persistence as well as changes in functional guilds and species composition are affected by burn-season (Howe 1995). Although much of the existing research on the effects of burning on tallgrass prairie focuses on dormant spring- and fall-burns (Risser *et al.* 1981), the importance of summer-burns is increasingly being explored (Copeland *et al.* 2002).

Burn-season effects

Tallgrass prairies in Manitoba are usually burned in May once runoff from snowmelt has occurred. Spring-burns are also traditionally used in rangeland (e.g. Anderson *et al.* 1970) and Military Reserve management (e.g. Shay *et al.* 2001) to increased dominant C_4 grass productivity (e.g. Collins 2002) and reduce the risk of wildfires, respectively. In this study, spring-burn had the least desirable effect on species diversity and composition. Although an anticipated decrease in exotic graminoid diversity and cover (e.g. Willson & Stubbendieck 1997) did occur, species composition in spring burns was relatively similar to the control and characterized by woody species including *Rosa* spp. and *Symphoricarpos* spp. Spring-burns on tallgrass prairie in Kansas also have negligible effects on woody species cover; indeed, some woody species, including *Amorpha canescens*, are favoured (Towne & Owensby 1984). Native graminoid species richness was also suppressed by spring-burn over the short-term, but had fully recovered three years after burning. These unusual responses may be attributed to the late timing, June 6, of the spring-burn, which was postponed because of a devastating 100-year flood. Other studies (e.g. Towne and Owensby 1984) also have found that responses to spring-burns is affected by burn date in ungrazed tallgrass prairie in Kansas and suggest burning earlier in the spring would reduce herb productivity, but promote species diversity and perennial forbs.

Summer-burns caused by lightning fires were historically common on large prairie tracts (Higgins 1984). Although less common, small-in-scale, and quickly extinguished by rain, they likely contributed to the landscape level patchiness of tallgrass prairies (Anderson 1997). They, however, are generally avoided in prairie management since they occur when dominant warm-season species are actively growing, thereby decreasing productivity of grass species that are important for livestock grazing (e.g. *Andropogon gerardii*) (Engle *et al.* 1998). Moreover, it is often assumed that summer-burns are ineffective because of low fuel, living plant tissue, and high moisture, especially on grazed prairies (e.g. Bragg 1982). However, they have the potential to increase subdominant early-flowering forbs and cool-season native and exotic grasses, in turn increasing overall species diversity (Howe 1994). They can also give early-season species a second autumn growing season, increasing plant vigor to be utilized the following growing season (Janer & Zedler 2001).

In general, graminoids including native *Carex* spp., *Juncus* spp. and exotic cool-season *Poa* spp. were favoured by summer-burns. Ewing and Engle (1988) also found that graminoids and exotic cool-season grasses respond favourably to summer-burns. If seedbanks are dominated by exotics, intense disturbance including fire may actually increase the prevalence of exotics and contribute to the further decline of desired species and functional guilds (Sveinson & McLachlan 2003, Appendix 1). That exotic species remained uncommon on this extant prairie following burning further emphasizes its high quality. In contrast, native forbs were suppressed by summer burning, as they tend to be more sensitive to disturbance than native graminoids (Willson & Stubbendieck 1996), have smaller populations and lower biomass (Briggs & Knapp 2001), and are susceptible to fire damage when actively growing (Howe 1994).

Fall-burn generally had the most favourable effect on species diversity and desired functional guilds in this high quality northern tallgrass prairie. Native forb and graminoid species diversity and cover were increased by fall-burn. Individual native forb (e.g. *Anemone canadensis* and *Aster ericoides*) and graminoid (e.g. *Andropogon gerardii* and *Panicum leibergii*) species also increased in cover with fall-burning, regardless of flowering-phenology. Grasses dominate this site, and fall-burning likely compromised their growth over the short-term, thereby reducing their competitiveness and promoting forb species growth and diversity. Forb diversity in northern mixed-grass prairie (Biondini *et al.* 1989) and forb cover in southern tallgrass prairie (Coppedge *et al.* 1998) were also enhanced by fall-burns. These findings seem to contradict those of other studies, in which early-flowering species are increased by fall-burns and late-flowering species by spring-burns (Anderson 1990; Howe 1994). Engle and Bidwell (2001) also found that tallgrass prairie plant responses to burn-season are highly variable and that other factors beyond phenology may be involved. These include differences in latitude, soil type, water and nutrient availability, burn interval, and species composition.

Woody cover was suppressed by fall-burn and to a lesser extent by summer-burn, whereas it was unaffected by spring-burns. Other studies suggest that summer-burns are effective at brush control (Anderson 1997), as fire damage is most severe while plants are actively growing and carbohydrate reserves are low (DeBano 1998). Woody species including *Rosa* spp. and *Symphoricarpos* spp. also responded similarly and cover tended to be lowest in the fall-burn. Woody species encroachment substantially contributes to the deterioration of tallgrass prairie (Mack & D'Antonio 1998; Heisler 2003) and effective short-term control is often achieved with burning (e.g. Leach & Givnish 1996). However, woody species were relatively uncommon in the treatment plots and further investigation into the effects of burn-season is needed.

Tallgrass prairies are characterized by low nitrogen and soil moisture as well as by high light (Knapp & Seastedt 1986), conditions that favour dominant warm-season grasses over forbs. Short-term increases in nutrient availability associated with burning, may promote native forb productivity in tallgrass prairie (Seastedt *et al.* 1991) because of their higher nitrogen requirement (Tuner & Knapp 1996). However, reductions in litter associated with burning increase dominant grass productivity at the expense of subdominant forb species (Vogel 1974; Howe 1994). Fall-burns are often criticized because of safety and unpredictable weather. It has also been suggested that they decrease productivity since they remove biomass prior to winter, thereby reducing the amount of trapped snow and increasing soil temperature, evaporation, and runoff in the spring (Willms *et al.* 1993). However, productivity in northern tallgrass prairie is not likely limited by soil moisture, especially during the years of above-average levels of precipitation experienced in this study. In contrast, it is limiting on northern mixed-grass prairies. Losses associated with burning far outweigh its benefits and thus, they are infrequently burned and usually in the spring (e.g. Shay *et al.* 2001).

Changes over time

In general, effects of burning on species composition, diversity and functional guilds were short-lived. An increase in native forb diversity was more pronounced for species richness than ESR, suggesting that rare or subdominant species are responding to fire and competitive release. Over time these subdominant species were displaced by dominant species, such as *Andropogon gerardii*, that can outshade shorter forbs (Hulbert 1969, 1988; Knapp & Seastedt 1986). Short-term increases in forbs have also been observed following late growing-season fire in mid-successional tallgrass prairie of Oklahoma (Engle *et al.* 1998). All burn treatments, except the fall-burn, increased in similarity as time-since-burning increased. Although burn effects may have been significant, vegetation was responding to other factors. Thus, an overall increase in woody cover, attributed to high precipitation, far out weighed vegetational responses to burn-season (e.g. Boindini *et al.* 1989; Coppedge *et al.* 1998).

Exotic forb cover showed a five-fold increased over time, even in the unburned controls. Although this increase also may have been associated with precipitation levels, it may also have been a research artifact. The parallel insect study (e.g. Wade 2003) required biweekly sampling over a six-month period, which resulted in trail creation, and in some cases trampling disturbance that was severe enough to remove vegetation. The later may have provided opportunities for weedy native or exotic species to colonize from the seedbank. Disturbed prairies are characterized by exotic species that are often ruderal and colonize effectively from the seedbank and seed rain following disturbance (Schott & Hamburg 1997). The characterization of both the seedbank and aboveground vegetation species composition can be important in determining future management practices and outcomes (Chapter 4).

When tracked over time, the effects of burn-season on flowering-phenology guilds was not as that of other studies (e.g. Howe 1994, Coppedge *et al.* 1998). Diversity of all flowering-phenology guilds were initially promoted by burning, regardless of burn-season. Early-flowering diversity was suppressed by all burn-seasons three years after burning, whereas no differences were found for late-flowering species. The latter are dominated by forbs, which tend to decline as time since burn increases as they are displaced by dominant late-flowering grass species (e.g. Briggs & Knapp 1995).

Limitations

This study suffered from some limitations, these, in part associated with differences in land use history across the study site. Block D has been ploughed in the 1930s and thus, differed in plant species composition from the other blocks, which were located in unbroken prairie. In contrast, no differences in spider diversity and composition were found (Wade 2003). Had vegetation been sampled prior to burning, vegetational changes associated with burn season would have been clearer. Site accessibility was also difficult, such that data were collected only once in year three, and thus could not be included in the analyses. This, in large part, was related to its being used as a military training facility, which prevents uncontrolled public access.

Management Recommendations

As habitat conversion for urban development continues, the protection and maintenance of SCRR is of extreme importance. The fact that high quality tallgrass prairie is found within the SCRR suggests current land-use has minimal impact. Very little tallgrass prairie remains within or near urban centres, especially in its northern region, and without active management these remnants are often degraded by surround land-use. Although military and conservation activities often conflict, SCRR provides an excellent opportunity for research, as the Department of National Defence (DND) is committed to ensuring the long-term persistence of this valuable tallgrass prairie.

Wildfires caused by training activities are of great concern for DND. Burning in the spring and fall can be used to reduce fuel buildup as well as promote diversity and reduce the dominance of competitive species (e.g. Collins & Steinauer 1998) at low-intensities (Connell 1978; Huston 1979). Although my results suggest fall-burns are most favourable, burn management plans should incorporate all burn-seasons to ensure all flowering-phenology (e.g. early, mid, and late) and growth form (e.g. forbs, graminoids, and woody) guilds are promoted. In addition, site- or region-specific constraints are crucial and must be considered, especially when dealing with endangered ecosystems such as tallgrass prairie. Characterization of the aboveground and belowground (i.e. propagule and seed banks) species composition prior to burning may prevent unexpected species responses (e.g. Sveinson & McLachlan 2003, Appendix 1) as well as help make informed decisions regarding burn-season. As information for this region is lacking, future efforts should be directed towards increasing the knowledge base and examine the roles of alterative management techniques, such as mowing and seeding, in tallgrass prairie management.

CHAPTER 4: Role of disturbance, soil fertility, and interseeding in rehabilitating degraded tallgrass prairie in southeastern Manitoba.

ABSTRACT

Most tallgrass prairie in North America has been eliminated by agriculture and urban development. Although extant prairie continues to be degraded by woody encroachment and invasion by exotics, little is rehabilitated, especially at the northern edge of its range. The objectives of this study were to assess how disturbance, fertilization, and interseeding might affect plant diversity and species composition, and how these treatment effects would change over time. In 1999, we initiated a replicated experiment in southeastern Manitoba, Canada. The main factor was herbicide (glyphosate), split factors were fertilizer (ammonium nitrate) and disturbance (mowing and burning), and the split-split factor was interseeding (seeding). Treatment-associated changes in plant diversity as well as the composition of species and guilds were compared to those of neighbouring high quality references sites. Glyphosate-treated plots were characterized by weedy and exotic species. Species richness and cover of exotic graminoids, including *Poa compressa*, were decreased by glyphosate whereas that of dominant weedy forbs, including *Potentilla arguta* and *Asclepias incarnata*, increased, their having been released from the seedbank. Native graminoids, including *Andropogon gerardii*, woody species, including *Rosa* spp., and forbs, including *Aster ciliolatus*, all were adversely affected by glyphosate. Mowing and burning had less effect than glyphosate, in large part because of long-term haying on this site. Dominant native warm season grass *A. gerardii* increased with mowing and decreased with fire, alone and when combined with glyphosate. In contrast, exotic graminoid *Poa compressa* increased with fire and decreased with mowing. Fertilizer increased native forbs *Aster ciliolatus* and *Solidago nemoralis,* native graminoid *Carex granularis*, and litter. In contrast, cover of exotic graminoid *Poa compressa* and native forb *Antennaria neglecta* declined Interseeding with native species increased native graminoid cover, decreased exotic graminoid cover, but had no overall effect on forbs. However, sown native forb species *Aster ericoides* and unsown graminoid *Panicum lanuginosum* both increased when seeding was combined with fire. In contrast, litter significantly declined with seeding, the latter only in the absence of fertilizer. Species composition of glyphosate treated plots became more similar to that of unsprayed and control plots over time, whereas effects of fertilizer and other disturbance factors showed relatively little change. Disturbance and fertilization can have desirable effect but only when seedbank and site-specific constraints have been identified. Effective techniques in rehabilitation are required if the degradation of existing and restored tallgrass prairie is to be mitigated.

***Key-words*:** exotic, fire, fertilizer, glyphosate, guild, mowing, restoration, seeding

4.1. INTRODUCTION

Most of the tallgrass prairie in Canada has been fragmented by agriculture and urbanization. Less than 1% of historical land cover in Manitoba remains, much of which is protected by a single preserve (CWHP 1998). Although these protection efforts are of fundamental importance, remnants are increasingly restored as they continue to be degraded by nutrient inputs, fire suppression, overgrazing by cattle, and invasion by exotic and woody plants. Most tallgrass prairie restoration is conducted as reconstruction, whereby new natural habitat is created (SER 2002). Although rehabilitation of already existing but degraded prairie habitat often has even greater potential for success (McDonald 2000), it receives relatively little attention in the literature. Prairie restoration is generally predicated on disturbing existing vegetation cover, in large part designed to decrease the dominance of exotic species as well as that of C_4 grasses. Historical disturbance types play a central role, most notably fire and grazing (e.g. Collins & Steinauer 1998; Howe 1999a), as well as management substitutes, including mowing (e.g. Howe 1999b; Bartels & Wilson 2001), herbicides (e.g. Choi & Pavlovic 1994; Wilson & Gerry 1995), and tillage (Morgan 1997; Wilson 2002).

Prescribed burns are commonly used throughout the tallgrass prairie region, tend to be adopted wherever logistically feasible, and vary according to intensity, timing, and frequency. Periodic low-intensity burns increase native species diversity and prevent competitive exotic and woody species from dominating remnants and restoration sites (Anderson 1990; Leach & Ginish 1996). Moreover, spring-burns increase the diversity of late-flowering species and fall-burns that of early-flowering species (Howe 1994). The productivity of dominant C_4 grasses also increases with spring-burns, at the expense of overall diversity, and especially the diversity of subdominant forbs (Davison & Kindscher 1999).

Effects of herbicides on existing tallgrass prairie are relatively unexplored, although they are commonly used to control weeds in degraded areas such as roadsides (Tyser *et al.* 1998) to deplete seedbanks prior to restoration, to increase productivity in rangelands (Engle *et al.* 1993), and to help establish warm-season grasses (Washburn *et al.* 1999). Their use in protected areas is often restricted as they can damage non-target or vulnerable species and, should seed banks be dominated by exotics, increase the presence of exotics (Sveinson & McLachlan 2003, Appendix 1).

Grazing also was an important disturbance type in the past (e.g. Vinton *et al.* 1993), but plays a less important role in tallgrass prairie restoration, and is increasingly being replaced by mechanical substitutes such as mowing and haying (Gibson *et al.* 1993; Collins & Steinauer 1998). Despite being relatively non-selective and uniform in impact (Clark & Wilson 2001; Janer & Zedler 2001), the latter is used effectively to manage high-priority endangered (Bartels & Wilson 2001), invasive (Solecki 1997), and woody (Leach & Givinish 1996) species. Mowing at stem elongation was effective in controlling *Bromus inermis* (Willson & Stubbendieck 1996), but had little effect on *Agropyron cristatum* (Romo *et al.* 1994), and some recent reviews question whether it preferentially favours native over exotic species (e.g. Wilson 2002). As with other forms of low intensity disturbance, mowing can reduce dominance of undesirable and dominant species, facilitating the emergence of uncommon and endangered species (Sveinson & McLachlan 2003, Appendix 1). Moreover, it and haying can also help reduce soil fertility in new restorations.

