University of Alberta

Ecology and Management of Crested Wheatgrass Invasion

by

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"*This land affords nothing but short, round, sticky grass*"

Henry Kelsey (1691) *The Kelsey Papers.* Champlain Society, Toronto ON.

"*...the conquest of the desert in the Palliser triangle in the 1930s is the greatest Canadian success story since the completion of the Canadian Pacific Railway...It is doubtful whether within the whole of our literature a single tale has been told with an agrostologist as the hero; and still less is there likely to have been one glorifying a grass seed...for few Canadians have ever played so large a role in changing the face of the earth as Dr. Lawrence Kirk, and few seeds of grass have ever been so face-changing as the crested wheat grass he developed at the University of Saskatchewan...Studies by Dr. S.E. Clarke [the Johnny Appleseed of crested wheat grass] definitely established the superiority of crested wheat grass and crested wheat and alfalfa mixtures, over the native prairie wool...* [and] *enough progress had been made to engender confidence that ultimate victory over the destructive forces in nature was assured. The beginning of the end was in sight.*"

James H. Gray (1967) *Men Against the Desert.* Western Producer Book Service, Saskatoon SK.

"*...the Dirty Thirties period was indeed a war in which no one had time to think about the long-term ecological effects of their best weapon [crested wheatgrass]. When I remind myself that topsoil rebuilds at a natural rate of about two centimeters per century, I know that we were right to try to preserve it at all costs. Now that the war is over, we can attempt to resolve some of the ecological fallout and find a balance between the competing demands of prairie agriculture and the threatened grassland ecosystem from which it sprang.*"

Don Gayton (1996) Turf wars. *Canadian Geographic*, 116, 70-78.

"*We presently lack the knowledge to determine the long-term effects of crested wheatgrass on the Great Plains. However, there is a growing body of knowledge that suggests that crested wheatgrass alters the environment in many undesirable ways...*[so] *the continued conversion of native prairie and planting of crested wheatgrass or other exotic species seems ill advised.*"

Peter Lesica & Thomas H. DeLuca (1996) Long-term harmful effects of crested wheatgrass on Great Plains grassland ecosystems. *Journal of Soil and Water Conservation*, 51, 408-409.

ABSTRACT

Crested wheatgrass (*Agropyron cristatum* Gaertn. [L.] *sensu amplo*), a perennial bunchgrass from the temperate steppes of Asia, was introduced to North America for livestock forage and land reclamation. Invasion by crested wheatgrass into adjacent native grasslands may impact biodiversity and ecosystem functioning, but documentation is lacking. Further, many land managers desire means to prevent invasion from economically valuable agricultural plantings and to restore invaded areas on lands set aside for biodiversity conservation.

A research program was designed to describe multiple scales of crested wheatgrass invasion patterns and impacts in mixed-grass prairie of Alberta and Saskatchewan, and to determine effective means for preventing invasion and restoring invaded grassland. Within the mixed-grass prairie region, crested wheatgrass invasion most commonly occurred on excellent condition rangeland and rarely on saline soils or poor condition rangelands. Among and within plant communities, invasion was associated with greater aboveground biomass and crested wheatgrass dominance, but lower species richness and vegetation diversity. Seedbank diversity was not different, but crested wheatgrass appeared to replace fringed sage (*Artemisia frigida* Willd.) as the most abundant species (40% of germinable seed), suggesting substantial seed inputs or seedbank persistence.

In field experiments, >90% of crested wheatgrass seed buried in the soil germinated or decomposed within 5 months. Conversely, >75% of seed elevated above the soil survived at least 26 months, suggesting seedbanks persist where sward management permits aerial seedbanks to form above the soil. Four years of repeated grazing, haying and glyphosate applications reduced or maintained low crested wheatgrass seedbank densities, but only glyphosate reduced adult plant cover. With the exception of glyphosate, no treatment significantly increased community diversity or similarity towards a native reference community. Selective glyphosate application allowed native species survival, and the flush of resource availability promoted native species germination from the seedbank and colonization from off-site. Restoration efficiency and effectiveness may be increased with a carefully sequenced combination of grazing to reduce crested wheatgrass seedbanks, then glyphosate to remove adult plants, then native grass seed additions to overcome dispersal barriers; particularly of those species competitively excluded by crested wheatgrass.

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CHAPTER I. ECOLOGY AND MANAGEMENT OF CRESTED WHEATGRASS

APPLIED PERSPECTIVES

Biological invasions by alien species are considered one of the greatest threats to biodiversity conservation world-wide, second only to direct habitat loss through human land use. Invasive alien plants simplify compositional structure by rapidly increasing in abundance, dominating communities, resisting further succession, and in some cases locally extirpating species or altering ecosystem function (Mack et al. 2000). Alien species (a.k.a. exotic, introduced or non-indigenous) include those that rapidly overcome natural dispersal barriers among continents or among oceanic islands via deliberate or accidental human transportation. Although inter-continental and inter-island dispersal and colonization is a natural process (MacArthur & Wilson 1967), over the last 500 years humans have increased this rate to unprecedented levels. What constitutes a native species is more problematic to define. Some simple definitions for North America limit native species to those associated with co-evolved competitors, predators and pathogens, and present in North America prior to 1492 (Haber 1999). However, this negates including recent colonists not associated with human vectors, long-established aliens that have hybridized with natives, or the subsequent evolution of aliens to become naturalized components of ecosystems (Mack et al. 2000).

Concern over biological invasions has stimulated considerable scientific inquiry, with the primary question for plants being why do some alien invasive species appear to compete so successfully with native species. A number of hypotheses have been proposed and reviewed by Mack et al. (2000) and Hierro et al. (2004). A species-centered view involves identifying whether some "novel attribute(s)" of the alien, not otherwise represented in the native flora, provides a competitive advantage and facilitates invasion. Some attributes investigated to date include phylogeny, allelopathy, greater fecundity, greater size, or greater tolerance to abiotic stresses (i.e. Rejmanek & Richardson 1996). A bottom-up view involves identifying whether the alien is pre-adapted to utilize a niche not otherwise used by native species. Human disturbance and eutrophication of the environment creates niches by increasing or disrupting natural "fluctuations in resource availability" (i.e. Davis et al. 2000). Local extirpation following disturbance is not necessary to create an "empty niche", as the local species pool may simply not include a species adapted to use a niche in time and space (i.e. Elton 1958). The latter also suggests community diversity, either taxonomic or functional, should confer some "invasion resistance" (i.e. Tilman 1997). Finally, a top-down view involves identifying whether an alien has experienced competitive release in a new environment devoid of co-evolved predators and pathogens. This "enemy escape" may allow reallocation of metabolic energy from defense toward growth and reproduction. Where this reallocation provides a selective advantage, aliens may undergo "evolution for increased competitive ability" (i.e. Blossey & Notzold 1995) and the time needed by a population to accumulate those adaptations could explain the lag phase preceding the exponential phase in many invasions (Lambrinos 2004). No single theory has emerged to explain why some aliens are successful, in part because different factors operate at different scales (Byers & Noonburg 2003) and invaders vary in so many attributes (Lodge 1993).

While biologists continue to pursue the ultimate causes of invasion, land managers are most concerned with the proximate extent of invasion and severity of the resulting ecological and economic impacts (Pimentel et al. 2001). Answers to these management questions are what justify policy changes and control efforts, but there is an unfortunate dichotomy between those researching the causes for invasion and those researching means or actively attempting to control invasions (Hobbs & Huenneke 1992; Hobbs & Humphries 1995). One group treats all alien species equally because the goal is to discover a universal cause in the scientific tradition. The other group treats a handful of dominating and economically damaging "weeds" differently from those with neutral or positive economic impacts. Rarely have the ecological impacts been evaluated for economically valued alien invasive species.

Crested wheatgrass (*Agropyron cristatum* L. [Gaertn.]) is an example of the latter case. This Eurasian species is one of the most widely distributed and abundant alien species in semiarid regions of western North America. The reasons for this deliberate proliferation are complex and have to do with human values. However, causation for the accidental proliferation in northern mixed-grass prairie, ecological impacts of this invasion, and means to prevent invasion and restore invaded grasslands are applied science questions that, to date, have been given relatively little attention.

FUNCTIONAL ECOLOGY OF NORTHERN MIXED-GRASS PRAIRIE

Many characteristics of semiarid, temperate environments are important to consider for alien plant invasions. To survive in these ecosystems a plant must possess life history strategies, morphological or physiological adaptations for persistence under climatic conditions that vary greatly in amplitude (Smoliak 1986; Burke et al. 1997). Perennial grasses dominate because the deep fibrous roots effectively forage for spatially and temporally variable supplies of soil moisture and nitrogen (Burke et al. 1998; Krueger-Mangold et al. 2004). Grasslands are also subject to frequent fire and grazing, and grasses in particular have co-evolved morphologically to withstand these disturbances (Langer 1972). To become invasive, a plant must possess superior adaptations to climate, grazing or fire relative to the dominant native species.

The coexistence of many grassland species has much to do with temporal and spatial variation in colonization, longevity and competitive ability (Tilman 1994). The mixed-grass prairie includes a wide variety of species representing monocotyledon and dicotyledon origins, caespitose and rhizomatous growth habits, annual and perennial life histories, woody and herbaceous life forms, and C_3, C_4 and Crassulacean Acid Metabolism photosynthetic pathways (Coupland 1950). The relative abundance of these functional groups at any point in time and space is affected by topoedaphics (Ayyad & Dix 1964; Barnes et al. 1983), soil disturbance (Costello 1944; Coffin & Lauenroth 1988; Umbanhowar 1992; Samuel & Hart 1994), grazing and fire history (Dyksterhuis 1949; Collins & Barber 1985), and their interactions (Milchunas et al. 1989).

Clines in these biological characteristics among these landscapes complicate functional classifications, but changes in the abundance of many ubiquitous species are useful indicators of microclimate, soil and grazing conditions (Lauenroth et al. 1997). For example, the C_4 short-grass, blue grama (*Bouteloua gracilis*) is an indicator of xeric or grazed sites while the C_3 mid-grass, needle and thread (*Stipa comata*) is an indicator of mesic or ungrazed sites, and the forb, fringed sage (*Artemisia frigida*) indicates prolonged heavy grazing or soil disturbance (Coupland 1950). Transitions between community types can progress linearly in the absence of disturbance (Clements 1936), or become retrogressive as grazing pressure increases (Dyksterhuis 1949), or jump irreversibly from one state to another under unique suites of conditions (Westoby et al. 1989).

INTENTIONAL PROLIFERATION OF CRESTED WHEATGRASS

Europeanization of the Northern Great Plains

To expedite settlement of the northern Great Plains c.1900, the region was subdivided into a grid of land parcels for "homesteading". To qualify for subsidized purchase of these homesteads, settlers were required to cultivate a portion of the parcel allotted, with no attention to the amenability of the soil to support cultivated plants (Jones 2002). As a result, large areas of land were cultivated except for those most sandy, stony, saline and steeply sloped. During the 1930s, much of the marginally productive cultivated lands were abandoned and left to revegetate naturally or were seeded with alien perennial forages adapted to continuous grazing by domestic livestock. Agricultural researchers imported productive, easily established and persistent forage species from semiarid regions of eastern Europe and central Asia. Of those species, crested wheatgrass was the most easily established and persistent under drought conditions of the 1930s (Coulman et al. 1999). Thus began the extensively documented (Rogler & Lorenz 1983) and even glorified (Gray 1967) process of crested wheatgrass proliferation; though a few details deserve attention for this dissertation.

Crested Wheatgrass Agronomy and Use

Crested wheatgrass is actually a complex of species native to the temperate steppes of Eurasia (Dillman 1946; Beetle 1961; Dewey 1986). In the late 1800s seeds of the diploid *Agropyron cristatum* (Gaertn.) and tetraploid *Agropyron desertorum* (Fisch. ex Link) were introduced to both Canada and the United States of America (USA). Generally, *A. cristatum* is a shorter, leafier plant whereas *A. desertorum* is taller and contains relatively more coarse stems. Multiple cultivated varieties have been developed from both species and subsequent introductions of additional species (*A. sibericum*, *A. mongolicum*, *A. fragile*). Varietal differences in morphology, phenology, nutritive quality, forage yield and germinability have been investigated (Asay & Johnson 1983, 1990; Ray et al. 1994, 1996, 1997), and these intra-complex differences tend to be less than between crested wheatgrass and native grass species. Due to confusion surrounding the taxonomy and usage of common names, both Beetle (1961) and Dewey (1986) proposed a single all-encompassing nomenclature (*A. cristatum sensu amplo* and *A.*

cristatum sensu lato, respectively) but neither term is commonly used. I will refer to the complex as *A. cristatum* from this point forward.

Following initial use for abandoned farmland revegetation c.1935, the high yielding, early growing and palatable properties of *A. cristatum* were promoted for use in complimentary grazing systems (Lodge 1970). Phenologically, *A. cristatum* is more productive earlier in the season relative to native mixed-grass prairie species, and a combination of these two pasture types can extend the grazing season and defer grazing native prairie; the latter contributing to long-term sustainability (Smoliak et al. 1980). In the 1960s and 70s Canadian and USA regulatory agencies began requiring resource extraction industries to revegetate disturbed lands, and in semiarid regions *A. cristatum* was the most popular species for this purpose (DePuit 1986). In recent decades the use of native species for revegetation has been promoted (Richards et al. 1998) and the use of *A. cristatum* for revegetation has been discontinued in Alberta (Alberta Environment 2003). Currently, changes in agricultural markets are increasing conversion of annually cultivated cropland to perennial hay and pasture. Government subsidies through the USA Conservation Reserve Program and Canadian Permanent Cover Program have helped convert several million ha, and in the northern Great Plains *A. cristatum* is the most commonly seeded species (Lesica & DeLuca 1996, Vaisey et al. 1996).

A more recent and somewhat paradoxical use for *A. cristatum* has been the deliberate seeding to prevent the spread of other alien invasive species. In semiarid Wyoming, seeding *A. cristatum* helped prevent cheatgrass (*Bromus tectorum*) seedling survival and reestablishment (Whitson & Koch 1998). In more arid portions of Utah, *A. cristatum* is being used as a "nurse crop" to facilitate succession away from cheatgrass dominance and toward native sagebrush and perennial bunchgrass dominance, in part because *A. cristatum* reduces cheatgrass in the short-term but is not persistent in the long-term (Cox & Anderson 2004). Elsewhere, competition with *A. cristatum* has reduced cover and prevented the spread of knapweed (*Centaurea* spp.) and leafy spurge (*Euphorbia esula*) (Berube & Myers 1982; Ferrell et al. 1998).

To date, *A. cristatum* has been seeded on approximately 1.7 million ha of the 24 million ha Canadian mixed-grass prairie, or 6.7% of the region (Appendix A). The area remaining as native mixed-grass prairie is considerably larger, approximately 7.9 million ha or 33% of the region, but these fragmented remnants are almost wholly surrounded by *A. cristatum* because of intentional seedling along roadside ditches and utility rights-of-way. This landscape configuration and juxtaposition of vegetation types may have a substantial influence on *A. cristatum* invasion (Forman et al. 2004).

CRESTED WHEATGRASS INVASION

Geographic Scope

Ideal conditions for *A. cristatum* persistence relate to the fundamental and realized niche of the species (Hutchinson 1957). In North America, *A. cristatum* is recommended for seeding semiarid rangelands within the temperate zones of western Canada and the USA (Johnson 1986). Within the native range of this species in Asia, climatic conditions vary from 200 to 450 mm mean annual precipitation, and -5 to 10 °C mean annual temperature (Appendix B). An overlay of these precipitation and temperature zones in North America corresponds with the cool semiarid portions of the western Great Plains and basins and plateaus between the Rocky Mountains and western Coastal Ranges (Figure 1.1). Smaller scale inductive models by Hill et al. (2000) based on climate and forage production records predicted a similar geographic distribution in Alberta.

Within this potential North American range of *A. cristatum* there are multiple reports of invasion into native grasslands (Table 1.1), and most occur within the northern Great Plains. The persistence of *A. cristatum* roughly correlates with this pattern, since pastures several decades old are common in Saskatchewan, Alberta and North Dakota (Lesica & DeLuca 1996), but pastures in Oregon, Nevada and Utah require reseeding at 10 to 20 year intervals to remain *A. cristatum*-dominated. This has led to some controversy categorizing *A. cristatum* as an invasive species, since managers and researchers in the Great Basin do not believe it is persistent or invasive and have gone so far as to call reports to the contrary "myths" (Johnson 1986).

Temporal Patterns of Dispersal

As a caespitose (bunch or tussock) grass the primary means of *A. cristatum* dispersal is by seed, and seedbank studies suggest high density annual seed production is the major factor in maintenance of *A. cristatum* monocultures (Marlette & Anderson 1986; Pyke 1990; Heidinga & Wilson 2002; Ambrose & Wilson 2003). Intraspecific competition can restrict *A. cristatum* seed production (Olson & Richards 1989; Jefferson & Kielly 1993), but seedbank densities greatly exceed those observed for native caespitose grasses (Romo & Bai 2004). Temporally, individual plants have asynchronous patterns of reproductive tiller development (Berdahl & Frank 1998), and this generates variability in seed maturity and subsequent shattering from culms. Pyke (1990) found *A. cristatum* seed can be retained on the spike for at least eight months which further extends the period of seed dispersal.

Under ideal moisture conditions for germination, only 20% of surface broadcast seed may germinate (Ambrose & Wilson 2003), and Pyke (1990) found germinable *A. cristatum* seed remained in the seedbank for at least one year. Taken together, this suggests the potential for invasion is not entirely a function of high annual seed production, but an interaction of this with long dispersal periods and potential dormancy contributing to seedbank persistence. Although the latter has been suggested as a cause for failure to eradicate *A. cristatum* (Wilson & Partel 2003), there is no direct evidence of seedbank persistence in a physiological sense (see Baskin & Baskin 1998; Thompson & Grime 1979).

Spatial Patterns of Invasion

Typically, invasion proceeds as a simple diffusion pattern from its point of origin, and over time multiple individuals form multiple patches leading to large-scale metapopulations (Radosevich et al. 2003). Marlette & Anderson (1986) found *A. cristatum* plants and seed up to 150 m from the edge of 20-year old stands, and Hull & Klomp (1966) and Heidinga & Wilson (2002) found plants at least 30 m from the edge of 30 and 50-year old stands, respectively. Because *A. cristatum* can retain seed into the winter (Pyke 1990) it is possible the smooth surface of snow drifts allows long-distance dispersal. For example, in Grasslands National Park individual plants have been discovered up to 5 km from the nearest possible seed source. These isolated cases of long-distance dispersal and the reported invasion rates of 1 to 2 m yr^{-1} may be extreme instances from the leeward edge of seeded patches. However, establishment of widely dispersed individuals or "nascent foci" can greatly accelerate invasion rates in the long-term (Moody & Mack 1988). Landscape fragmentation may be most important to consider, since the long and narrow transportation corridors seeded to *A. cristatum*, though small in area relative to rectangular fields, have relatively more edge exposed to adjacent native grasslands and are a greater potential source for invasion (Forman et al. 2004).

Potential Ecological Impacts of Invasion

Comparative descriptions of native grasslands and adjacent *A. cristatum* dominated fields indicate an overall community scale pattern of lower richness, evenness and diversity in the latter (Table 1.2). However, the structure of these comparisons often involves confounding or covarying influences, like mechanical shrub control or cultivation prior to seeding *A. cristatum* (Smoliak et al. 1967; Dormaar et al. 1978; Reynolds & Trost 1980; Marlette & Anderson 1986; Sutter & Brigham 1999; Broersma et al. 2000; Krzic et al. 2000), initial cultivation of both native and *A. cristatum* dominated communities (Wilson 1989; Christian & Wilson 1999), or gradients of *A. cristatum* abundance from dispersal onto native grasslands (Heidinga & Wilson 2002). These influences need to be considered when evaluating the potential impacts of *A. cristatum* invasion on native grassland community diversity. No study involved before and after comparisons of the same site, although Dormaar et al. (1978) resampled sites 12 years after Smoliak et al. (1967). As such, it is not possible to determine if reported patterns reflect pre-existing diversity, competitive displacement and colonization prevention of natives following invasion, or year and management effects from the time invasion began until measurements were made.

Controlled field competition experiments indicate variable performance of *A. cristatum* in seeded mixtures with native grass species. Schuman et al. (1982) observed *A. cristatum* out-compete native species after four years in semiarid Wyoming. In Saskatchewan, production and survival of *Bouteloua gracilis* transplants were greater in semiarid old fields than in *A. cristatum* pastures (Bakker & Wilson 2001). A survey of more than 80 *A. cristatum* pastures in southern Saskatchewan, 8 to 35 years after establishment, indicated *A. cristatum* still dominated vegetative cover (Looman & Heinrichs 1973). These studies from semiarid regions contrast with those from subhumid regions. McWilliams & Van Cleave (1960), observed *Pascropyrum smithii* and *Stipa viridula* out-compete *A. cristatum* within the subhumid foothills of western Montana. In addition, grazing *A. cristatum* monocultures promoted invasion by native grasses like

Stipa comata and *Stipa viridula* from adjacent research plots. Wilson (1989) observed a similar response among these species on reclaimed roadways in a subhumid transition zone between tallgrass and mixed-grass prairie in southern Manitoba.

Comparisons of soil beneath crested wheatgrass pastures and native prairie indicate no change or lower root biomass and organic matter under *A. cristatum* (Table 1.3). In most cases it is difficult to account for the covarying influence of cultivation on soil organic matter content, since that perturbation alone can cause the observed change. Only Christian & Wilson (1999) explicitly compared *A. cristatum* and native dominated soils on abandoned cultivated land. Low soil organic carbon and nitrogen beneath *A. cristatum* has been attributed to lower root biomass and plant residue inputs (Dormaar et al. 1978, Smoliak & Dormaar 1985, Dormaar et al. 1995, Christian & Wilson 1999). This interpretation seems surprising, since *A. cristatum* is known to produce more above-ground biomass than mixed-grass prairie communities (Smoliak et al. 1980). Thus, the deliberate conversion and accidental invasion of this species could have regional and global consequences for carbon sequestration and mitigation of greenhouse gas emissions (Christian & Wilson 1999).

CONTROL AND RESTORATION FOLLOWING CRESTED WHEATGRASS INVASION

Goals and Considerations

Two very different paradigms are implied by the terms control and restoration. Weed scientists are primarily focused on manipulating the demographic process of a single species, using techniques and approaches suitable for a range of plant community types (Huston 2004). For rangelands, the end goal is often a productive, palatable and nutritious mixture of plants suitable for livestock (DiTomaso 2000). In contrast, restoration ecologists are primarily focused on manipulating a range of successional processes, using techniques and approaches to achieve a targeted plant community composition (Hobbs & Harris 2001). For grasslands, the end goal is often a diverse mixture of perennial species representative of the richness and evenness observed in natural grassland communities. Integrating the two paradigms is absolutely necessary for simultaneously preventing or eradicating an invasive alien species while encouraging the development of a native-dominant plant community similar to the pre-invaded structure and composition (Hobbs & Humphries 1995; Randall 1996). This is a special case of restoration, where the presence of an invasive alien species is the primary biotic limitation that must be overcome for transition to a new compositional state to occur (D'Antonio & Meyerson 2002).

Approaches Taken for Control

Conventional methods to eradicate perennial herbaceous plants include repeated tillage and herbicide applications. Unfortunately, these high cost and energy intensive methods create a number of problems, including soil organic matter loss, selection for herbicide tolerant individuals and eradication of co-occurring desireable species. In addition, these disturbed soils are rapidly dominated by annuals and are dissimilar from perennial dominated grasslands. Though perennial plants will increase and replace the annuals over time (Costello 1944; Samuel & Hart 1994), many annual species are classified as noxious weeds, which introduces legal and social barriers to restoration (D'Antonio & Meyerson 2002).

Single applications of these techniques can reduce costs and may permit survival of seed and vegetative propagules, but often of both the invader and native species. For instance, tillage and broad-spectrum herbicides like glyphosate have been used to reinvigorate pastures of *A. cristatum* (Lorenz & Rogler 1962; Lym & Kirby 1991). In the short-term, tillage has neutral or negative effects on *A. cristatum* cover and production (Table 1.4), but in the long-term the reduced inter and intraspecific competition from neighbours stimulates vegetative and seed production (Olson & Richards 1989; Jefferson & Kielly 1993). Similarly, burning *A. cristatum* may cause short-term reductions in production but the effect does not persist in the long-term (Lodge 1960; Romo et al. 1994).

Timing and placement of particular disturbances appears to be important in reducing reproductive output and increasing mortality of *A. cristatum*. Defoliation after reproductive culms reach the ear stage of development can eliminate seed prior to fertilization and prevent further reproductive development in that year. Delaying defoliation until after anthesis can reduce vegetative production in the following year, but at the risk of allowing fertilized seed to enter the seedbank (Romo & Harrison 1999).

Although *A. cristatum* is generally tolerant of defoliating disturbances like mowing or grazing, seedlings may experience high mortality (Salihi & Norton 1987).

Elevated wick application of glyphosate early in the year can selectively increase the mortality of taller and earlier developing *A. cristatum*, while permitting survival of shorter and later developing native plants (Romo et al. 1994; Bakker et al. 2003). Spraying at this time only allows later developing native plants like *Bouteloua gracilis* to survive and increase over time (Bakker et al. 1997; Wilson & Partel 2003). In all cases, reinvasion by *A. cristatum* from an abundant soil seedbank has limited the success of these treatments. Romo et al. (1994) recommend three years of preventative treatment to deplete the soil seedbank prior to glyphosate application, but Wilson & Partel (2003) found seven years of repeated glyphosate application had no significant impact on seedbank density. The latter experiment did not control seed production from neighbouring buffer strips, and considerable annual seed rain from these invigorated neighbours may be a problem.

Approaches Taken for Restoration

Restoration of native grasslands typically involves seeding perennial species normally dominant in the vegetation. Perennial herbaceous species tend to produce short-lived or transient seedbanks (Thompson & Grime 1979) and landscapes subject to invasion or grazing tend to have few propagules of the dominant perennial grasses (Marlette & Anderson 1986; Heidinga & Wilson 2002; Romo & Bai 2004). Seeding can accelerate the occupation of space by native perennials (Bakker et al. 2003; Wilson et al. 2004), but this may produce communities very dissimilar from native reference communities (Hammermeister et al. 2003). Natural recovery depends on the emergence of persistent species from the seedbank or dispersal from adjacent patches, and perennials may be more dispersal limited on larger disturbances (Umbanhowar 1992; Coffin et al. 1996). Whether or not seed additions are necessary in the long-term is an important consideration, since this is an expensive approach and commercial suppliers may not provide genotypes of local provenance (Richards et al. 1998). Ideally, reliance on initial floristics to provide propagules sufficient for natural succession would reduce costs and biological conservation risks associated with alien genotypes of otherwise native species.

SUMMARY OF KNOWLEDGE GAPS

1. Although many anecdotal observations of *A. cristatum* invasion exist, the rate and extent of invasion among landscapes within the region remain unknown. In particular, there may be bottom-up factors associated with soil that limit invasion, and top-down factors associated with grazing that regulate invasion. A description of the realized niche for *A. cristatum* and quantification of invasion rates is needed to clarify the potential extent of this problem.
2. Where *A. cristatum* has been seeded on cultivated land, plant community diversity and soil quality appear to be lower than on comparable lands dominated by native species. Whether or not these patterns hold true following *A. cristatum* invasion of uncultivated, native mixed-grass prairie is unknown. An ecological impact assessment of *A. cristatum* invasion into mixed-grass prairie is needed to establish if and how plant community diversity and ecosystem function are altered.
3. The failure to eradicate *A. cristatum* after multiple years of control efforts has been attributed to persistence of a large soil seedbank. Persistence implies viable seed remains dormant in the soil for more than one year. This hypothesis has not been explicitly tested, and a number of microsite factors may influence the survival and fate of seed over time.
4. Experimental attempts to reduce *A. cristatum* abundance and simultaneously increase native species abundance have had mixed results. One of the greatest challenges is to reduce the seedbank of *A. cristatum* to halt rapid recruitment following mortality of adult plants. Carefully designed before-after control-impact experiments are necessary to test how a number of annually repeated disturbances affect the demographics of this invasive species, and successional trajectories towards a reference native community.
5. The synthesis of this information can provide insight on both the relative invasibility of different landscapes in the northern Great Plains, and the mechanisms for *A. cristatum* invasion in particular. Provided the gaps above can be addressed, management recommendations for different land use objectives can be provided where few are currently available. As well, hypotheses can be proposed and crucial experiments suggested to address knowledge gaps arising from this work.

LITERATURE CITED

Alberta Environment (2003) *Problem introduced forages on prairie and parkland reclamation sites: Guidance for non-cultivated land.* Alberta Environment R&R/03-05. Edmonton AB.

Allred, B.W. (1940) Crested wheatgrass in competition with the native grassland dominants of the northern Great Plains. *Soil Conservation*, **6**, 59-63.

Ambrose, L.G. (1999) *Seed persistence of an introduced and a native grass species in a prairie old field.* MSc Thesis, University of Regina. Regina SK.

Ambrose, L.G. & Wilson, S.D. (2003) Emergence of the introduced grass *Agropyron cristatum* and the native grass *Bouteloua gracilis* in a mixed-grass prairie restoration. *Restoration Ecology*, **11**, 110-115.

Asay, K.H. & Johnson, D.A. (1983) Genetic variability for characters affecting stand establishment in crested wheatgrass. *Journal of Range Management*, **36**, 703-706.

Asay, K.H. & Johnson, D.A. (1990) Genetic variances for forage yield in crested wheatgrass at six levels of irrigation. *Crop Science*, **30**, 79-82.

Ayyad, M.A.G. & Dix, R.L. (1964) An analysis of a vegetation-microenvironmental complex on prairie slopes in Saskatchewan. *Ecological Monographs*, **34**, 421-442.

Bakker, J.D., Christian, J., Wilson, S.D. & Waddington, J. (1997) Seeding blue grama in old crested wheatgrass fields in southwestern Saskatchewan. *Journal of Range Management*, **50**, 156-159

Bakker, J.D. & Wilson, S.D. (2001) Competitive abilities of introduces and native grasses. *Plant Ecology*, **157**, 117-125.

Bakker, J.D., Wilson, S.D., Christian, J.M., Li, X., Ambrose, L.G. & Waddington, J. (2003) Contingency of grassland restoration on year, site, and competition from introduced grasses. *Ecological Applications*, **13**, 137-153.

Barnes, P.W., Tiezen, L.L. & Ode, D.J. (1983) Distribution, production, and diversity of C3 and C4 dominated communities in a mixed prairie. *Canadian Journal of Botany*, **61**, 741-751.

Baskin, C.C. & Baskin, J.M. (1998) *Seeds: Ecology, biogeography, and evolution of dormancy and germination.* Academic Press, San Diego CA.