High soil nutrient levels are common in post-agricultural restoration sites and tend to increase the productivity of dominant warm-season grasses (Mitchell *et al.* 1996) at the expense of overall species diversity (Wilson & Tilman 1993). Under these conditions, introduced species tend to outcompete and displace native prairie species, which are adapted to nutrient-poor soils, further reducing overall diversity (McLachlan & Knispel 2003). Repeated haying reduces soil fertility (Schaffers *et al.* 1998), as do other soil impoverishment techniques including the use of sawdust and sugar (Morgan 1994; Gerry & Wilson 1995; Schultz 2001).

Although these prairie restoration techniques primarily focus on aboveground vegetation restoration, the composition of seed banks can have large ramifications for future vegetational change (Berger 1993). If seedbanks are dominated by exotics, disturbance of vegetation may actually increase the prevalence of exotics and contribute to the further decline of desired species (Sveinson & McLachlan 2003, Appendix 1). If prairie seedbanks are depauperate and sites are isolated, species can be introduced by broadcasting or, more successfully, drilling seed (Morgan 1997). Interseeding allows for the persistence of native species cover, and reduces the likelihood of soil erosion (Samson & Moser 1982; Packard 1997; Tharel *et al.* 2002) and subsequent invasion by exotics. However, interseeding is poorly understood and rarely used in reconstruction, in part because of its perceived inadequate control of exotic species (Wark *et al.* 1995).

The objective of this study was to determine the role of disturbance, soil fertility, and interseeding in rehabilitating degraded tallgrass prairie. I addressed four questions:

1. What are the differences in diversity and species composition for aboveground and seedbank components of degraded and neighbouring high quality prairie?
2. How do fertilization and disturbance factors including fire, mowing, and herbicide affect plant diversity and species composition?
3. What are the effects of interseeding on species composition and diversity?
4. How do these treatment-associated effects on vegetation change over time?

I anticipated that fertilization would decrease native diversity in undisturbed treatments; disturbance variables would increase native tallgrass prairie species, but only under nutrient-poor conditions; and seeding would increase native species richness, especially under disturbed and nutrient rich soil conditions.

4.2. METHODS

Study area and Site description

This three-year study was conducted within the Manitoba Tall Grass Prairie Preserve in southeastern Manitoba, Canada (49°15' N, 96 °45'W) (Fig. 2.5). This preserve is characterized by aspen and oak bluffs interspersed with prairies and sedge meadows, and surrounded by agricultural fields (Moore & Fortney 1994). It is 5,000 acres in area and contains over 300 vascular plant species. Low-lying areas are dominated by *Carex* species and drier uplands by *Andropogon gerardii* and *Sorghastrum nutans* (Borkowsky & Jones 1998). Much of the area escaped agricultural conversion due to the presence of large boulders, aspen groves, and wetlands.

The mean yearly daily temperature from 1971-2000, collected at the nearest meteorological station (49°32'N, 96°46W), was 2.7°C (36.86°F) (Environment Canada 2002). The mean daily temperatures in July and January over this time period were 19.1°C (66.4°F) and -17.4°C (68.0°F), respectively. The average annual rainfall was 440.2mm, approximately 40% falling in June and July, whereas average annual snowfall was 99.2cm, the majority of it falling between November and January.

In July 1999, we initiated a long-term replicated experiment on degraded tallgrass prairie. The annually hayed site was dominated by exotic grass species that included *Agrostis stolonifera*, *Poa compressa*, and *Bromus inermis* (Plate 4.1a). Native species were relatively less common and included *Andropogon gerardii*, *Carex granularis*, and *Solidago rigida*.

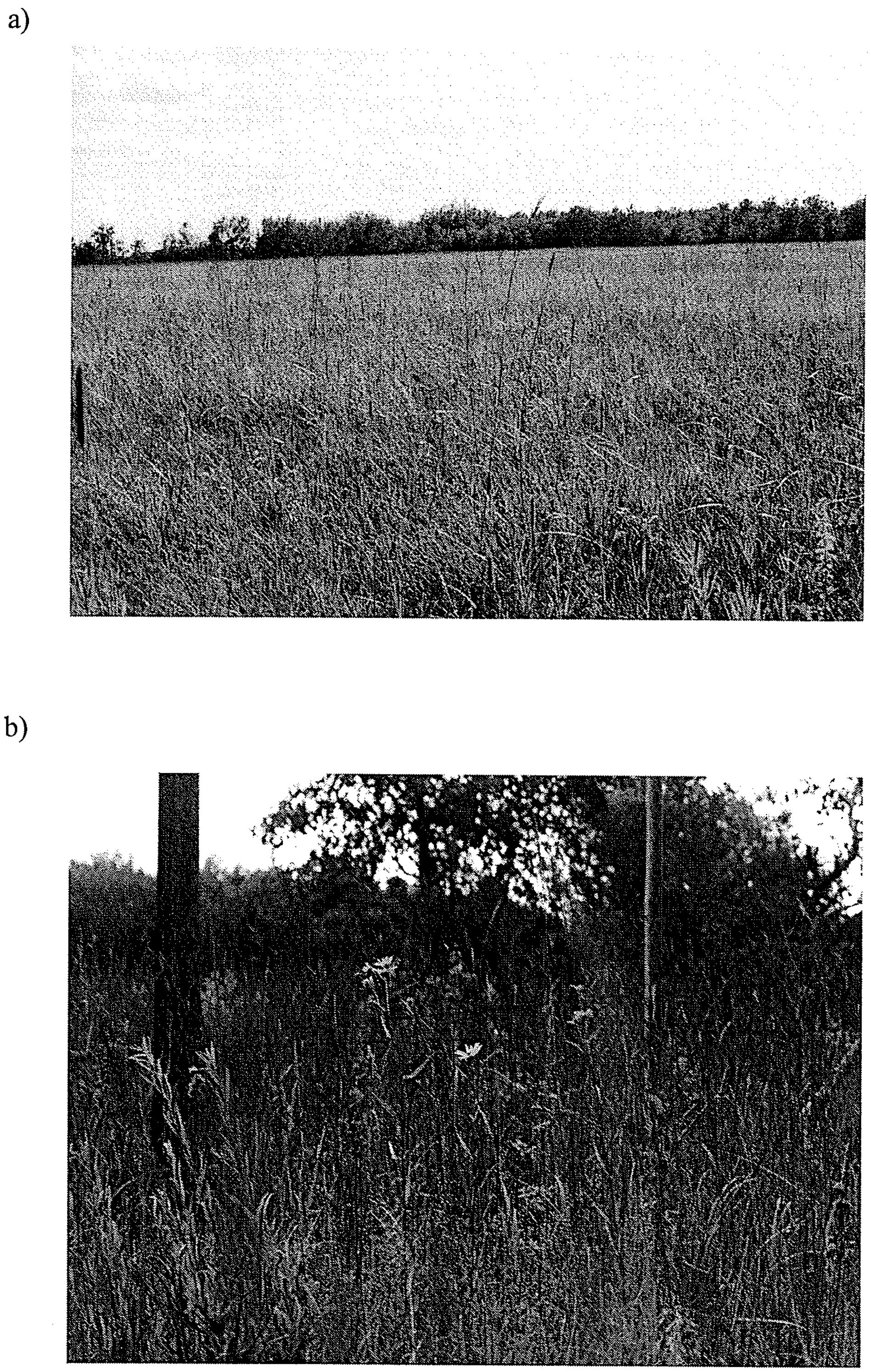


Plate 4.1. The Manitoba Tall Grass Prairie Preserve a) experimental and b) reference sites.

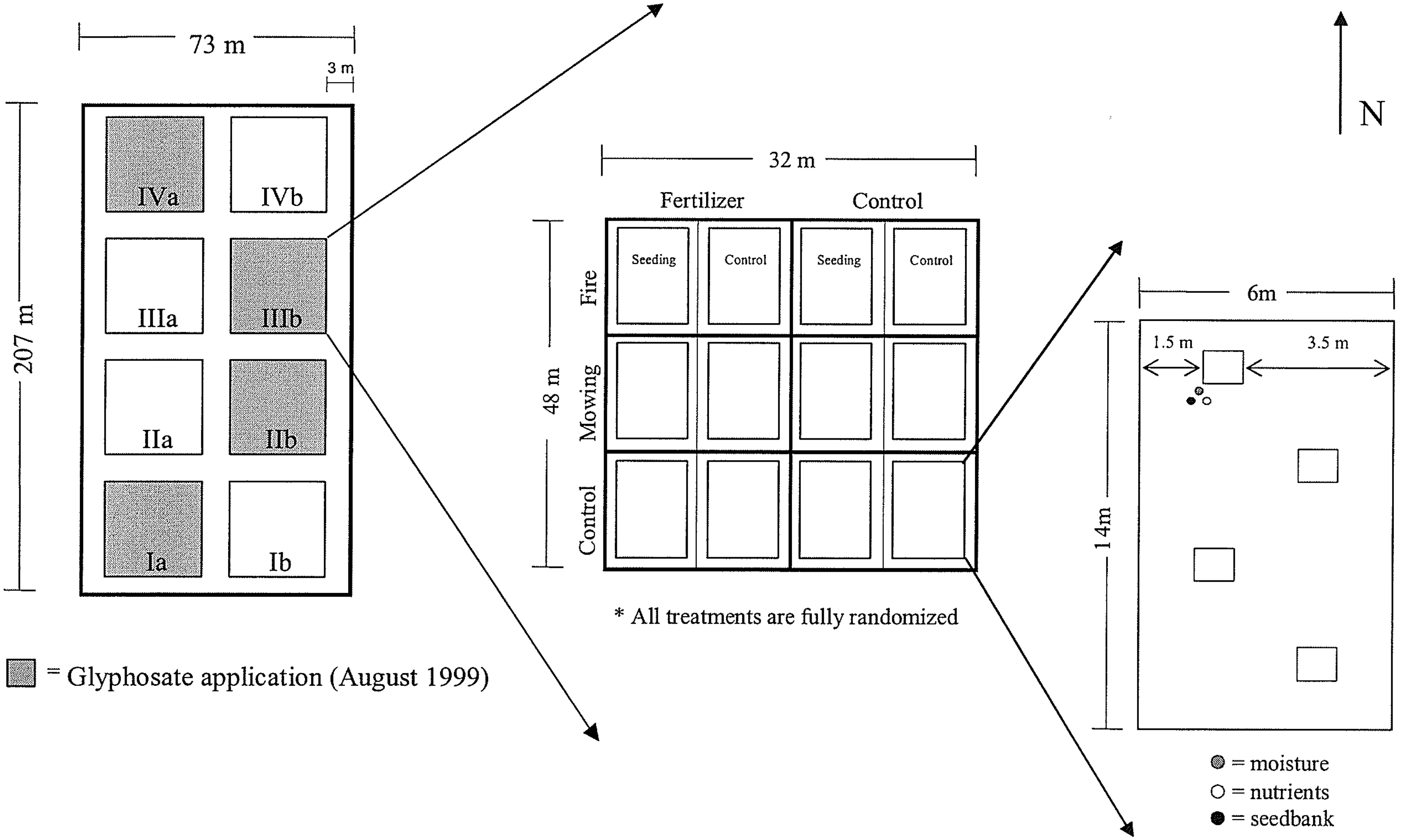
Experimental design

The four-times replicated experiment was 73m x 207m in size, and was conducted as a split-split-split design (Fig. 4.1). The main factor was herbicide (present, control). Glyphosate (Roundup®) was applied at 2 L/acre in August 1999 to each of the 32m x 48m main plots (Table 4.1). Although the site only was ranked "C" in quality (Moore 1996), provincially endangered *Spiranthes magnicamporum* emerged following herbicide application, precluding any subsequent tillage or herbicide use.

The split factors were fertilizer (present, control) and disturbance (mowing, burning, and control), these randomly applied within each of the main factor plots (Fig. 4.1). Each split plot was 6m x 14m in size and surrounded by a corridor 1m in width. Fertilizer, ammonium nitrate (34-0-0), was broadcast in May 2000 and 2001 at a rate of 14 g/m^2. Burning was conducted in October 2000, using headfires (i.e. burning with the wind) due to the lack of litter. Mowing was conducted in July and October 2000, and October 2001 (Table 4.1).

The split-split factor was interseeding (present, control), which, due to excessive moisture, was unavoidably delayed until October 2001 (Fig. 4.1). Randomized plots were mowed and raked in order to increase potential contact with mineral soil and seeded with a Truax native seed drill at 28 kg bulk seed/ha (25lbs/ac). Locally collected seed was used, and, by biomass, comprised 96% grasses and 4% forbs (Tables 4.2a & 4.2b). Dominant seed species, in order of importance, included *Elymus canadensis*, *Andropogon gerardii*, *Andropogon scoparius*, *Sorghastrum nutans*, *Veronicastrum virginicum*, *Solidago rigida*, and *Dalea purpurea*.

Fig. 4.1. The nested experimental design, including herbicide (glyphosate and control); soil fertility (ammonium nitrate and control); disturbance (fire, mowing, and control); and seeding introduction (seeding and control) as treatments and the location of 1m x 1m vegetation sampling quadrats and soil cores within each split-split-split plot.



* All treatments are fully randomized

Table 4.1. Schedule of disturbance, fertilizer, and seeding treatments and vegetation sampling from 1999 to 2002.

	1999						2000						2001						2002					
	May	June	July	Aug	Sept	Oct	May	June	July	Aug	Sept	Oct	May	June	July	Aug	Sept	Oct	May	June	July	Aug	Sept	Oct
Treatments																								
Glyphosate				▨																				
Fertilizer							▨						▨											
Mowing									▨			▨						▨						
Burn												▨												
Seeding																		▨						
Sampling																								
Restoration										▨						▨						▨		
Reference 1										▨														
Reference 2																▨								

Table 4.2a. Seeded native graminoid species ordered according to weight.

Species Name	**Common name**	**Weight (kg)**	**Proportion of mix**
Elymus canadensis	Canada wild rye	3.209	45.7
Andropogon gerardii	Big bluestem	2.015	28.7
Andropogon scoparius	Little bluestem	1.322	18.8
Sorghastrum nutans	Indian grass	0.372	5.3
Spartina pectinata	Prairie cord grass	0.064	0.9
Koeleria cristata	June grass	0.032	0.5
Sporobolus heterolepis	Prairie dropseed	0.007	0.1
Total Graminoids		7.022	100.0

Table 4.2b. Seeded native forb species ordered according to weight.