Beetle, A.A. (1961) The nomenclature of the crested wheatgrass complex. *Journal of Range Management*, **14**,

Berdahl, J.D. & Frank, A.B. (1998) Seed maturity in four cool-season forage grasses. *Agronomy Journal*, **90**, 483-488.

Berube, D.E. & Myers, J.H. (1982) Suppression of knapweed (*Centaurea diffusa*) invasion by crested wheatgrass (*Agropyron cristatum*) in the dry interior of British Columbia. *Journal of Range Management*, **35**, 459-461.

Blossey, B. & Notzold, R. (1995) Evolution of increased competitive ability in invasive non-indigenous plants: a hypothesis. *Journal of Ecology*, **83**, 887-889.

Broersma, K., Krzic, M., Thompson, D.J. & Bomke, A.A. (2000) Soil and vegetation of ungrazed crested wheatgrass and native rangelands. *Canadian Journal of Soil Science*, **80**, 411-417.

Burke, I.C., Lauenroth, W.K. & Parton, W.J. (1997) Regional and temporal variation in net primary productivity and nitrogen mineralization in grasslands. *Ecology*, **78**, 1330-1340.

Burke, I.C., Lauenroth, W.K., Vinton, M.A., Hook, P.B., Kelly, R.H., Epstein, H.E., Aguiar, M.R., Robles, M.D., Aguilera, M.O., Murphy, K.L. & Gill, R.A. (1998) Plant-soil interactions in temperate grasslands. *Biogeochemistry*, **42**, 121-143.

Byers, J.E. & Noonburg, E.G. (2003) Scale dependent effects of biotic resistance to biological invasion. *Ecology*, **84**, 1428-1433.

Christian, J.M. & Wilson, S.D. (1999) Long-term ecosystem impacts of an introduced grass in the northern Great Plains. *Ecology*, **80**, 2397-2407.

Clements, F.E. (1936) Nature and structure of the climax. *Journal of Ecology*, **24**, 252-284.

Coffin, D.P. & Lauenroth, W.K. (1988) The effects of disturbance size and frequency on a shortgrass plant community. *Ecology*, **69**, 1609-1617.

Coffin, D.P., Lauenroth, W.K. & Burke, I.C. (1996) Recovery of vegetation in a semiarid grassland 53 years after disturbance. *Ecological Applications*, **6**, 538-555.

Collins, S.L. & Barber, S.C. (1985) Effects of disturbance on diversity of mixed grass prairie. *Vegetatio*, **64**, 87-94.

Costello, D.F. (1944) Natural revegetation of abandoned plowed land in the mixed prairie association of northeastern Colorado. *Ecology*, **25**, 312-326.

Coulman, B., Harvey, B., McCurdy, B. & Willis, C. (1999) *Forages in the new millennium: A national strategy for research and development.* Canadian Agri-Food Research Council, Ottawa ON.

Coupland, R.T. (1950) Ecology of mixed prairie in Canada. *Ecological Monographs*, **20**, 271-315

Cox, R.D. & Anderson, V. (2004) Increasing native diversity of cheatgrass-dominated rangeland through assisted succession. *Journal of Range Management*, **57**, 203-210.

D'Antonio, C.D. & Meyerson, L.A. (2002) Exotic plant species as problems and solutions in ecological restoration: a synthesis. *Restoration Ecology*, **10**, 703-713.

Davis, M.A., Grime, J.P. & Thompson, K. (2000) Fluctuating resources in plant communities: a general theory of invasibility. *Journal of Ecology*, **88**, 528-534.

DePuit, E.J. (1986) The role of crested wheatgrass in reclamation of drastically disturbed lands. In Johnson, K.L. (ed.). *Crested wheatgrass: Its values, problems and myths. Symposium proceedings*. Utah State University, Logan UT. Pp. 323-330.

Dewey, D.R. (1986) Taxonomy of the crested wheatgrasses (*Agropyron*). In Johnson, K.L. (ed.). *Crested wheatgrass: Its values, problems and myths.* Symposium proceedings. Utah State University, Logan UT. Pp. 31-44.

Dillman, A. C. (1946) The beginning of crested wheatgrass in North America. *Agronomy Journal*, **38**, 237-250

DiTomaso, J.M. (2000) Invasive weeds in rangelands: species, impacts, and management. *Weed Science*, **48**, 255-265.

Dormaar, J.F., Johnston, A. & Smoliak, S. (1978) Long-term soil changes associated with seeded stands of crested wheatgrass in southeastern Alberta, Canada. In *Proceedings of The First International Rangeland Congress*. Pp. 623-625.

Dormaar, J.F., Naeth, M.A., Willms, W.D. & Chanasyk, D.S. (1995) Effect of native prairie, crested wheatgrass (*Agropyron cristatum* (L.) Gaertn.) and Russian wildrye (*Elymus junceus* Fisch.) on soil chemical properties. *Journal of Range Management*, **48**, 258-263.

Dyksterhuis, E.J. (1949) Condition and management of rangeland based on quantitative ecology. *Journal of Range Management*, **2**, 104-115.

Elton, C.S. (1958) *The ecology of invasions by plants and animals*. University of Chicago Press, Chicago IL.

Ferrell, M.A., Whitson, T.D., Koch, D.W. & Gade, A.E. (1998) Leafy spurge (*Euphorbia esula*) control with several grass species. *Weed Technology*, **12**, 374-380.

Forman, R.T.T., Sperling, D., Bissonette, J., Clevenger, A.P., Cutshall, C.D., Dale, V.H., Fahrig, L., France, R., Goldman, C.R., Heanue, K., Jones, J.A., Swanson, F.J., Turrentine, T. & Winter, T.C. (2004) *Road ecology: Science and solutions*. Island Press, Covelo CA.

Gray, J.H. (1967) *Men against the desert*. Western Producer Book Service, Saskatoon SK.

Haber, E. 1999. *Invasive plants of natural habitats in Canada: An integrated review of wetland and upland species and legislation governing their control*. Canadian Wildlife Service & Canadian Museum of Nature. Ottawa, ON.

Hammermeister, A.M., Naeth, M.A., Schoenau, J.J. & Biederbeck, V.O. (2003) Soil and plant response to wellsite rehabilitation on native prairie in southeastern Alberta, Canada. *Canadian Journal of Soil Science*, **83**, 507-519.

Heidinga, L. & Wilson, S.D. (2002) The impact of an invading alien grass (*Agropyron cristatum*) on species turnover in native prairie. *Diversity and Distributions*, **8**, 249-258.

Hierro, J.L., Maron, J.L. & Callaway, R.M. (2005) A biogeographical approach to plant invasions: the importance of studying exotics in their introduced and native range. *Journal of Ecology*, **93**, 5-15.

Hill, M.J., Willms, W.D. & Aspinall, R.J. (2000) Distribution of range and cultivated grassland plants in southern Alberta. *Plant Ecology*, **147**, 59-76.

Hobbs, R.J. & Harris, J.A. (2001) Restoration ecology: repairing the earth's ecosystems in the new millennium. *Restoration Ecology*, **9**, 239-246.

Hobbs, R.J. & Huenneke, L.F. (1992) Disturbance, diversity and invasion: Implications for conservation. *Conservation Biology*, **6**, 324-337.

Hobbs, R.J. & Humphries, S.E. (1995) An integrated approach to the ecology and management of plant invasions. *Conservation Biology*, **9**, 761-770.

Houston, W.R. (1957) Renovation and fertilization of crested wheatgrass stands in the northern Great Plains. *Journal of Range Management*, **10**, 9-11.

Hull, A.C. & Klomp, G.J. (1966) Longevity of crested wheatgrass in the sagebrush-grass type in southern Idaho. *Journal of Range Management*, **19**, 5-11.

Hull, A.C. & Klomp, G.J. (1967) Thickening and spread of crested wheatgrass stands on southern Idaho ranges. *Journal of Range Management*, **20**, 222-227.

Huston, M.A. (2004) Management strategies for plant invasions: manipulating productivity, disturbance, and competition. *Diversity and Distributions*, **10**, 167-178.

Hutchinson, G.E. (1957) Concluding remarks. *Cold Springs Harbour Symposium on Quantitative Biology*, **22**, 415-427.

Jefferson, P.G. & Kielly, G.A. (1993) Re-evaluation of row spacing/plant density of seeded pasture grasses for the semiarid prairie. *Canadian Journal of Plant Science*, **78**, 257-264.

Johnson, D.A. (1986) Seed and seedling relations of crested wheatgrass: A review. In Johnson, K.L. (ed.). *Crested wheatgrass: Its values, problems and myths. Symposium Proceedings*. Utah State University, Logan UT. Pp. 65-90.

Jones, D.C. (2002) *Empire of Dust: Settling and abandoning the prairie dry belt.* University of Calgary Press, Calgary AB.

Klement, K.D., Heitschmidt, R.K. & Kay, C.E. (2001) *Eighty years of vegetation and landscape changes in the northern Great Plains: a photographic record.* Conservation Research Report No. 45, United States Department of Agriculture, Agricultural Research Service, Washington DC.

Kotanen, P.M., Bergelson, J. & Hazlett, D.L. (1998) Habitats of native and exotic plants in Colorado shortgrass steppe: a comparative approach. *Canadian Journal of Botany*, **76**, 664-672.

Kuchler, A.W. (1964) *Potential natural vegetation of the conterminous United States.* American Geographical Society Special Publication 36, New York NY.

Krueger-Mangold, J., Sheley, R., Engel, R., Jacobsen, J., Svejcar, T. & Zabinski, C. (2004) Identification of the limiting resources within a semi-arid plant association. *Journal of Arid Environments*, **58**, 309-320.

Krzic, M., Broersma, K., Thompson, D.J. & Bomke, A.A. (2000) Soil properties and species diversity of grazed crested wheatgrass and native rangelands. *Journal of Range Management*, **53**, 353-358.

Lambrinos, J.G. (2004) How interactions between ecology and evolution influence contemporary invasion dynamics. *Ecology*, **85**, 2061-2070.

Langer, R.H.M. (1972) *How grasses grow.* Institute of Biology, Studies in Biology no. 34. Edward Arnold Publishers Ltd. London UK.

Larson, D.L. (2003) Native weeds and exotic plants: relationships to disturbance in mixed-grass prairie. *Plant Ecology*, **169**, 317-333.

Larson, D.L., Anderson, P.J. & Newton, W. (2001) Alien plant invasion in mixed-grass prairie: effects of vegetation type and anthropogenic disturbance. *Ecological Applications*, **11**, 128-141.

Lauenroth, W.K., Coffin, D.P., Burke, I.C. & Virginia, R.A. (1997) Interactions between demographic and ecosystem processes in a semi-arid and an arid grassland: a challenge for plant functional types. In: Smith, T.M., Shugart, H.H. & Woodward, F.I. (eds) *Plant functional types: Their relevance to ecosystem properties and global change.* Cambridge University Press, New York NY. Pp. 234-254.

Lesica, P. & DeLuca, T.H. (1996) Long-term harmful effects of crested wheatgrass on Great Plains grassland ecosystems. *Journal of Soil and Water Conservation*, **51**, 408-409.

Lodge, D.M. (1993) Biological invasions: Lessons for ecology. *Trends in Ecology and Evolution*, **8**, 133-137.

Lodge, R.W. (1960) Effects of burning, cultivating and mowing on the yield and consumption of crested wheatgrass. *Journal of Range Management*, **13**, 318-321.

Lodge, R.W. (1970) Complimentary grazing systems for the northern Great Plains. *Journal of Range Management*, **23**, 268-271.

Looman, J. & Heinrichs, D.H. (1973) Stability of crested wheatgrass pastures under long-term pasture use. *Canadian Journal of Plant Science*, **53**, 501-506.

Lorenz, R.J. & Rogler, G.A. (1962) A comparison of methods of renovating old stands of crested wheatgrass. *Journal of Range Management*, **15**, 215-219.

Lym, R.G. & Kirby, D.R. (1991) Effect of glyphosate on introduced and native grasses. *Weed Technology*, **5**, 421-425.

MacArthur, R.H. & Wilson, E.O. (1967) *The theory of island biogeography*. Princeton University Press, Princeton NJ.

Mack, R.N., Simberloff, D., Lonsdale, W.M., Evans, H., Clout, M. & Bazzaz, F.A. (2000) Biotic invasions: causes, epidemiology, global consequences and control. *Ecological Applications*, **10**, 689-710.

Marlette, G.M. & Anderson, J.E. (1986) Seed banks and propagule dispersal in crested wheatgrass stands. *Journal of Applied Ecology*, **23**, 161-175.

McWilliams, J.L. & vanCleve P.E. (1960) A comparison of crested wheatgrass and native grass mixtures seeded on rangeland in eastern Montana. *Journal of Range Management*, **13**, 91-94.

Milchunas, D.G., Lauenroth, W.K., Chapman, P.L., Kazempour, M.K. (1989) Effects of grazing, topography, and precipitation on the structure of a semiarid grassland. *Vegetatio*, **80**, 11-23.

Moody, M.E. & Mack, R.N. (1988) Controlling the spread of plant invasions: The importance of nascent foci. *Journal of Applied Ecology*, **25**, 1009-1021.

Olson, B.E. & Richards, J.H. (1989) Crested wheatgrass growth and replacement following fertilization, thinning, and neighbor plant removal. *Journal of Range Management*, **42**, 93-97.

Pimentel, D., McNair, S., Janecka, J., Wightman, J., Simmonds, C., O'Connel, C., Wong, E., Russel, L., Zern, J., Aquino, T. & Tsomondo, T. (2001) Economic and environmental threats of alien plant, animal, and microbe invasions. *Agriculture, Ecosystems and Environments,* **84**, 1-20.

Pyke, D.A. (1990) Comparative demography of co-occurring introduced and native tussock grasses: Persistence and potential expansion. *Oecologia*, **82**, 537-543.

Radosevich, S.R., Stubbs, M.M. & Ghersa, C.M. (2003) Plant invasions - process and patterns. *Weed Science*, **51**, 254-259.

Randall, J.M. (1996) Weed control for the preservation of biological diversity. *Weed Technology*, **10**, 370-383.

Ray, I.M., Frank, A.B. & Berdahl, J.D. (1994) Genetic variances of agronomic traits in tetraploid crested wheatgrass under competitive conditions. *Crop Science,* **34**, 1436-1439.

Ray, I.M., Frank, A.B. & Berdahl, J.D. (1997) Genetic variances of agronomic and morphological traits of diploid crested wheatgrass. *Crop Science,* **37**, 1503-1507.

Ray, I.M., Karn, J.F. & Data, S.T. (1996) Heritabilities of nutritive quality factors and interrelationships with yield in tetraploid crested wheatgrass. *Crop Science,* **36**, 1488-1491.

Rejmanek, M. & Richardson, D.M. (1996) What attributes make some plant species more invasive? *Ecology*, **77**, 1655-1661.

Reynolds, T.D. & Trost, C.H. (1980) The response of native vertebrate populations to crested wheatgrass planting and grazing sheep. *Journal of Range Management*, **33**, 122-125.

Richards, R.T., Chambers, J.C. & Ross, C. (1998) Use of native plants on federal lands: policy and practice. *Journal of Range Management*, **51**, 625-632.

Rogler, G.A. & Lorenz, R.J. (1983) Crested wheatgrass - early history in the United States. *Journal of Range Management*, **36**, 91-93.

Romo, J.T. & Bai, Y. (2004) Composition of seed banks and plant communities in the mixed prairie of Saskatchewan. *Journal of Range Management*, **57**, 300-304.

Romo, J.T. & Harrison, T. (1999) Regrowth of crested wheatgrass following defoliation. *Canadian Journal of Plant Science*, **79**, 557-563.

Romo, J.T., Grilz P.L. & Delanoy L. (1994) Selective control of crested wheatgrass (*Agropyron cristatum* [L.] Gaertn. and *A. desertorum* Fisch.) in the northern Great Plains. *Natural Areas Journal*, **14**, 308-309.

Salihi, D.O. & Norton, B.E. (1987) Survival of perennial grass seedlings under intensive grazing in semiarid rangelands. *Journal of Applied Ecology*, **24**, 145-151.

Samuel, M.J. & Hart, R.H. (1994) Sixty-one years of secondary succession on rangelands of the Wyoming high plains. *Journal of Range Management*, **47**, 184-191.

Schuman, G.E., Rauzi, F. & Booth, D.T. (1982) Production and competition of crested wheatgrass-native grass mixtures. *Agronomy Journal*, **74**, 23-26.

Smoliak, S. (1986) Influence of climatic conditions on production of *Stipa-Bouteloua* prairie over a 50 year period. *Journal of Range Management*, **39**, 100-103.

Smoliak, S., Johnston, A. & McLean, A. (1980) *Management of crested wheatgrass pastures*. Publication 1473, Agriculture Canada, Research Branch, Ottawa ON.

Smoliak, S. & Dormaar, J.F. (1985) Productivity of Russian wild rye and crested wheatgrass and their effect on prairie soils. *Journal of Range Management*, **38**, 403-405.

Smoliak, S., Johnston, A. & Lutwick, L.E. (1967) Productivity and durability of crested wheatgrass in southeastern Alberta. *Canadian Journal of Plant Science*, **47**, 539-548.

Soil Classification Working Group (1998) *The Canadian System of Soil Classification*, 3rd edn. Agriculture and Agri-Food Canada, Publication 1646, Ottawa ON.

Sutter, G.C. & Brigham, R.M. (1999) Avifaunal and habitat changes resulting from conversion of native prairie to crested wheat grass: patterns at songbird community and species levels. *Canadian Journal of Zoology*, **76**, 869-875.

Thompson, K. & Grime, J.P. (1979) Seasonal variation in the seed banks of herbaceous species in ten contrasting habitats. *Journal of Ecology*, **67**, 893-921.

Tilman, D. (1994) Competition and biodiversity in spatially structured habitats. *Ecology*, **75**, 2-16.

Tilman, D. (1997) Community invasibility, recruitment limitation, and grassland biodiversity. *Ecology*, **78**, 81-92.

Umbanhowar, C.E. (1992) Abundance, vegetation and environment of four patch types in a northern mixed prairie. *Canadian Journal of Botany*, **70**, 277-284.

USGS (1999) *Climate-vegetation atlas of North America.* United States Department of the Interior - United States Geological Survey, Washington D.C.

Vaisey, J.S., Weins, T.W. & Wettlaufer, R.J. (1996) *The permanent cover program: Is twice enough?* Prairie Farm Rehabilitation Administration, Regina SK.

Westoby, M., Walker, B., Noy-Meir, I. (1989) Opportunistic management of rangelands not at equilibrium. *Journal of Range Management*, **42**, 266-274.

Whitson, T.D. & Koch, D.W. (1998) Control of downy brome with herbicides and perennial grass competition. *Weed Technology*, **12**, 391-396.

Wiken, E.B. (1986) *Terrestrial Ecozones of Canada.* Ecological Land Classification Series No. 19., Environment Canada, Hull QB.

Wilson, S.D. (1989) The suppression of native prairie by alien species introduced for revegetation. *Landscape and Urban Planning*, **17**, 113-119.

Wilson, S.D. & Partel, M. (2003) Extirpation or coexistence? Management of a persistent introduced grass in a prairie restoration. *Restoration Ecology*, **11**, 410-416.

Wilson, S.D., Bakker, J.D., Christian, J.M., Li, X., Ambrose, L.G. & Waddington, J. (2004) Semiarid old-field restoration: is neighbor control needed? *Ecological Applications*, **14**, 476-484.

Wilson, S.D. & Gerry, A.K. (1995) Strategies for mixed-grass prairie restoration: Herbicide, tilling, and nitrogen manipulation. *Restoration Ecology*, **3**, 290-298.

Table 1.1 Reported cases of *A. cristatum* invasion in North America.

Province/State(s)	Ecoregion[a]	Habitat Association	Reference
Saskatchewan	Mixed-grass prairie	Ungrazed 15 years	Heidinga & Wilson 2002
Saskatchewan	Mixed-grass prairie	Abandoned cultivation	Wilson et al. 2004
Alberta	Mixed-grass prairie	Reclaimed lands	Alberta Environment 2003
North & South Dakota, Montana & Wyoming	Mixed-grass prairie	Various	Klement et al. 2001
North Dakota	Mixed-grass prairie	Cultivated land	Allred 1940
North & South Dakota	Mixed-grass prairie	Prairie dog towns & proximity to roads	Larson et al. 2001; Larson 2003
Colorado	Short-grass steppe	Roadside ditches & soil disturbance	Kotanen et al. 1999
Colorado	Short-grass steppe	Abandoned cultivation	Coffin et al. 1996
Idaho	Sagebrush steppe	Light intensity sheep grazing	Marlette & Anderson 1986
Idaho	Sagebrush steppe	Light intensity sheep grazing	Hull & Klomp 1966; Hull & Klomp 1967

[a] Ecoregion names for Canada follow Wiken (1986), and for the U.S.A. follow Kuchler (1964).

Table 1.2 Comparisons of vascular plant community diversity between adjacent native-dominated and *A. cristatum*-dominated fields.

Native Community Dominants[a]	*A. cristatum* (+/–)[b]			Reference
	R	E	D	
Agropyron smithii & Koeleria macrantha	–	+	–	Sutter & Brigham 1999
Stipa comata & Bouteloua gracilis	nsd	–	na	Wilson 1989
Stipa comata & Bouteloua gracilis	–	na	–	Christian & Wilson 1999
Stipa comata & Bouteloua gracilis (sampled twice, in 1965 & 1977)	na	–	na	Smoliak et al. 1967; Dormaar et al. 1978
Stipa comata & Bouteloua gracilis	–	na	na	Heidinga & Wilson 2002
Pseudoregneria spicata & Artemisia tridentata	nsd	–	–	Krzic et al. 2000
Pseudoregneria spicata & Artemisia tridentata	–	nsd	–	Broersma et al. 2000
Pseudoregneria spicata & Artemisia tridentata	–	na	na	Marlette & Anderson 1986
Pseudoregneria spicata & Artemisia tridentata	–	na	–	Reynolds & Trost 1980

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[a] Two most abundant native species reported for native-dominant sites.

[b] (+/–) = increase or decrease associated with *A. cristatum* dominance; R = vascular plant species richness; E = evenness and D = diversity (Shannon-Weiner indices); na = not applicable; nsd = not statistically different.

Table 1.3 Comparisons of soil organic matter characteristics between adjacent native-dominated and *A. cristatum*-dominated fields.

Soil Type & Condition[a]	*A. cristatum* (+/–)[b]			Reference
	Selected Variables	Depth & Response	Depth & Response	
		0-13 cm		
Brown chernozem, grazed & abandoned	Root mass	–		Dormaar et al. 1978
	SOC	nsd		
		0-15 cm	0-10 cm	
Brown chernozem, grazed & abandoned	Root mass	–		Smoliak & Dormaar 1985
	SOC		–	
	Total N		nsd	
		0-7.5 cm	7.5-40 cm	
Brown chernozem & Brown solonetz, grazed & undisturbed	Root mass	–	nsd	Dormaar et al. 1995
	SOM	–	+	
	Total N	–	nsd	
	Avail N	–	+	
		0-10 cm		
Brown chernozem, ungrazed & abandoned	Root mass	–		Christian & Wilson 1999
	SOC	–		
	Total N	–		
	Avail N	–		
		0-7.5 cm	7.5-15 cm	Krzic et al. 2000
Dark-brown chernozem, grazed & undisturbed	Root mass	nsd	nsd	
	SOC	nsd	+	
	Total N	nsd	nsd	
		0-7.5 cm	7.5-15 cm	
Dark-brown chernozem, ungrazed & undisturbed	Root mass	nsd	nsd	Broersma et al. 2000
	SOC	nsd	nsd	
	Total N	nsd	nsd	

[a] Soil type according to the Canadian System of Soil Classification (Soil Survey Working Group 1998); abandoned = formerly cultivated then abandoned and revegetated naturally; undisturbed = never cultivated.

[b] SOC = soil organic carbon; Total N = total soil nitrogen; Avail N = available soil nitrogen (NO3 & NH4); (+/–) = increase or decrease associated with *A. cristatum* dominance; nsd = not statistically different.

Table 1.4 Response of *A. cristatum* parameters following various disturbance treatments.

Disturbance Type	Years Elapsed	Measured Variable	*A. cristatum* (+/–)[a]	Reference
Tillage	1	basal cover	–	Houston 1957
	1	phytomass	–	Lorenz & Rogler 1962
	1	phytomass	–	Lodge 1960
	1	foliar cover	nsd	Wilson & Gerry 1995
	1	foliar cover	–	Bakker et al. 1997; 2003
	2	phytomass	nsd	Lodge 1960
	2	basal cover	+	Houston 1957
	2 to 12	phytomass	+	Lorenz & Rogler 1962
	4	foliar cover	nsd	Bakker et al. 1997; 2003
Surface Harrow	2	basal cover	nsd	Houston 1957
Burn (fall)	2	basal cover	nsd	Romo et al. 1994
Burn (spring)	2	phytomass	–	Lodge 1960
	2	basal cover	nsd	Romo et al. 1994
Glyphosate (fall)	1	phytomass	nsd	Lym & Kirby 1991
Glyphosate (spring)	1	foliar cover	–	Wilson & Gerry 1995
	1	foliar cover	–	Bakker et al. 1997; 2003
annually repeated	2	basal cover	–	Romo et al. 1994
annually repeated	4	foliar cover	–	Bakker et al. 1997; 2003
annually repeated	4	seedbank density	+	Ambrose 1999
annually repeated	7	foliar cover	–	Wilson & Partel 2003
annually repeated	7	seedbank density	nsd	Wilson & Partel 2003
Glyphosate & Clipping	1	foliar cover	–	Wilson & Partel 2003
	1	seedbank density	nsd	Wilson & Partel 2003
Clipping (50% tillers)	1	tiller replacement	nsd	Olson & Richards 1989
Clipping (fall)	1	phytomass	–	Romo & Harrison 1999
Clipping (spring)	1	foliar cover	–	Wilson & Partel 2003
	1	seedbank density	nsd	Wilson & Partel 2003
	1	phytomass	nsd	Romo & Harrison 1999
Mowing	1	phytomass	–	Lodge 1960
	2	phytomass	+	Lodge 1960
	1	basal cover	nsd	Romo et al. 1994
Grazing	1	seedling survival	–	Salihi & Norton 1987

[a] (+/–) = increase or decrease associated with *A. cristatum* parameter relative to an undisturbed control; nsd = not statistically different from undisturbed control.

Figure 1.1 Estimated potential geographic distribution of *A. cristatum* in North America (white area bound by 30 to 52 °N latitude and 100 to 125 °W longitude). *A. cristatum* is expected to occur in cool, temperate, semiarid environments bound by -5 °C < mean annual temperature < 10 °C and 200 mm < mean annual precipitation < 450 mm. Spatial climate data were adapted from large format *.tiff images available from USGS (1999).

CHAPTER 2. OUTLINING THE ECOLOGICAL NICHE FOR CRESTED WHEATGRASS IN NORTHERN MIXED-GRASS PRAIRIE

INTRODUCTION

Alien plant species are often persistent and can become invasive in regions where geoclimatic conditions resemble those of the region in which the species evolved (Peterson & Vieglais 2001). Knowledge of this fundamental niche can be used to screen and quarantine species prior to importation (Mack et al. 2000). For alien species already introduced and invasive, there are abiotic and biotic limitations on survival and reproduction that affect spatial distribution within a region (Huston 2004). Knowledge of this realized niche can help natural area managers identify invasion-susceptible landscapes and management regimes (Higgins et al. 1999). In semiarid grasslands, there have been a few empirical studies of native species distributions along regional or landscape gradients (i.e. Milchunas et al. 1989; Paruelo & Lauenroth 1996), but few have explicitly dealt with alien invasive species (McClaran & Anable 1992; Ibarra-F. et al. 1995; Lambrinos 2002).

Descriptive studies have associated alien species richness with landscape factors such as livestock grazing, soil nutrients and human disturbance, and one result has been that alien richness is often correlated with native richness (Gelbard & Harrison 2003; Stohlgren et al. 1999; Kotanen et al. 1998; Larson et al. 2001). Conversely, experimental studies have manipulated soil nutrients, taxonomic and functional group richness, and results often suggest species rich communities are most resistant to invasion (Fargione et al. 2003; Symstad 2000). This contradictory and aggregate information remains problematic for land managers, because few alien species are persistent, dominating and invasive, while most are transient naturalized ruderals (Byers et al. 2002).

Crested wheatgrass (*Agropyron cristatum*) is an alien invasive species in the northern Great Plains of North America. This Asian species was introduced for land reclamation and livestock forage on several million ha of northern mixed-grass prairie (Lesica & DeLuca 1996), and subsequent invasion into native grasslands can be as great as 1-2 m yr^{-1} (Marlette & Anderson 1986; Heidinga & Wilson 2002). Invasion by *A. cristatum* has raised environmental concerns because invaded grasslands are less diverse (Heidinga & Wilson 2002) and may accumulate less soil organic carbon (Dormaar et al.

1995; Christian & Wilson 1999) relative to native grasslands. Although climatic limits for this species have been modeled for the region (Hill et al. 2000), invasion is not a universal phenomenon on landscapes within the region. It is unknown how invasion is affected by seed production and dispersal or seed germination and establishment limitations, which are directly or indirectly limited by landscape characteristics and regulated by management.

The objective of this research was to describe how landscape factors and their interactions facilitate or inhibit *A. cristatum* invasion in northern mixed-grass prairie. This large-scale realized niche investigation used a combination of field surveys and greenhouse experiments. For the field survey, invasion distances and landscape factors easily measured and understood by managers were selected, whereas for greenhouse experiments a number of *A. cristatum* germination and seedling development responses were related to a number of soil chemical and physical predictors.

MATERIALS AND METHODS

Study Area Description

The northern mixed-grass prairie encompasses the glaciated semiarid plains of Alberta and Saskatchewan, Canada and portions of Montana and North Dakota, USA. The climate is temperate continental with 300 to 400 mm mean annual precipitation, most falling as rain from convective storms between May and September. Temperatures vary from winter lows of -40 °C in January to summer highs of +40 °C in July (Environment Canada 2000). Native vegetation in the region is dominated by perennial grasses with *Stipa comata*, *Bouteloua gracilis*, *Koeleria macrantha* and *Carex* spp. ubiquitous, and inter-spaces are often carpeted by cryptogams (Coupland 1950). More than 70% of the native vegetation cover has been lost to agricultural and urban developments since 1900; and an extensive network of roads, fences and utility rights-of-way fragment the remaining native grassland (Samson & Knopf 1994).

Regional Belt Transect Investigation

In 1976, a 5 m wide pipeline right-of-way (RoW) was constructed, and seeded in spring 1977 to a mixture of *A. cristatum* and *Elymus junceus*. The RoW spans 138 km of the mixed-grass prairie region along a nearly straight line from 110° 5' West, 50° 55'

North to 111° 45' West, 51° 30' North. More than 65 km of this RoW bisects patches of native vegetation, and *A. cristatum* invasion from the 1977 RoW onto adjacent native grassland was evident in 2002. The RoW was oriented West-Northwest and in 2000 a parallel RoW was constructed along the North-Northeast edge, which obliterated most of the invading population along that edge. Therefore, unobstructed invasion patterns were only evident along the South-Southwest edge. During the period of maximum seed dispersal (August-March, from Pyke 1990), prevailing winds in this region parallel the RoW and invasion patterns were generally representative of lateral dispersal across the wind over a 25-year period. This arrangement provided an ideal natural experiment, whereby a source population along a single linear corridor spanned multiple repeated landscape units. Such an arrangement eliminated confounding effects of *A. cristatum* population age, genotype and prevailing wind direction, so I could more confidently assume invasion pattern variation was related to other landscape factors.

In August 2002, *A. cristatum* invasion was measured as the maximum distance plants had spread into adjacent native grassland, perpendicular to the 1977 RoW. Relative to native grasses, *A. cristatum* was easily and rapidly distinguished by its larger tussock growth form. The RoW bisected large areas of native grassland, far from any other potential sources of *A. cristatum*, so I was confident that invading plants originated from the RoW population. These invasion distance responses were recorded for discrete RoW segments divided on the basis of soil type, slope gradient and range condition.

Prior to field work, discrete soil polygons were identified along 61,915 m of the RoW using 1:50,000 scale soil survey maps classified according to the Canadian System of Soil Classification (Soil Classification Working Group 1998). Many small internal drainage basins and eroded slopes were not indicated at the 1:50,000 scale, so more fine-scale modifications were made using 1:20,000 scale monochromatic aerial photos, resulting in 151 discrete soil polygons (Table 2.1). Segments of the RoW crossing through each soil polygon were further divided into 10 m lengths to reflect changes in slope gradient. Percent slope was calculated from engineering profile surveys conducted at the time of RoW construction (Jim Robert, BP Canada Energy Co., personal communication). To simplify analyses and reduce measurement errors, nine equidistant slope gradient classes were created to assign values to each segment. Where two or more contiguous segments had the same slope class within a polygon, the segments were concatenated and maximum invasion distance was applied to the new larger segment. The result was a nested arrangement of 594 slope segments among 151 soil polygons.

While in the field, range condition was classified for all 594 slope segments. Range condition uses information about individual plant species responses to grazing on a given soil type (or "range site") within an ecoclimatic region, to score the current plant community composition (or "range type") relative to an ungrazed potential natural community composition (Dyksterhuis 1949; Wroe et al. 1988; Abouguendia 1990). Conducting a detailed vegetation inventory for 594 segments was not practical in the time available for this investigation, so an abridged version of range condition evaluation was used for reconnaissance-scale classification (Abouguendia 1990). Among the possible plant species indicators of range condition, only the most common and easily identified species were used for evaluation. One of three range condition categories: excellent, good–fair, or poor, which covered 21, 36 and 43% respectively of the surveyed RoW was applied to each segment (Table 2.2). The goal was to obtain a relative measure of past grazing intensity on each RoW segment, but the spatial distribution of indicator species is often modified by topoedaphic influences independent of grazing (Ayyad & Dix 1964). This is why a number of physical indicators of grazing activity were also incorporated in the reconnaissance-scale classification (Table 2.2).

Several characteristics of the sampling design and data distributions complicated analysis. Not all possible factor level combinations were sampled, and invasion distance response distributions were often skewed and unbalanced for each factor level combination, which contributed to heteroscedasticity. Not all of these problems could be accommodated in a traditional analysis of variance (ANOVA) (Shaw & Mitchell-Olds 1993), and the combination of categorical and quantitative independent variables prevented most other forms of multivariate analyses (Kachigan 1991). Non-parametric multiplicative regression (NPMR) in the program Hyperniche® was selected to identify the variance components of each factor and best fit multi-factor model for the single response variable of invasion distance (McCune & Mefford 2004). NPMR can accommodate categorical and quantitative predictors, with unbalanced, non-normal and heteroscedastic responses, and the multiplicative nature reduces problems of additivity and multicolinearity. Unlike most model fitting procedures that require a priori selection of overall response functions, NPMR generates local means for combinations of factor levels to fit and evaluate a single multi-dimensional response surface a posteriori.

In the case of the quantitative response invasion distance, local means were calculated using a distance weighting function that assumed a Gaussian distribution (the non-parametric component). The weighting function for each datum was adjusted between 0 and 1 by adjusting the tolerance, or standard deviation of the Gaussian distribution, for each iteration. In effect, adjusting tolerance is like adjusting the volume of a multidimensional window around each local mean. In Hyperniche®, tolerance is adjusted 16 times for quantitative factors to include up to 75% of the data as fully weighted, and for categorical factors tolerance is adjusted only twice because data are either in or out. For all possible combinations of the three factors range condition, soil type, and slope gradient, NPMR generated 514 models. The amount of data captured for a given tolerance level and model iteration varies for each factor level combination, so the average amount of data required to estimate a single local mean was reported as N*. The N* estimates how much data were contained in each multidimensional window around each mean. To prevent response surface discontinuities or overfitting, only those models with N* > 5% of total N were included in model selection. Within these constraints, models with low tolerance and high N* were desired. The best one, two and three factor models were selected based on these criteria and where the cross-validated regression coefficient ($xR^2 = 1 -$ [residual sums of squares/total sums of squares]) was maximized (McCune & Mefford 2004).

Based on the variance explained in NPMR, original factors were eliminated or combined into a single "site" factor, and levels were compared through a non-parametric ANOVA. To accommodate the unbalanced number of replicates for each site factor level, Dunn's multiple comparison procedure was used to pool variances and generate a separate standard error to identify differences ($\alpha = 0.05$) in each pair-wise comparison (Zar 1999). Ordering site factor levels by mean rank then segregating levels into their original factors allowed exploration of how each original factor level was separated, much like cluster analysis (Kachigan 1991). Both NPMR and ANOVA require the assumption that factors are independent and spatial autocorrelation of sample units violated this assumption (Shaw & Mitchell-Olds 1993; McCune & Mefford 2004). Autocorrelation was handled by eliminating data where sample units for a given factor combination were restricted to a single pasture, and small sample bias was reduced by eliminating factor combinations with $n < 4$. Any additional role spatial autocorrelation may have played was dampened by sample units distributed over a 138 km distance.

Greenhouse Experiments

To further test the role of soil on *A. cristatum* germination and seedling establishment, two experiments were conducted in spring 2003. Soils represented Ah horizons from a range of soil types in the mixed-grass prairie region (Table 2.3). All soils were originally sampled between May and July 2001 using 24 to 30 cylindrical soil cores (7.5 cm deep x 7.9 cm diameter) randomly distributed within a 0.5 ha area at each of 12 sites. Soils were sieved to remove roots and stones >2 mm, air dried at ~25 °C for two weeks, and stored at ~20 °C for 18 months. In January 2003, between 100 and 125 g of soil from each subsample were mixed to create a 3 kg composite sample for each of the 12 sites. The percentage of sand, silt and clay were determined using the hydrometer method (Sheldric & Wang 1993). Organic carbon was analyzed by the Walkley-Black method (Nelson & Sommers 1996), and total soil nitrogen by dry combustion and gas chromatography (Yeomens & Bremner 1991). Soil electrical conductivity (EC), Na^+ concentration and sodium adsorption ratio (SAR) were determined from a saturation paste extract as per Janzen (1993), and soil pH as per Hendershot et al. (1993).

To determine the number of days to 50% germination of *A. cristatum* seeds, 10 replicate petri dishes were first filled with 40 g of soil from each of the 12 sites. To each dish, 60 ml of distilled water was initially added to saturate the soil. Twenty-five seeds of the "Kirk" variety of *A. cristatum* (91% germinability) were placed on the moist soil surface of each dish, and petri dish covers were placed overtop to reduce evaporation. This variety of *A. cristatum* was most readily obtained from commercial suppliers, but differed from the variety seeded along the RoW 25 years earlier. Although I cannot exclude the possibility of local adaptation changing the seed germination and seedling establishment responses to soil type, results of the field and greenhouse work will be discussed as though the two genotype sources are one. Under ambient laboratory conditions of approximately 21 °C and 12:12 light:dark hours, it was necessary to add 20 ml of distilled water each day to resaturate the soil. The number of seeds that germinated in each dish was recorded every one to three days over a six week period.

To determine seedling growth rates of *A. cristatum*, 10 replicate greenhouse pots (10 x 10 x 15 cm) were filled to within 1 cm of the lip with soil from each of 12 soil types. To each pot, a single seed of the "Kirk" variety of *A. cristatum* was placed ~0.5 cm below the surface. All pots were maintained under greenhouse conditions of approximately 25 °C and 12:12 light:dark hours, and watered every other day to maintain field capacity. Seedling height (soil surface to tip of tallest leaf, laid flat along a ruler) and leaf emergence were measured daily for 60 days. Seedling growth rate was calculated as the increase in height between measurement intervals and averaged among intervals. Greenhouse experiment data were analyzed with linear bivariate regression to test for significant ($\alpha = 0.05$) relationships between soil chemical and physical parameters with *A. cristatum* germination rate, seedling growth rate, leaf emergence dates and final seedling height.

RESULTS

Maximum *A. cristatum* invasion distance varied from 0 to 20 m, which converts to a rate from 0 to 0.80 m yr^{-1}. Range condition appeared to be the most important predictor of invasion distance, and resulted in the best fit single factor NPMR model (Table 2.4). Addition of slope gradient did not improve the best fit model, so this factor was excluded from further analyses. The combination of range condition and soil type nearly doubled the amount of variation explained for invasion; however, only half the total variation was explained by the combination of these two factors. Nonetheless, range condition and soil type were combined into 21 levels of a single site factor, of which only 18 levels with $n > 3$ were used in an ANOVA. There were significant differences among site factors ($X^2 = 58.30$; df = 17; $p < 0.001$), and excellent range condition was associated with the six greatest invasion distance values. Differences between good–fair and poor range condition were less clear, as these often overlapped (Table 2.5; Figure 2.1). Soil type did not sort out as clearly, but invasion appeared to be least on saline internal drainage basin soils and greatest on coarse-textured eroded and fine-textured glacial moraine soils. Although there was a single instance of invasion as great as 0.80 m yr^{-1}, the greatest median rate on excellent condition, glacial lacustrine soil was 0.21 m yr^{-1}.

The time required for 50% of *A. cristatum* seed to germinate increased directly with increases in all indicators of soil salinity: Na^+ ($y = 2.96x - 13.73$; $r^2 = 0.54$; $p = 0.01$), SAR ($y = 0.11x - 0.63$; $r^2 = 0.51$; $p = 0.01$) and EC ($y = 0.14x + 2.92$; $r^2 = 0.49$; $p = 0.01$). Removal of the most extreme saline soil still resulted in significant regressions among Na^+ and SAR, but not EC. The time required for the 2nd leaf to emerge on *A. cristatum* seedlings decreased indirectly as sand content increased ($y = -8.95x + 160.03$; $r^2 = 0.32$; $p = 0.07$), and increased directly as silt content increased ($y = 6.39x - 47.06$; $r^2 = 0.44$; $p = 0.03$). Removal of the most sandy soil still resulted in significant regressions among these variables, and an even better fit with silt content ($y = 4.27x - 17.62$; $r^2 = 0.56$; $p = 0.01$). Seedling growth rate, final height, and final leaf or tiller numbers were not significantly related to any soil physical or chemical characteristic.

DISCUSSION

At each stage in the life cycle of *A. cristatum*, landscape factors potentially limit germination, establishment and seed dispersal. A slower rate of germination and relatively little invasion on saline soils suggests salinity is an important and early limiting factor. Salinity is known to impose a physiological constraint on imbibition and slows the rate of seed germination (Johnson 1990). This is a particularly crucial limitation in semiarid environments for two reasons. First, low relief and precipitation are not conducive to leaching or runoff removal of salts from the landscape. Regionally, most drainage is internal and salts accumulate at toe slopes from groundwater discharge, or in playas where runoff collects and evaporates (Miller et al. 1985). Second, precipitation events are short and separated by long intervals, which limit the availability of soil water in time, and seeds need to quickly germinate and establish because drought is a constant threat (Lauenroth et al. 1994). It appears saline soils limit *A. cristatum* invasion, and the efficiency of future monitoring programs could be improved by reduced frequency of re-visiting these sites.

Once a seedling has emerged it must develop sufficient leaf and root area to accumulate carbohydrate reserves for surviving winter dormancy. Water and nutrient availability are crucial at this stage, and soil texture modifies the availability of both (Brady & Weil 1999). More rapid seedling development on sandy soils in the greenhouse suggests these soils may provide a short-term establishment advantage. Coarse textured soils provide less resistance to the movement of water and penetration of plant roots relative to fine textured soils, and if water is not limiting *A. cristatum* seedling establishment and growth rates are more rapid on coarse soils (Cluff et al. 1983; Evers & Parsons 2003). Ibarra-F. et al. (1995) also found coarse textured soils low in organic matter were more easily invaded by buffelgrass (*Cenchrus ciliatus* L.) in desert grasslands of North America. However, *A. cristatum* invasion patterns were not related to soil textural patterns alone, perhaps because the greater water holding capacity of fine textured soils confers a long-term survival advantage during periods of drought.

Functionally, the preferential invasion by *A. cristatum* into excellent condition range types and near absence of invasion from poor condition types suggests the species should be classified a rangeland "decreaser" (Dyksterhuis 1949), which is similar to most native C_3 mid-height grasses in the region (Wroe et al. 1988; Abouguendia 1990). This pattern implies a response to grazing, soil or an interaction of the two. Although much of the region is characterized by a mixture of C_3 grasses and the C_4 grass *Bouteloua gracilis* (Coupland 1950), the latter is more common and often dominant on moisture-limited soils and landscape positions, and C_3 grasses increase in abundance as moisture increases (Ayyad & Dix 1964; Barnes et al. 1983; Archer 1984). *A. cristatum* may simply prefer the habitat of physiologically and morphologically similar species, but this response conflicts with experimental evidence that invader establishment is limited where functionally similar species are already dominant (Fargione et al. 2003). It may be that interspecific competition plays a small role in defining the realized niche at larger, landscape scales (Byers & Noonburg 2003).

A second possibility for the relatively strong response to range condition is that grazing was more important than soil in generating the range type, and grazing directly reduced *A. cristatum* seed production and dispersal for invasion. Within the native range of *A. cristatum*, light to moderate grazing has no affect on persistence, but the absence of this species is an indicator of severe overgrazing (Xie & Wittig 2003). Experimental work in North America indicates *A. cristatum* responds to grazing by transferring energy into new leaves and tillers instead of reproductive culms (Romo & Harrison 1999). The absence of grazing may increase the susceptibility of an area to *A. cristatum* invasion by not limiting seed inputs, although other seed-limited grasses like Lehmann lovegrass (*Eragrostis lehmanniana* Necs.) have rapidly spread across landscapes regardless of grazing intensity (McClaran & Anable 1992). If grazing directly limits *A. cristatum* invasion, this is also a factor most easily monitored and manipulated by managers.

A third possibility for the observed invasion patterns, also supported by the analysis, is the interaction of landscape factors. Livestock distribution is known to vary in relation to water availability, topography and animal density. For reasons of energetic efficiency, cattle spend proportionately more time near water and on landscape positions with < 10% slope (Ganskopp & Vavra 1987; Pinchak et al. 1991). A corollary is that grazing intensity should decrease as slope gradient increases, at least to some threshold density of cattle. This could account for increased invasion on steeply sloped eroded and hummocky moraine soils, and the alluvial channels that commonly dissect these landscapes. Most of the sampled eroded slopes were classified as excellent condition. Similarly, most water sources for cattle were located within saline internal drainage basins, and these landscapes were associated with poor to good range condition but not excellent condition. Thus, fencing sloped areas to concentrate cattle grazing, or using sheep that have lower water demands and use slope gradients up to 45% (McDaniel & Tiedeman 1981) may be useful techniques for further limiting *A. cristatum* invasion.

Landscapes are complex and much of the invasion distance variation could not be accounted for in this reconnaissance-scale field survey. Range condition was particularly problematic to interpret because of correlations with slope, aspect, soil and grazing. Soil salinity and texture naturally change along slope gradients because erosion at steep grades and leaching in uplands results in deposition at more level grades and groundwater discharge at toe slopes, respectively (Seelig & Richardson 1994). Both salt and clay accumulate in level basins and toe slopes, leaving coarser and less saline soils at shoulder and midslope positions (Burke et al. 1995; Florinsky et al. 2000). Because more than 90% of the slope segments had a grade between 0 and 5%, it was difficult to accurately or precisely estimate how slope interacted with soil type or range condition. This problem may have been further exacerbated by differences in slope aspect as slope gradient increased, but aspect was not measured. Most of these bottom-up patterns should have been captured within the spatial scales measured, but it was not possible to directly measure top-down variation in past grazing intensity, frequency or timing. Grazing is also not a homogenous ecological process, and can generate changes in plant community composition and bare ground cover at scales < 10 m. These details were overlooked in this survey, but may have been key factors influencing invasion and generating among sample variation.

CONCLUSION

Invasion of northern mixed-grass prairie by *A. cristatum* was most strongly associated with non-saline, excellent condition rangeland. Soil salinity appears to impose a bottom-up limitation on seed germination and grazing may impose a top-down limitation on seed production and dispersal. Although slope gradients modify the spatial distribution of salts, soil particles and grazing animals, slope was not a good predictor of invasion. Under the most ideal conditions, *A. cristatum* invasion rates were slow (1 m every 5 years), although this effect size was relative to the orientation of the linear corridor studied, and best represents lateral movement across the prevailing wind. The regional belt transect was useful for identifying several ecological niche dimensions, but the spatially nested arrangement and variable representation of landscape factors complicated data analysis. Still, landscape-scale responses provided direction for experimentation and hypothesis testing which corresponded with descriptive data.

LITERATURE CITED

Abouguendia, Z.M. (1990) *A practical guide to planning for management and improvement of Saskatchewan rangeland.* Saskatchewan Research Council, Saskatoon SK.

Archer, S. (1984) The distribution of photosynthetic pathway types on a mixed-grass prairie hillside. *American Midland Naturalist*, **111**, 138-142.

Ayyad, M.A.G. & Dix, R.L. (1964) An analysis of a vegetation-microenvironmental complex on prairie slopes in Saskatchewan. *Ecological Monographs*, **34**, 421-442.

Barnes, P.W., Tieszen, L.L. & Ode, D.J. (1983) Distribution, production and diversity of C3 and C4 dominated communities in a mixed prairie, South Dakota. *Canadian Journal of Botany*, **61**, 741-751.

Brady, N.C. & Weil, R.R. (1999) *The nature and properties of soils.* 12th edition. Prentice Hall, Upper Saddle River NJ.

Burke, I.C., Elliott, E.T. & Cole, C.V. (1995) Influence of macroclimate, landscape position and management on soil organic matter in agroecosystems. *Ecological Applications*, **5**, 124-131.

Byers, J.E., Reichard, S., Randall, J.M., Parker, I.M., Smith, C.S., Lonsdale, W.M., Atkinson, I.A.E., Seastedt, T.R., Williamson, M., Chornesky, E. & Hayes, D. (2002) Directing research to reduce the impacts of nonindigenous species. *Conservation Biology*, **16**, 630-640.

Byers, J.E., & Noonburg, E.G. (2003) Scale dependent effects of biotic resistance to biological invasion. *Ecology*, **84**,1428-1433.

Christian, J.M. & Wilson, S.D. (1999) Long-term ecosystem impacts of an introduced grass in the northern Great Plains. *Ecology*, **80**, 2397-2407.

Cluff, G.J., Young, J.A. & Evans, R.A. (1983) Edaphic factors influencing the control of Wyoming big sagebrush and seedling establishment of crested wheatgrass. *Journal of Range Management*, **36**, 786-792.

Coupland, R.T. (1950) Ecology of mixed prairie in Canada. *Ecological Monographs*, **20**, 271-315.

Dormaar, J.F., Naeth, M.A., Willms, W.D. & Chanasyk, D.S. (1995) Effect of native prairie, crested wheatgrass (*Agropyron cristatum* (L.) Gaertn.) and Russian wildrye (*Elymus junceus* Fisch.) on soil chemical properties. *Journal of Range Management*, **48**, 258-263.

Dyksterhuis, E.J. (1949) Condition and management of rangeland based on quantitative ecology. *Journal of Range Management*, **2**, 104-115.

Environment Canada (2000) *Canadian Climate Normals 1971-2000.* Environment Canada, Ottawa ON.

Evers, G.W. & Parsons, M.J. (2003) Soil type and moisture level influence on Alamo switchgrass emergence and seedling growth. *Crop Science*, **43**, 288-294

Fargione, J., Brown, C.S. & Tilman, D. (2003) Community assembly and invasion: An experimental test of neutral versus niche processes. *Proceedings of the National Academy of Sciences of the United States of America*, **100**, 8916-8920.

Florinsky, I.V., Ellers, R.G. & Lelyk, G.W. (2000) Prediction of soil salinity risk by digital terrain modeling in the Canadian prairies. *Canadian Journal of Soil Science*, **80**, 455-463.

Ganskopp, D. & Vavra, M. (1987) Slope use by cattle, feral horses, deer, and bighorn sheep. *Northwest Science*, **61**, 74-81

Gelbard, J.L. & Harrison, S. (2003) Roadless habitats as refuges for native grasslands: Interactions with soil, aspect and grazing. *Ecological Applications*, **13**, 404-415.

Heidinga, L. & Wilson, S.D. (2002) The impact of an invading alien grass (*Agropyron cristatum*) on species turnover in native prairie. *Diversity and Distributions*, **8**, 249-258.

Hendershot, W.H., Lalande, H. & Duquette, M. (1993) Soil reaction and exchangeable acidity. In: Carter, M.R. (ed) *Soil Sampling and Methods of Analysis.* Lewis Publishers, Boca Raton FL. Pp. 141-146.

Higgins, S.I., Richardson, D.M., Cowling, R.M. & Trinder-Smith, T.H. (1999) Predicting the landscape-scale distribution of alien plants and their threat to plant diversity. *Conservation Biology*, **13**, 303-313.

Hill, M.J., Willms, W.D. & Aspinall, R.J. (2000) Distribution of range and cultivated grassland plants in southern Alberta. *Plant Ecology*, **147**, 59-76.

Huston, M.A. (2004) Management strategies for plant invasions: manipulating reproductivity, disturbance, and competition. *Diversity and Distributions*, **10**, 167-178.

Ibarra-F., F.A., Cox, J.R., Martin-R., M.H., Crow, T.A. & Call, C.A. (1995) Predicting buffelgrass survival across a geographical and environmental gradient. *Journal of Range Management*, **48**, 53-59.

Janzen, H.H. (1993) Soluble salts. In: Carter, M.R. (ed) *Soil Sampling and Methods of Analysis*). Lewis Publishers, Boca Raton FL. Pp. 161-166.

Johnson, R.C. (1990) Salinity and germination in *Agropyron desertorum* accessions. *Canadian Journal of Plant Science*, **70**, 707-716.

Kachigan, S.K. (1991) *Multivariate statistical analysis: A conceptual introduction*, 2nd edn. Radius Press, New York NY.

Kotanen, P.M., Bergelson, J. & Hazlett, D.L. (1998) Habitats of native and exotic plants in Colorado shortgrass steppe: a comparative approach. *Canadian Journal of Botany*, **76**, 664-672.

Lambrinos, J.G. (2002) The variable invasive success of *Cortaderia* species in a complex landscape. *Ecology*, **83**, 518-529.

Larson, D.L., Anderson, P.J. & Newton, W. (2001) Alien plant invasion in mixed-grass prairie: effects of vegetation type and anthropogenic disturbance. *Ecological Applications*, **11**, 128-141.

Lauenroth, W.K., Sala O.E., Coffin D.P. & Kirchner T.B. (1994) The importance of soil water in the recruitment of *Bouteloua gracilis* in the shortgrass steppe. *Ecological Applications*, **4**, 741-749.

Lesica, P. & DeLuca, T.H. (1996) Long-term harmful effects of crested wheatgrass on Great Plains grassland ecosystems. *Journal of Soil and Water Conservation*, **51**, 408-409.

Mack, R.N., Simberloff, D., Lonsdale, W.M., Evans, H., Clout, M. & Bazzaz, F.A. (2000) Biotic invasions: causes, epidemiology, global consequences, and control. *Ecological Applications*, **10**, 689-710.

Marlette, G.M. & Anderson, J.E. (1986) Seed banks and propagule dispersal in crested wheatgrass stands. *Journal of Applied Ecology*, **23**, 161-175.

McClaran, M.P. & Anable, M.E. (1992) Spread of introduced Lehmann lovegrass along a grazing intensity gradient. *Journal of Applied Ecology*, **29**, 92-98.

McCune, B. & Mefford, M.J. (2004) *Nonparametric multiplicative habitat modeling, Version 1*. MjM Software, Gleneden Beach OR.

McDaniel, K.C. & Tiedeman, J.A. (1981) Sheep use on mountain winter range in New Mexico. *Journal of Range Management*, **34**, 102-105.

Milchunas, D.G., Lauenroth, W.K., Chapman, P.L. & Kazempour, M.K. (1989) Effects of grazing, topography, and precipitation on the structure of a semiarid grassland. *Vegetatio*, **80**, 11-23.

Miller, J.J., Acton, D.F. & St. Arnaud, R.J. (1985) The effect of groundwater in soil formation in a morainal landscape in Saskatchewan. *Canadian Journal of Soil Science*, **65**, 293-307.

Nelson, D.W. & Sommers, L.E. (1996) Total carbon, organic carbon, and organic matter. In: Klute, A. (ed) *Methods of soil analysis. Part 3. Chemical methods.* Soil Science Society of America, Madison, WI. Pp. 961-1010.

Paruelo, J.M. & Lauenroth, W.K. (1996) Relative abundance of plant functional types in grasslands and shrublands of North America. *Ecological Applications*, **6**, 1212-1224.

Peterson, A.T. & Vieglais, D.A. (2001) Predicting species invasions using ecological niche modeling: New approaches from bioinformatics attack a pressing problem. *Bioscience*, **51**, 363-371.

Pinchak, W.E., Smith, M.A., Hart, R.H. & Waggoner, J.W. Jr. (1991) Beef cattle distribution patterns on foothill range. *Journal of Range Management*, **44**, 267-275.

Pyke, D.A. (1990) Comparative demography of co-occurring introduced and native tussock grasses: persistence and potential expansion. *Oecologia*, **82**, 537-543.

Romo, J.T. & Harrison, T. (1999) Regrowth of crested wheatgrass following defoliation. *Canadian Journal of Plant Science*, **79**, 557-563.

Samson, F. & Knopf, F. (1994) Prairie conservation in North America. *Bioscience*, **44**, 418-421.

Seelig, B.D. & Richardson, J.L. (1994) Sodic soil toposequence related to focused water flow. *Soil Science Society of America Journal*, **58**, 156-163.

Shaw, R.G. & Mitchell-Olds, T. (1993) ANOVA for unbalanced data: an overview. *Ecology*, **74**, 1638-1645.

Sheldric, B.H. & Wang, C. (1993) Particle size analysis. In: Carter, M.R. (ed) *Soil Sampling and Methods of Analysis.* Lewis Publishers, Boca Raton FL. Pp. 507-511.

Soil Classification Working Group (1998) *The Canadian System of Soil Classification*, 3rd edn. Agriculture and Agri-Food Canada, Publication 1646, Ottawa ON.

Soil Survey Staff (1999) *Soil Taxonomy: A basic system of soil classification for making and interpreting soil surveys*, 2nd edn. United States Department of Agriculture, Natural Resources Conservation Service, Agriculture Handbook Number 436. Washington D.C.

Stohlgren, T.J., Schell, L.D. & Vanden Heuvel, B. (1999) How grazing and soil quality affect native and exotic plant diversity in Rocky Mountain grasslands. *Ecological Applications*, **9**, 45-64.

Symstad, A.J. (2000) A test of the effects of functional group richness and composition on grassland invasibility. *Ecology*, **81**, 99-109.

Wroe, R., Smoliak, S., Adams, B., Willms, W.D. & Anderson, M.L. (1988) *Guide to range condition and stocking rates for Alberta grasslands.* Alberta Forestry, Lands and Wildlife, Edmonton AB.

Xie, Y. & Wittig, R. (2003) Growth parameters of characteristic species of *Stipa* steppes in northern China as indicators of the grazing intensity. *Journal of Applied Botany*, **77**, 68-74.

Yeomens, J.C. & Bremner, J.M. (1991) Carbon and nitrogen analysis of soils by automated combustion techniques. *Communications in Soil Science and Plant Analysis,* **22**, 843-850

Zar, JH. 1999. *Biostatistical Analysis*, 4th edn. Prentice Hall, Upper Saddle River NJ.

Table 2.1 Soil type characteristics and sample unit distribution along the belt transect.

Code	Landform/Parent Material	Soil (s)[a]	Surface Texture	Polygon Descriptors[b]	
				Length (m)	Number (n)
COL	Colluvial slope	Brown Chernozem Haplustoll	sandy-loam	283	10
ERO	Eroded slope	Regosol Ustorthent	gravelly-loam	95	15
ALV	Channel floodplain	Humic Regosol Ustifluvent	silt-loam	69	20
GLA	Glacial lacustrine plain	Brown Chernozem Haplustoll	loam	446	24
GMO	Glacial hummocky moraine	Brown Chernozem Calciustoll	clay-loam	506	34
IDB	Internal drainage basin	Humic Gleysol Natraquoll	clay-loam	132	18
SHL	Marine shale bedrock	Solonetz/Solod Natrargid/Natrustoll	silt-loam	872	30

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[a] Follows nomenclature in the Canadian System of Soil Classification (Soil Classification Working Group 1998) and USA Soil Taxonomy (Soil Survey Staff 1999).

[b] Length is the mean RoW length in meters across polygons of that category; Number is the count of discrete polygons of that category.

Table 2.2. Range condition classification criteria for each of the 594 slope segments along the belt transect.

Range Condition Category[a]	Indicator Species[b] Abundance (%)		Cattle Dungpat Density	Litter Cover (%)
	Decreaser	Increaser		
Poor	< 25	> 75	> 2 per 10 m	0-10
Good–Fair	25–75	25–75	1-2 per 10 m	11-50
Excellent	> 75	< 25	rare/absent	> 51

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[a] Modified from Dyksterhuis (1949) and Abouguendia (1990).