Species Name	Common name	Weight (g)	Proportion of mix
Veronicastrum virginicum	Culver's root	40.0	15.1
Solidago rigida	Stiff goldenrod	38.6	14.6
Dalea purpurea	Purple prairie clover	36.5	13.8
Solidago missouriensis	Low goldenrod	29.0	10.9
Anemone cylindrica	Long fruited anemone	24.8	9.4
Aster ptarmicoides	Upland aster	16.8	6.3
Geum triflorum	Three flowered avens	15.5	5.8
Gaillardia aristata	Gaillardia	13.0	4.9
Rudbeckia hirta	Black eyed Susan	11.0	4.1
Dalea candida	White prairie clover	10.0	3.8
Eupatorium maculatum	Joe pie weed	5.0	1.9
Galium boreale	Northern bedstraw	4.8	1.8
Aster ericoides	Many flowered aster	4.0	1.5
Antennaria neglecta	Field pussy-toes	3.0	1.1
Anemone multifida	Cut leaved anemone	2.5	0.9
Sisyrinchium montanum	Blue eyed grass	2.4	0.9
Artemisia ludoviciana	Prairie sage	2.0	0.8
Liatris ligulistylis	Meadow blazingstar	1.5	0.6
Heuchera richardsonii	Alumroot	1.0	0.4
Gentiana andrewsii	Closed gentian	1.0	0.4
Aster novae-angliae	New England aster	1.0	0.4
Campanula rotundifolia	Harebell	0.6	0.2
Zigadenus elegans	Smooth camas	0.6	0.2
Penstemon gracilis	Lilac flowered penstemon	0.5	0.2
Total Forbs		265.1	100.0

Two adjacent high-integrity remnants were used as reference sites to identify the desirability of inevitable treatment-associated changes in vegetation (Plate 4.1b). Both reference sites were dominated by native species that included *Andropogon gerardii*, *Carex* spp., and *Solidago rigida*. One reference site (Ref 1) was also characterized by native species *Galium boreale* and *Deschampsia caespitosa* and the other (Ref 2) by exotic *Agrostis stolonifera* and native *Juncus* species.

Biotic sampling

Absolute percent cover (i.e. the ground cover within a defined area which is occupied by the above-ground parts of each species when viewed from above) (Kent & Coker 1992) of all plant species was sampled within four randomly assigned permanent 1m x 1m quadrats within each split-split plot ($n = 384$) (Fig. 4.1) in late August 2000, 2001, and 2002 during the peak growth of dominant species. The spatial arrangement of the 16 1m x 1m control split-split plots was replicated in and used to characterize each reference site. Percent cover of all plant species was sampled for Ref 1 and Ref 2 in August 2000 and 2001, respectively.

To assess seedbank species composition, four 3 cm x 15cm soil cores were collected from the corner of each split-split plot for both restoration ($n = 384$) and Ref 1 sites ($n = 16$) in July 2000. Samples were combined with an equal proportion of sterile mix (Sunshine Mix 4 Aggregate Plus) and spread on top of 10cm x 15cm x 8cm pots, which were randomly located in trays within the greenhouse. Ten control pots, containing only sterile mix, were interspersed among the experimental pots to monitor greenhouse contamination. Pots were maintained under a 16-hour photoperiod at 25°C day/10°C night temperatures, and watered weekly. As seedlings emerged, they were identified according to Royer and Dickinson (1999) and Looman and Best (1987) and removed. Unidentified seedlings were transplanted and maintained until flowering or identification was possible. When emergence was exhausted (2 to 4 months), pots were cold-stratified at 2°C (36°F) for six weeks. When returned to the greenhouse, soil was stirred to promote seed germination and pots again randomly located within the greenhouse. Pots were cold stratified twice after which emergence had largely ceased, and the germination trials ended after 13 months.

Abiotic sampling

To estimate soil nutrient status, soil cores were collected in August 2000. Four 3 x 15 cm soil cores were collected from the centre of each main treatment plot ($n = 32$) and duplicated control plots ($n = 16$) at the restoration and Ref 1 sites, respectively. Samples from each plot were homogenized, dried, ground, and sieved through a 2 mm screen to remove plant material and rock. Soil texture (i.e. percent sand, silt, and clay) was estimated using the Boucycous Hydrometer Method on four randomly selected samples from each main plot. Conductivity and pH were measured in a 2:1 deionized water:soil slurry using an ohmmeter for conductivity and a standard hydrogen electrode for pH (Karla & Maynard 1991). Organic matter was estimated using the weight loss on-ignition method. Soil nitrate was determined using spectroscopy on sample 2.0 M KCl extracts (Carter 1993).

To assess soil moisture, soil cores were collected in August 2001. Four 3cm x 15cm soil cores ($n = 32$) were collected from each main plot of restoration site and the matching control plots at Ref 1 and Ref 2 ($n = 16$). Cores were immediately weighed and subsequently oven-dried at 50°C for 24 hours, or until no further weight loss was observed, and reweighed to determine gravimetric water content (Black 1965).

Statistical analysis

Treatment-associated changes in diversity were estimated using Hill's (1973) diversity measures, consisting of N_0 (i.e. species richness), which is the total number of species and is sensitive to rare species, and N_2 (i.e. effective species richness), which is the reciprocal of Simpson's index and emphasizes dominance. Species also were categorized according to functional guilds, these including origin (native or exotic); growth form (graminoid, forb, or woody). Delays in treatment application precluded repeated measures analysis, thus differences in plant diversity, species composition, and guilds among sites and treatments were assessed using one-way ANOVA for 2002 data (SAS 1988) (Appendix 3). All data were log transformed to meet the assumptions of ANOVA (Zar 1999) and original data are presented. Post-hoc Tukey's tests ($\alpha = 0.05$) were used to separate means when overall treatment effects were significant ($\alpha = 0.01$). Differences in seedbank N_0, N_2 and density (number of seedlings/33cm^3) between the restoration and Ref 1 were assessed using t-tests.

Changes in species composition of reference and restoration sites were examined using correspondence analysis (CA), a multivariate statistical method that maximally separates samples according to differences in species composition (ter Braak 1990).

Canonical correspondence analysis (CCA) was further used to determine relationships among species composition, site, and the constraining treatment and year variables (ter Braak 1987). The CCA is a direct ordination technique that maximally separates samples according to differences in species composition and then constrains them to independent variables. Species were only included if they occurred in more than one treatment plot. Data were log +1 transformed and rare species down-weighted.

4.3 RESULTS

Baseline site evaluation

Abiotic Measurements

Pre-treatment soil characteristics of the restoration and Ref 1 sites generally were similar to each other (Table 4.3). No significant differences were found either for soil texture (i.e. percent sand, silt, and clay) or for pH and nitrate. However, soils from Ref 1 had 50% greater organic matter ($p<0.01$) and gravimetric soil moisture ($p<0.01$) as well as higher conductivity ($p<0.05$) than those of the restoration (Table 4.3). Gravimetric water content also varied significantly ($p<0.001$) across the experimental blocks at the restoration, ranging from 19% in Block 1 to 12% in Block 4. Indeed, Block 1 was covered by standing water in 2001, which precluded subsequent seeding and vegetation sampling.

Biotic Measurements

Aboveground diversity

Diversity and percent cover of native aboveground plant species, when grouped according to origin and growth form guilds, differed between restoration and reference sites (Table 4.4). Both reference sites had significantly greater native graminoid species richness ($p<0.0001$), effective species richness ($p<0.01$), and cover ($p<0.001$) than the restoration. Native forb diversity and cover were similar across all sites, although species richness and effective species richness tended to be greater in Ref 1 (Table 4.4). Native woody species were relatively uncommon on Ref 1 and restoration, whereas Ref 2 had the highest native woody diversity and cover.

Aboveground exotic species were generally much more prevalent at the restoration (Table 4.4). Exotic graminoid species richness, effective species richness, and cover were significantly greater ($p<0.0001$) than those of the reference sites. Moreover, exotic forb species richness ($p<0.0001$), effective species richness ($p<0.001$), and cover ($p<0.001$) were also greater at the restoration (Table 4.4).

Seedbank diversity

In general, graminoids accounted for 60% of all species in the seedbank. Seedbanks of the reference sites were dominated by native and those of the restoration by exotic species (Table 4.4). Unlike aboveground vegetation, native forb species richness and effective species richness ($p<0.0001$) and density ($p<0.001$) of the seedbank were significantly greater in the reference site; indeed, no native forbs emerged from the restoration seedbank. Native graminoid density was significantly ($p<0.01$) greater for the restoration, whereas species richness and effective species richness were similar for both sites. As with the aboveground, exotic graminoids species richness ($p<0.01$), effective species richness ($p<0.001$), and density ($p<0.0001$) were significantly greater in the restoration, whereas, exotic forbs only tended to be more prevalent (Table 4.4).

Aboveground species composition

Species composition differed substantially between reference and restoration sites (Fig. 4.2a). Correspondence analysis (CA) axes 1 and 2 accounted for 18.9% and 14.9% of the variation, respectively, and represented 33.8% of the total variation within the species data. Ref 1 was positively associated with axis 1 (Fig. 4.2a) and characterized by native *Astragalus agrestis*, *Glycyrrhiza lepidota*, *Campanula rotundifolia*, and *Andropogon scoparius* (Fig. 4.2b). In contrast, the restoration was negatively associated with axis 1 and characterized by exotic *Trifolium repens*, *Festuca elatior*, *Trifolium pratense*, and *Bromus inermis*. Axis 2 was positively associated with Ref 1, these again including the native *A. agrestis*, *C. rotundifolia*, and *A. scoparius*. In contrast, axis 2 was negatively associated with the both reference sites, these being characterized by species found in wet habitats including *Muhlenbergia richardsonis*, *Melilotus* spp., *Deschampsia caespitosa*, and *Calamagrostis inexpansa* (Fig. 4.2b).

Seedbank species composition

Seedbank composition also differed between the reference and restoration sites (Fig. 4.3a). In general, the restoration was characterized by native and exotic graminoids, and Ref 1 by native graminoid and forbs. Correspondence analysis (CA) axes 1 and 2 accounted for 19.4% and 14.2% of the variation, respectively, and represented 33.6% of the total variation within the seedbank data. Ref 1 was positively associated with axis 1 and characterized by native graminoid species *Panicum leibergii*, *Andropogon scoparius*, and *Deschampsia caespitosa*. In contrast, the restoration was negatively associated with axis 1 and characterized by native graminoids *Carex granularis*, *Andropogon gerardii*, and exotic forb *Brassica* sp. (Fig. 4.3b). Axis 2 was positively associated to the restoration and characterized by weedy and exotic graminoids *Bromus inermis*, *Juncus interior*, and *Agrostis stolonifera*. In contrast, Ref 1 was negatively associated with axis 2 and was characterized by native species *Allium stellatum*, *Galium boreale*, and *C. granularis* (Fig. 4.3b).

Restoration outcomes

Treatment effects on diversity

Treatments had significant effects on diversity and all functional guilds, especially native forbs (Table 4.5). Three years after application, glyphosate significantly decreased native forb species richness ($F_{1,2} = 55.80$, $p = 0.0175$) and cover ($F_{1,2} = 16.22$, $p = 0.0561$), as well as native woody species cover ($F_{1,2} = 25.83$, $p = 0.0366$). Whereas exotic graminoid effective species richness also decreased ($F_{1,2} = 18.04$, $p = 0.0512$) with glyphosate, exotic forb effective species richness increased ($F_{1,2} = 39.47$, $p = 0.0244$). In general, fertilizer and disturbance treatments had little effect on functional guilds. Seeding, in contrast, significantly increased native graminoid cover ($F_{1,24} = 16.22$, $p = 0.0005$) and decreased exotic graminoid cover ($F_{1,24} = 5.62$, $p = 0.0261$) (Table 4.5). Exotic forb effective species richness showed a significant ($F_{1,24} = 7.42$, $p = 0.0118$) interaction between glyphosate and seeding, decreasing only when both seeded and sprayed with glyphosate (Table 4.5).

Treatment effects on species composition

Disturbance, fertilization, and seeding all had a significant impact on species composition (Table 4.6). CA axes 1 and 2 accounted for 28.6% and 3.2% of the variation, respectively, and represented 31.8% of the total variation within the species data. When constrained by the environmental treatments in canonical correspondence analysis (CCA), the species-environment correlation values were 0.955, 0.832, 0.589, and 0.583 for axes 1, 2, 3, and 4 respectively (Table 4.6). Glyphosate was positively correlated with CCA axis 1 (Fig. 4.4a) and was characterized by weedy and exotic species *Epilobium* spp., *Potentilla arguta*, *Asclepias incarnata* and *Setaria glauca* (Fig. 4.4b). No-glyphosate plots were characterized by desirable native forb species including *Helianthus maximiliani*, *Smilacina stellata*, *Gentiana andrewsii*, and the native graminoid *Andropogon gerardii* (Fig. 4.4b). Fertilizer was positively correlated with CCA axis 2 (Table 4.6), and was characterized by native *Juncus balticus*, *Zizia aptera*, *Asclepias ovalifolia*, and exotic *Polygonum* spp. Non-fertilized plots were associated with native *Salix* spp., *Galium boreale*, *Astragalus agrestis*, and *Asclepias incarnata* (Fig. 4.4b). Fire was positively associated with CCA axis 3 (Table 4.6) and characterized by *A. incarnata* and *Juncus balticus* and interseeding negatively associated with CCA axis 3 (Table 4.6) and characterized by *Deschampsia caespitosa* and *Apocynum cannabinum* (data not shown). In turn, mowing was positively associated with CCA axis 4 (Table 4.6) and characterized by *Erigeron canadensis*, *Cirsium flodmanii*, and *Ranunculus* spp. (data not shown).

When species were examined separately, 11 species and litter responded significantly to treatments (Table 4.7). Glyphosate significantly reduced cover of native forb *Aster ciliolatus* ($F_{1,2} = 22.31, p = 0.0420$), graminoid *Andropogon gerardii* ($F_{1,2} = 18.47, p = 0.0501$), and woody *Rosa* spp. ($F_{1,2} = 28.62, p = 0.0332$). The exotic graminoid *Poa compressa* ($F_{1,2} = 15.76, p = 0.0580$) also decreased whereas graminoids that increased in glyphosate plots included native *Carex granularis* ($F_{1,2} = 60.84, p = 0.0160$) and exotic *Agrostis stolonifera* ($F_{1,2} = 145.83, p = 0.0068$).

Other disturbance types also had a significant effect on *Poa compressa* and *Andropogon gerardii* (Table 4.7). Exotic graminoid *P. compressa* was significantly ($F_{2,24} = 4.51, p = 0.0219$) increased by fire and decreased by mowing. Conversely, native graminoid *A. gerardii* was significantly increased by mowing and decreased by fire ($F_{2,24} = 3.29, p = 0.0546$). *Andropogon gerardii* was also decreased when these disturbance treatments were combined with glyphosate, although, alone, the latter had a significantly adverse effect on the cover ($F_{2,24} = 3.29, p = 0.0546$). Despite these interactions, its cover was greatest in the untreated control plots.

Fertilizer significantly increased percent cover of native forbs *Aster ciliolatus* ($F_{1,24} = 5.36, p = 0.0294$) and *Solidago nemoralis* ($F_{1,24} = 4.20, p = 0.0515$), and litter ($F_{1,24} = 9.74, p = 0.0047$) (Table 4.7). However, litter decreased in cover when fertilizer was combined with glyphosate. In contrast, fertilization decreased the cover of exotic graminoid *P. compressa* ($F_{1,24} = 4.21, p = 0.0512$). and native forb *Antennaria neglecta* ($F_{1,24} = 21.72, p < 0.0001$)., and the latter was almost entirely removed when fertilizer was combined with glyphosate.

Seeding significantly increased sown native forb species *Aster ericoides* ($F_{1,24} = 4.90, p = 0.0366$) (Table 4.7). Unsown native graminoid *Panicum lanuginosum* also increased ($F_{1,24} = 10.27, p = 0.0038$) with seeding when combined with fire, but decreased when seeding was combined with mowing ($F_{2,24} = 4.33, p = 0.0249$). Exotic forb *Prunella vulgaris* significantly declined with seeding, although it increased when seeding was combined with glyphosate ($F_{1,24} = 9.41, p = 0.0053$). Litter was also significantly decreased by seeding, but only in the absence of fertilizer ($F_{1,2} = 6.98, p = 0.0143$).