[b] Indicators differed for four primary kinds of range site. For upland sites with coarse to loam textured soils, decreasers were *Stipa comata*, *Stipa curtiseta* and *Elymus lanceolatus*, and increasers were *Bouteloua gracilis*, *Carex* spp. and *Artemisia frigida*. For upland sites with fine to loam textured soils, decreasers were *Elymus lanceolatus*, *Pascopyrum smithii* and *Stipa comata*, and increasers were *Bouteloua gracilis*, *Carex* spp. and *Artemisia frigida*. For lowland saline sites with fine to loam textured soils, the decreaser was *Pascopyrum smithii*, and the increaser was *Carex* spp. For lowland alluvial sites with coarse to loam textured soils, decreasers were *Pascopyrum smithii* and *Stipa curtiseta*, and increasers were *Artemisia frigida* and *Poa pratensis*. Adapted from Abouguendia (1990).

Table 2.3. Chemical and physical parameters of 12 soils from the Canadian mixed-grass prairie region used for germination and seedling growth rate experiments.

Soil Suborder[a]	Sand (%)	Silt (%)	Clay (%)	Organic Carbon (%)	Total Nitrogen (%)	pH	EC[b] (dS m^{-1})	Na^+ (mg L^{-1})	SAR[c]
Rego-brown Chernozem	79	13	8	1.7	0.14	6.9	3.3	4	0.6
Brown Chernozem	55	31	14	3.5	0.29	6.8	3.5	4	0.6
Brown Chernozem	45	34	21	4.9	0.38	6.4	3.5	5	0.9
Brown Chernozem	39	45	16	2.8	0.27	6.7	3.5	4	0.6
Brown Chernozem	33	48	19	3.6	0.31	6.7	3.4	4	0.6
Brown Chernozem	30	39	31	3.0	0.27	7.0	4.7	9	1.1
Brown Solonetz	49	34	17	3.0	0.30	6.1	4.0	22	3.8
Brown Solonetz	38	40	22	3.0	0.27	7.1	4.4	21	2.6
Brown Solonetz	33	42	25	2.1	0.19	6.6	4.1	26	3.4
Calcareous Dark-brown Chernozem	25	37	38	3.7	0.37	6.9	5.6	3	0.3
Solonetzic Dark-brown Chernozem	45	34	21	4.5	0.39	6.5	5.3	10	1.6
Dark-brown Solonetz	52	34	14	3.2	0.29	6.1	7.0	82	18.4

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[a] Follows nomenclature in the Canadian System of Soil Classification (Soil Classification Working Group 1998).

[b] Soil electrical conductivity is indicative of ions in the soil and is most influenced by clay and dissolved salt concentrations.

[c] Sodium Adsorption Ratio has no units, and is the concentration of Na^+ divided by the square root sum of Ca^{2+} and Mg^{2+} and is indicative of soil sodicity.

Table 2.4. One and two predictor models from nonparametric multiplicative regression for *A. cristatum* invasion distance. Best fit (high xR^2, high N*, low Tolerance) models used local mean smoothing assuming a Gaussian distribution for weighting values in mean calculations.

Model	xR^2	$xR^2\delta$	N*	Tolerance Graze	Tolerance Soil	Tolerance Slope
Range condition	0.22	- -	225.6	10.0	- -	- -
Soil type	0.08	- -	184.2	- -	0.0	- -
Slope gradient	0.02	- -	418.5	- -	- -	6.0
Range condition x Soil type	0.40	0.18	70.0	7.5	0.0	- -

Table 2.5. Comparison of *A. cristatum* invasion distance distributions among combined range condition and soil type site factor levels. Site factor levels are sorted in descending order using mean ranks from a Kruskal-Wallis ANOVA, and differences among site levels (ranks in same column followed by different letters) were identified with Dunn's multiple comparison procedure for groups with unbalanced replication ($\alpha = 0.05$).

Range Condition	Soil Type[a]	n[b]	Mean Rank
Excellent	GLA	4	129.6 a
Excellent	GMO	9	124.8 a
Excellent	ALV	5	113.7 a,b
Good-Fair	GMO	9	93.5 b,c
Excellent	SHL	4	88.9 b,c
Excellent	ERO	9	88.1 a,b,c,d
Good-Fair	COL	4	85.1 a,b,c,d,e
Poor	ERO	5	84.8 b,c,d
Good-Fair	ALV	7	83.9 a,b,c,d,e
Poor	GLA	8	78.9 b,c,d,e
Poor	GMO	16	72.4 c,d,e
Poor	ALV	8	70.9 b,c,d,e
Good-Fair	SHL	5	62.2 b,c,d,e
Poor	SHL	21	55.7 e,f
Good-Fair	GLA	12	52.1 d,e,f
Poor	COL	4	41.0 d,e,f
Good-Fair	IDB	4	41.0 d,e,f
Poor	IDB	13	41.0 f

a. Soil type code descriptions in Table 2.1.

b. n refers to the statistical sample number of polygons for each soil type associated with each range condition class. Because slope gradient was not significant in NPMR, slope segments within a soil polygon were concatenated to create 151 sample units, and only the 147 sample units where n > 3 for any site factor level were used in the ANOVA.

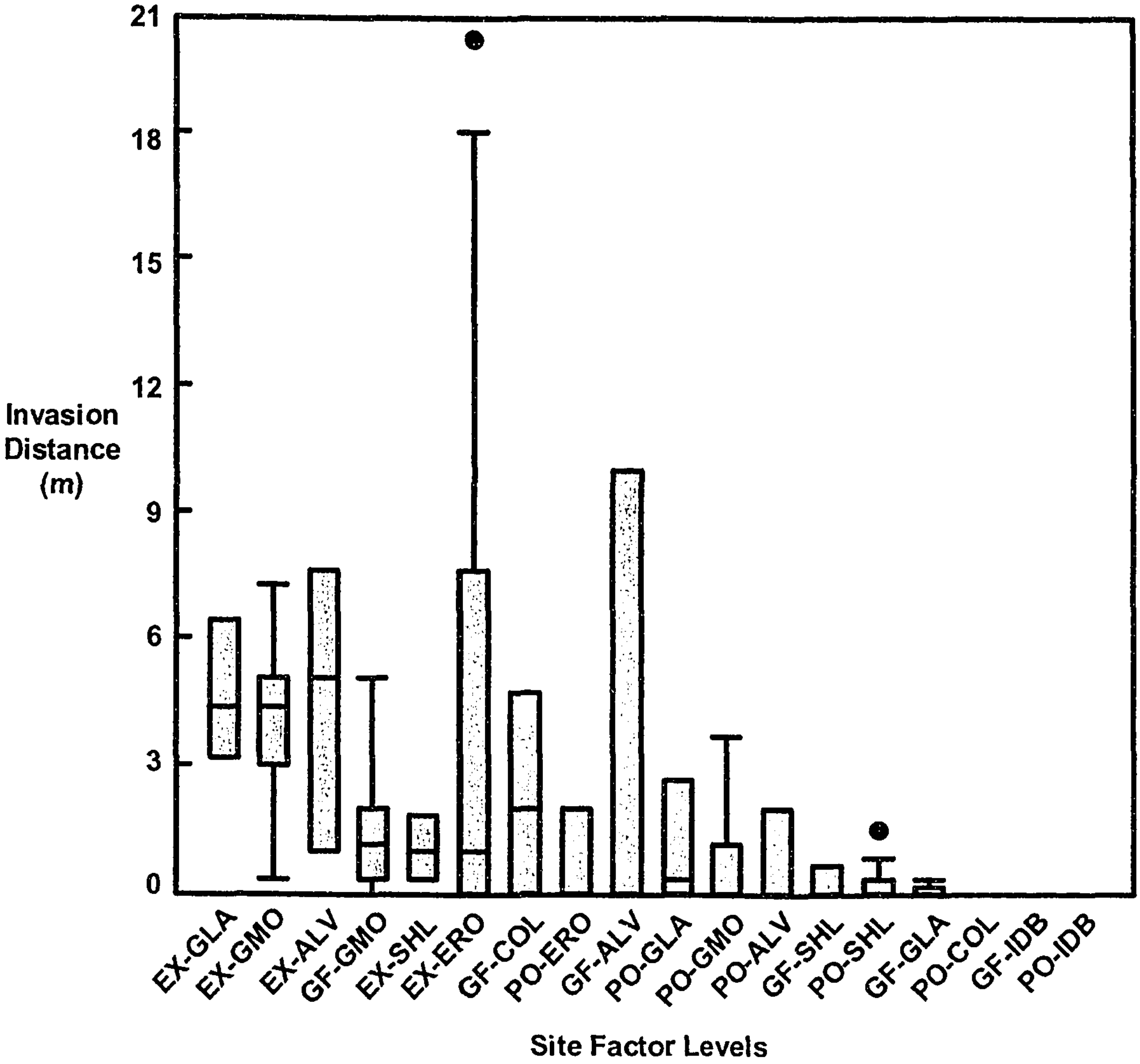

Figure 2.1 Box and whisker plots of *A. cristatum* invasion distance response to combined range condition and soil type site factor levels (EX = excellent condition; GF = good-fair condition; PO = poor condition; soil type codes are listed in Table 2.1). Levels of site factors are sorted by descending mean ranks from a Kruskal-Wallis test, and dots are outliers beyond the 5% or 95% percentiles.

CHAPTER 3. MULTI-SCALE IMPACTS OF CRESTED WHEATGRASS INVASION IN MIXED-GRASS PRAIRIE

INTRODUCTION

Semi-arid grasslands are particularly susceptible to alien plant invasions because recent and extensive agricultural land transformations have involved multiple deliberate and accidental introductions (D'Antonio & Vitousek 1992; Williams & Baruch 2000). As a result, there has been continual growth in weed control costs for natural areas (Mack et al. 2000; Pimentel et al. 2001). Despite widespread and early concern over invasive species (Elton 1958), few studies have sufficiently quantified the impacts of these invasions on native ecosystems (Parker et al. 1999) while policies and actions for control are too often based on anecdotal observations (Hobbs & Humphries 1995; Byers et al. 2002).

Crested wheatgrass (*Agropyron cristatum*) is a complex of perennial caespitose species from Eurasia that were artificially selected and intentionally introduced for agriculture in North America (Rogler & Lorenz 1983; Dewey 1986). The popularity of this species is due to greater grazing resistance, productivity and ability to establish under drought conditions relative to native grass species (Smoliak et al. 1980). In addition, *A. cristatum* has spread into adjacent natural grasslands (see Chapter 2) raising concerns over the ecological impacts (Lesica & DeLuca 1996). Whatever those impacts are, the extent of *A. cristatum* invasion is of most concern since it dominates roadside ditches throughout the network of farm access roads in the northern Great Plains. This network fragments much of the 1 million km^2 region into rectangular patches 1.6 to 3.2 km wide.

Invasion requires seed dispersal and the rate of spread can be as much as 1 to 2 m yr^{-1} (Hull & Klomp 1966; Marlette & Anderson 1986; Heidinga & Wilson 2003). Further, *A. cristatum* tends to outcompete native grasses (Schuman et al. 1982) and dominate communities for decades following establishment (Looman & Heinrichs 1973; Dormaar et al. 1995; Christian & Wilson 1999). The combination of dispersal rate, long-term dominance over and exclusion of native species is what defines *A. cristatum* as an invader in this region. Paradoxically, *A. cristatum* competes so successfully it is seeded in the semiarid Intermountain region of the USA to prevent the invasion of economically undesirable alien species like cheatgrass (*Bromus tectorum*) and knapweed (*Centaurea* spp.) (Johnson 1986).

A. cristatum pastures are less diverse (Looman & Heinrichs 1973; Marlette & Anderson 1986; Sutter & Brigham 1998; Broersma et al. 2000; Krzic et al. 2000; Heidinga & Wilson 2003) and have less soil organic matter than native-dominant grasslands that developed on formerly cultivated land (Smoliak & Dormaar 1985; Dormaar et al. 1995; Christian & Wilson 1999). However, cultivated and seeded pastures of *A. cristatum* may not be suitable analogues for evaluating impacts of invasion into uncultivated native grassland, particularly since cultivation alone reduces soil organic matter (Aguilar et al. 1988; Burke et al. 1995). Few investigations have involved *A. cristatum* dominated communities established from natural encroachment or broadcast seeding without soil disturbance (Marlette & Anderson 1986; Pyke 1990; Heidinga & Wilson 2003), and these were limited to single-site analyses of demographic and/or alpha diversity parameters. Parker et al. (1999) suggests a general problem with impact assessments of invasive species has been this limited spatial and organizational scope. Thus, I designed an investigation to avoid the covarying impact of cultivation and expand both the scale and parameters of inference.

The objective of this investigation was to identify if *A. cristatum* invasion significantly impacted population, community and ecosystem level parameters in northern mixed-grass prairie. *A. cristatum* invasion was hypothesized to reduce native plant species abundance, within community (alpha) and among community (beta) diversity and soil organic matter, and increase aboveground biomass. Only patterns can be described by sampling sites where *A. cristatum* invasion has already occurred, so multiple hypotheses for the mechanisms were also proposed.

METHODS

Site Characteristics and Selection

Sampling was conducted in 2001 within the mixed-grass prairie region of Canada. Mean annual precipitation ranges from 300 to 400 mm, with a distinct winter-dry summer-wet pattern. Mean annual temperature ranges from 3 to 7 °C, with maximum summer highs of 40 °C and minimum winter lows of –40 °C (Wiken 1986). The C_3 and

C_4 grasses *Stipa comata, Koeleria macrantha* and *Bouteloua gracilis* are dominant (Coupland 1950), however, ~70% of this region has been transformed into annual cropland, perennial forage crops, roadways and other developments since 1900 (Samson & Knopf 1994). Fragmented remnants of Canadian mixed-grass prairie typically occur where steep slopes, stony, salty or sandy soil prevented sustainable crop production.

Eight sites were selected where *A. cristatum* had dispersed from a seeded field into an adjacent native grassland community and visibly dominated the invaded vegetation. Adjacent invaded and uninvaded patches were then sampled in the context of a control-impact design (Appendix C). Abandoned cultivated land was avoided since *A. cristatum* preferentially invades disturbed sites (Kotanen et al. 1998; Larson et al. 2001) and soil organic matter depletion from cultivation can persist for decades (Dormaar et al. 1995; Christian & Wilson 1999). Otherwise, site selection incorporated a variety of *A. cristatum* introduction dates, soil types, grazing regimes, native plant community types and cardinal direction of invasion from the seed source (Table 3.1). Variability among sites was intended to expand the scale of inference to all invaded sites in the region. This decision sacrifices some statistical precision in order to gain ecological accuracy for the desired population of inference (Oksanen 2001). Differences in patterns between invaded and uninvaded grasslands were tested, but the mechanisms or processes generating these differences can only be hypothesized.

Specific sampling locations within sites were selected along a linear field edge on level ground, where *A. cristatum* had invaded 5 to 15 m from the cultivated source into adjacent native grassland. Uniformity of slope and width of the invaded area was required to reduce spatial variability within each site. A 20 m long transect was established in each of the invaded and uninvaded areas at each site, for a total of 16 transects. Transects were approximately parallel, 10 to 20 m apart, and placed at least 2.5 m from the cultivated edge or the invading front to avoid edge effects.

Vegetation Sampling

In July 2001, 0.1 m^2 (20 x 50 cm) quadrats were placed at 1 m intervals along each transect (20 quadrats), with the shorter dimension parallel to the transect. Visual estimates of basal cover for bare ground, litter and each vascular plant, bryophyte and terricolous lichen species were recorded as per methods outlined by Wroe et al. (1988).

Species nomenclature followed Moss (1994). Basal cover was preferred because changes in precipitation and grazing from year to year can affect foliar or canopy cover estimates in semi-arid grassland, without altering basal cover. Litter and vegetation biomass were sampled from a subset of 10 randomly selected quadrats. Surface and standing dead plant litter were hand raked and removed to the mineral soil or cryptogamic crust. Live rooted vegetation was clipped at ground level and removed. Both litter and vegetation were oven dried at 70 °C for 48 hours and weighed.

Soil sampling and processing

Three cylindrical soil cores (7.9 cm diameter x 7.5 cm deep) were removed within each of the 10 quadrats where litter and vegetation biomass had been sampled. The organic, or Ah, horizon of grassland soils varies in thickness from 10 to 20 cm and contains 80% of the soil organic matter; thus, the upper 7.5 cm represents a large portion of the soil organic matter pool (Soil Classification Working Group 1998). Each core area included plant crowns and interspaces in proportion to the basal cover for each quadrat, instead of stratifying cores among crowns and interspaces. The three cores were bulked for each quadrat, sealed in plastic bags and temporarily stored in coolers (~5 °C) while in transport from the field to the lab. Samples were stored at 0.5 °C to minimize organic carbon and nitrogen loss due to mineralization and volatilization for up to 5 days before soil organic matter fractionation.

Each soil sample was air-dried (~25 °C lab temperature) for one week following removal from cold storage and prior to soil analyses. Soil organic matter fractionation began by hand-crushing each sample to pass a 2 mm sieve, and stones >2 mm were discarded. Particulate organic matter (POM) including roots, litter, seeds and insect exuviae >2.0 mm were retained. Soil was again sieved to pass 0.5 mm, and additional POM 0.5 to 2.0 mm was removed by hand and composited with POM >2.0 mm to comprise the POM fraction. POM was then oven dried at 70 °C for 48 hours and weighed for each sample. Remaining soil particles 0.5 to 2.0 mm were composited with soil particles that passed through the 0.5 mm sieve, to comprise the soil fraction. Soil organic carbon was determined for fine ground (<0.1 mm particle size) subsamples by the Walkley-Black method (Nelson and Sommers 1996), total soil nitrogen by dry-combustion and gas chromatography (Yeomens & Bremner 1991), and total soil phosphorus by perchloric acid digestion and inductively coupled plasma spectrometry (Kuo 1996a, b). All soil elemental concentrations were reported as a percent of dry soil mass.

Germinable seedbank sampling and enumeration

In early October 2001, all transects were relocated and the soil seedbank was sampled within the remaining quadrats where vegetation and litter biomass was not sampled earlier in July. Most seed produced by perennial and annual species had shattered by this time of year; thus, samples included both transient and persistent seedbanks (Thompson & Grime 1979). Three cylindrical soil cores (7.9 cm diameter x 5.0 cm deep), including overlying vegetation and litter, were removed from within each quadrat. This method was selected because more than 70% of the seedbank is found in the upper 5 cm of soil and a large portion can also occur in surface litter (Iverson & Wali 1982; Willms & Quinton 1995). The three cores were bulked for each quadrat and sealed in plastic bags for transport from the field to the lab, where samples were stored at –5.0 °C for 6 months. This duration of cold storage was intended to stratify and break dormancy of some species (Baskin & Baskin 1998), although the constant temperature did not entirely simulate the winter climate.

In mid April 2002, each thawed subsample was hand crushed and spread to a 1 cm depth over 3 cm of potting soil (1:4 vermiculite:peat) in greenhouse trays. Plant crowns were removed by hand to eliminate seedling enumeration errors due to regrowth from dormant plant crowns. The 160 trays were maintained under greenhouse conditions, where temperature varied from 15 to 30 °C and the ambient daily light:dark cycle averaged 16:8 hours, from April 28 to July 28, 2002. Trays were watered every other day and flowering plant seedlings were identified and enumerated at 3 week intervals. Identified seedlings were removed to avoid competition with subsequent seedlings and recounting errors. Seedlings that could not be identified to species by July 28 were transplanted into pots and grown for an additional two months until identification could be confirmed. The abundance of each species per sample was scaled up and reported as germinable seed m^{-2} of soil sampled.

Data analyses

To calculate within-community, or alpha diversity, the Shannon-Weiner index (H') was selected. For each transect at each site, the total richness and average vegetation basal cover or seed density per species, were used in the calculation. The H' is less sensitive to the influence of dominant species abundances (Kent & Coker 1992), and should dampen bias introduced in site selection for *A. cristatum* dominated areas. To calculate among-community, or beta diversity, the Czechanowski dissimilarity index (D_C) was selected. The D_C is a percentage value calculated from the equation: 1 – [(2 x sum of minimum proportional abundances of species occurring in both samples)/(sum of proportional abundances of both samples)], where 0 represents two identical communities and 100 represents completely distinct communities (Kent & Coker 1992). All possible combinations of 8 invaded or 8 uninvaded areas for vegetation or seedbank dissimilarity generated four distributions of 28 D_C values, from which mean D_C was calculated and to which statistical tests were applied.

To test for differences in functional group (Appendix D) abundance associated with *A. cristatum* invasion, species in both vegetation and the seedbank were assigned to commonly used groups: C_3 graminoids, C_4 graminoids, perennial forbs, annual and biennial forbs and cryptogams (Kindscher & Wells 1995; Willms & Quinton 1995; Paruelo & Lauenroth 1996). Morphologically, phenologically or physiologically similar species may respond similarly to invasion by a single species representing one functional group (Symstad 2000).

Differences between invaded and uninvaded areas ($n = 8$) were identified ($\alpha = 0.05$) with a non-parametric Wilcoxon Signed-Rank (WSR) test for paired or related samples because the distribution of differences among pairs was frequently non-normal. The WSR test is not normally applied when $n < 10$ because the parametric paired t test is robust for small samples, but WSR is more conservative and reduces type 1 error (Blair & Higgins 1985).

RESULTS

The abundance of several native species differed between *A. cristatum* invaded and uninvaded areas (Table 3.2). Generally, *A. cristatum* invasion was associated with lower abundance of C_3 mid-height grasses *E. lanceolatus*, *S. comata*, *K. macrantha* and perennial forbs like *Artemisia frigida*. Vegetative cover of the short-grasses *B. gracilis*, *Carex eleocharis* and *Poa sandbergii* was not different. Similarly, cover of most ubiquitous cryptogams was not different, with one exception. Although the annual forb *Androsace septentrionalis* was infrequently encountered in the vegetation, germinable seed was common in both invaded and uninvaded areas.

Both alpha and beta diversity were greater for uninvaded vegetation (Figure 3.1). Lower alpha diversity of invaded vegetation was attributable to fewer forb species and lower forb cover (Figure 3.2). Annual and biennial forbs were rare, and grouped with perennials. At the beta scale, invaded vegetation had 35 species with *A. cristatum* the single dominant; whereas uninvaded had 49 species (more sparse perennial forbs) and different dominant species among sites.

Seedbank alpha and beta diversity were not different between invaded and uninvaded areas (Figure 3.1). However, alpha diversity did not reflect the change in seedbank richness and evenness (Figure 3.3). *A. cristatum* dominated the invaded seedbank (37% of total density) to the same degree *A. frigida* dominated the uninvaded seedbank (37% of total seedlings) with no substantial change in overall species richness (invaded = 11, uninvaded = 12) or total seedbank density (invaded = 1084 m^{-2}, uninvaded = 1090 m^{-2}). Generally, perennial forb seedbank density was lower in invaded areas largely due to lower *A. frigida* density, although richness was not different. Seedbank density of C_3 graminoids was greater in invaded areas largely due to abundant *A. cristatum* seed, and lower richness reflected lower frequency of *K. macrantha* and *S. comata* seed. At the beta scale, richness was similar (invaded = 31, uninvaded = 34) and the most frequent and abundant species were CWG in invaded and *A. frigida* in uninvaded seedbanks.

Above ground vegetation and litter mass of invaded areas were 63 and 89% greater than uninvaded areas, but below ground POM was not different (Figure 3.4). These differences reflected a change in vertical structure of the communities, but there were no differences ($P > 0.05$) in mean vegetation, litter, bare ground or cryptogam cover. In addition, the means of soil organic carbon, nitrogen and phosphorus were not different ($P > 0.05$).

DISCUSSION

Invasion impacts on biodiversity

The pattern of lower alpha richness and abundance of native species within *A. cristatum* dominated prairie has been observed elsewhere in the northern Great Plains (Sutter & Brigham 1998; Christian & Wilson 1999), and inter-mountain Palouse prairie (Krzic et al. 2000). In cases where a gradient of *A. cristatum* abundance was sampled on uncultivated native grassland adjacent to *A. cristatum* pastures, native plant cover and seed rain were inversely related to *A. cristatum* cover and seed rain (Marlette & Anderson 1986; Heidinga & Wilson 2003). These patterns indicate either competitive effects of *A. cristatum*, or pre-existing patterns of diversity prior to *A. cristatum* invasion.

Potentially, *A. cristatum* invasion may preferentially occur in species-poor neighborhoods where unused resources are available; vis-a-vis the empty niche hypothesis (Elton 1958). Theoretically, if an empty niche is being exploited the abundance of all other species should not change, or decrease equally in response to random gap colonization by *A. cristatum*. Because *A. cristatum* is a larger plant than all other herbaceous species encountered a decrease in species richness may simply be related to sampling scale (Oksanen 1996), which is why the minimal area from species area curves was intentionally exceeded in this study. Despite these possibilities, native C_3 mid-height grasses and forbs were lower in abundance, while some other species (cryptogams, annual forbs, the C_4 grass *B. gracilis*, and C_3 shortgrasses *C. eleocharis* and *P. sandbergii*) did not change in abundance. Overall, *A. cristatum* invasion was associated with "non-random" differences in native species abundance, similar to patterns observed by Heidinga & Wilson (2002).

An alternative explanation is that *A. cristatum* competed more effectively for resources and occupied a niche that overlapped that of more than one native species; vis-a-vis the competitive exclusion hypothesis (Grime 1973). Characteristics of *A. cristatum* like greater size, litter production and relative growth rate are consistent with general traits of highly competitive plants (Grime 1973), and in arid to semiarid grasslands most competition is focused on the most limiting resource, soil water (Fowler 1986; Call & Roundy 1991). Eissenstat & Caldwell (1988a, b) concluded *A. cristatum* was a superior competitor with the C_3 perennial grass *Pseudoregneria spicata*, because earlier spring root growth by the former led to rapid soil water depletion and reduced moisture availability for the latter. Frank et al. (1985) drew a similar conclusion to explain the competitive relations between *A. cristatum* and the C_3 perennial grass *P. smithii*. Huber-Sannwald et al. (1998) concluded something other than soil nutrient availability was the cause for reduced biomass and clonal expansion of *E. lanceolatus* in field competition experiments with *A. cristatum*. Taken together, these studies suggest the early growth of *A. cristatum* provides advantageous access to soil water, which may confer a competitive advantage over later developing native species. Native C_3 mid-height grasses and forbs seem most susceptible to competitive exclusion.

Additional support for this hypothesis is provided by abundance patterns of persistent native graminoids. Peak production of the C_4 perennial *B. gracilis* is later than C_3 species (Kemp & Williams 1980), suggesting this C_4 grass may largely avoid competing with *A. cristatum* for water over the course of a year. However, Bakker & Wilson (2001) found the growth of transplanted *B. gracilis* was suppressed more in *A. cristatum* pastures than old-fields dominated by native grasses; thus, the long-term persistence of *B. gracilis* in *A. cristatum* dominated communities remains unknown. The C_3 perennials *C. eleocharis* and *P. sandbergii* grow and reproduce much earlier than all other grasses, and this phenological asynchrony with *A. cristatum* may allow persistence.

The abundance of native species in the seedbank was also less in *A. cristatum* invaded prairie, but diversity measures did not reflect this change because a single species (*A. frigida*) dominated the uninvaded seedbank, and *A. cristatum* dominated the invaded seedbank. Dormant seed persistence may account for the high abundance of *A. frigida* in uninvaded native seedbanks (Bai & Romo 1994), but *A. cristatum* seedbanks should be transient (Thompson & Grime 1979) with high densities maintained only by annual seed additions (Pyke 1990). This is truly the distinguishing feature of *A. cristatum*, since most grasses that produce large or persistent seedbanks are vegetatively short-lived or annual whereas long-lived perennials generally produce transient, low density seedbanks (Thompson & Grime 1979; Romo & Bai 2004). The seedbank of annual and biennial forbs was unaffected by *A. cristatum* invasion, perhaps because these forbs have persistent seed that remains dormant despite successional changes in the vegetation (Baskin & Baskin 1998). In South African fynbos, Holmes & Cowling (1997) also found the seedbank of largely annual forbs changed little after decades of *Acacia* invasion had eliminated most herbaceous vegetation.

Of greatest concern for conservation was the greater beta dissimilarity of native uninvaded sites relative to that among *A. cristatum* invaded sites. These sites differed in native species composition, soil type and grazing regime, and *A. cristatum* was capable of invading each one. Overall, invasion homogenized compositional structure at community and landscape scales within the region.

Invasion impacts on ecosystem function

Above ground production in *A. cristatum*-invaded prairie was nearly twice that of uninvaded prairie, which is consistent with long-term production monitoring (Smoliak et al. 1980). Despite greater above ground biomass in *A. cristatum* invaded areas there was no difference in POM or soil organic matter, similar to patterns observed where *A. cristatum* was directly seeded into uncultivated Palouse prairie (Broersma et al. 2000; Krzic et al. 2000). These results contrast with soil organic matter and root biomass responses where Great Plains old fields dominated by native grasses were compared to those dominated by *A. cristatum* (Smoliak & Dormaar 1985; Dormaar et al. 1995; Christian & Wilson 1999). These researchers suggested lower root biomass and residue additions by *A. cristatum* were the cause for less soil organic matter, relative to native species 50 to 70 years post cultivation. Klein et al. (1988) further point to nitrogen-poor *A. cristatum* root residues, relative to native grasses, limiting microbial mineralization and soil organic matter formation. Why then was there no change in root biomass and below ground litter (POM), or soil organic matter approximately 10 to 65 years after *A. cristatum* had invaded uncultivated prairie?

The process of soil organic matter recovery following a discrete disturbance like cultivation may be very different from temporally diffuse invasion impacts on an uncultivated soil organic matter pool already at equilibrium. Uncultivated soil organic matter pools may be highly resistant to invasion or successional changes in herbaceous vegetation. Alternatively, insufficient time may have elapsed for soil responses to a gradual change in herbaceous vegetation, because equilibrium turnover rates of soil organic matter in the northern Great Plains greatly exceed the elapsed time since *A.*

cristatum invasion (Henderson et al. 2004). This could account for no detectable difference in aggregate-associated soil organic matter, but not POM.

Another possibility has more to do with the physiological efficiency of the grasses themselves. In greenhouse trials by Levang-Brilz & Biondini (2002), the depth, biomass, water and nitrogen use efficiencies of *A. cristatum* roots were similar to C_4 tall-grasses, and greater than native C_3 mid-grasses and C_4 short-grasses. Davidson et al. (1995) suggested increased soil respiration, and water and nitrogen use were the cause for soil organic matter degradation under rapidly growing alien grasses. In the short-term, increased aboveground production and soil respiration from *A. cristatum* invaded prairie could result in no detectable change in soil organic matter (Curtin et al. 2000). In the long-term, greater efficiency of invaders could simultaneously increase aboveground biomass at the expense of soil nutrient pools, but confirmation of this hypothesis requires physiological comparisons of *A. cristatum* invaded and uninvaded prairie.

CONCLUSION

Once established in a community, *A. cristatum* dominated vegetation and the seedbank, and was associated with lower abundance and richness of native plant functional groups in both components of the community. This effect and the non-random changes in native species abundance, indicate a broad though incomplete niche overlap with the dominant vascular plants in northern mixed-grass prairie. Controlling *A. cristatum* invasion and restoring invaded prairie will require suppression of *A. cristatum* seed production, eradication of *A. cristatum* plants, and addition of native grass and forb seed. Without these restorative measures, it is possible meta-populations of many native plant species will decline, compositional structure of communities and landscapes will be simplified, and primary production patterns will be altered.

LITERATURE CITED

Aguilar, R., Kelly, E.F. & Heil, R.D. (1988) Effects of cultivation on soils in northern Great Plains rangeland. *Soil Science Society of America Journal*, **52**,1081-1085.

Bai, Y. & Romo, R.T. (1997) Seed production, seed rain, and the seedbank of fringed sagebrush. *Journal of Range Management*, **50**, 151-155.

Bakker, J. & Wilson, S.D. (2001) Competitive abilities of introduced and native grasses. *Plant Ecology*, **157**, 117-125.

Baskin, C.C. & Baskin, J.M. (1998) *Seeds: ecology, biogeography, and evolution of dormancy and germination.* Academic Press, Toronto ON.

Blair, R.C. & Higgins, J.J. (1985) A comparison of the paired samples t test to that of the Wilcoxon's signed-rank test under various population shapes. *Psychological Bulletin*, **97**, 119-128.

Broersma, K., Krzic, M., Thompson, D.J. & Bomke, A.A. (2000) Soil and vegetation of ungrazed crested wheatgrass and native rangelands. *Canadian Journal of Soil Science*, **80**, 411-417.

Burke, I.C., Lauenroth, W.K. & Coffin, D.P. (1995) Soil organic matter recovery in semiarid grasslands: implications for the conservation reserve program. *Ecological Applications*, **5**, 793-801.

Byers, J.E., Reichard, S., Randall, J.M., Parker, I.M., Smith, C.S., Lonsdale, W.M., Atkinson, A.E., Seastedt, T.R., Williamson, M., Chornesky, E. & Hays, D. (2002) Directing research to reduce the impacts of nonindigenous species. *Conservation Biology*, **16**, 630-640.

Call, C.A. & Roundy, B.A. (1991) Perspectives and processes in revegetation of arid and semiarid rangelands. *Journal of Range Management*, **44**, 543-549.

Christian, J.M. & Wilson, S.D. (1999) Long-term ecosystem impacts of an introduced grass in the northern Great Plains. *Ecology*, **80**, 2397-2407.

Coupland, R.T. (1950) Ecology of mixed prairie in Canada. *Ecological Monographs*, **20**, 271-315.

Curtin, D., Selles, F., Wang, H., Zentner, R.P. & Campbell, C.A. (2000) Restoring organic matter in a cultivated, semiarid soil using crested wheatgrass. *Canadian Journal of Soil Science,* **80**, 429-435.

D'Antonio, C.M. & Vitousek, P.M. (1992) Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annual Review of Ecology and Systematics*, **23**, 63-87.

Davidson, E.A., Nepstad, D.C., Klink, C. & Trumbore, S.E. (1995) Pasture soils as carbon sink. Scientific correspondence. *Nature*, **376**, 472-473.

Dewey, D.R. (1986) Taxonomy of the crested wheatgrasses (*Agropyron*). In: Johnson KL (ed) *Crested wheatgrass: Its values, problems and myths*, symposium proceedings, pp 31-44. Utah State University, Logan UT.

Dormaar, J.F., Naeth, M.A., Willms, W.D. & Chanasyk, D.S. (1995) Effect of native prairie, crested wheatgrass (*Agropyron cristatum* (L.) Gaertn.) and Russian wild rye (*Elymus junceus* Fisch.) on soil chemical properties. *Journal of Range Management,* **48**, 258-263.

Eissenstat, D.M. & Caldwell, M.M. (1988a) Competitive ability is linked to rates of water extraction: a field study of two aridland tussock grasses. *Oecologia*, **75**, 1-7.

Eissenstat, D.M. & Caldwell, M.M. (1988b) Seasonal timing of root growth in favorable microsites. *Ecology*, **69**, 870-873.

Elton, C.S. (1958) *The ecology of invasions by animals and plants.* University of Chicago Press, Chicago.

Fowler, N. (1986) The role of competition in plant communities in arid and semiarid regions. *Annual Review of Ecology and Systematics*, **17**, 89-110.

Frank, A.B., Berdahl, J.D. & Barker, R.E. (1985) Morphological development and water use in clonal lines of four range grasses. *Crop Science*, **25**, 339-344.

Grime, J.P. (1973) Interspecific competitive exclusion in herbaceous vegetation. *Nature*, **242**, 344-347.

Heidinga, L. & Wilson, S.D. (2003) The impact of an invading alien grass (*Agropyron cristatum*) on species turnover in native prairie. *Diversity and Distributions*, **8**, 249-258.

Henderson, D.C., Ellert, B.H. & Naeth, M.A. (2004) Utility of ^{13}C for ecosystem carbon turnover estimation in grazed mixed grass prairie. *Geoderma*, **119**, 219-231.

Hobbs, R.J. & Humphries, S.E. (1995) An integrated approach to the ecology and management of plant invasions. *Conservation Biology*, **9**, 761-770.

Holmes, P.M. & Cowling, R.M. (1997) Diversity, composition and guild structure relationships between soil-stored seed banks and mature vegetation in alien plant-invaded South African fynbos shrublands. *Plant Ecology*, **133**, 107-122.

Huber-Sannwald, E., Pyke, D.A., Caldwell, M.M. & Durham, S. (1998) Effects of nutrient patches and root systems on the clonal plasticity of a rhizomatous grass. *Ecology*, **79**, 2267-2280.

Hull, A.C. & Klomp, G.J. (1966) Longevity of crested wheatgrass in the sagebrush-grass type in southern Idaho. *Journal of Range Management*, **19**, 5-11.

Iverson, L.R. & Wali, M.K. (1982) Buried, viable seeds and their relation to revegetation after surface mining. *Journal of Range Management*, **35**, 648-652.

Johnson, K.L. (1986) The social values of crested wheatgrass: pros, cons and tradeoffs. In: Johnson, K.L. (ed) *Crested wheatgrass: Its values, problems and myths*, symposium proceedings, pp 331-335. Utah State University, Logan UT.

Kemp, P.R. & Williams, G.J. (1980) A physiological basis for niche separation between *Agropyron smithii* (C_3) and *Bouteloua gracilis* (C_4). *Ecology*, **61**, 846-858.

Kent, M. & Coker, P. (1992) *Vegetation description and analysis: a practical approach.* John Wiley and Sons, Toronto ON.

Kindscher, K. & Wells, P.V. (1995) Prairie plant guilds: A multivariate analysis of prairie species based on ecological and morphological traits. *Vegetatio*, **117**, 29-50.

Klein, D.A., Frederick, B.A., Biondini, M. & Trlica, M.J. (1988) Rhizosphere microorganism effects on soluble amino acids, sugars and organic acids in the root zone of *Agropyron cristatum*, *Agropyron smithii* and *Bouteloua gracilis*. *Plant and Soil*, **110**, 19-25.

Kotanen, P.M., Bergelson, J. & Hazlett, D.L. (1998) Habitats of native and exotic plants in Colorado shortgrass steppe: a comparative approach. *Canadian Journal of Botany*, **76**, 664-672.

Krzic, M., Broersma, K., Thompson, D.J. & Bomke, A.A. (2000) Soil properties and species diversity of grazed crested wheatgrass and native rangelands. *Journal of Range Management*, **53**, 353-358.

Kuo, S. (1996a) Total phosphorus, digestion with perchloric acid. In: Klute, A. (ed) *Methods of soil analysis: Part 3 Chemical methods*, third edition, pp 870-872. Soil Science Society of America, Madison, WI.

Kuo, S. (1996b) Phosphorus determination, inductively coupled plasma spectrometry. In: Klute, A. (ed) *Methods of soil analysis: Part 3 Chemical methods*, third edition, pp 910-911. Soil Science Society of America, Madison, WI.

Larson, D.L., Anderson, P.J. & Newton, W. (2001) Alien plant invasion in mixed-grass prairie: Effects of vegetation type and anthropogenic disturbance. *Ecological Applications,* **11**, 128-141.

Lesica, P. & DeLuca, T.H. (1996) Long-term harmful effects of crested wheatgrass on Great Plains grassland ecosystems. *Journal of Soil and Water Conservation*, **51**, 408-409.

Levang-Brilz, N. & Biondini, M.E. (2002) Growth rate, root development and nutrient uptake of 55 plant species from the Great Plains grasslands, USA. *Plant Ecology*, **165**, 117-144.

Looman, J. & Heinrichs, D.H. (1973) Stability of crested wheatgrass pastures under long-term pasture use. *Canadian Journal of Plant Science*, **53**, 501-506.

Mack, R.N., Simberloff, D., Lonsdale, W.M., Evans, H., Clout, M. & Bazzaz, FA. (2000) Biotic invasions: causes, epidemiology, global consequences and control. *Ecological Applications,* **10**, 689-710.

Marlette, G.M. & Anderson, J.E. (1986) Seed banks and propagule dispersal in crested-wheat grass stands. *Journal of Applied Ecology*, **23**, 161-175.

Moss, E.H. (1994) *The flora of Alberta.* University of Toronto Press, Toronto, ON.

Nelson, D.W. & Sommers, L.E. (1996) Total carbon, organic carbon, and organic matter. In: Klute, A. (ed) *Methods of soil analysis. Part 3. Chemical methods*, pp 961-1010. Soil Science Society of America, Madison, WI.

Oksanen, J. (1996) Is the humped relationship between species richness and biomass an artifact due to plot size? *Journal of Ecology*, **84**, 293-295.

Oksanen, L. (2001) Logic of experiments in ecology: Is pseudoreplication a pseudoissue? *Oikos*, **94**, 27-38.

Parker, I.M., Simberloff, D., Lonsdale, W.M., Goodell, K., Wonham, M., Kareiva, P.M., Williamson, M.H., Von Holle, B., Byers, J.E. & Goldwasser, L. (1999) Impact: toward a framework for understanding the ecological effects of invaders. *Biological Invasions*, **1**, 3-19.

Paruelo, J.M. & Lauenroth, W.K. (1996) Relative abundance of plant functional types in grasslands and shrublands of North America. *Ecological Applications*, **6**, 1212-1224.

Pimentel, D., McNair, S., Janecka, J., Wightman, J., Simmonds, C., O'Connel, C., Wong, E., Russel, L., Zern, J., Aquino, T. & Tsomondo, T. (2001) Economic and environmental threats of alien plant, animal, and microbe invasions. *Agriculture, Ecosystems and Environments,* **84**, 1-20.

Pyke, D.A. (1990) Comparative demography of co-occurring introduced and native tussock grasses: persistence and potential expansion. *Oecologia*, **82**, 537-543.

Rogler, G.A. & Lorenz, R.J. (1983) Crested wheatgrass - early history in the United States. *Journal of Range Management*, **36**, 91-93.

Romo, J.T. & Bai, Y. (2004) Composition of seed banks and plant communities in the mixed prairie of Saskatchewan. *Journal of Range Management*, **57**, 300-304.

Samson, F.B. & Knopf, F.L. (1994) Prairie conservation in North America. *Bioscience*, **44**, 418-421.

Schuman, G.E., Rauzi, F. & Booth, D.T. (1982) Production and competition of crested wheatgrass-native grass mixtures. *Agronomy Journal*, **74**, 23-26.

Smoliak, S., Johnston, A. & McLean, A. (1980) *Management of crested wheatgrass pastures*. Publication 1473, Agriculture Canada, Research Branch, Ottawa.

Smoliak, S. & Dormaar, J.F. (1985) Productivity of Russian wild rye and crested wheatgrass and their effect on prairie soils. *Journal of Range Management*, **38**, 403-405.

Soil Classification Working Group (1998) *The Canadian System of Soil Classification*, 3rd edn. Agriculture and Agri-Food Canada Publication 1646, Ottawa ON.

Sutter, G.C. & Brigham, R.M. (1998) Avifaunal and habitat changes resulting from conversion of native prairie to crested wheatgrass: patterns at songbird community and species levels. *Canadian Journal of Zoology*, **76**, 869-875.

Symstad, A.J. (2000) A test of the effects of functional group richness and composition on grassland invasibility. *Ecology*, **81**, 99-109.

Thompson, K. & Grime, J.P. (1979) Seasonal variation in the seed banks of herbaceous species in ten contrasting habitats. *Journal of Ecology*, **67**, 893-921.

Wiken, E.B. (1986) *Terrestrial Ecozones of Canada*. Ecological Land Classification Series No. 19., Environment Canada, Hull QB.

Williams, D.G. & Baruch, Z. (2000) African grass invasion in the Americas: ecosystem consequences and the role of ecophysiology. *Biological Invasions*, **2**, 123-140.

Willms, W.D. & Quinton, D.A. (1995) Grazing effects on germinable seeds on the fescue prairie. *Journal of Range Management*, **48**, 423-430.

Wroe, R.A., Smoliak, S., Adams, B.W., Willms, W.D. & Anderson, M.L. (1988) *Guide to Range Conditions and Stocking Rates for Alberta Grasslands*. Alberta Forestry, Lands and Wildlife, Public Lands, Edmonton AB.

Yeomens, J.C. & Bremner, J.M. (1991) Carbon and nitrogen analysis of soils by automated combustion techniques. *Communications in Soil Science and Plant Analysis*, **22**, 843-850.

Table 3.1 Characteristics of sampling locations (site number locations in Appendix C).

Site #	Soil Texture and Suborder[a]	Dominant Native Graminoids[b]	Year[c] *A. cristatum* Introduced	Grazing Regime[c]
1	sandy clay loam Orthic Dark-brown Chernozem	*B. gracilis, P. smithii,* *E. lanceolatus*	1975	continuous May-Oct heavily grazed 1979 to 1990
2	silt loam Orthic Brown Solonetz	*K. macrantha,* *C. eleocharis, S. comata*	1960	continuous Jul-Nov heavily grazed 1960 to 2000
3	clay loam Orthic Dark-brown Chernozem	*S. comata, E. lanceolatus,* *C. eleocharis*	1965	continuous May-Oct lightly grazed 1965 to 2001
4	sand Regosolic Brown Chernozem	*P. smithii, S. comata,* *K. macrantha*	1980	short-duration Aug-Sep lightly grazed 1980 to 2001
5	clay loam Solonetzic Brown Chernozem	*S. comata, E. lanceolatus,* *K. macrantha*	1950	ungrazed 1988 to 2001
6	silty clay loam Orthic Brown Solonetz	*P. smithii, C. eleocharis,* *P. sandbergii*	1935	continuous Oct-Apr lightly grazed 1927 to 2001
7	sandy loam Orthic Brown Chernozem	*S. comata, K. macrantha,* *B. gracilis*	1954	continuous May-Oct heavily grazed 1954 to 2001
8	sandy loam Orthic Brown Chernozem	*S. comata, E. lanceolatus,* *B. gracilis*	1990	ungrazed 1980 to 2001

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[a] Based on soil survey maps and field classifications using the Canadian System of Soil Classification (Soil Classification Working Group 1998).

[b] Three most abundant listed in declining order, nomenclature from Moss (1994): *Bouteloua gracilis, Carex eleocharis, Elymus lanceolatus, Koeleria macrantha, Pascopyrum smithii, Poa sandbergii, Stipa comata.*

[c] Based on landowner interviews.

Table 3.2 Abundance of ubiquitous species (n>5 of 8 sites) within *A. cristatum* invaded and uninvaded vegetation and seedbanks.

	Vegetation Basal Cover (%)			Seedbank Density (# m^{-2})		
Species	Uninvaded	Invaded	P (n)	Uninvaded	Invaded	P (n)
	mean ± SE	mean ± SE		mean ± SE	mean ± SE	
Perennial C3 Graminoids						
Agropyron cristatum	0.0 ± 0.0	13.8 ± 2.5	0.01 (8)	9 ± 6	404 ± 164	0.01 (8)
Carex eleocharis	3.6 ± 1.1	3.6 ± 1.4	0.99 (8)	63 ± 29	32 ± 12	0.29 (8)
Elymus lanceolatus	3.5 ± 0.7	0.1 ± 0.1	0.02 (7)		n < 6	
Koeleria macrantha	2.9 ± 0.8	0.2 ± 0.1	0.01 (6)	53 ± 20	5 ± 4	0.03 (7)
Poa sandbergii	1.5 ± 0.7	0.8 ± 0.2	0.46 (6)		n < 6	
Stipa comata	7.9 ± 2.0	1.5 ± 0.5	0.01 (8)	30 ± 6	7 ± 2	0.01 (8)
Perennial C4 Graminoids						
Bouteloua gracilis	2.6 ± 0.9	3.6 ± 0.8	0.40 (7)	9 ± 4	7 ± 4	0.49 (6)
Perennial Forbs						
Artemisia frigida	2.3 ± 1.0	0.2 ± 0.1	0.02 (8)	405 ± 185	158 ± 53	0.02 (8)
Phlox hoodii	0.9 ± 0.3	0.1 ± 0.1	0.03 (6)		n < 6	
Sphaeralcea coccinea	0.4 ± 0.2	0.2 ± 0.1	0.17 (6)		n < 6	
Annual & Biennial Forbs						
Androsace septentrionalis		n < 6		211 ± 132	227 ± 170	0.92 (6)
Cryptogams						
Cladonia pyxidata	8.3 ± 2.3	7.3 ± 1.8	0.75 (6)		not applicable	
Selaginella densa	15.7 ± 5.1	12.9 ± 4.0	0.45 (7)		not applicable	
Xanthoparmelia chlorochroa	2.8 ± 1.5	1.4 ± 1.1	0.03 (6)		not applicable	

P values are from the Wilcoxon Signed-Rank test for paired samples.

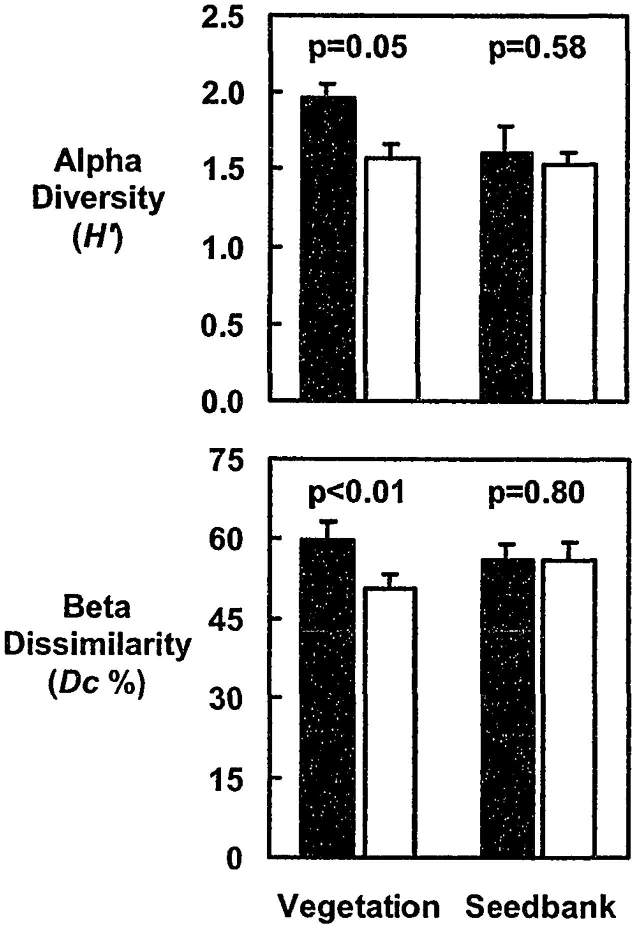

Figure 3.1 Alpha diversity (within community) and beta dissimilarity (among communities) of *A. cristatum* invaded (white columns) and uninvaded (black columns) grasslands. Columns are means with standard error bars, and P values are from the Wilcoxon Signed-Rank test (n = 8 alpha, n = 28 beta) for paired samples.

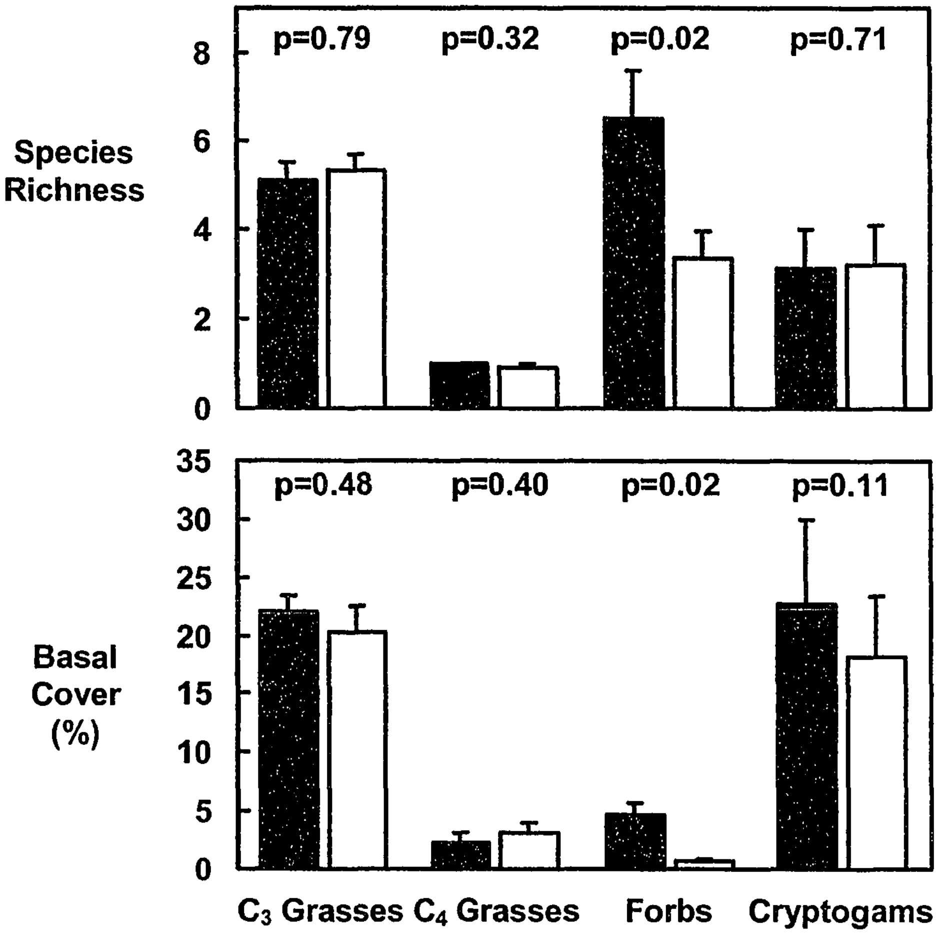

Figure 3.2 Alpha richness and abundance of vegetation functional groups in *A. cristatum* invaded (white columns) and uninvaded (black columns) grasslands. Columns are means with standard error bars, and P values are from the Wilcoxon Signed-Rank test (n = 8) for paired samples.

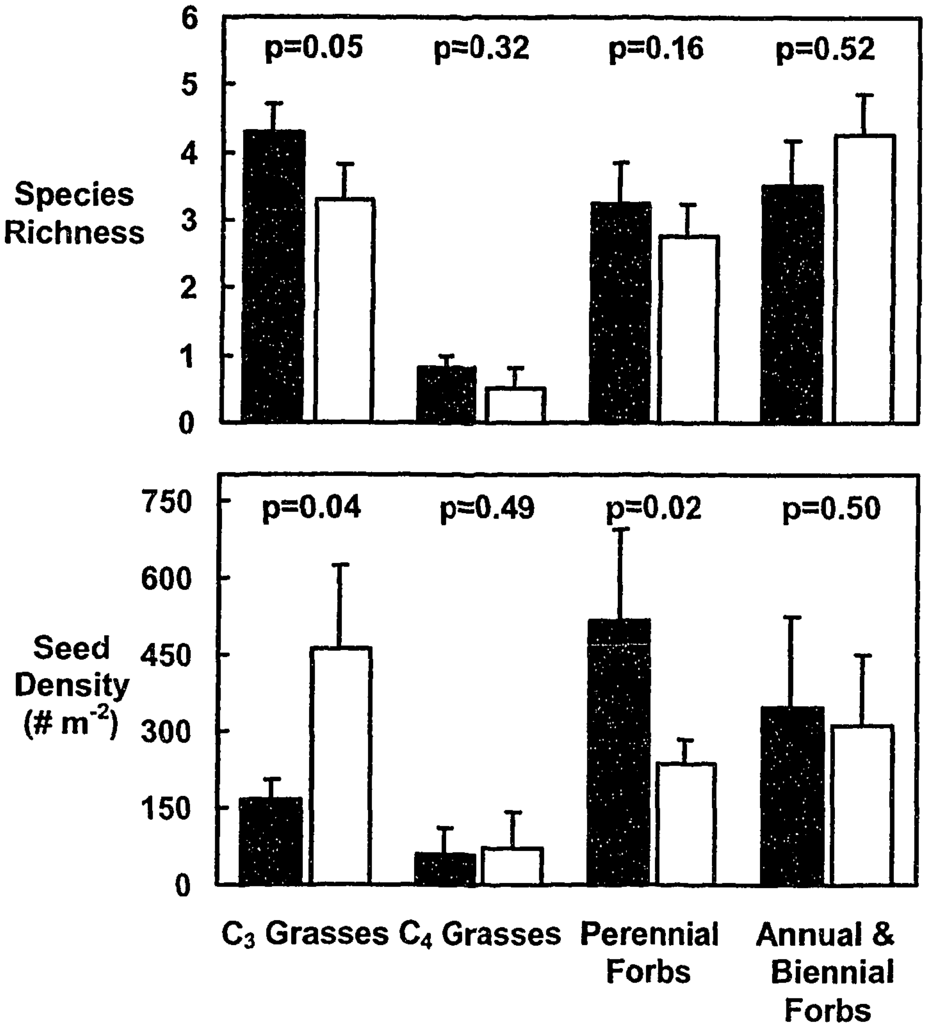

Figure 3.3 Alpha richness and abundance of seedbank functional groups in *A. cristatum* invaded (white columns) and uninvaded (black columns) grasslands. Columns are means with standard error bars, and P values are from the Wilcoxon Signed-Rank test (n = 8) for paired samples.

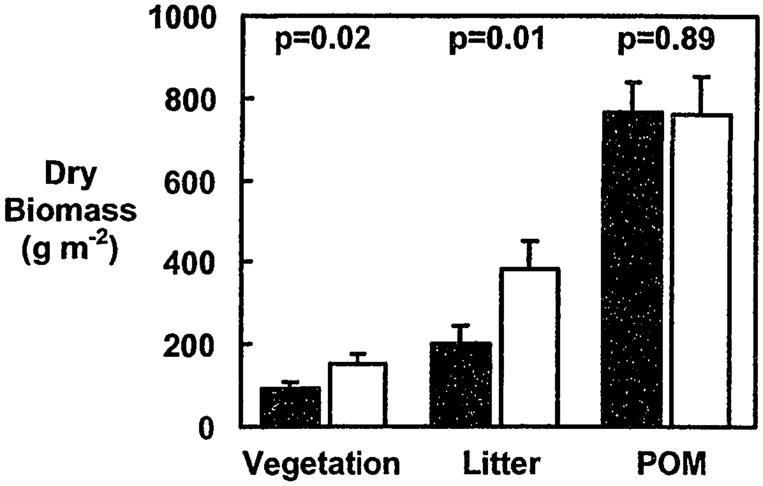

Figure 3.4 Oven dried mass of above ground vegetation and litter, and below ground particulate organic matter (POM) in *A. cristatum* invaded (white columns) and uninvaded (black columns) grasslands. Columns are means with standard error bars, and P values are from the Wilcoxon Signed-Rank test (n = 8) for paired samples.

CHAPTER 4. PARTITIONING THE APPARENT PERSISTENCE OF CRESTED WHEATGRASS SEEDBANKS: AN EXPERIMENTAL APPROACH

INTRODUCTION

Patterns of seed survival following dispersal have substantial impacts on the population dynamics of individual species, and the structure of plant communities (Baskin & Baskin 1998). Seed that survives and remains dormant but viable in the soil for at least one year post-dispersal is considered persistent, while seed that either germinates or decomposes within a year post-dispersal is considered transient. Species with persistent seedbanks are typically short-lived in the vegetative phase, while species with non-dormant seed form transient seedbanks and are typically long-lived in the vegetative phase (Thompson & Grime 1979). This presents a regeneration challenge for land managers who wish to maintain dominant populations of perennial species. Efficient maintenance of perennial forage crop productivity requires conspecific regeneration in gaps that follow adult plant mortality. This is particularly problematic for bunchgrasses that rely almost wholly on seedling establishment for population growth.

Crested wheatgrass (*Agropyron cristatum*) is a perennial bunchgrass from Asia that was introduced on the northern Great Plains of Canada for livestock forage and land reclamation. Pastures and hayfields seeded as far back as the 1930s remain dominated by this one species and produce consistently high yields (Looman & Heinrichs 1973; Smoliak et al. 1980). Crested wheatgrass seed production and seedbank densities vary from a few hundred to a few thousand m^{-2} (Marlette & Anderson 1986; Pyke 1990; Jefferson & Kielley 1993; Ambrose & Wilson 2003), and greatly exceed the densities achieved by native grasses (Romo & Bai 2004; Willms & Quinton 1995). Difficulty eradicating crested wheatgrass for conversion to native grass or other tame species, has been attributed to this large and potentially persistent seedbank (Pyke 1990; Wilson & Partel 2003; Bakker et al. 2004). However, this apparent persistence may simply be a density/mortality function, whereby high seed mortality rates are offset by greater annual input rates and the chance accumulation of a few survivors from each generation. If seedbank persistence does occur, it facilitates goals of maintaining pasture or hay field productivity, but complicates goals of eradication and conversion.

Patterns of survivorship do not always fit a rigid classification, and the same species can exhibit different seed survival patterns in different years due to changed environmental conditions (Donald 1993). *A. cristatum* seed can remain germinable for several decades when stored at freezing temperatures, but rates were considerably less for seed stored at room temperature (Ackigoz & Knowles 1983). Fluctuating temperature, humidity and light under field conditions tend to hasten germination (Maynard & Gates 1963; Wilson 1973; Young & Evans 1986) but how this affects long-term survival is unknown. In the field, short-term survival of *A. cristatum* seed was greater at the surface relative to shallow depths, because of fewer losses to germination (Ambrose & Wilson 2003). Conversely, increasing depth of burial will reduce *A. cristatum* seedling emergence (Redman & Qi 1992), and deep buried seed may enter secondary dormancy rather than germinate and fail to emerge (Benvenuti et al. 2001).