Restoration changes over time

The one-time application of glyphosate had a strong effect on species composition (Fig. 4.5a). Over time, the species composition of glyphosate treated plots predictably became more similar to that of plots of unsprayed as well as reference sites, changing from weedy ruderal species to ones that are characteristic of poor-to- intermediate habitat quality (Fig. 4.5b). Species associated with glyphosate treated plots sampled in 2000 included exotic *Setaria glauca*, *Erigeron canadensis*, and *Epilobium* spp. as well as weedy native *Potentilla arguta*, *Oenothera biennis*, and *Panicum capillare*. Three years later, native species were still rare but *Rudbeckia hirta*, *Solidago graminifolia*, and *Achillea millefolium* had become established. Exotics also remained, but now included *Trifolium repens*, *Medicago lupulina*, and *Phleum pratense* (Fig. 4.5b).

Effects of fertilizer and other disturbance showed relatively little change over time (Fig. 4.5a). Glyphosate effects out-dominated those of other disturbance types and fertilizer. However, when combined with glyphosate, fertilizer was associated with an increase in native graminoid *Eleocharis palustris* (Fig. 4.5b). As seeding was delayed until 2002 because of excess precipitation, plots were only sampled once after treatment and, thus, showed no change.

Increases in precipitation may also have been associated with changes in species composition over the study period that were exhibited by all treatments plots, including the controls (Appendix 5). In part, this shift was associated with an increase in the presence of hydrophilic and mesic species including *Juncus* spp, *Agrostis stolonifera*, and *Zizia aptera* (Fig. 4.5b). Although glyphosate-treated plots shifted towards those of reference sites, ultimately restoration and reference plots remained distinct, the latter with native species including *Galium boreale*, *Populus tremuloides*, and *Vicia americana* (Fig. 4.5b).

Table 4.3. Soil characteristic summary (means ± S.E.) and t-test results for the restoration ($n = 16$) and reference site 1 ($n = 16$).

	Site		
	Restoration	Reference 1	p-value
pH	8.15 ± 0.27	8.04 ± 0.10	*ns*
Conductivity (μS/cm)	91.60 ± 4.45	127.75 ± 10.62	*
Percent organic matter	6.09 ± 0.34	12.27 ± 1.07	**
Gravimetric soil moisture	14.43 ± 2.29	28.98 ± 1.42	**
Nitrate (mg/L)	0.20 ± 0.41	0.10 ± 0.00	*ns*
Soil composition			
Percent sand	50.19 ± 1.37	46.98 ± 0.40	*ns*
Percent silt	42.18 ± 2.86	42.99 ± 1.39	*ns*
Percent clay	7.63 ± 1.52	10.37 ± 1.37	*ns*

* $p<0.05$, ** $p<0.01$, and *ns* = not significant

Table 4.4. Aboveground and seedbank species richness, effective species richness (ESR), and total cover means (± S.E.) for the restoration and reference sites ordered according to origin^1 and growth form^2. Mean followed by different letters are significantly different according to Tukey-Kramer ($p>0.05$).

	Aboveground				Seedbank			
Site	Restoration	Ref 1	Ref 2	p-value	Restoration	Ref 1	Ref 2	p-value
Species Richness[3]								
Native								
Forbs	3.75 ± 0.58	5.44 ± 0.81	3.31 ± 0.56	*ns*	0.00 ± 0.00	0.81 ± 0.19	-	***
Graminoids	1.69 ± 1.08 a	3.06 ± 1.44 b	4.81 ± 1.17 c	***	1.75 ± 0.19	1.50 ± 0.27	-	*ns*
Woody	0.75 ± 0.14	0.69 ± 0.20	1.56 ± 0.27	*ns*	-	-	-	-
Exotic								
Forbs	2.13 ± 0.26 a	0.50 ± 0.18 b	0.88 ± 0.27 b	***	0.50 ± 0.16	0.13 ± 0.13	-	*ns*
Graminoids	3.69 ± 0.30 a	0.38 ± 0.13 b	1.50 ± 0.18 c	***	0.94 ± 0.11	0.44 ± 0.13	-	*
ESR[4]								
Native								
Forbs	2.29 ± 0.28	3.45 ± 0.45	2.08 ± 0.26	*ns*	0.00 ± 0.00	0.80 ± 0.73	-	***
Graminoids	1.07 ± 0.14 a	1.34 ± 0.18 b	1.80 ± 0.15 b	*	1.52 ± 0.62	1.29 ± 0.80	-	*ns*
Woody	0.74 ± 0.14	0.58 ± 0.16	1.26 ± 0.20	*ns*	-	-		-
Exotic								
Forbs	1.52 ± 0.16 a	0.54 ± 0.19 b	0.57 ± 0.16 b	**	0.50 ± 0.63	0.13 ± 0.50	-	*ns*
Graminoids	1.81 ± 0.16 a	0.38 ± 0.13 b	1.25 ± 0.13 a	***	0.91 ± 0.39	0.44 ± 0.51	-	**

Table 4.4. Cont'd

	Aboveground				Seedbank			
Site	Restoration	Ref 1	Ref 2	p-value	Restoration	Ref 1	Ref 2	p-value
Cover[5]								
Native								
Forbs	2.48 ± 0.34	2.00 ± 0.19	2.04 ± 0.27	*ns*	0.00 ± 0.00	1.13 ± 0.30	-	**
Graminoids	4.42 ± 0.67 a	6.01 ± 0.41 b	7.63 ± 0.36 b	**	7.25 ± 1.85	2.56 ± 0.54	-	*
Woody	1.34 ± 0.29	0.82 ± 0.23	1.85 ± 0.31	*ns*	-	-	-	-
Exotic								
Forbs	1.91 ± 0.22 a	0.32 ± 0.11 b	1.10 ± 0.41 b	**	0.56 ± 0.18	0.13 ± 0.13	-	*ns*
Graminoids	5.66 ± 0.46 a	0.28 ± 0.10 b	3.11 ± 0.54 c	***	3.06 ± 0.64	0.63 ± 0.20	-	**

[1] Origin: native; exotic

[2] Growth form: forbs; graminoids; and woody

[3] Species richness: total number of species

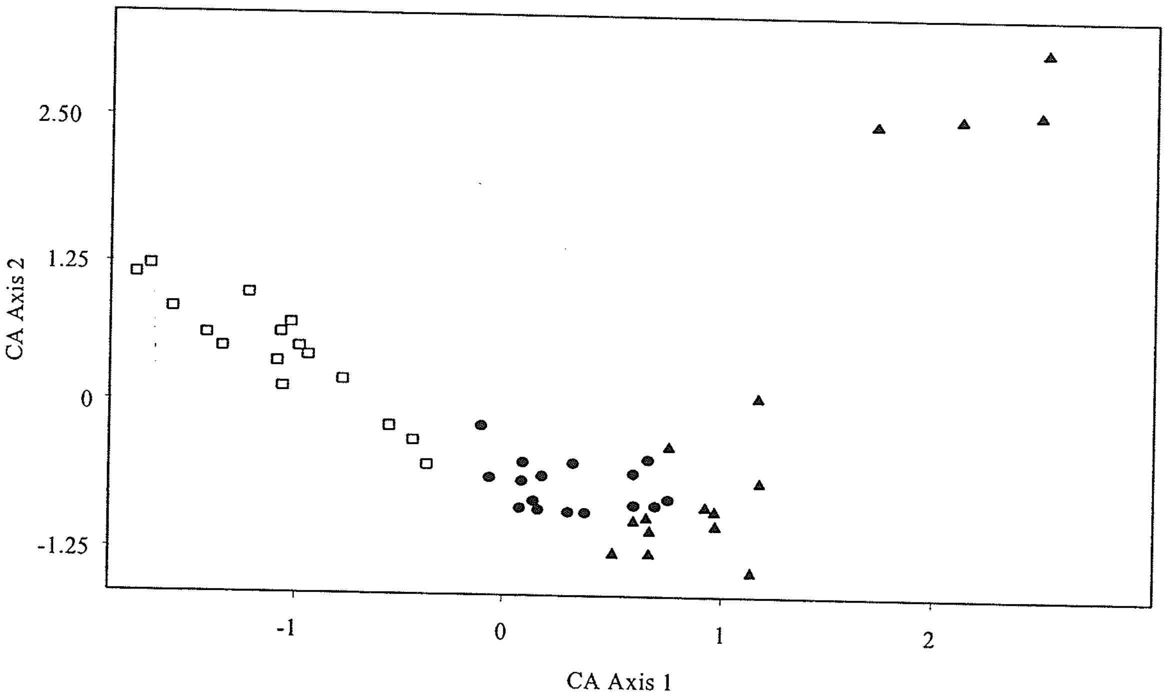
[4] Effective species richness: the reciprocal of Simpson's index

[5] Seedbank: density (seedlings/33cm3) instead of cover

ns = not significant; * $p < 0.01$; ** $p < 0.001$; and *** $p < 0.0001$

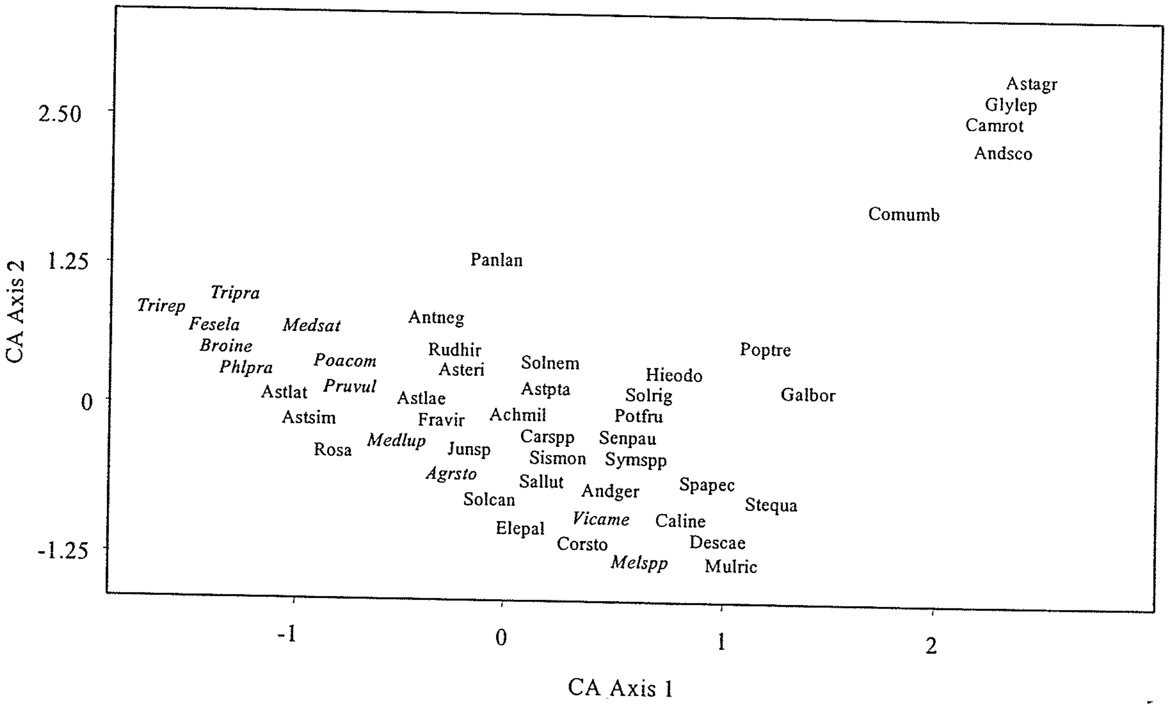
Fig. 4.2. Correspondence analysis (CA) ordination of the a) restoration (open squares), reference 1 (closed triangles), and reference 2 (closed circles) sites ($n = 48$) and b) associated aboveground plant species (exotic species italicized) (Appendix 2).

a)



2.50
1.25
0
-1.25
CA Axis 2
-1
0
1
2
CA Axis 1

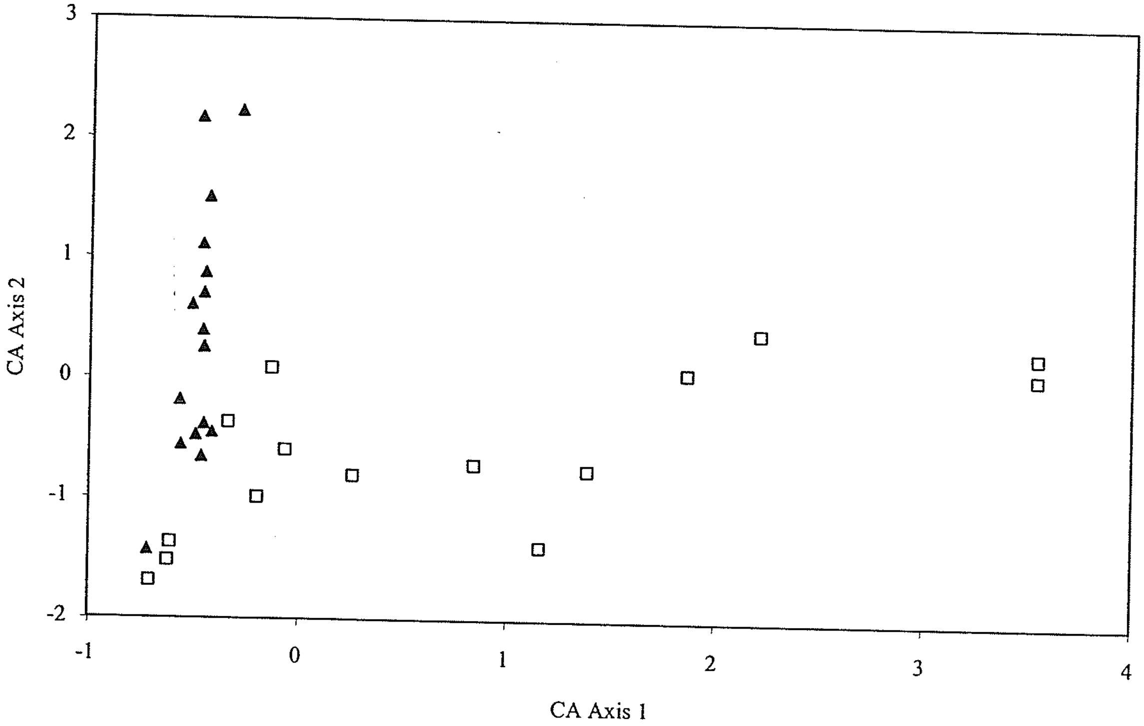
b)



2.50
1.25
0
-1.25
CA Axis 2
Astagr
Glylep
Camrot
Andsco
Comumb
Panlan
Tripra
Trirep
Fesela
Medsat
Antneg
Broine
Rudhir
Poptre
Solnem
Phlpra
Poacom
Asteri
Hieodo
Astlat
Pruvul
Astpta
Galbor
Astlae
Solrig
Astsim
Fravir
Achmil
Potfru
Carspp
Senpau
Rosa
Medlup
Junsp
Sismon
Symspp
Agrsto
Sallut
Spapec
Andger
Solcan
Stequa
Vicame
Caline
Elepal
Corsto
Descae
Melspp
Mulric
-1
0
1
2
CA Axis 1

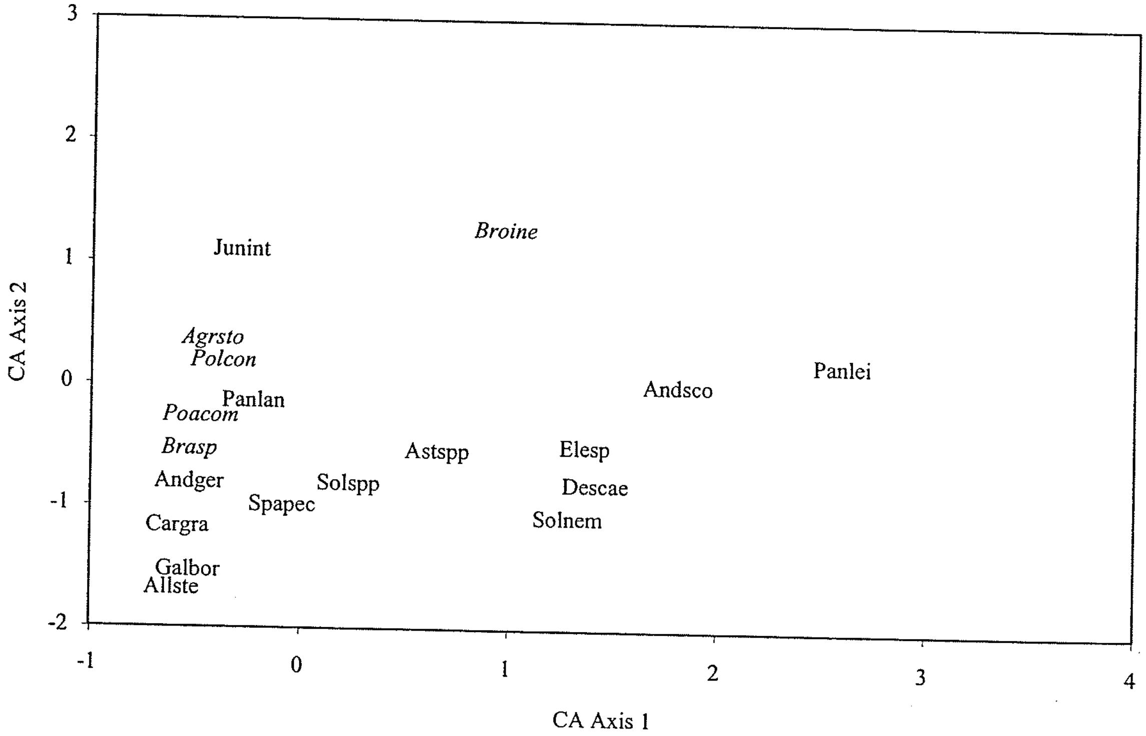
Fig. 4.3. Correspondence Analysis (CA) ordination of a) restoration (open squares) and reference 1 sites (triangles) ($n = 32$) and b) associated seedbank species (exotic species codes are italicized) (Appendix 2).

a)



3
2
1
0
-1
-2
CA Axis 2
-1
0
1
2
3
4
CA Axis 1

b)



3
2
1
0
-1
-2
CA Axis 2
Junint
Broine
Agrsto
Polcon
Panlei
Andsco
Panlan
Poacom
Brasp
Astspp
Elesp
Andger
Solspp
Descae
Spapec
Cargra
Solnem
Galbor
Allste
-1
0
1
2
3
4
CA Axis 1

Table 4.5. Summary of ANOVA showing the effects of the glyphosate, fertilizer, disturbance (fire and mowing), and seeding on diversity (species richness = SR and effective species richness = ESR) and cover in 2002. Only significant effects are shown and trends are indicated as increased (+) or decreased (-).

	Overall model	Glyphosate	Fertilizer	Disturbance	Seeding	G*F	G*D	G*S	G*F*D*S
Native									
Forb Cover	***	* (-)	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*
Forb SR	*	** (-)	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*
Graminoid Cover	**	*ns*	*ns*	*ns*	*** (+)	*ns*	*ns*	*ns*	*
Woody Cover	***	* (-)	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*
Woody ESR	*	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*
Exotic									
Forb ESR	***	* (+)	*ns*	*ns*	*ns*	*ns*	*ns*	**	*ns*
Graminoid Cover	***	*ns*	*ns*	*ns*	* (-)	*ns*	*ns*	*ns*	*ns*
Graminoid ESR	****	* (-)	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*

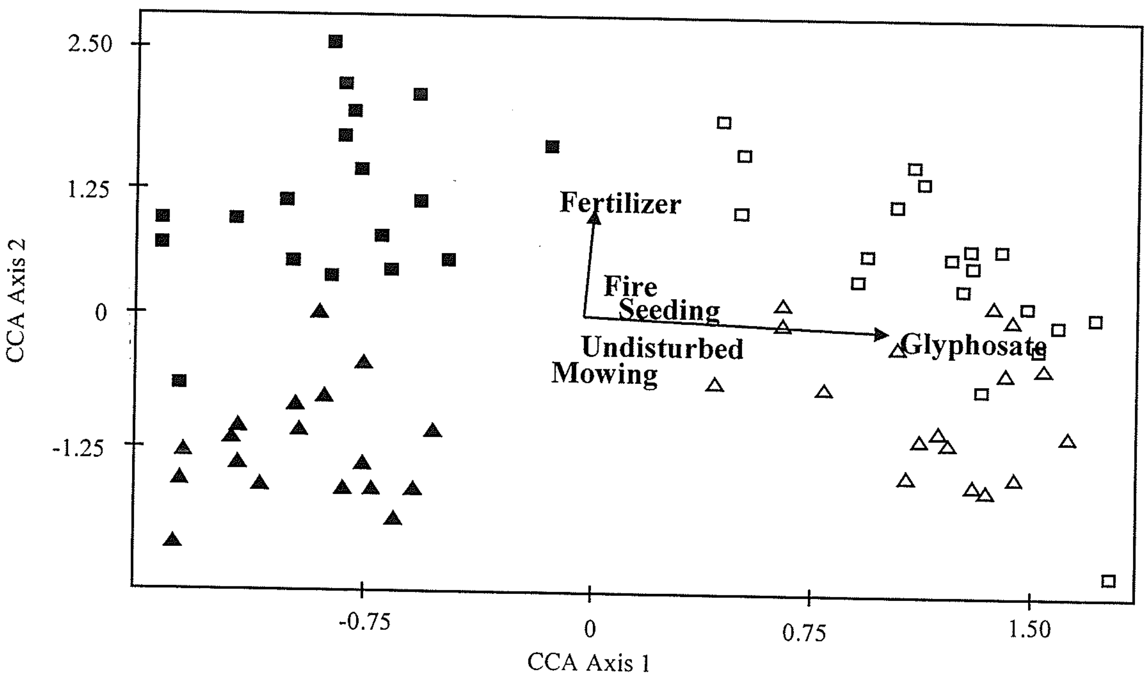
ns = not significant; * p <0.05; ** p <0.01; ***p <0.001; and ****p <0.0001

Table 4.6 . Eigenvalues and intraset correlations of treatment variables for the four CCA axes. The cumulative percentage variance and the rank order of the correlations are given in brackets.

	Axis			
	1	2	3	4
Eigenvalue	0.215	0.024	0.015	0.001
Species-environment correlations	0.955	0.832	0.589	0.583
% variance of species data	28.6	3.2 (31.8)	2.0 (33.8)	1.1 (34.9)
% variance for species-treatment data relation	80.1	8.8 (88.9)	5.8 (94.7)	3.1 (97.8)
Intraset correlations (Rank)				
Glyphosate	0.951	-0.026	0.002	0.027
Fertilizer	0.018	0.821	-0.014	0.030
Control	-0.018	-0.030	-0.136	-0.479
Fire	0.679	0.102	0.320	-0.041
Mowing	-0.050	-0.073	-0.188	0.518
Seeding	0.479	0.065	-0.491	-0.686

Fig. 4.4. Canonical correspondence analysis (CCA) ordination of a) treatment plots showing glyphosate (open); no glyphosate (closed); fertilizer (squares); and no fertilizer (triangles) (*n* = 72) and b) associated aboveground species (Appendix 2). Exotic species names are italicized and species (*n* = 74) have been removed from the centre of the ordination.

a)


2.50
1.25
0
-1.25
CCA Axis 2
-0.75
0
0.75
1.50
CCA Axis 1
Fertilizer
Fire
Seeding
Undisturbed
Mowing
Glyphosate

b)

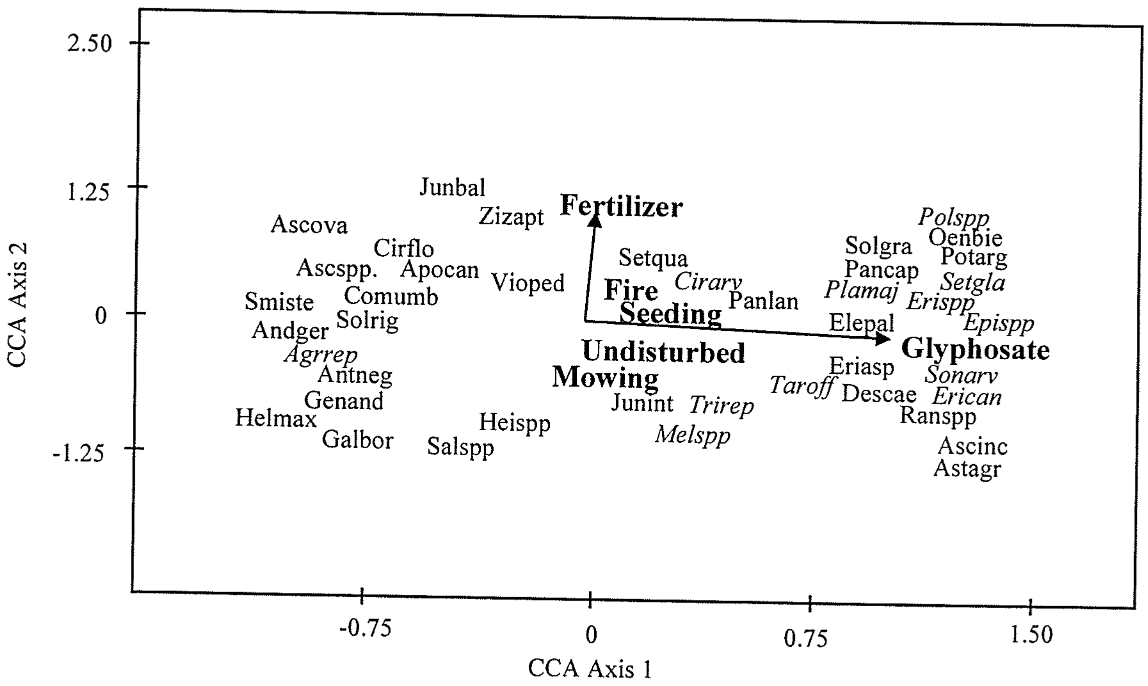

2.50
1.25
0
-1.25
CCA Axis 2
-0.75
0
0.75
1.50
CCA Axis 1
Junbal
Zizapt
Fertilizer
Ascova
Cirflo
Ascspp.
Apocan
Vioped
Smiste
Comumb
Andger
Solrig
Agrrep
Antneg
Genand
Helmax
Galbor
Salspp
Heispp
Setqua
Cirary
Fire
Seeding
Panlan
Undisturbed
Mowing
Junint
Trirep
Melspp
Polspp
Solgra
Oenbie
Pancap
Potarg
Plamaj
Setgla
Erispp
Elepal
Epispp
Glyphosate
Eriasp
Sonarv
Taroff
Descae
Erican
Ranspp
Ascinc
Astagr

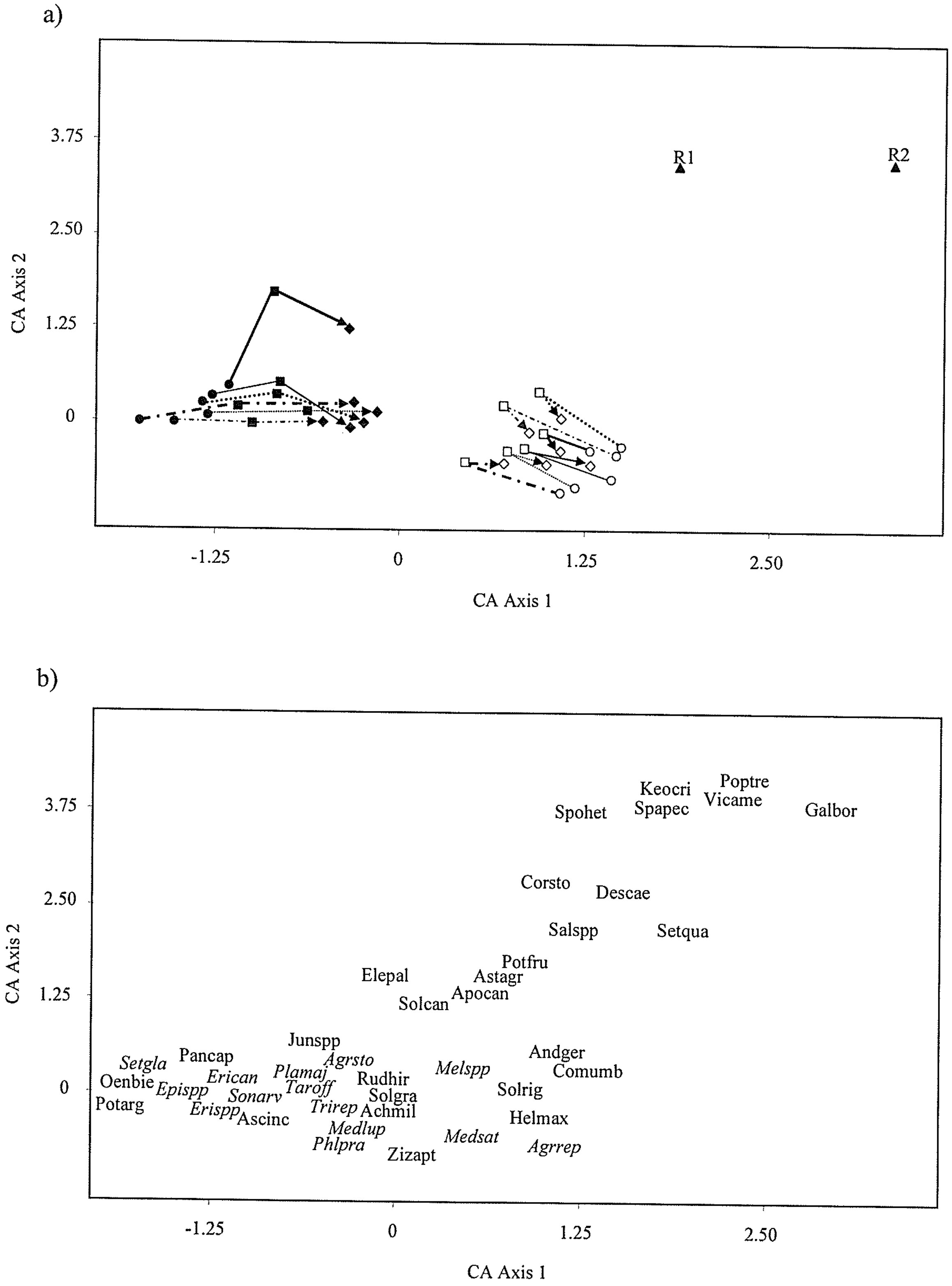
Table 4.7. Summary of ANOVA showing the effects of the glyphosate, fertilizer, disturbance (fire and mowing), and seeding on individual species in 2002. Only significant effects are shown and trends are indicated as increased (+) or decreased (-).