The objective of this experiment was to determine the survival and relative germinability of *A. cristatum* seed cohorts under field conditions. Specifically, I was interested in testing how seed survival and germinability differed over three years between cohorts placed in four vertical positions. Greater moisture availability in the soil was expected to increase mortality rates due to germination and decomposition, while greater temperature and humidity fluctuations aboveground were expected to increase seed germinability in the first year (stratification benefits) but decrease germinability in the second year (lost viability).

METHODS

In mid-April 2002, *A. cristatum* seed ("Kirk" variety) was obtained from a commercial supplier, and the certificate of seed analysis indicated 93% germinability for this fall 2001 harvested seed. Experimental units were prepared by sealing lots of 100 seeds in 15 x 15 cm nylon packets, constructed from commercial tent screening (mesh size = 0.5 mm). This mesh size prevents macroinvertebrates from removing seed, but allows soil particles, gases, moisture and microorganisms to penetrate. Initial germination was determined from four lots of 100 seeds by counting the number that produced a radicle >1 mm after 21 days incubation on moist filter paper at 22 °C and approximately 14:10 light:dark cycle. These conditions should be ideal for rapid and complete germination of *A. cristatum* (Young & Evans 1986), and all subsequent laboratory germination tests were conducted similarly.

In late April 2002, a completely randomized factorial field experiment was established in an ungrazed mixed-grass prairie near Lethbridge AB (49° 42' lat, 112° 51' lon; Appendix C). Vegetation on site was dominated by the grasses *Pascopyrum smithii*, *Elymus lanceolatus*, *Stipa viridula* and *Bouteloua gracilis*, and scattered shrubs of *Eurotia lanata*. Soil was a sandy-clay, dark brown chernozem formed on glacio-lacustrine parent materials. Climate normals for Lethbridge are 365 mm annual precipitation, 2251 hours annual sunshine, 5.8 °C annual temperature and 2995 degree days above 0 °C (Environment Canada 2000). Considerable daily and seasonal climatic variation occurs, but temperature fluctuations below ground decrease with increasing depth particularly when snow insulates the ground in winter (Figure 4.1).

The combination of four levels of the seed placement factor and seven levels of the duration factor, created 28 factor level combinations. Four replicates of each combination necessitated 112 experimental units, and these were placed 50 cm apart within a 6 x 6 m area. Four levels of seed placement were devised by burying packets at 15 cm and 2 cm depths, placing packets on the soil surface beneath grass litter, and suspending other packets 10 cm above ground. The 15 cm depth represented a potential position seed could be buried from topsoil inversion during agricultural tillage. The 2 cm depth represented the optimum for cultural establishment (Redmann & Qi 1992). Clay and a dense mat of roots allowed excavation of intact soil blocks 2 or 15 cm thick. Buried units were placed horizontally at the bottom of each excavation, then soil blocks were replaced over top and compressed with foot pressure until the surface was level with adjacent non-excavated soil. The soil surface placement represented the most likely position of naturally broadcast seed, and the elevated treatment represented a potential aerial seed bank that results when seed fails to shatter from reproductive culms (Pyke 1990) or becomes lodged in litter above ground. To prevent predation by granivorous vertebrates, surface and elevated units were covered by metal hardware cloth cages (7 mm mesh, cube dimensions 20 x 20 x 20 cm) and fixed in place with iron spikes. These cages allowed air movement, rain and light penetration, snow accumulation and vegetative growth around the surface and elevated packets.

There were seven removal intervals from mid-July 2002 to mid-July 2004. At each interval, packets were excavated or removed from cages and transported in a darkened container for approximately 6 hours enroute to the lab. Seed from each packet were removed and examined at 12 x magnification to determine the proportion that germinated (radicles and coleoptiles present), decomposed (empty seed coats crushed with forceps), or survived (whole seed that could not be compressed with forceps). After 15 months tissue degradation made it difficult to distinguish germinated and decomposed seeds, so these two were grouped thereafter. Despite this degradation and occasional beetle (Coleoptera) parasitism, all seeds were recovered from the nylon packets over the full duration of the experiment. Germinability tests of remaining whole seed that survived were conducted (see procedure above), but no other viability tests were applied.

To determine if patterns of survivorship were different among seed placement treatments, a nonparametric log-rank test was computed for curves using interval means for each treatment pair combination. The same test was used to compare each survivorship curve to linear and negative exponential functions to distinguish curves as Deevey type 2 or 3 (Pyke & Thompson 1986). In both cases, the log-rank test generates a χ^2 test statistic, and for paired comparisons the χ^2 critical = 3.84 (df = 1; $\alpha = 0.05$). For treatment comparisons of seed fate at two particular intervals, proportional data were arcsine transformed prior to conducting a factorial analysis of variance (time = 2, treatment = 3) and Tukey's multiple comparison procedure (SAS Institute 1999). Significant differences among treatments and intervals were identified where $\alpha = 0.05$.

RESULTS & DISCUSSION

Seedbank Survival

Survivorship curves were significantly different among elevated, surface and buried treatments, but the two burial depths were not different (Figure 4.2, Table 4.1). Where *A. cristatum* seed was in contact with the soil, survivorship approximated a negative exponential Deevey type 3 curve ($\chi^2 = 0.19$ shallow, $\chi^2 = 0.03$ deep), because initially high rates of mortality declined with time. Total mortality of seed in the first 5 months exceeded the 70 to 88% germination rates observed by Ambrose & Wilson (2003) under varying soil moisture. Unusually high precipitation and cool temperatures at

Lethbridge between June and September 2002 appear to have resulted in relatively greater decomposition rates and lower germination rates than Ambrose & Wilson (Table 2). Crist & Friese (1993) found decomposition rates tend to be greater under cool and moist winter conditions, and Young & Evans (1986) indicate temperatures above 20 to 25 °C are ideal for *A. cristatum* germination. Decomposition rates increased over the first winter for surface laid seed, and germination in all treatments was concentrated during the first summer (Table 4.2). The persistence of a few seeds (1 to 5%) from 12 to 26 months may reflect experimental errors from seeds lodged in the nylon mesh that avoided soil contact altogether, or a portion of the population in physiological dormancy.

Survival of elevated seed was linear ($\chi^2 < 0.00$) and did not change over a 26.5 month period (Figure 4.2, Table 4.1). A small proportion of surface-laid seed germinated or decomposed intermittently and mortality rates were linear (2.5% mo^{-1}; $\chi^2 < 0.00$) for the first 15 months, and a linear model was also the best fit over the whole 26.5 month period ($\chi^2 = 0.06$) approximating a Deevey type 2 curve. Ambrose & Wilson (2003) found seedling germination and emergence rates for surface sown seeds were much lower than buried seeds, with 20% under high precipitation and 5% under low precipitation after six months. Static survivorship near 78% for the last 11.5 months partly reflects an experimental error whereby ramets of *Pascopyrum smithii* lifted surface-laid packets above the soil surface. The apparent resurrection of seed in fall 2003 may be a small sample problem given the high variation in this particular treatment. Greater variation at the soil surface may be influenced by differences in light and moisture availability among microsites. Marlette & Anderson (1986) found more *A. cristatum* seed in the soil beneath patches of litter and Fowler (1988) found grass seedling emergence and survival were greater in exposed microsites. Thus the survival of seed may be greater beneath dense patches of litter where light penetration and the amplitude of temperature and moisture variation are reduced (Willms et al. 1993). These latter fluctuations are known to progressively hasten germination rates (Maynard & Gates 1963), which could accelerate seed loss during brief periods of sufficient moisture and heat.

The different patterns of seed survival have implications for the dynamics of *A. cristatum* seedbanks. Disturbances like grazing that remove litter and compress standing culms to the ground, should increase seed-soil contact and reduce total seedbank survival.

As much as 75% of broadcast seed can be buried beneath the surface after a short period of grazing, and as little as 7% is buried in the absence of grazing (Winkel et al. 1991). A lack of grazing or haying disturbance that allows litter accumulations and maintains standing culms above the soil surface will generate an aerial seedbank and contribute to persistence of cohorts over multiple generations. For example, an annual carryover of seed equivalent to 20 to 50% of maximum seedbank density has been observed in lightly grazed *A. cristatum* stands; however, much of that carryover could be an artifact of delayed dispersal from standing culms (Pyke 1990) and does not imply soil seedbank persistence. In native grasslands, Willms & Quinton (1995) found several thousand seeds m^{-2} were present in above ground litter and constituted approximately 30% of the total seedbank to a 6 cm depth. A combined persistent aerial and transient soil seedbank create the appearance of overall seedbank persistence, and management will influence the proportion of these components, and the number of generations and seed present. Managers wanting to renovate *A. cristatum* pastures should weigh the costs and benefits of tillage and seeding, vs. simply letting the field remain idle for a year to build-up a seedbank that could be stimulated to germinate following a short-duration, high-intensity grazing event or harrowing.

Dormancy and Germinability

For below ground persistence to occur, suitable conditions for germination must be lacking for prolonged periods or a portion of the seed remains physiologically dormant (Baskin & Baskin 1998). Germinability patterns of *A. cristatum* seeds were consistent with survival patterns for buried seed, but deviated from those for surface and elevated seeds (Figure 4.2). In particular, an initial decline in germinability for 15 months was followed by a 20 to 40% increase in September 2003, then decline to previous levels by mid-summer 2004. Patterns of seed dormancy for perennial grasses from temperate environments are typically synchronized with annual climate cycles, such that seed can be dormant at dispersal and require cold or heat stratification to increase germinability (Baskin & Baskin 1998). Increased *A. cristatum* germinability after July 2003 coincided with the end of a cooler and moister than normal period, and the start of one hotter and drier than normal. Fluctuating moisture and temperature cause seeds to germinate more rapidly than those stored for long periods under constant conditions (Maynard & Gates

1963; Wilson et al. 1974; Young & Evans 1986), and this may be an adaptation to drought stress whereby a wetting and drying event preconditions seed to imbibe more quickly the next time moisture becomes available (Wilson 1973; Briede & McKell 1992).

Another possibility for the timing of decreased dormancy and increased germinability is a genetic based adaptation for fall germination. Several researchers report that seedling emergence, survival and adult plant density are greater when *A. cristatum* pastures are seeded in the fall (McLean & Wikeem 1983; White 1984; Ries & Hofmann 1996). Seedlings that establish in fall are capable of overwintering on the northern Great Plains, and more of these seedlings survive late spring frosts than spring emerged seedlings (White 1984). In the central Asian steppes where *A. cristatum* evolved, a late summer to early fall wet season and more severe winter drought relative to the northern Great Plains, may have selected for seed that breaks dormancy and germinates most readily in the fall (Appendix A).

CONCLUSION

A small portion of *A. cristatum* seed does survive and remain germinable in the environment after three years. The vertical position of that seed has a major influence on the proportion surviving and persisting, and this could be manipulated by land management activities like tillage or grazing. Dormancy may also occur in seed not exposed to suitable germination conditions in the first year. The queues that induce and break dormancy were not entirely clear, but a combination of land management and environmental conditions can create patterns of seedbank persistence that defy the traditional classification by Thompson & Grime (1979). This may be a widespread phenomenon among perennial grasses normally thought to produce transient seedbanks, or a distinguishing feature of this Asian species.

LITERATURE CITED

Ackigoz, E. & Knowles, R.P. (1983) Long-term storage of grass seeds. *Canadian Journal of Plant Science*, **63**, 669-674.

Ambrose, L.G. & Wilson, S.D. (2003) Emergence of the introduced grass *Agropyron cristatum* and the native grass *Bouteloua gracilis* in a mixed-grass prairie restoration. *Restoration Ecology*, **11**, 110-115.

Baskin, C.C. & Baskin, J.M. (1998) *Seeds: Ecology, biogeography, and evolution of dormancy and germination.* Academic Press, San Diego CA.

Benvenuti, S., Macchia, M. & Miele, S. (2001) Quantitative analysis of emergence of seedlings from buried weed seeds with increasing soil depth. *Weed Science*, **49**, 528-535.

Briede, J.W. & McKell, C.M. (1992) Germination of seven perennial arid land species, subjected to soil moisture stress. *Journal of Arid Environments*, **23**, 263-270.

Crist, T.O. & Friese, C.F. (1993) The impact of fungi on soil seeds: Implications for plants and granivores in a semiarid shrub-steppe. *Ecology*, **74**, 2231-2239.

Donald, W.W. (1993) Models and sampling for studying weed seed survival with wild mustard (*Sinapis arvensis*) as a case study. *Canadian Journal of Plant Science*, **73**, 637-645.

Environment Canada (2000) *Canadian Climate Normals 1971-2000.* Environment Canada, Ottawa ON.

Fowler, N.L. (1988) What is a safe site?: Neighbour, litter, germination date, and patch effects. *Ecology*, **69**, 947-961.

Looman, J. & Heinrichs, D.H. (1973) Stability of crested wheatgrass pastures under long-term pasture use. *Canadian Journal of Plant Science*, **53**, 501-506.

Marlette, G.M. & Anderson, J.E. (1986) Seed banks and propagule dispersal in crested wheatgrass stands. *Journal of Applied Ecology*, **23**, 161-175.

Maynard, M.L. & Gates, D.H. (1963) Effects of wetting and drying on germination of crested wheatgrass seed. *Journal of Range Management*, **16**, 119-121.

McLean, A. & Wikeem, S.J. (1983) Effect of time of seeding on emergence and long-term survival of crested wheatgrass in British Columbia. *Journal of Range Management*, **36**, 694-700.

Pyke, D.A. (1990) Comparative demography of co-occurring introduced and native tussock grasses: persistence and potential expansion. *Oecologia*, **82**, 537-543.

Pyke, D.A. & Thompson, N.J. (1986) Statistical analysis of survival and removal rate experiments. *Ecology*, **67**, 240-245.

Redmann, R.E. & Qi, M.Q. (1992) Impacts of seeding depth on emergence and seedling structure in eight perennial grasses. *Canadian Journal of Botany*, **70**, 133-139.

Ries, R.E. & Hofmann, L. (1996) Perennial grass establishment in relationship to seeding dates in the northern Great Plains. *Journal of Range Management*, **49**, 504-508.

Romo, J.T. & Bai, Y. (2004) Composition of seed banks and plant communities in the mixed prairie of Saskatchewan. *Journal of Range Management*, **57**, 300-304.

SAS Institute Inc. (1999) *Statistical Analysis Software Version 8.0.* SAS Institute Inc., Cary NC.

Thompson, K. & Grime, J.P. (1979) Seasonal variation in the seed banks of herbaceous species in ten contrasting habitats. *Journal of Ecology*, **67**, 893-921.

White, R.S. (1984) Stand establishment: The role of seedling size and winter injury in early growth of three perennial grass species. *Journal of Range Management*, **37**, 206-211.

Willms, W.D., McGinn, S.M. & Dormaar, J.F. (1993) Influence of litter on herbage production in the mixed prairie. *Journal of Range Management*, **46**, 320-324.

Willms, W.D. & Quinton, D.A. (1995) Grazing effects on germinable seeds on the fescue prairie. *Journal of Range Management*, **48**, 423-430.

Wilson, A.M. (1973) Responses of crested wheatgrass seeds to environment. *Journal of Range Management*, **26**, 43-46.

Wilson, A.M., Wondercheck, D.E. & Goebel, C.J. (1974) Responses of range grass seeds to winter environments. *Journal of Range Management*, **27**, 120-122.

Winkel, V.K., Roundy, B.A. & Blough, D.K. (1991) Effects of seedbed preparation and cattle trampling on burial of grass seeds. *Journal of Range Management*, **44**, 171-175.

Young, J.A. & Evans, R.A. (1986) Seed and seedbed ecology of crested wheatgrass. In: *Crested wheatgrass: Its values, problems and myths; Symposium proceedings* (Johnson, K.L. ed). Utah State University, Logan UT. Pp. 61-64.

Table 4.1 Matrix of χ^2 test statistics from log-rank tests to determine if survivorship curves differ among treatments.

	Elevated (10 cm)	Surface (0 cm)	Shallow (2 cm)
Elevated (10 cm)	0.00	--	--
Surface (0 cm)	3.98	0.00	--
Shallow (2 cm)	91.90	66.23	0.00
Deep (15 cm)	87.47	64.73	0.11

Significant differences occur where $\chi^2 > 3.84$ ($df = 1$, $\alpha = 0.05$).

Table 4.2 Percentage of the total seedbank that germinated or decomposed over the first summer (5 month duration) and the first year (12 month duration). No seed germinated or decomposed from the Elevated placement treatment.

Fate	Duration	Placement		
		Surface (0 cm)	Shallow (2 cm)	Deep (15 cm)
		mean ± sterr	mean ± sterr	mean ± sterr
Germinated	5 months	13 ± 4 b	51 ± 11 a	61 ± 2 a
	12 months	14 ± 8 b	47 ± 5 a	54 ± 8 a
Decomposed	5 months	5 ± 2 b*	40 ± 9 a	30 ± 4 a
	12 months	19 ± 2 b*	46 ± 6 a	35 ± 8 a

Within rows, values followed by the same letter were not significantly different, and between rows within a fate category and placement treatment values followed by an asterix were significantly different (Tukey $\alpha = 0.05$).

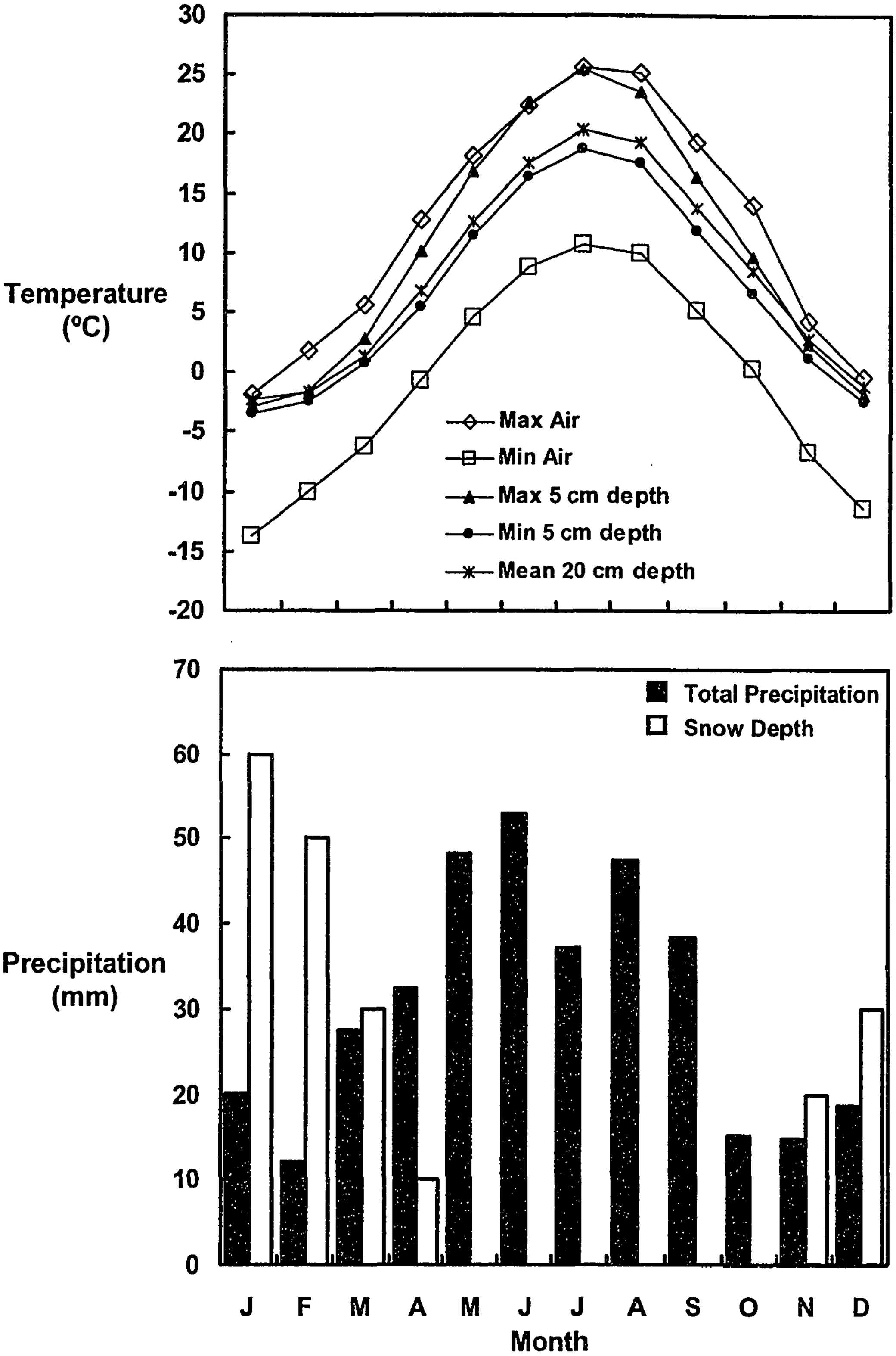

Figure 4.1 Mean monthly air and soil temperatures, and mean monthly precipitation and snow depth for Lethbridge, AB (adapted from Environment Canada 2002).

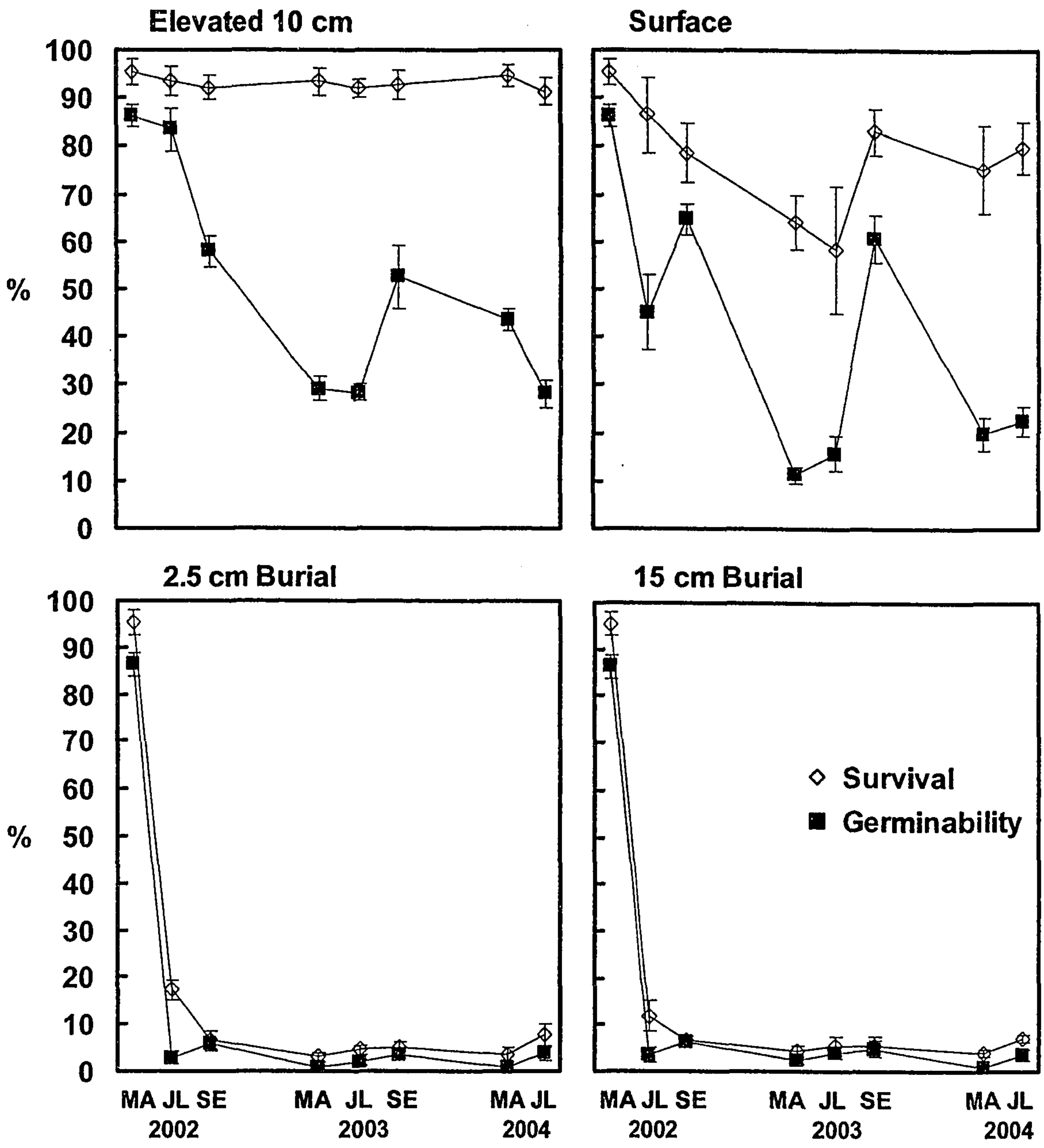

Figure 4.2 Survival and germinability of *A. cristatum* seed, as a percentage of total seed density, in four seed placement treatments over a 26.5 month period at Lethbridge, AB. Bars are standard errors (n = 4).

CHAPTER 5. PRAIRIE RESTORATION USING INITIAL FLORISTICS AND ALIEN PERENNIAL GRASS CONTROL

INTRODUCTION

Native grassland restoration is limited by a number of factors, including availability of a diverse propagule mix of local provenance and resource capture by competitive alien plants (Wilson et al. 2004). Some of these aliens are economically beneficial, which presents a number of dilemmas for both conservation and restoration (Pimentel et al. 2001). The Eurasian bunchgrass *A. cristatum* was intentionally seeded in North America for reclamation and forage production, and has accidentally invaded adjacent native grasslands. This species remains dominant in fields for decades (Looman & Heinrichs 1973; Christian & Wilson 1999) and both seeded and invaded grasslands are less diverse at community to landscape scales (see Chapter 3). At the same time, grazing *A. cristatum* during peak production in spring can defer grazing native grasslands until these natives are better able to withstand this disturbance (Smoliak et al. 1980). Those wishing to eradicate *A. cristatum* for native grassland restoration must recognize the ecological and economic risks associated with lost forage availability in a region dominated by private agricultural land-owners. Combining techniques to prevent invasion from agricultural pastures and to restore invaded or seeded areas on adjacent public grasslands could result in a regional benefit to biodiversity conservation. Techniques that selectively inhibit undesired aliens yet promote desired natives already present will also reduce costs and genetic risks associated with adding native seed (Richards et al. 1998).

Bunchgrasses disperse primarily through seed production, so preventing *A. cristatum* invasion must focus on limiting seed availability. Defoliation of bunchgrasses by grazing or clipping stimulates vegetative tillering and suppresses reproductive culm development (Olson & Richards 1988: Busso & Richards 1995; Romo & Harrison 1999) and may be the most effective means to prevent invasion. However, soil seedbanks provide another propagule source that complicates eradication and restoration efforts, and tillage or herbicides may stimulate seedling emergence and reinvasion (Lodge 1960; Lorenz & Rogler 1962; Olson & Richards 1989; Wilson & Gerry 1995). Seedbank persistence may also be a problem (Pyke 1990) and disturbances that promote germination or decomposition can potentially reduce seedbanks. Grazing and burning are known to reduce grass litter and increase bare ground (Collins & Barber 1985; Dormaar et al. 1994; Shay et al. 2001), and may increase germination and prevent seedbank accumulation. Past research on how disturbances affect *A. cristatum* populations has been limited to a few treatments (Bakker et al. 2003) or few repetitions (Romo et al. 1994; Wilson & Gerry 1995; Wilson & Partel 2003).

To achieve large-scale and long-term conservation goals, successful manipulation of the invasive species population is insufficient to evaluate the success of restorative techniques (Huston 2004). In particular, conservation goals of maintaining native biological diversity and restoration goals of increasing community similarity to a reference ecosystem must both be measured (Sheley & Krueger-Mangold 2003). Intermediate levels or interactions of disturbance from grazing and burning are expected to increase community diversity in grasslands by reducing dominance and increasing richness (Collins & Barber 1985). Glyphosate applications have neutral or positive effects on plant community diversity (Sullivan & Sullivan 2003), and in the case of *A. cristatum* dominated grasslands glyphosate consistently increases diversity and soil resource availability (Bakker et al. 2003). Achieving similarity to a native reference community is more elusive, since the previous community composition is not known in fields dominated by *A. cristatum* for decades. Adjacent native grasslands with similar soils may substitute as accurate references, but the history of grazing and fire can create different compositional patterns (Westoby et al. 1989) further complicating the precision of reference estimation.

The objectives of this field experiment were to test the impact of annually repeated disturbance on the structure of *A. cristatum* populations, grassland plant communities, biomass and soil resource availability. Conservation goals were evaluated by comparing these responses after four years of grazing, haying, burning, glyphosate, glyphosate plus burning, and a control treatment excluded from all of the above. Restoration goals were evaluated by comparing community patterns in these same treatments to a synthetic reference community. Hypotheses for future restoration trajectories were developed from the results of these comparisons.

METHODS

Study Area

The northern mixed-grass prairie encompasses the semiarid Great Plains of Alberta and Saskatchewan, Canada and portions of Montana, Wyoming, North and South Dakota, U.S.A. The climate is temperate continental, and temperatures vary from winter lows in January of -40 °C to summer highs in July of 40 °C. Mean annual precipitation (MAP) is 300 to 400 mm, and most falls as rain between May and September (Environment Canada 2000). Inter-annual variability is common, and over the course of this experiment there was drought from September 2000 to June 2002 characterized by less than 50% MAP, while June 2002 to July 2003 was wetter with greater than 150 % MAP, and 2004 was near average (PFRA 2004). The perennial grasses *Stipa comata*, *Bouteloua gracilis*, *Koeleria macrantha* and *Agropyron smithii* dominate native vegetation in the region (Coupland 1950), but in Canada approximately 70% of this vegetation has been lost to cultivation since 1900. *A. cristatum* now occupies 6 to 7% of the region along roadside ditches, utility corridors and on pastures and hayfields (Appendix A).

Experimental Design

A randomized complete block experiment was established in May 2001, using four blocks at locations separated by 150 to 500 km. Each block was established on an *A. cristatum* field that was seeded 25 to 65 years earlier (Table 5.1; Appendix C). Among block variability in soil type, *A. cristatum* genotype, seeding date and management history was intended to expand the scale of inference to the entire region. While this variability sacrifices some statistical precision, it increases the ecological accuracy for the desired scale of inference (Oksanen 2001). Each 70 x 90-m block was fenced with barbed wire to control livestock access, and selecting level sites at least 50 m from the nearest road, cultivated field or other major disturbance reduced within block variability. Within each block, six 10 x 30-m plots were separated and surrounded by 10-m buffers, and these buffers were mowed once or twice each year to prevent *A. cristatum* seed dispersal into adjacent plots. At small scales of variability, plots were large enough to encompass ant mounds, mammal burrows and wallows that occupied <10% of each plot.