	Overall	Glyphosate (G)	Fertilzer (F)	Disturbance (D)	Seeding (S)	G*F	G*D	G*S	G*F*D	F*S	D*S
Litter	**	*ns*	* (+)	*ns*	**** (-)	***	*ns*	*ns*	*ns*	*	*ns*
Native forbs											
Antennaria neglecta	****	*ns*	**** (-)	*ns*	*ns*	*	*ns*	*ns*	*ns*	*ns*	*ns*
Aster ciliolatus	*	* (-)	* (+)	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*
Aster ericoides	*	*ns*	*ns*	*ns*	* (+)	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*
Solidago nemoralis	**	*ns*	* (+)	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*
Native graminoids											
Andropogon gerardii	*	* (-)	*ns*	* (+M) (-F)	*ns*	*ns*	*	*ns*	*	*ns*	*ns*
Carex granularis	****	* (+)	*ns*	*ns*	*ns*	*	*ns*	*ns*	*ns*	*ns*	*ns*
Panicum lanuginosum	**	*ns*	*ns*	*ns*	** (+)	*ns*	*ns*	*ns*	*ns*	*ns*	*
Native woody											
Rosa spp.	****	* (-)	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*
Exotic forbs											
Prunella vulgaris	*	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*	**	*ns*	*ns*	*ns*
Exotic graminoids											
Agrostis stolonifera	***	** (+)	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*
Poa compressa	**	* (-)	* (-)	* (+F) (-M)	*ns*	*	*	*ns*	*ns*	*ns*	*ns*

* $p < 0.05$; ** $p < 0.01$; ***$p < 0.001$; and ****$p < 0.0001$

ns = not signficiant; F = fire; and M = mowing

Fig. 4.5. Correspondence analysis (CA) ordination of a) treatment plots showing glyphosate (open shapes); no glyphosate; year (2000 = square; 2001 = triangle; and 2002 = circle); fertilizer (bold lines); and disturbance (undisturbed = solid line; fire = dotted line; and mowing = dot hyphen line) (*n* = 38) and b) associated aboveground species (Appendix 2). Exotic species names are italicized and species (*n* = 69) have been removed from the centre of the ordination.


a)
CA Axis 2
3.75
2.50
1.25
0
R1
R2
-1.25
0
1.25
2.50
CA Axis 1
b)
CA Axis 2
3.75
2.50
1.25
0
Keocri
Poptre
Spapec
Vicame
Spohet
Galbor
Corsto
Descae
Salspp
Setqua
Potfru
Elepal
Astagr
Apocan
Solcan
Junspp
Pancap
Setgla
Agrsto
Andger
Plamaj
Melspp
Comumb
Oenbie
Erican
Rudhir
Epispp
Taroff
Solrig
Sonarv
Solgra
Potarg
Trirep
Achmil
Erispp
Ascinc
Helmax
Medlup
Medsat
Phlpra
Agrrep
Zizapt
-1.25
0
1.25
2.50
CA Axis 1

4.4 . DISCUSSION

Although much extant tallgrass prairie is characterized by continued declines in native diversity and invasion by exotics, restoration efforts generally focus on constructing new habitat rather than rehabilitating these important habitat remnants. In this study I assessed the use of disturbance, fertilization, and interseeding in the rehabilitation of degraded tallgrass prairie in southern Manitoba. Glyphosate and, to a lesser degree, burning and mowing, had substantial effects on plant diversity and species composition, as did fertilization and interseeding. Disturbance and fertilizer effects were greatest immediately after treatment application, declining over the next three years, whereas the effects of seeding will only increase over time.

Disturbance effects

Glyphosate had the greatest impact on both native and exotic flora of any treatment in this study. Native diversity, especially that of forb and woody species, decreased substantially when glyphosate was applied. Forbs also have been adversely affected by this nonselective herbicide in mountain rangelands (Ralphs 1995) and, predictably, by broadleaf herbicides including 2,4-D in tallgrass prairie (Engle *et al.* 1993) and clopyralid in roadside prairie restoration (Tyser et al. 1998). Native forbs in prairies are generally more sensitive to herbicides than are native graminoids (Willson & Stubbendieck 1996), as they typically have smaller populations and lower biomass (Briggs & Knapp 2001). As the seedbank was low in diversity and dominated by exotic forbs, it was not able to function as an effective source for native forb species following herbicide application (Sveinson & McLachlan 2003, Appendix 1).

Native graminoids also were vulnerable to glyphosate, especially *Andropogon gerardii*. It, along with other C_4 grasses, characterizes high quality northern tallgrass prairies and is a highly desirable and useful indicator species during restoration (Morgan et al. 1995). Glyphosate, alone and when combined with fire, had a substantial and adverse effect on *A. gerardii*. In contrast, other studies suggest that early spring-application of glyphosate will increase *A. gerardii* production during rangeland improvement (e.g. Waller & Schmidt 1983; Gillen *et al.* 1987), as will annual spring burning on both rangeland and tallgrass prairies (Svejcar 1990; Collins & Steinauer 1998). In this study, however, glyphosate and burn treatments were implemented in the fall. Other studies have similarly found that disturbance such as burning (e.g. Howe 1995) and herbicide use (e.g. Grace *et al.* 2000) adversely affects plants that are actively growing.

Encroachment by native woody species also contributes substantially to the decline of tallgrass prairie (Anderson 1990; Mack & D'Antonio 1998) and effective short-term control is often achieved with herbicides (e.g. Bowes & Spurr 1996), as well as mowing and burning (e.g. Leach & Givnish 1996). Although glyphosate significantly reduced the cover of *Rosa* spp. in this study, woody species were relatively uncommon because of the long-time haying.

Exotic graminoid diversity was temporarily reduced by glyphosate. Some exotic graminoids, including *Poa compressa*, declined when sprayed whereas others, including *Agrostis stolonifera*, had fully recovered after three years, and, in many cases, dominated earlier sprayed plots. In some studies (e.g. Choi & Pavlovic 1994), glyphosate also has been effective in reducing exotic graminoid cover, especially during stem elongation (e.g.

Willson & Stubbendieck 1996), whereas, in others, it only has achieved poor control (e.g. Wilson & Gerry 1995). *Agrostis stolonifera* cover may have increased because of its dominance in both seedbank and surrounding vegetation (Sveinson & McLachlan 2003, Appendix 1), and due to the relatively great precipitation levels observed during this experiment.

Exotic forb diversity, on the other hand, generally increased with glyphosate. It seems that glyphosate-associated reductions in native and exotic graminoid cover may have released exotic forbs that were otherwise suppressed by these established species. Most of those characterizing sprayed plots were ruderal and some, including *Polygonum convolvulus* and *Brassica* sp., dominated the seedbank (Sveinson & McLachlan 2003, Appendix 1). Exotic forbs that typify disturbed prairies are often ruderal and colonize effectively from the seedbank and seed rain following disturbance (Schott & Hamburg 1997).

The other disturbance treatments, i.e. mowing and fire, had relatively less effect on species composition and diversity, and were compromised by the past management of the study site. Although prescribed burning is a dominant management activity in prairie restoration and conservation (Grace *et al.* 2002), neither exotic nor native species diversity was affected. An important exception was *Andropogon gerardii*, which was adversely affected by fall burns, conducted when this warm season grass was still actively growing (e.g. Howe 2000). The less-than-anticipated effects of burning were likely related to the low fuel loads associated with prolonged haying (Clark & Wilson 2001) and the previous application of glyphosate. Indeed, burning was only effective when combined with fertilizer, as the latter increased productivity and subsequent litter accumulation, thereby increasing the amount of fuel available for burning.

Mowing is increasingly used for restoration and conservation in European grasslands (Scheffers *et al.* 1998) and North American prairies (Wilson & Clark 2001), especially when burning opportunities are restricted. However, like burning, it relatively little effect on species composition or diversity in this study. Mowing had a positive effect on *A. gerardii*, although the opposite effect was observed when combined with the more dominant and adverse effects of glyphosate. Plots were mowed twice during each growing season and this treatment was generally less intensive than the other disturbance treatments. Moreover, it is often used to reduce the competitiveness of cool-season grasses (e.g. Willson & Stubbendieck 1996). Possible effects of mowing were again mitigated by the similar haying practices that have been conducted annually over the last decade.

Fertilizer effects

Many studies suggest that increases in soil nutrients benefit competitive species, thus reducing overall diversity (e.g. Tilman 1993; Wilson & Tilman 1993). Although diversity as a whole was unaffected in this study, the cover of litter and native forbs *Aster ciliolatus* and *Solidago nemoralis* all increased with fertilization. Soils of the restoration had low organic matter and they, like most prairie soils, were characterized by low nitrogen and water and high light availability (Knapp & Seastedt 1986), conditions that favour dominant warm-season grasses over forbs. Increases in nitrogen concentration associated with fire and grazing, may promote the productivity and diversity of native forbs in tallgrass prairie (Seastedt *et al.* 1991) because of their higher nitrogen and water requirements (Turner & Knapp 1996). Although, fertilization is generally discouraged in prairie restoration (Packard & Mutel 1997), as it often increases the productivity of exotic species (Wilson & Gerry 1995; Maron & Jefferies 2001), the cover of exotic graminoid *Poa compressa* actually declined with fertilized in this study. Thus, fertilization may have a role when seeding forbs in degraded tallgrass prairies, especially when soil nutrient levels are low.

Interseeding effects

In general, prairie rehabilitation and associated interseeding are poorly understood, as they are more complicated than habitat reconstruction and provide less direct control over desired vegetational change (Wark *et al.* 1996). Seeding-associated changes to existing vegetation are less predictable than those to weed-free seedbed, and management effects less immediate and obvious (McDonald 2000). In this study, interseeding generally increased the cover of native graminoids, in particular unsown *Panicum lanuginosum*, while decreasing that of exotic graminoids. Although there was no significant effect on forb diversity, cover of the sown forb *Aster ericoides* increased. Seeding was delayed for two years by excess precipitation and only occurred in the fall before the project ended, partially accounting for the reduced forb response. The greater response by graminoids might have been associated with the use of a seed drill, which tends to favour graminoid establishment (John Morgan *pers. comm.*) rather than that of sod and forb plugs (Morgan *et al.* 1995). Although most species that were sown were forbs (77%), seed weight of the mixture was dominated by grasses (96%). Indeed, grass-dominated seed mixtures characterize most restoration seeding practices, perhaps explaining why assessments of long-term tallgrass prairie restoration often indicate that managers are better at constructing grasslands than prairies comprising both graminoids and forbs (e.g. McLachlan & Knispel 2003).

Prior to seeding, plots were mowed and raked to ensure maximum soil-to-seed contact, thus significantly reducing litter levels. Raking may also have had an effect on species composition and growth, as it minimally disturbed the soil and, by increasing light availability, may have reduced the competitiveness of dominant species. The long-term impacts of interseeding on degraded prairie merit further research, especially as some studies suggest that rehabilitation will ultimately be more successful than reconstruction (e.g. McDonald 2000).

Reference sites and restoration success

The reference and restoration sites differed in aboveground and seedbank species diversity and composition. That the restoration was characterized by exotic species, and the reference site by native and woody species, is attributable to differences in land-use. The restoration site has been annually hayed, whereas the reference sites are managed for conservation. Although the latter are burned frequently, they continue to be encroached by woody species and have reduced diversity of C_3 grasses and forbs. In contrast, the woody cover in the restoration was reduced by repeated mowing (e.g. Bartel & Wilson 2001).

Reference sites are often used to assess the effectiveness of restoration (Pywell *et al.* 2002). Although data were only collected over three years, they do suggest that the similarity of glyphosate-treated plots and reference sites increased over time. The uses of reference sites are often criticized in the restoration literature, as they are not mechanism based and often centre on some arbitrary state in the past (e.g. Pickett & Parker 1994). Rather than an end-point of restoration, the reference sites were used to assess the direction, degree, and desirability of inevitable vegetational change associated with restoration (e.g. McLachlan & Bazely 2003).

Limitations of the study

This study was restricted by its limited size. Little tallgrass prairie remains in Manitoba compared with extant prairie to the south, making it difficult to find large homogeneous patches of native habitat. Although plots were large as possible and buffer areas constructed among plots, treatments including fertilization were difficult to isolate completely, especially in light of excess moisture.

Most of the upland tallgrass prairie in Manitoba has been successfully converted to agriculture or settled, leaving only wet prairie or sloughs for conservation and restoration. A moisture gradient was identified at this study site and the experiment was designed to minimize any confounding effects. However, excess summer precipitation (40% and 30% higher than the 30-year mean in 2000 and 2001, respectively) resulted in standing water for much of the growing season, hampering the application of many treatments. Thus, burning was delayed one year and seeding two years. Replicated experimental research is generally more difficult to conduct under these conditions than are retroactive assessments of long-term prairie restoration projects (e.g. McLachlan & Knispel 2003) or formal monitoring programs (e.g. Tyser *et al.* 1998).

Management Implications

Although rehabilitation, when used in combination with habitat protection, has potential to slow or reverse further degradation of tallgrass prairie, it has received little attention in the literature, in part because it is less predictable, less immediate and takes many years to achieve any desired outcomes. Also, by definition, threatened habitat is less available for active management than are post-agricultural sites, which, in turn, are more amenable to reconstruction techniques derived from agronomic practices. Although much tallgrass prairie is actively managed, primarily through the use of prescribed burns and, to a lesser extent, the control of exotics, interseeding rarely takes place. Even less is known about the rehabilitation of tallgrass prairie at the northern limit of its range. Most of the studies regarding prairie restoration in the Canadian prairies have been conducted in the mixed-grass prairie region to the west (e.g. Wilson & Shay 1990; Shay *et al.* 2001; Wilson 2002) and management practices, such as burning and mowing, also have been developed elsewhere. Although, any low-intensity disturbance might promote diversity (Connell 1978; Huston 1979) and reduce the dominance of competitive species (e.g. Collins & Steinauer 1998), long-term research and monitoring is needed for this region.

Glyphosate clearly had the most immediate effect on vegetation, whereas ongoing haying likely reduced the effects of mowing and burning. Although herbicides might be a useful tool in rehabilitation, glyphosate is difficult to use, as it is a non-selective herbicide and can severely damage non-target or vulnerable species. The application of glyphosate in this study occurred in late summer, resulting in substantial and often undesirable changes in diversity. The initial removal of exotic cover would have facilitated interseeding, but was delayed in this experiment by excess precipitation. Although, respraying would normally occur the following spring, it was prohibited by the unanticipated emergence of an endangered species, *Spiranthes magnicamporum*. Ironically, it is likely that the use of glyphosate likely released this low-lying species, which would have otherwise been suppressed by dominant and more competitive species. As native forbs were highly sensitive to glyphosate, selective herbicides including, sethoxydim (Poast®) and imazapic (Plateau®), might be better used to remove undesirable grass and forb species, respectively. Glyphosate might be more effective if it was spot-sprayed on monodominant stands of exotics as well as wick-applied when removing undesirable tall herbaceous (Grilz & Romo 1995) and woody species (Solecki 1997). In this study, glyphosate concentrations were originally chosen to eliminate all vegetation and the seedbank for future reconstruction. If it were used for rehabilitation, lower concentrations would have likely have reduced the cover of the dominant vegetation without removing populations in their entirety or without affecting low-lying plants.

Burning and mowing had relatively less effect on the vegetation in this study and was attributed to the long term haying and associated reductions in fuel load. If haying was eliminated or reduced in frequency, burning would become more effective, but it helps generate income for the preserve and maintains support by neighbouring rural communities, which is important in these agriculture-dominated landscapes. Alternative approaches might be to increase fuel loads by adding native straw or by fertilizing. Fertilizer had a positive impact on native forbs (e.g. *Aster ericoides* and *Solidago nemoralis*) in this study, and is worth further investigation, but might create further problems in sites dominated by exotics. Low-cost alternatives to commercial fertilizer such as hog and cattle manure are available in agriculture-dominated landscapes, but may also create future problems as they often contain weed seeds. Fertilizing immediately prior to interseeding with native species might facilitate forb establishment in nutrient-poor sites.

Although ecological theory is important when developing management plans for prairie restoration (Hobbs & Norton 1996), results of this study also suggest that site- or region-specific constraints are crucial, especially when rehabilitating existing but degraded prairie. These results further suggest that outcomes from reconstruction-based research are not immediately generalizable to rehabilitation, also indicating that more research on rehabilitation is needed if degraded extant prairie and restoration sites are to be effectively managed in the future.

CHAPTER 5: Thesis Discussion and Implications

SUMMARY

Less than 1% of the original tallgrass prairie remains and it is one of the most endangered ecosystems in North America. Although much of the remaining tallgrass prairie in Manitoba is protected, it continues to be degraded by surrounding land-use, invasion by woody and exotic species, and inappropriate management. Restoration combined with protection provides an opportunity to enhance degraded remnants as well as construct new prairie habitat. Much of the prairie restoration in Manitoba is end-point oriented (i.e. Ecological Restoration), including the seeding of native species in post-agricultural fields and small-scale schoolyard projects. A complimentary approach that examines underlying processes that affect vegetation change (i.e. Restoration Ecology) is equally important and may even have greater long-term potential. Ideally, both approaches are necessary for prairie restoration to succeed. Although prairie restoration is common place across the prairies, we still have little ability to predict restoration success, and, indeed, their seems to be a movement away from prairie to forest restoration in Manitoba

SCOPE OF RESEARCH

My study examined two long-term tallgrass prairie restoration projects. Long-term ecological research is extremely important in restoration, but difficult to accomplish in the relatively short-term research of a Masters thesis. These studies provided the opportunity to study both the initiation and completion of long-term research. They also facilitated a more complete study of tallgrass prairie restoration, in that, one study examined high quality prairie while the other was degraded. Furthermore, these studies investigated high priority management concerns of exotic and woody species invasion.

RESEARCH OUTCOMES

Prescribed burning is the dominant management practice in tallgrass prairie conservation and restoration. When appropriately timed, it can be used to increase and maintain tallgrass prairie species diversity and suppress woody and exotic species invasion. However, outcomes vary depending on site-level characteristics, including vegetation and seedbank composition as well as environmental conditions, past land-use and management practices, and burn-season. Until recently, the impacts of burn-season on tallgrass prairie have received very little attention. Tallgrass prairies have been traditionally burned in the spring and to a lesser extent in the fall. Burn-season had a substantial impact on diversity and species composition of high quality tallgrass prairie. In the St. Charles Rifle Range study, fall-burn had the most desirable effects, increasing native graminoid (e.g. *Andropogon gerardii* and *Panicum leibergii*) and forb (e.g. *Anemone canadensis* and *Aster ericoides*) diversity, regardless of time-of-flowering. In contrast, the relatively late spring-burn decreased exotic graminoid cover, but had little effect on species composition and was characterized by woody species (e.g. *Rosa* spp. and *Symphoricarpos* spp.). Although summer-burns are rarely used in Manitoba because of the associated safety risks, this treatment increased both native (e.g. *Carex torreyi*. and *Juncus* spp.) and exotic (e.g. *Poa pratensis*) graminoid species diversity. Burning was one of many treatments in the Manitoba Tall Grass Prairie Preserve study and, in contrast, this fall-burn had relatively little effect on species composition of that degraded tallgrass prairie, in large part because of long-term haying on this site.

Prairie restoration is commonly associated with the reconstruction of new habitat based on historical data. However, the role of alternative management techniques in rehabilitating degraded tallgrass prairie shows great potential, but has seen relatively little emphasis in the literature. Fall application of glyphosate had the greatest impact on native and exotic diversity and species composition. Weedy and exotic species, such as *Poa compressa*, slowly recovered their former cover and replaced native species in glyphosate-treated plots. Native graminoids, such as *Andropogon gerardii*, were adversely affected by glyphosate over the short-term, whereas native forbs, such as *Aster ciliolatus*, for the most part were eliminated in these treatments. Native woody species, such as *Rosa* spp., were also decreased by glyphosate. Herbicide-associated mortality of vegetation likely resulted in recolonization from the seed and propagule banks, most of these exotic, and further created opportunities for establishment by wind-dispersed species. The removal of existing vegetation also created an opportunity for interseeding of native species. Unfortunately, interseeding in this study was delayed for two years because of above-average levels of precipitation, and had relatively little effect on species composition.

Fertilization had no effect on the diversity of origin-growth form guilds, but increased native forbs *Aster ciliolatus* and *Solidago nemoralis,* native graminoid *Carex* granularis, and litter. In contrast, litter, exotic graminoid *Poa compressa* and native forb *Antennaria neglecta*, decreased in cover when fertilizer was combined with glyphosate, in part reflecting the dominant effect of the herbicide. Similarly, disturbance, mowing and burning, treatments had relatively minor main effects on species composition and diversity but interacted significantly with glyphosate. Native graminoid *Andropogon gerardii* cover was increased by mowing and decreased by fire, alone, and, again decreased when these treatments were combined with glyphosate. In direct contrast, exotic graminoid *Poa compressa* cover was increased by fire and decreased by mowing.

Over time, the species composition of glyphosate treated plots became increasingly similar to that of plots that had not been sprayed as well as high quality reference sites, changing from weedy species to ones that are characteristic of poor-to-intermediate habitat quality. Effects of fertilizer and other disturbance, mowing and burning, showed relatively little change over time, as the effects of glyphosate were so strong.

FUTURE DIRECTION

This research is the first of its kind at the northern edge of the tallgrass prairie region. It has provided baseline data and generated many questions for future research. As this study initiated a long-term research project within the Manitoba Tall Grass Prairie Preserve, the next step would be to monitor treatment-associated changes in aboveground vegetation, seed and propagule bank, and seed rain composition. Underlying mechanisms responsible for vegetational change, such as competitive interactions between dominant native (e.g. *Andropogon gerardii* and *Carex granularis*) and exotic (e.g. *Agrostis stolonifera* and *Poa compressa*) graminoid species when exposed to varying treatment factors, also should be examined.

Restoration activities and outcomes are highly dependant on site-level environmental conditions. Future research that focuses on the effects of environmental conditions, including moisture and soil type, on native seedling establishment and survival could increase the success of prairie restoration. In this study, interseeding was delayed for two years due to above average levels of precipitation. Greenhouse and field trials could be used to determine the effects of elevated soil moisture and soil type on native tallgrass prairie species and contribute to the development of seed mixtures for differing soil conditions. In addition, these results show that fertilization promotes native forb species diversity and has relatively no effect on exotic species. As fertilization is highly discouraged in prairie restoration, these findings merit further exploration.

Although interseeding has great potential for rehabilitating degraded tallgrass prairie, it was relatively unsuccessful in this study. Future research might investigate the use of alternatives to seeding, these including transplanting seedlings or sod, for native species re-introduction and establishment. Interseeding combined with herbicides that specifically select for graminoids or forbs as well as varied timing of application may also be useful in prairie rehabilitation, especially when exotic species dominate both above and belowground species composition. A study that documents the effective use of selective herbicides in prairie rehabilitation also would be extremely useful for managers.

Over the past decade, small-scale tallgrass prairies or wildflower gardens have become a popular alternative to traditional landscaping in urban areas. Many small patches of tallgrass prairie have been constructed in public green spaces by local community groups and the City of Winnipeg's Naturalist Services Branch. However, many of these prairies have become dominated by exotic and woody species due to the loss of community group interest and constraints in resources, preventing any required maintenance. An evaluation or retroactive study of these small but important urban prairie restorations that could develop indicator species and management recommendations for rehabilitation would be extremely useful (e.g. McLachlan and Knispel 2003). This study might contrast restoration success of urban community group initiated gardens, urban prairies, and rural prairies. Similarity to high quality remnant urban and rural prairies could also be examined. As these sites are situated within human-dominated landscapes, it would be important to include human involvement, use, and perception of these prairies. Impacts of human activity in restoration, such as accidental or intentional seed dispersal, vegetation trampling, introduction of non-native horticultural plants to increase aesthetic value, and selective weeding of undesirable species, is increasingly growing in interest and is of extreme importance when trying to restore natural habitat in urban settings (e.g. Benvie *In progress*).

MANAGEMENT IMPLICATIONS

Much of the remaining tallgrass prairie in Manitoba is highly fragmented and dominated by exotic species. Although the original land cover of tallgrass prairie will never be recovered, restoration can be used to increase the quality, patch size, and connectivity of existing degraded prairies. Conflicting land-use, such as herbicide use, fertilization, dumping, and development, in surrounding areas should be mitigated to prevent further decline. In addition, restoration has great potential for degraded habitats. Rather than rationalizing further habitat destruction, conservation activities should focus on both protection and management that includes restoration.

Both components of my research study specifically examined rehabilitation of tallgrass prairie degraded by exotic and woody species invasion. In contrast to traditional prairie restoration (i.e. reconstruction of new prairie that existed historically), I examined ways to enhance existing high quality and degraded prairie. Although the quick results of prairie reconstruction are often more appealing to agencies and the public, rehabilitation is potentially more successful over the long-term. Even high quality prairies are subject to woody species colonization and without active management, quality will likely decline in future. Rehabilitation techniques, such as prescribed burn, mowing, herbicide, and seeding, can be used to maintain and enhance native species diversity, when appropriately implemented. In addition, rehabilitation can also be used to increase habitat quality when endangered species are present. However, little information exists; moreover results from reconstruction do not seem to be generalizable.

Rehabilitation aims to conserve as well as enhance existing species diversity through native species re-introduction. Although rehabilitation allows exotic species to remain, native species will eventually dominate and non-invasive exotic species should be of low management concern. In general, restoration (i.e. both rehabilitation and reconstruction) will not likely eradicate exotic species. Management efforts should focus on maintaining exotic species at desirable levels within the plant community. As tallgrass prairie is a disturbance-dependent ecosystem, restoration activities should also re-introduce natural disturbance (e.g. fire and grazing) regime as well as explore alternative technique (e.g. mowing and herbicide) when feasible.

Although not examined in this study, prairie reconstruction can be used to create new prairie habitat in highly disturbed areas and post-agricultural fields dominated by exotic species and weedy native species. Seed and propagule banks under these conditions also tend to be dominated by exotic species and have been effectively controlled by removing existing vegetation and re-introducing native species (e.g. herbicide application, tilling, and seed drilling). However, once established, these prairies typically become invaded by exotic species due to dispersal from surrounding areas. Thus, rehabilitation techniques may also be used to increase the quality of degraded reconstructed prairies.

Current tallgrass prairie management tends to be opportunistic and based on logistical concerns rather than ecological data. Management decisions also should be informed by and based on site-specific needs, such as above- and below-ground species composition and management history. Proper characterization of the seed and propagule bank is extremely important when managing degraded tallgrass prairie and can prevent unexpected management outcomes, such as an increase in exotic species.

This study greatly contributes to the knowledge base on tallgrass prairie. As much of the tallgrass prairie has disappeared, restoration has an extremely important role in its long-term survival. It clearly shows that prairie restoration has great potential, but future research is needed to increase our ability to predictably restore prairie. The largest continuous patch of remnant tallgrass prairie is protected within a single Preserve and efforts should be made to identify other patches of tallgrass prairie for protection and restoration, thereby increasing land cover of this important habitat in Manitoba.

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APPENDIX 1. Role of seedbanks in the restoration of tallgrass prairie (Manitoba)
Sveinson, J. and McLachlan, S. 2003. Ecological Restoration, 21: 43-44.

Most restored tallgrass prairies in Manitoba are constructed habitats. Although restoration of existing but degraded natural habitat has great potential for success (McDonald 2000), little information about restoring degraded tallgrass prairie exists for this region. Since 1999, we have investigated the effects of various treatments--including fertilization, disturbance, and seeding--on a 4-acre (1.6-ha), post-agricultural site (Sveinson 2003) within the Manitoba Tall Grass Prairie Preserve in southeastern Manitoba. In this note, we highlight one part of this study in which we examined the potential use of glyphosate herbicide as a tool for releasing the native seedbank of degraded sites.

Prior to treatment, the study site was dominated by non-native grass species, including redtop (*Agrostis stolonifera*), timothy (*Phleum pratensis*), Canada bluegrass (*Poa compressa*), and smooth brome (*Bromus inermis*). Native species were less common and included big bluestem (*Andropogon gerardii*), granular sedge (*Carex granularis*) and stiff goldenrod (*Solidago rigida*). We established four 48-m x 32-m herbicide treatment plots in this four-times replicated experiment and an equivalent number of untreated control plots. Originally, we were interested in comparing a conventional restoration technique (tillage and herbicide application) with interseeding. However, a previously undocumented population of the endangered Great Plains ladies'-tresses (*Spiranthes magnicamporum*) emerged three days after we applied herbicide, precluding any subsequent mechanical or chemical treatments.

We sampled the vegetation cover of all plant species within four permanent 1-m x 1-m quadrats in each treatment plot. We also sampled four plots at a neighboring reference site that we used to identify any treatment-related changes in vegetation. To assess the seedbank species composition, we collected four soil samples within each of the treatment and reference plots. We mixed soil samples with equal proportions of a sterile mix (Sunshine Mix 4 Aggregate Plus) and placed them in 4-inch x 6-inch x 3-inch (10-cm x 15-cm x 8-cm) pots within the greenhouse. We identified and removed seedlings as they emerged. When the seedbank was exhausted, we cold-stratified the samples at 36°F (2°C) for six weeks and repeated the procedure once. We found that the seedbank of the degraded prairie had significantly higher diversity and density of both native and exotic graminoids (grasses, sedges, and rushes), and it tended to have higher diversity of exotic forbs. In contrast, the reference site had significantly higher native forb diversity and density.

In spring 2000, we observed that 80-95 percent of aboveground vegetation in the treatment plots died following the glyphosate application the previous August. Plant re-growth was extremely slow and vegetation did not green-up until late August 2000. We used t-tests to determine whether glyphosate had a significant effect on aboveground species richness (total number of species) and effective species richness (reciprocal of Simpson's diversity measure). We measured the latter because it is relatively insensitive to rare species. Two years after glyphosate application, we found that effective species richness for both exotic and native species had decreased significantly. Native species richness also decreased significantly, whereas no difference was found in exotic species richness (Sveinson 2003). Both glyphosate-treated and untreated plots were dominated by exotics redtop, Canada bluegrass, and common self-heal (*Prunella vulgaris*). In contrast, reference plots were dominated by native graminoids such as big bluestem and prairie cordgrass (*Spartina pectinata*) (Table 1).