Treatments in the six plots consisted of an exclusion (CTRL), graze, hay, burn, herbicide and combined burn x herbicide. Glyphosate (HERB) was annually applied in late May to two plots in each block. In 2001 and 2002 a mixture of 1:10 concentrate: water was applied using a sponge or 'wick' elevated 10 cm above ground. At this time of year *A. cristatum* was the tallest herbaceous plant, and wick application was intended to selectively remove taller *A. cristatum* before seed head development while avoiding shorter and later developing native plants present in the plot (Romo et al. 1994). In 2003 and 2004 the density of surviving *A. cristatum* was low and spot applications with a back-pack sprayer (same glyphosate concentration) became more efficient.

Grazing (GRAZE) treatments involved additional fencing 5 to 10 m from the plot edge. The grazed buffers prevented edge effects within the plot from excessive trampling near fences, gates and water sources. In mid June of each year, herbage utilization equivalent to ~50% was achieved using variable numbers and sizes of domestic cattle over a period of 48 to 96 hours. This short-duration, high-intensity (SD-HI) grazing event was intended to remove *A. cristatum* seed heads at the boot to ear stage of development, and no further reproductive culm emergence was expected for the year (Romo and Harrison 1999). Haying (HAY) treatments were conducted in late June to remove *A. cristatum* near the peak of forage production and quality (Smoliak et al. 1980), but prior to anthesis and seed fertilization. Haying was simulated by using a rotary mower to clip all vegetation at a 10 cm height, then swaths were raked and removed from the plot.

Prescribed burns were planned for late August of each year, prior to *A. cristatum* seed dispersal and after senescence of leaves and stems. Burning at this time was intended to eliminate seed additions by combusting seed on the stem and recently dispersed on the soil surface, although no effect on seed already in the soil seedbank was expected (Abrams 1988). There were two burn plots in each block, a burn only (BURN) and a combined burn and glyphosate treatment (HBRN). In 2001 a 2 m wide fireguard was burned around each plot, and 10 m wide head fires were set at 5 m intervals along the plot length. Fuel and weather conditions resulted in hot fires at Onefour, Brooks and Hanna blocks but humidity and green fuels at Eastend resulted in cool fires. A combination of insufficient fuels and poor weather prevented burning at all sites from 2002 to 2004.

Sampling

Initial vegetation and seedbank sampling was conducted in May 2001. In each plot, 20 quadrats (0.1 m^2) were randomly distributed within the 300 m^2 area to encompass the minimal sampling area based on species area curves for all sites. In each quadrat the basal cover of bare ground, litter and all cryptogamic and vascular plant species were recorded as per methods outlined by Wroe et al. (1988). A random subset of 8 quadrats was selected for soil seedbank sampling, and three cylindrical cores of soil and overlying litter (7.8 cm diameter x 5 cm deep) were extracted and composited for each quadrat. Sampling at this time of year includes the persistent and transient seedbanks (Thompson and Grime 1979). Cores were kept in coolers (~5 °C) for up to 7 days before setting up the greenhouse for germinable seedbank estimation.

Seedbank cores were hand crushed and spread to a 1 cm depth over 3 cm of potting soil (1:4 vermiculite:peat) in greenhouse trays. Plant crowns were removed by hand at this stage to eliminate seedling enumeration errors due to regrowth from dormant plant crowns. The 192 trays were maintained under greenhouse conditions from May 15 to July 30, where ambient temperature varied from 15 to 30 °C and the daily light:dark cycle averaged 16:8 hours. Trays were watered every other day and flowering plant seedlings were identified and enumerated at 3 week intervals. Identified seedlings were removed to avoid competition with subsequent seedlings and recounting errors. Seedlings that could not be identified to species by July 30 were transplanted into pots and grown for an additional two months until identification could be confirmed.

Final sampling was spread over a 12 month period from August 2003 to July 2004. Seed production was sampled for each plot in August 2003. Within eight square quadrats (0.25 m^2), the number and length of all *A. cristatum* seedheads were counted. From each quadrat, a subsample of five seedheads, representative of average length, was removed to count the number of spikelets on each. Seedbank sampling was conducted in May 2004 using the same method for initial sampling. At this time, root biomass was also sampled from eight randomly distributed points in each plot. At each point three cylindrical soil cores excluding the overlying litter (7.8 cm diameter x 7.5 cm deep) were extracted and composited for each point. Root biomass soil cores were air-dried (~25 °C lab temperature) for one week, then crumbled by hand to pass a 2 mm sieve, and stones

>2 mm were discarded. Roots and below ground litter >2.0 mm were retained. The soil that passed through the 2 mm sieve, was again sieved to pass 0.5 mm, and additional roots 0.5 to 2.0 mm were removed by hand and composited with those >2.0 mm. Roots were then oven dried at 70 °C for 48 hours and weighed. Vegetation cover and composition were sampled in early July 2004 using the same method for initial sampling. A random subset of 10 vegetation quadrats was selected to hand rake all standing and surface litter, and clip all live vascular plant biomass. Biomass samples were then oven dried at 70 °C for 48 hours and weighed.

Additional soil cores (2 cm diameter x 10 cm deep) were extracted in April, May and June 2004 to measure soil moisture and available nitrogen. These two parameters are the main limiting resources for plant growth in semiarid grasslands (Krueger-Mangold et al. 2004), and may help explain population and community differences among treatments. From 10 randomly selected points in each plot, two soil cores were removed (one for moisture and one nitrogen), and the 10 cores for each parameter were composited for each plot. Composite samples were kept in coolers (~5 °C) up to 5 days between collection and transport to the lab. Gravimetric moisture was reported as a percentage, determined by subtracting the oven dried weight (110 °C for 48 hours) from the field wet weight (Topp 1993), and these samples were also used to estimate soil bulk density (Culley 1993). Available nitrogen (NH_4^+ and NO_3^{-2}) was determined by KCl extraction and spectrophotometry (Maynard & Kalra 1993).

Data Analyses

Multivariate compositional data were summarized in several ways prior to analysis. Shannon-Weiner diversity and evenness indices (Kent & Coker 1992) were calculated at the plot level for vegetation cover and richness, or seedbank density and richness. Detrended correspondence analysis (DCA) was used to represent trajectories for each treatment relative to initial and reference conditions. To avoid outliers and reduce species variation among blocks relative to that among treatments, 14 aggregate functional groups were created (Appendix E) and scales were further constrained by calculating proportional abundances among functional groups within vegetation and seedbanks. To most effectively separate "plots" the number of "species" should be maximized relative to "plots" (Hill & Gauch 1980; McCune et al. 2002), so functional group abundances were averaged among blocks for each treatment at initial and final intervals. A reference community cluster was created using functional group abundances for eight native grassland sites. This data was gathered at scales (quadrat size, number and dispersion) similar to that in experimental plots (see Chapter 3).

Univariate treatment differences were tested in several ways. To determine if significant ($\alpha = 0.05$) changes from initial to final conditions occurred in a single treatment, a paired t-test ($n = 4$) was performed. The paired analysis removes variation due to blocking, controls for initial conditions and is robust for small samples exhibiting non-normality or heteroscedasticity (Zar 1999). To determine the direction of, and if, significant changes occurred among treatments, the magnitude and sign (- or +) of differences were determined for each plot by subtracting the initial value from the final value. An analysis of variance (ANOVA) was performed on these derived variables using the MIXED procedure and Tukey's multiple comparisons on LSMEANS. For variables where only final samples were collected, an ANOVA was performed using the same procedure. The MIXED procedure is robust for small samples and, when used with the Tukey-Kramer adjustment on least squared means, it accounts for heteroscedasticity resulting from block variation (SAS Institute Inc. 1999).

RESULTS

Survival and reproduction of *A. cristatum* were affected differently by each treatment. Cover decreased significantly where glyphosate was applied alone or in combination with fire (Figure 5.1). Although grazing and haying visibly reduced *A. cristatum* canopy cover, basal cover was not significantly altered by these treatments. Seedbank density increased significantly where disturbance was excluded in control and burn treatments, and this change in density appeared to correlate with that of seedheads (Figure 5.2). However, surviving *A. cristatum* plants in glyphosate treated plots tended to be taller and more robust, in particular the number of spikelets per spike was significantly greater relative to all other treatments.

Vegetation richness and total seedbank density both increased significantly ($p < 0.05$) in all treatments from May 2001 to July 2004. Because this response may reflect phenological differences due to season of sampling or climatic differences across years, tests for community-scale treatment differences were restricted to 2004 data. Community composition was affected differently by each disturbance (Figure 5.3a), and DCA separated treatment and reference sites by perennial to annual life histories along Axis 1 ($r^2 = 0.39$) and alien vs. native origin along Axis 2 ($r^2 = 0.50$). Richness, evenness and diversity of the seedbank were not different, although total density was different among treatments (Table 5.2). One to three species of annual and perennial forbs dominated the larger seedbanks in glyphosate alone and glyphosate plus fire treatments. Ubiquitous and abundant species included *Amaranthus retroflexus*, *Androsace septentrionalis*, *Artemisia frigida* and *Thlaspi arvense*. These species also dominated the significantly smaller seedbanks in grazed and hayed treatments, but intermediate sized seedbanks were dominated by *A. cristatum* in control and burn treatments.

Richness, evenness and diversity of vegetation were significantly greater where glyphosate was applied alone or in combination with fire (Table 5.2). Reduction in the single dominant, *A. cristatum*, allowed three mechanisms of community change to follow. First, many annual forbs emerged from the seedbank and increased over time, in particular: *Chenopodium leptophyllum*, *Descurainia sophia*, *Kochia scoparia* and *Thlaspi arvense*. Second, native perennial forbs grew larger and produced more seedlings or ramets, in particular: *Artemisia frigida*. Third, several native perennial grasses not originally recorded in the vegetation or seedbank had colonized the plots, in particular: *Hordeum jubatum*, *Agrostis scabra* and *Stipa viridula*. No treatment increased native perennial grass cover, and most successional trajectories veered laterally relative to the native reference (Figure 5.3a). Although the grazing trajectory was towards the native reference, the end point fell within the cluster of variation associated with *A. cristatum* pastures.

Ecosystem structure and function were also affected by repeated disturbance. Vegetation biomass was significantly greater where glyphosate and fire were applied in combination, relative to grazed and hayed treatments (Figure 5.4). Most biomass in glyphosate treatments was comprised of annual plant stems, while grazed and hayed treatments were largely *A. cristatum* leaves. The pattern of root biomass was the exact opposite, and was significantly greater under repeated grazed and hayed treatments, relative to where glyphosate and fire were applied in combination. Although burning visibly reduced litter biomass in 2002, after four years there were no significant differences among treatments. Soil bulk density was greatest in grazed treatments relative to burned, but did not differ among other treatments (Figure 5.5). Soil moisture averaged over a growing season, was significantly less after repeated grazing relative to glyphosate alone, but differences among sampling intervals reflected regional patterns of precipitation more than any treatment effect. Available soil nitrogen was also greater where glyphosate was applied alone or combined with fire, but the magnitude of this difference greatly exceeded that for soil moisture.

DISCUSSION

Reduced Invader Abundance

For long-term prevention of invasion and no additional losses of biological diversity, SD-HI spring grazing appears ideal. Grazing and haying successfully reduced or maintained low densities of *A. cristatum* seedbanks, with little change in adult plant cover. Complete elimination of seed production was not possible, because grazing animals avoided small patches of grass covered by urine or feces, and both livestock and haying equipment sometimes trample culms without destroying them (Balph & Malachek 1985). For large-scale prevention on rough ground, SD-HI grazing can be effective and provide economic returns despite added fencing and labor costs. For small-scale prevention, particularly urban and suburban conservation areas, haying or mowing may be most efficient. Regardless of the scale or technique, timing is crucial to ensure disturbance coincides with important phenological stages. Disturbing too early before reproductive culm initiation will merely delay seedhead emergence for the year (Romo & Harrison 1999), and retreatment will be necessary. If left until after flowering has occurred, there is a risk viable seed will be dispersed in baled hay or livestock dung. Further, *A. cristatum* begins to senesce soon after flowering and simultaneously declines in nutritive quality and palatability (Ganskopp et al. 1992); thus, late-season grazing may be ineffective to prevent seed dispersal.

Spring glyphosate wicking nearly eradicated the adult population of *A. cristatum* in a single year, but only where seedbank densities were low to begin with (Hanna and Onefour blocks). Where substantial seedbank densities were present at the onset of the experiment (Brooks and Eastend blocks), large numbers of *A. cristatum* seedlings emerged in the second year. Romo et al. (1994) and Bakker et al. (1997) were able to reduce *A. cristatum* cover by 10 to 80% after a single year of glyphosate application on ungrazed sites, where seedling emergence partly compensated for adult plant mortality. Burning after glyphosate application removed litter and increased bare soil, which seemed to enhance *A. cristatum* seedling establishment. After two years of wicking, *A. cristatum* was reduced below 5% cover and spot application from that point forward helped avoid non-target species losses, but this method required approximately 30 person hrs ha^{-1} yr^{-1}. Wilson and Partel (2003) found seven years of repeated spraying and wicking did not reduce *A. cristatum* foliar cover below an average of 7%. Interestingly, in this same experiment seedbank densities were up to six times higher in herbicide treated plots (1500 m^{-2}) than untreated plots (250 m^{-2}) (Ambrose 1999). This was interpreted as evidence of either seedbank persistence or invigorated seed production on surviving plants within plots (Bakker et al. 2003), or possibly on unmowed plot buffers.

From work completed in Chapter 4 and this Chapter, it appears *A. cristatum* soil seedbanks are not persistent (sensu Thompson & Grime 1979) and can be reduced by repeated glyphosate and other treatments. Seed production on surviving plants in glyphosate plots was enhanced, as expected from reduced intraspecific competition (Jefferson & Kielly 1993). Dispersal from surviving tussocks formed clusters of seedlings that were easily located and treated, but some long-distance dispersal, late germination following summer rains, and restriction of control efforts to early spring resulted in a persistent though small cover (<1%) of *A. cristatum* after four years. Eradication of this perennial bunchgrass requires equal attention to established plants and viable seedbanks, and the ideal balance is to reduce seedbank density before and during treatments designed to increase plant mortality; otherwise, glyphosate alone leads to perpetual and labour-intensive control.

Disturbance and Community Invasibility

Fields dominated by *A. cristatum* were resistant to compositional change, and repeated disturbance did not increase diversity or similarity towards the native reference community. These patterns are contrary to expectations from the intermediate disturbance hypothesis, where repeated grazing or fire can increase diversity (Collins & Barber

1985). Although many native perennial and annual forb species were present, most native perennial grasses were absent or rare in association with *A. cristatum*. Looman & Heinrichs (1973) surveyed *A. cristatum* pastures varying in soil, management history and age, and found essentially the same pattern. The impacts of protection and burning treatments were similar, because *A. cristatum* seedbank density increased and perennial and annual forb cover decreased slightly. Perennial grass seedbank density is expected to increase with protection from grazing (Romo & Bai 2004), and where *A. cristatum* invades, forb richness and cover decline most substantially (Chapter 3).

Grazing and haying were similar in that *A. cristatum* seedbank density remained low and cover did not change. Defoliation removes biomass and is generally associated with proliferation of tillers above ground and shallow roots below ground (Busso & Richards 1995; Arredondo & Johnson 1998), and this was consistent with our results. Where the two treatments diverged resulted from the scale at which each operates. Haying was homogenous, because all vegetation and seedheads 10 cm aboveground were removed in a single event. In contrast, grazing added heterogeneity by trampling, defecating, urinating and selectively defoliating. The apparent trend of increased similarity to the native reference community may have resulted from the combination of these ungulate impacts and careful timing to reduce *A. cristatum* seed production. Still, there was no substantial overall change after four years of repeated treatment, and the dominant species appears well adapted to SD-HI grazing (McCartney & Bittman 1994).

Glyphosate was successful in removing *A. cristatum*, and this increased bare ground and soil resource availability, which stimulated germination of dormant annuals and biennials in the seedbank. In these respects, glyphosate resulted in patterns consistent with early successional stages during abandoned farmland recovery in the northern Great Plains (Judd 1940; Tolstead 1941; Samuel & Hart 1994). This compositional shift also increased vegetation richness and evenness, but the lack of deep, fibrous rooted perennials made available significantly more soil moisture and nitrogen. This suggests a portion of *A. cristatum* dominance was due to successful competition for nitrogen, although in experiments elsewhere it successfully competes for both nitrogen and water (Eissenstat & Caldwell 1988; Bilborough & Caldwell 1997). The remaining problem is that high resource availability leaves a site vulnerable to reinvasion (Davis et al. 2000), not only by desired native species but also *A. cristatum* and other potentially noxious species. This instability could be reduced once the roots of perennial grasses occupy the soil volume (Burke et al. 1998).

Restoration Trajectories

Compositional changes following four years of repeated disturbance only tell part of the story, and the question for restoration is how communities will continue to change. Forcing a transition to native perennial grass dominance requires inputs to overcome the abiotic threshold of nitrogen availability and the biotic threshold of *A. cristatum* competition (Figure 5.3b). Glyphosate was the only treatment to cause a significant compositional shift away from *A. cristatum* dominance, but towards annual forb dominance, and in similar experiments glyphosate was always necessary for this transition (Romo et al. 1994; Wilson & Gerry 1995). In the short-term, discontinued annual glyphosate applications may return sites to *A. cristatum* dominance within a few years given the high rates of seed production that results from incomplete control (Bakker et al. 2003) and soil nitrogen availability. As such, continued prevention measures are necessary if restoration is to be successful. This illustrates how the restoration process may have a clear beginning, but to achieve long-term goals must become a component of ecosystem management.

Pretreatment with 2 to 3 years of grazing could reduce *A. cristatum* seedbank additions prior to glyphosate treatment and perhaps speed the initial restoration process 2 to 3 years by reducing the probability of *A. cristatum* seedling emergence following glyphosate. This will still result in an initial community dominated by annual forbs, although in the long-term selective grazing could simultaneously favour some native forbs to a greater extent than glyphosate alone (Figure 5.3b). Wilson & Partel (2003) found native plant cover was greatest where glyphosate and hand clipping *A. cristatum* was combined. Continued grazing could also allow increases in rhizomatous grasses and unpalatable native forbs, which could out-compete annuals. The rhizomatous *Pascopyrum smithii* is well known to rapidly recolonize and dominate bare soil (Reichhardt 1982; Samuel & Hart 1994). Unfortunately, grazing is likely to retard recovery of seed-limited caespitose grasses by directly reducing seed production and dispersal, although which species will depend on the season of grazing disturbance. High variability and low similarity in native grass composition on 50 to 70 year old abandoned fields relative to adjacent native grasslands has been attributed to the species-specific interactions between grazing response and dispersal ability (Dormaar & Smoliak 1985; Dormaar et al. 1994; Coffin et al. 1996).

Seed availability of native grasses appears to be a major limitation in long-term grassland restoration. Rapid increases in cover of dominant native grasses on disturbed soil tends to be greater where disturbances are small (Umbanhowar 1992) or adjacent to an undisturbed native grassland (Coffin et al. 1996). Pastures of *A. cristatum* tend to be 400 to 1600 m across in the northern Great Plains, and native grass seed limitations for restoration are likely. In the pastures I studied, the vegetative abundance of native grasses was relatively low and seedbank densities were lower still. Conversely, *A. cristatum* plantings along road and utility rights-of-way are rarely more than 10 m across, and may be more conducive to natural recovery following control. Additions of native grass seed could speed the restoration process, but by how much is not known. Relative to the initial floristics following glyphosate application, Bakker et al. (2003) and Wilson et al. (2004) found *B. gracilis* cover increased significantly after seeding, but few C_3 species emerged or were initially present. Seed establishment limitations are often greater for *B. gracilis* than most other native grasses (Lauenroth et al. 1994; Ambrose & Wilson 2003), but *S. comata* and *Elymus lanceolatus* are generally considered good colonizers and dominants of ungrazed native grasslands. The near complete absence of these C_3 mid-height grasses from *A. cristatum* pastures is possibly due to competitive exclusion (see Chapter 3).

CONCLUSION

No single treatment and no single attempt effectively suppressed *A. cristatum* and lead to native grassland restoration in the northern Great Plains. SD-HI spring grazing appears to be a suitable long-term technique for preventing invasion and short-term technique to reduce seedbank densities without disrupting land use. For native grassland restoration, at least two years of spring-timed wick application of glyphosate was necessary to eradicate most *A. cristatum* plants. In subsequent years, spot applications of glyphosate to eradicate individual plants required the greatest labour expenditure, and continued SD-HI grazing could provide a no-cost alternative that simply prevents *A.*

cristatum seed dispersal. Initial floristics will provide propagules for some mixed-grass prairie species in the short-term, and could succeed in establishing native perennial dominance in the long-term. However, reliance on initial floristics could result in low similarity to a reference community because many native species are dispersal limited. In the case of large isolated patches, *S. comata* and *E. lanceolatus* may need to be seeded, because these naturally dominant species are most frequently absent from *A. cristatum* pastures.

LITERATURE CITED

Abrams, M.D. (1988) Effects of burning regime on buried seed banks and canopy coverage in a Kansas tallgrass prairie. *The Southwestern Naturalist*, **33**, 65-70.

Ambrose, L.G. (1999) *Seed persistence of an introduced and a native grass species in a prairie old field.* MSc Thesis, University of Regina. Regina, SK.

Ambrose, L.G. & Wilson, S.D. (2003) Emergence of the introduced grass *Agropyron cristatum* and the native grass *Bouteloua gracilis* in a mixed-grass prairie restoration. *Restoration Ecology*, **11**, 110-115.

Arredondo, J.T. & Johnson, D.A. (1998) Clipping effects on root architecture and morphology of 3 range grasses. *Journal of Range Management*, **51**, 207-214.

Bakker, J.D., Wilson, S.D., Christian, J.M., Li, X., Ambrose, L.G. & Waddington, J. (2003) Contingency of grassland restoration on year, site, and competition from introduced grasses. *Ecological Applications*, **13**, 137-153.

Bakker, J.D., Christian, J., Wilson, S.D. & Waddington, J. (1997) Seeding blue grama in old crested wheatgrass fields in southwestern Saskatchewan. *Journal of Range Management*, **50**, 156-159.

Balph, D.F. & Malecheck, J.C. (1985) Cattle trampling of crested wheatgrass under short-duration grazing. *Journal of Range Management*, **38**, 226-227.

Bilbrough, C.J. & Caldwell, M.M. (1997) Expoitation of springtime ephemeral N pulses by six Great Basin plant species. *Ecology*, **78**, 231-243.

Burke, I.C., Lauenroth, W.K., Vinton, M.A., Hook, P.B., Kelly, R.H., Epstein, H.E., Aguiar, M.R., Robles, M.D., Aguillera, M.O., Murphy, K.L. & Gill, R.A. (1998) Plant-soil interactions in temperate grasslands. *Biogeochemistry*, **42**, 121-143.

Busso, C.A. & Richards, J.H. (1995) Drought and clipping effects on tiller demography and growth of two tussock grasses in Utah. *Journal of Arid Environments*, **29**, 239-251.

Christian, J. M., and S. D. Wilson. 1999. Long-term ecosystem impacts of an introduced grass in the northern Great Plains. Ecology **80**:2397-2407.

Coffin, D.P., Lauenroth, W.K. & Burke, I.C. (1996) Recovery of vegetation in a semiarid grassland 53 years after disturbance. *Ecological Applications*, **6**, 538-555.

Collins, S.L. & Barber, S.C. (1985) Effects of disturbance on diversity of mixed grass prairie. *Vegetatio*, **64**, 87-94.

Coupland, R.T. (1950) Ecology of mixed prairie in Canada. *Ecological Monographs*, **20**, 271-315

Culley, J.L.B. (1993) Density and compressibility. In: Carter, M.R. (ed) Soil sampling and methods of analysis. Lewis Publishers, Boca Raton FL. Pp. 529-540.

Davis, M.A., Grime, J.P. & Thompson, K. (2000) Fluctuating resources in plant communities: A general theory of invasibility. *Journal of Ecology*, **88**, 528-534.

Dormaar, J.F. & Smoliak, S. (1985) Recovery of vegetative cover and soil organic matter during revegetation of abandoned farmland in a semiarid climate. *Journal of Range Management*, **38**, 487-491.

Dormaar, J.F., Adams, B.W. & Willms, W.D. (1994) Effect of grazing and abandoned cultivation on a *Stipa-Bouteloua* community. *Journal of Range Management*, **47**, 28-32.

Eissenstat, D.M. & Caldwell, M.M. (1988) Competitive ability is linked to rates of water extraction: a field study of two aridland tussock grasses. *Oecologia*, **75**, 1-7.

Environment Canada (2000) *Canadian Climate Normals 1971-2000.* Environment Canada, Ottawa ON.

Ganskopp, D., Angell, R. & Rose, J. (1992) Response of cattle to cured reproductive stems in a caespitose grass. *Journal of Range Management*, **45**, 401-404.

Hill, M.O. & Gauch H.G. (1980) Detrended correspondence analysis: an improved ordination technique. *Vegetatio,* **42**, 47-58.

Huston, M.A. (2004) Management strategies for plant invasions: manipulating reproductivity, disturbance, and competition. *Diversity & Distributions*, **10**, 167-178.

Jefferson, P.G. & Kielly, G.A. (1993) Reevaluation of row spacing/plant density of seeded pasture grasses for the semiarid prairie. *Canadian Journal of Plant Science*, **78**, 257-264.

Judd, B.I. (1940) Natural succession of vegetation on abandoned farm lands in Teton County, Montana. *Journal of the American Society of Agronomy*, **32**, 330-336.

Kent, M. & Coker, P. (1992) *Vegetation description and analysis: a practical approach.* John Wiley and Sons, Toronto ON.

Krueger-Mangold, J., Sheley, R., Engel, R., Jacobsen, J., Svejcar, T. & Zabinski, C. (2004) Identification of the limiting resource within a semi-arid plant association. *Journal of Arid Environments*, **58**, 309-320.

Lauenroth, W.K., Sala, O.E., Coffin, D.P. & Kirchner, T.B. (1994) The importance of soil water in the recruitment of *Bouteloua gracilis* in the shortgrass steppe. *Ecological Applications*, **4**, 741-749.

Lodge, R.W. (1960) Effects of burning, cultivating and mowing on the yield and consumption of crested wheatgrass. *Journal of Range Management*, **13**, 318-321.

Looman, J. & Heinrichs, D.H. (1973) Stability of crested wheatgrass pastures under long-term pasture use. *Canadian Journal of Plant Science*, **53**, 501-506.

Lorenz, R.J. & Rogler, G.A. (1962) A comparison of methods of renovating old stands of crested wheatgrass. *Journal of Range Management*, **15**, 215-219.

Maynard, D.G. & Kalra, Y.P. (1993) Nitrate and exchangeable ammonium nitrogen. In: Carter, M.R. (ed) *Soil sampling and methods of analysis.* Lewis Publishers, Boca Raton FL. Pp. 25-38.

McCartney, D.H. & Bittman, S. (1994) Persistence of cool season grasses under grazing using the mob grazing technique. *Canadian Journal of Plant Science*, **74**, 723-728.

McCune, B., Grace, J.B. & Urban, D.L. (2002) *Analysis of ecological communities.* MjM Software Design.

Oksanen, L. (2001) Logic of experiments in ecology: Is pseudoreplication a pseudoissue? *Oikos*, **94**, 27-38.

Olson, B.E. & Richards, J.H. (1988) Tussock regrowth after grazing: intercalary meristem and bud activity of tillers of *Agropyron desertorum. Oikos*, **51**, 374-382.

Olson, B.E. & Richards, J.H. (1989) Crested wheatgrass growth and replacement following fertilization, thinning, and neighbor plant removal. *Journal of Range Management*, **42**, 93-97.

PFRA (2004) *Drought watch web* site (http://www.agr.gc.ca/pfra/drought/index_e.htm). Prairie Farm Rehabilitation Administration, Agriculture & Agri-Food Canada. Regina SK.

Pimentel, D., McNair, S., Janecka, J., Wightman, J., Simmonds, C., O'Connel, C., Wong, E., Russel, L., Zern, J., Aquino, T. & Tsomondo, T. (2001) Economic and environmental threats of alien plant, animal, and microbe invasions. *Agriculture, Ecosystems and Environments,* **84**, 1-20.

Pyke, D.A. (1990) Comparative demography of co-occurring introduced and native tussock grasses: persistence and potential expansion. *Oecologia,* **82**, 537-543.

Reichhardt, K.L. (1982) Succession of abandoned fields on the shortgrass prairie, northeastern Colorado. *The Southwestern Naturalist*, **27**, 299-304.

Richards, R.T., Chambers, J.C., & Ross C. (1998) Use of native plants on federal lands: policy and practice. *Journal of Range Management,* **51**, 625-632.

Romo, J.T. & Bai, Y. (2004) Composition of seed banks and plant communities in the mixed prairie of Saskatchewan. *Journal of Range Management*, **57**, 300-304.

Romo, J.T. & Harrison, T. (1999) Regrowth of crested wheatgrass following defoliation. *Canadian Journal of Plant Science*, **79**, 557-563.

Romo, J.T., Grilz, P.L. & Delanoy, L. (1994) Selective control of crested wheatgrass (*Agropyron cristatum* [L.] Gaertn. and *A. desertorum* Fisch.) in the northern Great Plains. *Natural Areas Journal*, **14**, 308-309.

Samuel, M.J. & Hart, R.H. (1994) Sixty-one years of secondary succession on rangelands of the Wyoming high plains. *Journal of Range Management*, **47**, 184-191.

SAS Institute Inc. (1999) *Statistical Analysis Software Version 8.0.* SAS Institute Inc., Cary NC.

Shay, J., Kunec, D. & Dyck, B. (2001) Short-term effects of fire frequency on vegetation composition and biomass in mixed prairie in south-western Mantioba. *Plant Ecology*, **155**, 157-167.

Sheley, R.L. & Krueger-Mangold, J. (2003) Principles for restoring invasive plant-infested rangeland. *Weed Science*, **51**, 260-265.

Smoliak, S. (1968) Grazing studies on native range, crested wheatgrass, and Russian wildrye pastures. *Journal of Range Management*, **21**, 47-50.

Smoliak, S., Johnston, A. & McLean, A. (1980) *Management of crested wheatgrass pastures.* Publication 1473, Agriculture Canada, Research Branch, Ottawa.

Soil Classification Working Group (1998) *The Canadian System of Soil Classification*, 3rd edn. Agriculture and Agri-Food Canada Publication 1646, Ottawa ON.