Herbicide-associated mortality of vegetation in the treatment plots likely resulted in recolonization of exotic species that dominated the seed and propagule banks, and further created opportunities for establishment by wind- and/or vector-dispersed species (Sveinson 2003). All exotic graminoids that increased in dominance in the herbicide-treated plots--redtop and Canada bluegrass--were found in the seedbank. Other exotic forb species, such as Canada thistle (*Cirsium arvensis*) and common self-heal, were not found in the seedbank, but were present in neighbouring seedbanks and may have colonized from surrounding areas. These results suggest that seedbanks can greatly affect the outcome of a restoration project. We strongly recommend characterizing both aboveground and seedbank species in order to increase the likelihood of success.

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Table 1. Five most dominant species found in the treatment and reference plots. Species were ranked based on average percent cover estimates in 1m x 1m quadrats.

Latin Name	Common Name	Glyphosate[1]	No Glyphosate	Reference site
Native species				
Andropogon gerardii	Big bluestem	-	6	1
Antennaria neglecta	Field pussytoes	28	5	32
Carex granularis	Granular sedge	2	2	13
Carex spp.	Sedge species	8	4	4
Eleocharis palustris	Common spike rush	5	-	6
Juncus spp.	Rush species	15	18	43
Spartina pectinata	Prairie cordgrass	-	-	2
Exotic speceis				
Agrostis stolonifera	Redtop	1	3	3
Festuca elatior	Tall meadow fescue	4	10	-
Poa compressa	Canada Bluegrass	7	1	20
Prunella vulgaris	Common self-heal	3	8	5

[1] - indicates species is not present

APPENDIX 2. Scientific and common name (Punter 1998)*, growth form (F = forb; G = graminoid; and W = woody), and origin (N = native and E = exotic) for all species found within the Manitoba Tall Grass Prairie Preserve (MTGPP) and St. Charles Rifle Range (SCRR) study sites. Species codes for ordinations use the first three letters of the genus and species of the scientific name (e.g. Achmil = *Achillea millefolium*).

Scientific name	Common name	Origin	Form	MTGPP	SCRR
Achillea millefolium	Common yarrow	N	F	*	*
Agalinis tenuifolia	Slenderleaf false foxglove	N	F	*	
Agoseris glauca	False dandelion	N	F	*	*
Agropyron repens	Quackgrass	E	G	*	
Agropyron subsecundum	Slender wheatgrass	N	G		*
Agropyron trachycaulum	Slender wheatgrass	N	G	*	*
Agropyron trachycaulum var. unilaterale	Awned wheatgrass	N	G	*	*
Agrostis stolonifera	Redtop	E	G	*	
Allium stellatum	Pink-flowered onion	N	F	*	*
Ambrosia sp.	Ragweed	E	F		*
Amelanchier alnifolia	Saskatoon	N	W	*	*
Amorpha nana	Dwarf flase indigo	N	W		*
Andropogon gerardii	Big bluestem	N	G	*	*
Andropogon scoparius	Little bluestem	N	G	*	*
Anemone canadensis	Canada anemone	N	F	*	*
Anemone cylindrica	Thimbleweed	N	F		*
Anemone multifida	Cut-leaved anemone	N	F	*	*
Anemone patens	Prairie crocus	N	F		*
Antennaria neglecta	Field pussy-toes	N	F	*	
Apocynum cannabinum	Indian-hemp	N	F	*	
Artemisia ludoviciana	Pasture sage	N	F		*
Asclepias incarnata	Swamp milkweed	N	F	*	
Asclepias ovalifolia	Dwarf milkweed	N	F	*	*
Asclepias spp.	Milkweed	N	F	*	
Aster ciliolatus	Lindley's aster	N	F	*	
Aster ericoides	Many-flowered aster	N	F	*	*
Aster laevis	Smooth aster	N	F	*	*
Aster lateriflorus	Wood aster	N	F	*	
Aster ptarmicoides	Upland aster	N	F	*	

APPENDIX 2. cont'd

Scientific name	Common name	Origin	Form	MTGPP	SCRR
Aster simplex	Small blue aster	N	F	*	
Aster spp.	Aster	N	F	*	
Astragalus agrestis	Purple milkvetch	N	F	*	*
Berteroa incana	Hoary alyssum	E	F		*
Brassica sp.	Mustard	E	F	*	*
Brassica spp.	Mustard	E	F	*	
Bromus inermis	Smooth brome	E	G	*	*
Calamagrostis canadensis	Marsh reed grass	N	G	*	
Calamagrostis inexpansa	Northern reed grass	N	G	*	*
Campanula rotundifolia	Harebell	N	F	*	*
Carex aurea	Golden sedge	N	G	*	
Carex buxbaumii	Brown sedge	N	G	*	
Carex crawei	Crawe's sedge	N	G	*	
Carex granularis	Granular sedge	N	G	*	
Carex lanuginosa	Woolly sedge	N	G	*	*
Carex praegracilis	Northern meadow sedge	N	G		*
Carex praticola	Graceful sedge	N	G		*
Carex sartwellii	Sartwell's sedge	N	G	*	
Carex spp.	Sedge	N	G	*	*
Carex tetanica	Rigid sedge	N	G		*
Carex torreyi	Torrey's sedge	N	G		*
Carex umbellata	Umbellate sedge	N	G	*	
Cerastium sp.	Chickweed	N	F		*
Cirsium arvense	Canada thistle	E	F	*	*
Cirsium flodmanii	Flodman's thistle	N	F	*	*
Cirsium vulgare	Bull thistle	E	F	*	
Comandra umbellata	Bastard toadflax	N	F		*
Cornus stolonifera	Red-osier dogwood	N	W	*	
Crataegus chrysocarpa	Round-leaved hawthorn	N	W	*	
Dalea purpurea	Purple prairie clover	N	F	*	*
Deschampsia caespitosa	Tufted hair grass	N	G	*	
Eleocharis palustris	Creeping spike-rush	N	G	*	
Eleocharis sp.	Spike-rush	N	G	*	
Elymus canadensis	Canada wild rye	N	G	*	*
Epilobium spp.	Willow-herb	E	F	*	
Erigeron asper	Rough fleabane	N	F	*	
Erigeron canadensis	Canada fleabane	E	F	*	

APPENDIX 2. cont'd

Scientific name	Common name	Origin	Form	MTGPP	SCRR
Erigeron philadelphicus	Philadelphia fleabane	N	F	*	*
Erigeron spp.	Fleabane spp.	E	F	*	
Festuca elatior	Meadow fescue	E	G	*	
Fragaria virginiana	Smooth wild strawberry	N	F	*	*
Gaillardia aristata	Great-flowered gaillardia	N	F		*
Galium boreale	Northern bedstraw	N	F	*	*
Gentiana andrewsii	Closed gentian	N	F	*	*
Geum triflorum	Three-flowered avens	N	F	*	*
Glycyrrhiza lepidota	Wild licorice	N	F	*	*
Helianthus laetiflorus	Beautiful sunflower	N	F	*	
Helianthus maximiliani	Narrow-leaved sunflower	N	F	*	*
Helianthus subrhomboideus	Stiff sunflower	N	F		*
Heliopsis helianthoides	Rough false sunflower	N	F		*
Heuchera richardsonii	Alumroot	N	F	*	*
Hieracium scabriusculum	Hawkweed	N	F	*	*
Hieracium spp.	Hawkweed	N	F	*	
Hierochloe odorata	Sweet grass	N	G	*	*
Juncus balticus	Baltic rush	N	G	*	*
Juncus interior	Inland rush	N	G	*	*
Juncus sp.	Rush	N	G	*	
Juncus spp.	Rush	N	G	*	
Keoleria cristata	June grass	N	G	*	*
Lactuca pulchella	Blue lettuce	N	F		*
Lathyrus palustris	Marsh vetchling	N	F		*
Lathyrus venosus	Wild peavine	N	F		*
Liatris ligulistylis	Meadow blazingstar	N	F	*	*
Linum sulcatum	Grooved yellow flax	N	F		*
Lithospermum canescens	Hoary pucoon	N	F	*	*
Lobelia kalmii	Kalm's Lobelia	N	F	*	
Lobelia spicata	Palespike Lobelia	N	F	*	
Lycopus americanus	Water-horehound	N	F	*	*
Medicago lupulina	Black medick	E	F	*	
Medicago sativa	Alfalfa	E	F	*	
Melilotus alba	White sweet clover	E	F	*	
Melilotus officinalis	Yellow sweet clover	E	F	*	
Melilotus spp.	Sweet clover	E	F	*	
Monarda fistulosa	Wild bergamot	N	F		*

APPENDIX 2. cont'd

Scientific name	**Common name**	**Origin**	**Form**	**MTGPP**	**SCRR**
Muhlenbergia richardsonis	Mat muhly	N	G	*	*
Oenothera biennis	Evening primrose	N	F	*	
Oxalis stricta	Yellow woodsorrel	E	F	*	
Panicum capillare	Witch grass	N	G	*	
Panicum lanuginosum	Soft millet	N	G	*	
Panicum leibergii	Leiberg's panic grass	N	G	*	*
Panicum sp.	Panic grass	N	G	*	
Phleum pratense	Common Timothy	E	G	*	
Plantago major	Common plantain	E	F	*	
Platanthera praeclara	Western prairie fringed orchid	N	F	*	
Poa compressa	Canada blue grass	E	G	*	
Poa pratensis	Kentucky blue grass	E	G	*	*
Poa spp.	Blue grass	E	G	*	*
Polygonum convolvulus	Black bindweed	E	F	*	
Polygonum spp.	Bindweed	E	F	*	
Populus tremuloides	Trembling aspen	N	W	*	*
Potentilla anserina	Silverweed	N	F	*	
Potentilla arguta	Tall prairie cinquefoil	N	F	*	
Potentilla fruticosa	Shrubby cinquefoil	N	W	*	
Prunella vulgaris	Heal-all	E	F	*	
Psoralea argophylla	Silverleaf psoralea	N	F		*
Psoralea esculenta	Indian breadroot	N	F		*
Ranunculus spp.	Buttercup	N	F	*	
Rhus radicans	Poison-ivy	N	F	*	
Rosa spp.	Rose	N	W	*	*
Rudbeckia hirta	Black eyed Susan	N	F	*	
Salix bebbiana	Beaked willow	N	W	*	*
Salix lutea	Yellow willow	N	W	*	*
Salix petiolaris	Basket willow	N	W		*
Salix spp.	Willow	N	W	*	*
Senecio pauperculus	Balsam groundsel	N	F	*	
Setaria glauca	Yellow foxtail	E	G	*	
Setaria viridis	Green foxtail	E	G	*	
Sisyrinchium montanum	Common blue-eyed grass	N	F	*	*
Smilacina stellata	False Soloman's seal	N	F		
Solidago canadensis	Graceful goldenrod	N	F	*	*
Solidago gigantea	Late goldenrod	N	F		*

APPENDIX 2. cont'd

Scientific name	**Common name**	**Origin**	**Form**	**MTGPP**	**SCRR**
Solidago graminifolia	Flat-topped goldenrod	N	F	*	
Solidago juncea	Sharp-toothed goldenrod	N	F		*
Solidago nemoralis	Showy goldenrod	N	F	*	*
Solidago rigida	Stiff goldenrod	N	F	*	*
Solidago spp.	Goldenrod	N	F	*	*
Sonchus arvensis	Field sow-thistle	E	F	*	*
Spartina pectinata	Prairie cord grass	N	G	*	*
Spiraea alba	Meadowsweet	N	W	*	*
Spiranthes magnicamporum	Great Plains ladies'-tresses	N	F	*	
Spiranthes romanzoffiana	Hooded ladies'-tresses	N	F	*	
Sporobolus heterolepis	Prairie dropseed	N	G	*	*
Stachys palustris	Woundwort	N	F	*	*
Steironema quadriflorum	Whorled loosestrife	N	F	*	
Stipa sp.	Porcupine grass	N	G		*
Stipa spartea	Porcupine grass	N	G	*	*
Symphoricarpos albus	Snowberry	N	W		*
Symphoricarpos occidentalis	Western snowberry	N	W		*
Symphoricarpos spp.	Snowberry	N	W	*	*
Taraxacum officinale	Common dandelion	E	F	*	*
Thalictrum dasycarpum	Tall meadow-rue	N	F	*	*
Thalictrum venulosum	Veiny meadow-rue	N	F		*
Trifolium pratense	Red clover	E	F	*	
Trifolium repens	White clover	E	F	*	
Vicia americana	American vetch	E	F	*	*
Vicia cracca	Tufted vetch	E	F		*
Viola adunca	Early blue violet	N	F		*
Viola nephrophylla	Northern bog violet	N	F	*	*
Viola pedatifida	Birdfoot violet	N	F	*	*
Zigadenus elegans	White camas	N	F	*	
Zizia aptera	Heart-leaved Alexanders	N	F	*	*
Zizia aurea	Golden Alexanders	N	F	*	*

*Punter, E. 1998. Manitoba Conservation Data Centre Vascular Plant Species Listing (Confirmed Reports). Unpublished report prepared for Conservation Manitoba. Manitoba, Canada.

APPENDIX 3. ANOVA model statement for a) Manitoba Tall Grass Prairie Preserve experiment and b) St. Charles Rifle Range study.

a)

Factor	d.f.
Block	2
Glyphosate	1
Block * Glyphosate	2
Disturbance	2
Fertilizer	1
Disturbance * Fertilizer	2
Glyphosate * Disturbance	2
Glyphosate * Fertilizer	1
Glyphosate * Disturbance * Fertilizer	2
Block * Disturbance	4
Block * Fertilizer	2
Block * Disturbance * Fertilizer	4
Block * Disturbance * Glyphosate	4
Block * Fertilizer * Glyphosate	2
Block * Disutrbance * Fertilizer * Glyphosate	4
Seeding	1
Seeding * Block	2
Seeding * Glyphosate	1
Seeding * Fertilizer	1
Seeding * Disturbance	2
Seeding * Glyphosate * Fertilizer	1
Seeding * Glyphosate * Disturbance	2
Seeding * Fertilizer * Disturbance	2
Seeding * Fertilizer * Disturbance * Glyphosate	2
Seeding * Glyphosate * Block	2
Seeding * Fertilizer * Block	2
Seeding * Disturbance * Block	4
Seeding * Glyphosate * Fertilizer * Block	2
Seeding * Glyphosate * Disturbance * Block	4
Seeding * Fertilizer * Disturbance * Block	4
Seeding * Fertilizer * Disturbance * Glyphosate * Block	4
Total d.f.	71

b)

Factor	d.f.
Block	3
Burn-season	3
Block * Burn-season	9
Year	2
Block * Year	6
Burn-season * Year	6
Block * Burn-season * Year	18
Total d.f.	47

APPENDIX 4. The Domin Scale used in the St. Charles Rifle Range study (Kent & Coker 1996).

Domin Scale	Value	Midpoint
+	1 individual, no measurable cover	0.25%
1	1-2 individuals, no measurable cover	0.5%
2	Several individuals but <1%	0.75%
3	1 – 4%	2.5%
4	4 – 10%	7.0%
5	11 – 25%	18.0%
6	26 – 33%	28.5%
7	34 – 50%	42.0%
8	51 – 75%	63.0%
9	76 – 90%	83.0%
10	91 – 100%	95.5%

APPENDIX 5. Mean precipitation and temperature for Winnipeg, Manitoba from April to September in 2000, 2001, and 2002 (http://www.gorilla-wx.net/).