Sullivan, T.P. & Sullivan, D.S. (2003) Vegetation management and ecosystem disturbance: impact of glyphosate herbicide on plant and animal diversity in terrestrial systems. *Environmental Reviews*, **11**, 37-59.

Thompson, K. & Grime, J.P. (1979) Seasonal variation in the seed banks of herbaceous species in ten contrasting habitats. *Journal of Ecology*, **67**, 893-921.

Tolstead, W.L. (1941) Plant communities and secondary succession in south-central south Dakota. *Ecology*, **22**, 322-328.

Topp, G.C. (1993) Soil water content. In: Carter, M.R. (ed) *Soil sampling and methods of analysis*. Lewis Publishers, Boca Raton FL. Pp. 541-558.

Umbanhowar, C.E. (1992) Early patterns of revegetation of artificial earthen mounds in a northern mixed prairie. *Canadian Journal of Botany*, **70**, 145-150.

Westoby, M., Walker, B., Noy-Meir, I. (1989) Opportunistic management of rangelands not at equilibrium. *Journal of Range Management*, **42**, 266-274.

Wilson, S.D., Bakker, J.D., Christian, J.M., Li, X., Ambrose, L.G. & Waddington, J. (2004) Semiarid old-field restoration: is neighbor control needed? *Ecological Applications*, **14**, 476-484.

Wilson, S.D. & Gerry, A.K. (1995) Strategies for mixed-grass prairie restoration: Herbicide, tilling, and nitrogen manipulation. *Restoration Ecology*, **3**, 290-298.

Wilson, S.D. & Partel, M. (2003) Extirpation or coexistence? Management of a persistent introduced grass in a prairie restoration. *Restoration Ecology*, **11**, 410-416.

Wroe, R.A., Smoliak, S., Adams, B.W., Willms, W.D. & Anderson, M.L. (1988) *Guide to Range Conditions and Stocking Rates for Alberta Grasslands*. Alberta Forestry, Lands and Wildlife, Public Lands, Edmonton AB.

Zar, JH. 1999. *Biostatistical Analysis*, 4th edn. Prentice Hall, Upper Saddle River NJ.

Table 5.1 Initial characteristics of the four experimental blocks on *A. cristatum* fields in southern Alberta and Saskatchewan, Canada.

Characteristic	Block Name			
	Hanna	Brooks	Onefour	Eastend
Location (lat/lon)	51°40'/112°10'	50°35'/112°40'	49°07'/110°28'	49°10'/109°06'
A. cristatum seeding date & composition[a]	c. 1938 (2n)	c. 1976 (2n & 4n)	c. 1940 (2n) *M. sativa*	c. 1967 (4n) *E. junceus* *M. sativa*
Grazing history[b]	continuous, high intensity	continuous, mod. intensity	ungrazed since 1968	spring only, low intensity
Mean annual precipitation (mm)	375	325	350	350
Soil Great Group[c]	dark-brown solonetz	solonetzic brown chernozem	orthic brown chernozem	solonetzic brown chernozem
Soil textural class	loam	sandy-loam	clay-loam	loam
Soil organic carbon (%)	3.2	3.0	3.0	2.1
Soil conductivity (dS m^{-1})	7.0	4.0	4.7	4.1

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[a] Species names: *Agropyron cristatum* (2n) is the diploid Fairway variety, while (4n) refers to the *A. desertorum* tetraploid Standard variety. *Elymus junceus* (Russian wild rye) and *Medicago sativa* (alfalfa) were the other forages seeded simultaneously.

[b] Based on landowner interviews.

[c] Follows nomenclature in the Canadian System of Soil Classification (Soil Classification Working Group 1998).

Table 5.2 Comparison of community composition responses from 2004 among treatments (same small case letters within a row indicate $p > 0.05$).

Responses	Treatment					
	BURN	CTRL	GRAZE	HAY	HBRN	HERB
Vegetation						
Basal cover (%)	35 ab	32 ab	39 a	28 b	29 b	34 ab
Richness	13.5 b	12.5 b	14.3 b	11.5 b	27.3 a	27.5 a
Evenness (Shannon's E)	0.49 b	0.41 b	0.50 b	0.42 b	0.67 a	0.68 a
Diversity (Shannon's H')	1.26 b	1.00 b	1.30 b	1.05 b	2.21 a	2.23 a
Seedbank						
Seedling density (m^{-2})	2722 bc	3030 bc	2087 bc	1785 c	6316 a	4229 ab
Richness	19.8 a	16.8 a	18.3 a	19.0 a	19.8 a	18.5 a
Evenness (Shannon's E)	0.64 a	0.67 a	0.65 a	0.65 a	0.57 a	0.58 a
Diversity (Shannon's H')	1.89 a	1.90 a	1.87 a	1.90 a	1.71 a	1.68 a

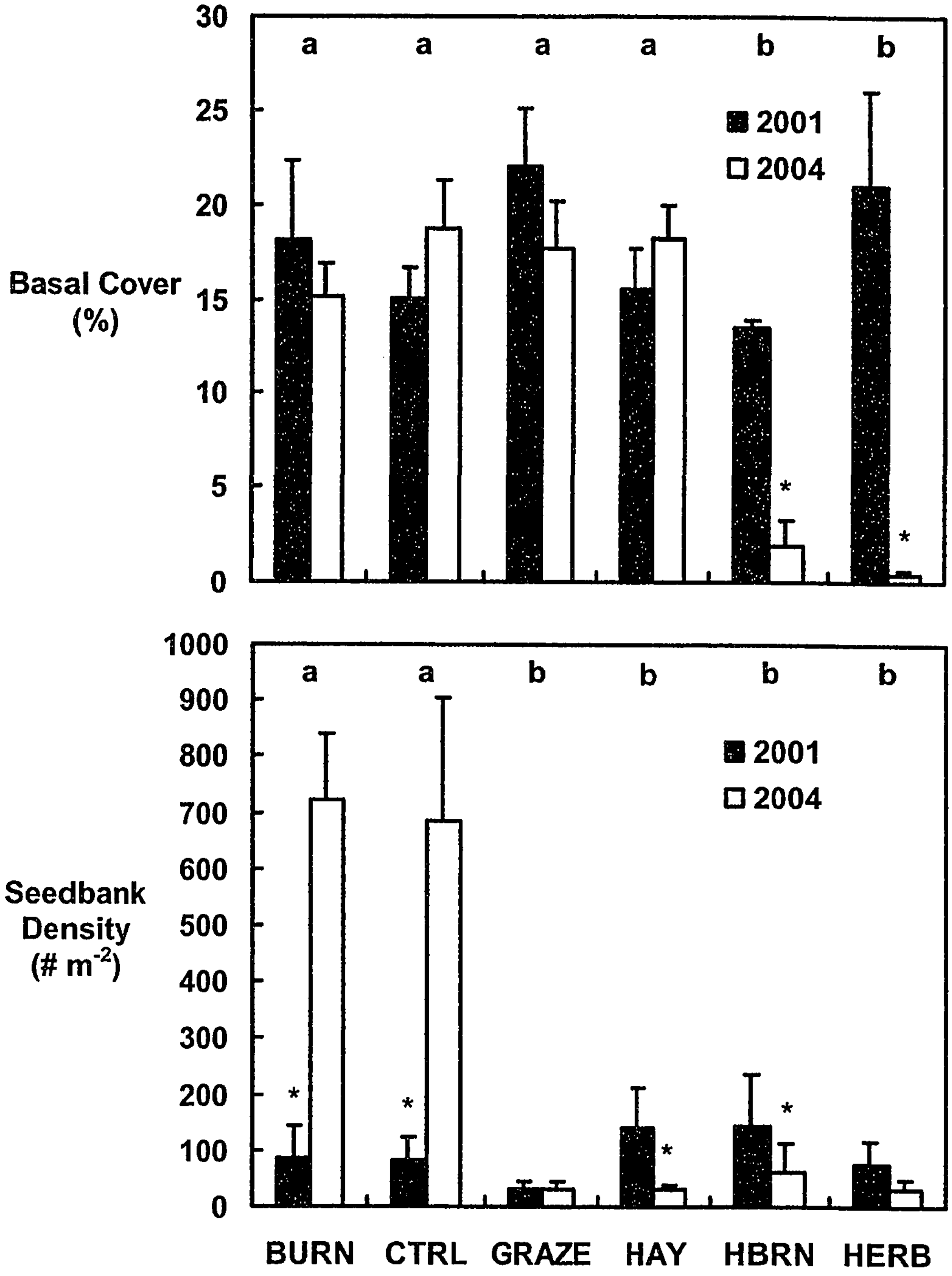

Figure 5.1 Comparison of *A. cristatum* basal cover and germinable seedbank density between initial and final conditions within a treatment (* indicates $p < 0.05$), and among treatments (same small case letters indicate $p > 0.05$).

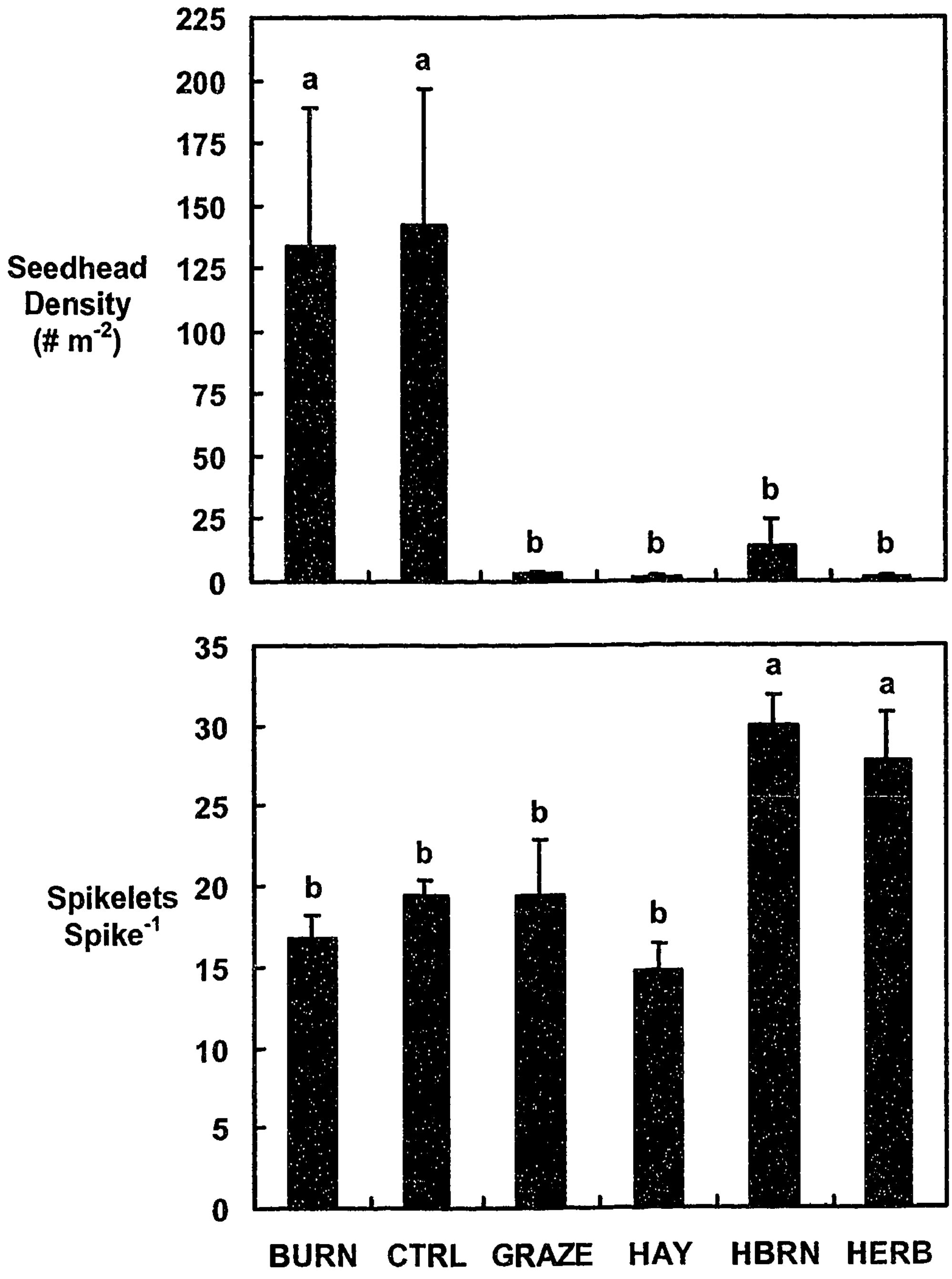

Figure 5.2 Comparison of *A. cristatum* seedhead density and spikelets per seedhead in 2004 among treatments (same small case letters indicate $p > 0.05$).

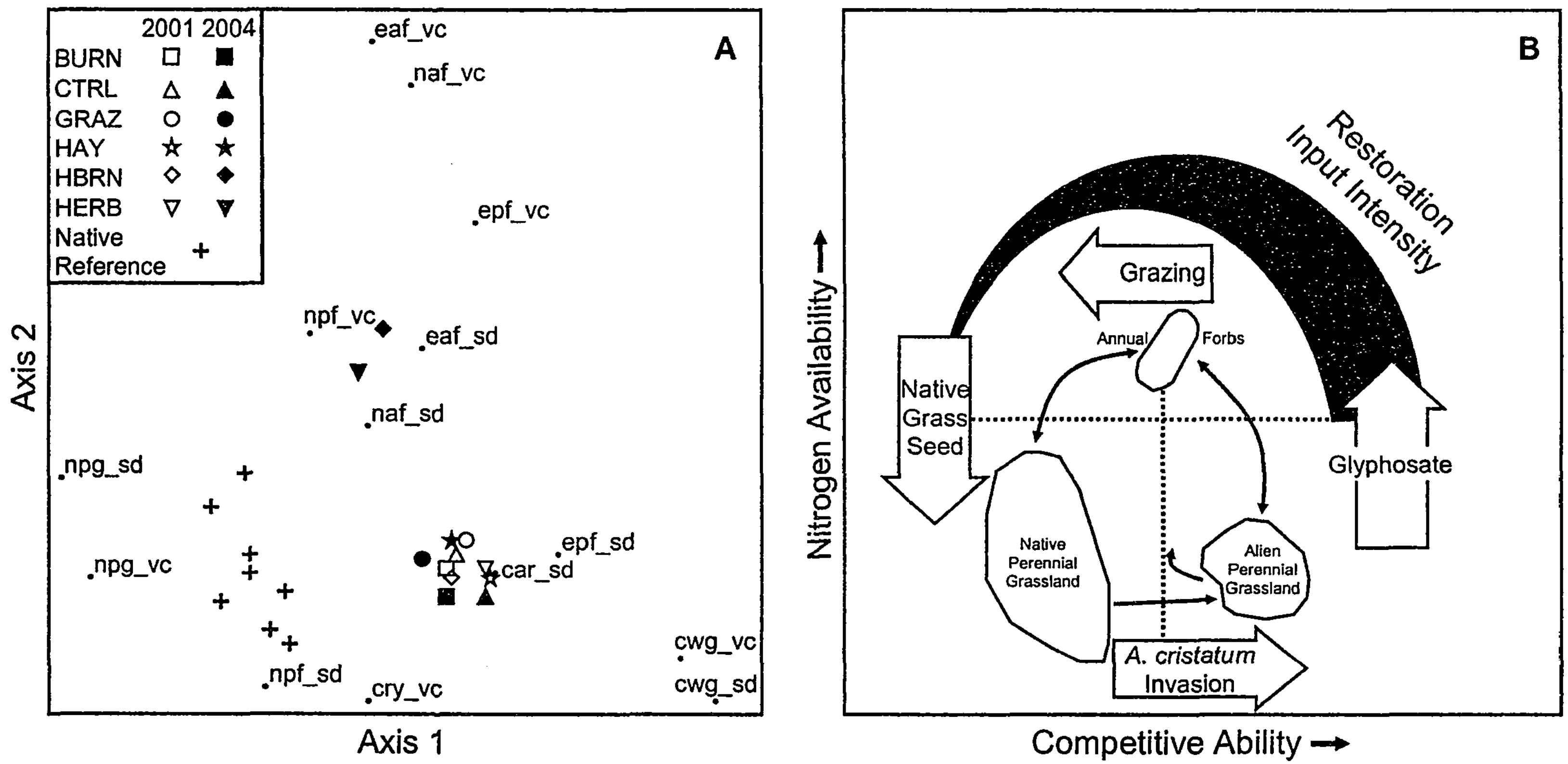

Figure 5.3a. Detrended correspondence analysis of crested wheatgrass communities before and after four years of treatment and relative to eight native grassland reference communities (inertia = 0.81). Functional group labels are defined in Appendix F. Suffixes to functional groups are seedbank density (sd) and vegetation cover (vc). 5.3b. Conceptual model of underlying abiotic and biotic gradients (axes) associated with community clusters in a, and how these are related to ecological processes and management inputs (block arrows) for conservation and restoration. Dotted lines indicate thresholds in nitrogen availability and competitive ability, and solid arrows indicate possible community transitions.

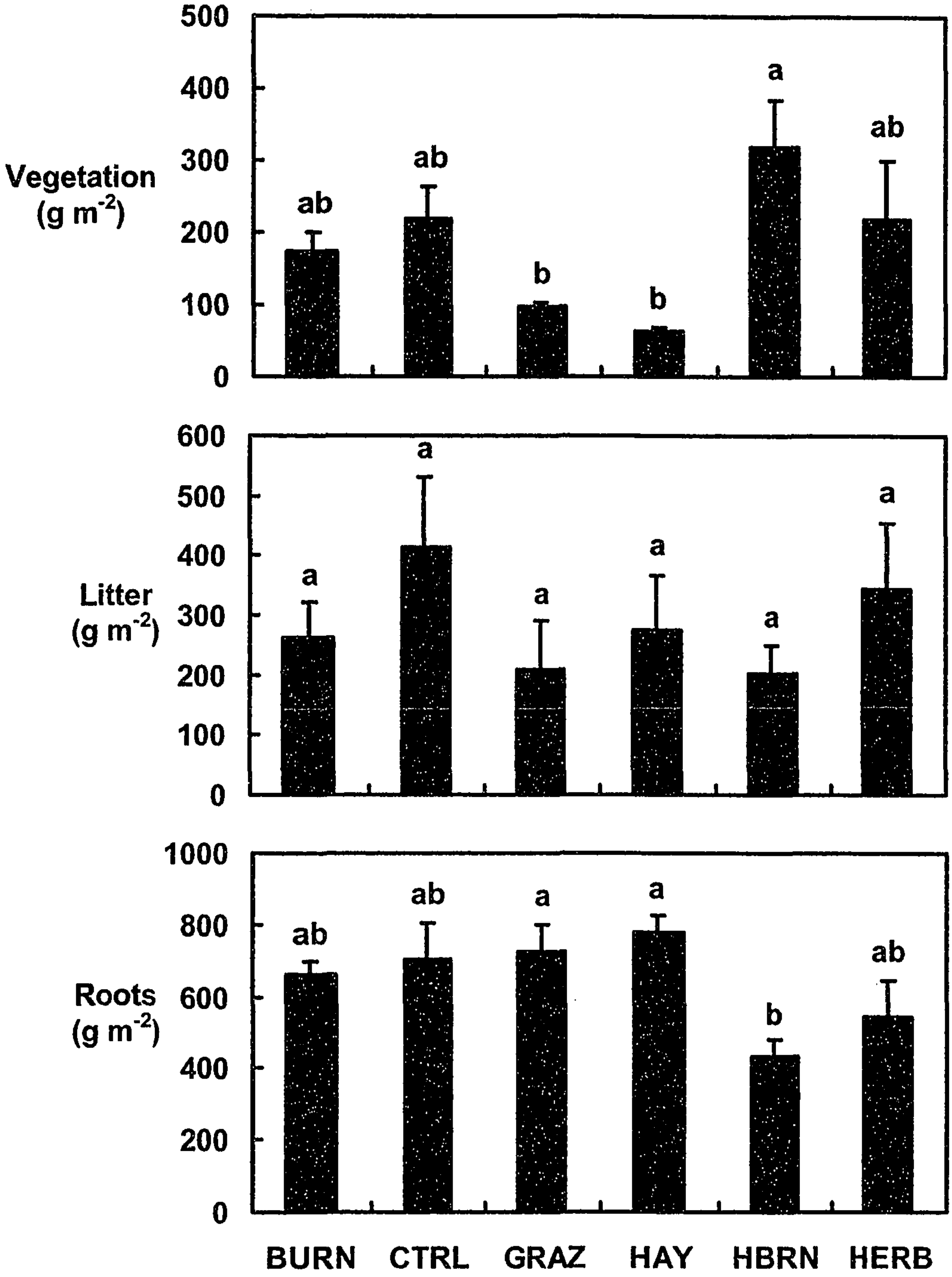

Figure 5.4 Comparison of vegetation, litter and root biomass in 2004 among treatments (same small case letters indicate $p > 0.05$).

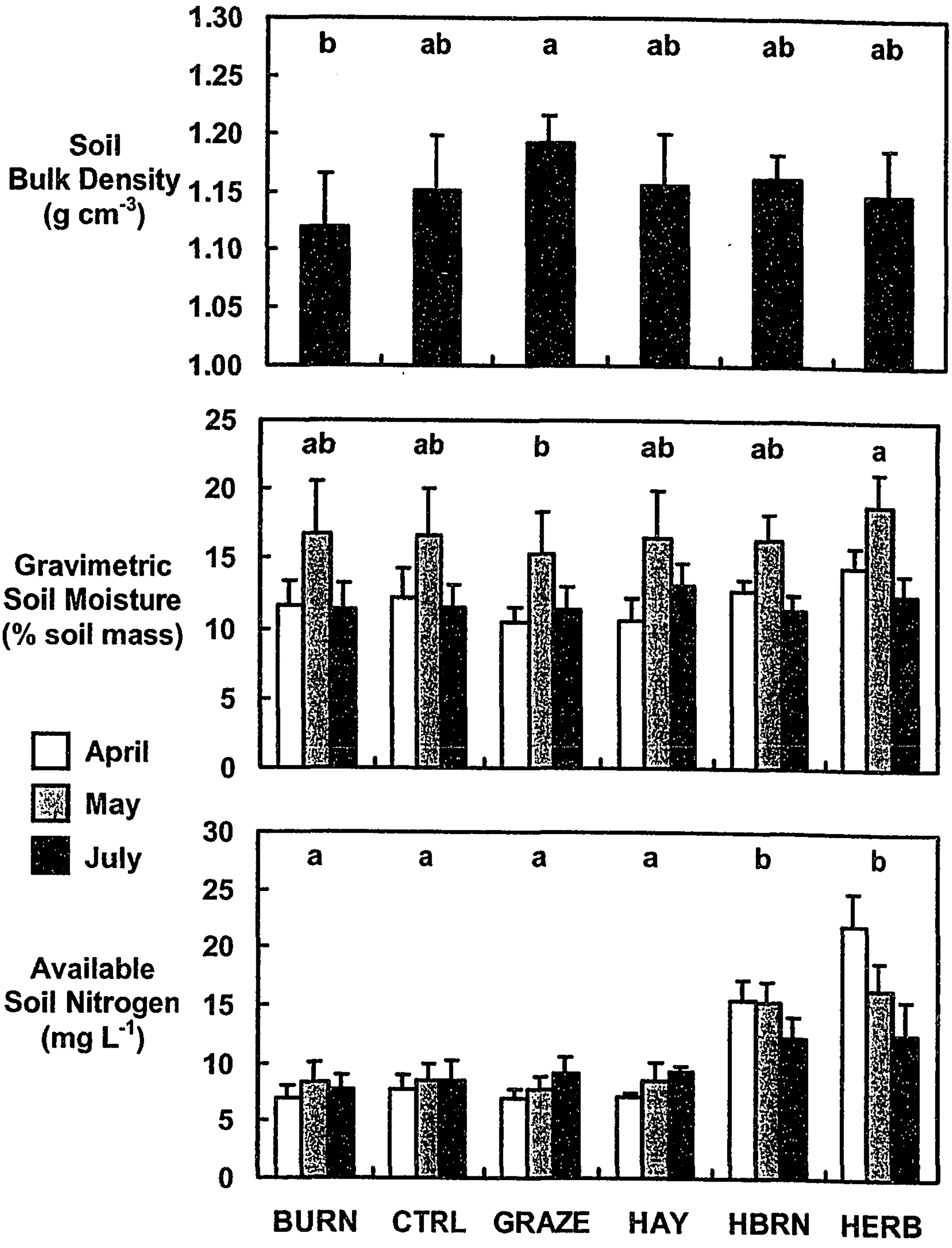

Figure 5.5 Comparison of soil bulk density, gravimetric moisture and available nitrogen (NH_4 & NO_3) in 2004 among treatments (same small case letters indicate $p > 0.05$).

CHAPTER 6. SYNTHESIS: DYNAMICS OF CRESTED WHEATGRASS INVASION

WHAT IS REALLY LIMITING OR PROMOTING INVASION TODAY?

The rate of *A. cristatum* invasion was much less than at first thought (Chapter 2), but widespread distribution in the form of linear corridors helps *A. cristatum* overcome dispersal barriers (Appendix A). A number of factors potentially limit invasion rates, and from those measured it was not entirely clear how grazing, plant communities and soil interacted to limit seed inputs and seedling establishment. The ideal experimental test of how and to what degree different factors contribute to crested wheatgrass invasion requires a complex factorial design. Gradients of moisture, propagule availability and bareground could be created in the field or greenhouse to determine multivariate thresholds for germination and establishment of *A. cristatum* seedlings. Additional factors could be added or separate experiments conducted to determine how soils varying in texture and salinity, and native grass competitors varying in size and phenology affect established or transplanted *A. cristatum* plant survival and reproductive output. Research elsewhere has investigated some factors, such as varying soil moisture effects on germination rates (Ambrose & Wilson 1999), varying moisture, bareground and propagule availability on establishment rates (Jim Romo, pers. comm..), and competition effects on transplant survival and biomass (Bakker & Wilson 2001).

The greatest median invasion rate (laterally to the prevailing wind) was only 0.21 m yr^{-1}, and this linear distance was true for only a few soil types with excellent condition range communities. What may be more important to consider at the regional scale, is how these rates interact with the juxtaposition of *A. cristatum* populations on the landscape as a result of deliberate human introductions. The cumulative effect of these landscape fragmentation patterns and grazing intensity gradients can lead to a number of invasion scenarios. Even with invasion rates as low as 0.21 m yr^{-1}, this scales up to a potentially invaded area equal to several thousand ha yr^{-1} within the 24 million ha ecoregion. High-intensity grazing appears to reduce *A. cristatum* seed rain from nearly 700 to nearly 30 seeds m^{-2}, a 23 fold decrease (Chapter 5), and could be used as both a modeling and management tool to simulate and test the interaction of grazing and fragmentation on *A. cristatum* invasion and the loss of native mixed-grass prairie.

WHAT ARE THE ULTIMATE CAUSES AND CONSEQUENCES OF INVASION?

Several characteristics of *A. cristatum* may help it gain dominance over most native herbaceous species in the northern mixed-grass prairie. These characteristics include greater size, seed and litter production, and physiological efficiency relative to all co-occurring native species; consistent with characteristics Grime (1973) predicted for highly competitive species. However, these mechanistic hypotheses do not explain how *A. cristatum* developed these advantages and why no native species occupies a similar niche (Elton 1958). The answer to this question requires understanding the different selection pressures in North America and Asia. Temperate semiarid grasslands on both continents share a number of dominant plant genera (i.e. *Stipa*, *Festuca*, *Koeleria*, *Poa*, *Elymus*, *Carex* and *Artemisia*), and have a long evolutionary history of grazing by ungulates, rodents and invertebrates. However, *A. cristatum* is rarely listed as a common species in semiarid steppes of Asia (Appendix B), and it is not generally recognized as an invasive species in North American semiarid sagebrush steppe or subhumid grasslands adjacent to the northern mixed-grass prairie. The environmental variable that differs most among these regions is the seasonal distribution of precipitation.

The steppes of Mongolia, Siberia and China experience greater seasonal amplitude in precipitation than either the northern Great Plains or Great Basin of North America, despite similar mean annual precipitation (Figure 6.1). In addition, seasonal water deficits for plant growth occur at different times in these three environments. In the Great Basin, there is little seasonal variation in precipitation, but hot summer weather results in mid-summer to fall water deficits. In the northern Great Plains, a combination of early spring snowmelt and late spring to early summer precipitation results in water deficits from late summer to fall. In central Asian steppes, there is little snow for soil moisture recharge in spring, and peak precipitation does not occur until late summer to early fall. The unique result is an early spring to early summer soil water deficit.

The period of maximum *A. cristatum* growth (Smoliak et al. 1980) is correlated with the period of extreme water deficit within its natural range (Figure 6.1). The combination of cool, dry weather, and continuous grazing by domestic and wild ungulates selected for a species that is both drought and grazing tolerant. Adaptations such as high water and nitrogen use efficiency, and rapid growth at low temperatures would be advantageous in such an environment. Similarly, mortality rates may be high under these conditions and a metabolic tradeoff for survival would be increased seed production for recruitment. The rainy season in Asia coincides with the period of maximum seed dispersal (Pyke 1990), and may be key for annual recruitment to maintain a population subject to high winter-spring mortality.

On the northern Great Plains of North America, there is relatively more water available during the period of maximum *A. cristatum* growth (Figure 6.1), and this increase in resource availability can contribute to greater size and seed production. Seed dispersed in fall may not germinate due to water deficits, but the pulse of spring moisture may be sufficient for germination and establishment. In the sagebrush steppe of the Great Basin, there is relatively more water available during the winter and spring; however, summer water deficits should reduce seed production and certainly preclude germination until after October. Seedlings that develop this late are susceptible to frost injury and mortality, which could explain why *A. cristatum* is not self-replacing in this region. Overall, a climatic threshold along the North American continental divide separates the potential range of this species in two. The sagebrush steppes in the Great Basin support marginal habitats within the fundamental niche of *A. cristatum*, but the northern mixed-grass prairie in the Great Plains provides an optimal realized niche where the species persists and readily invades new habitats.

Why no species native to North America evolved to similarly exploit an early spring pulse of soil resources has to do with these climatic differences and, in the case of the Great Basin, different grazing histories. Abundant spring moisture in the northern Great Plains likely selects for plants that compete more intensely when soil moisture resources become limiting in early summer (Tilman 1985), and for plants that survive regular grazing disturbance. Conversely, two species in the Great Basin did evolve to grow rapidly and develop during a short period of spring moisture, but the region has had no large herds of ungulates for at least 10,000 years. *Pseudoregneria spicata* and *Poa sandbergii* are the closest ecological equivalents to *A. cristatum*, with two important exceptions. Although *P. spicata* is similar in size and phenology to *A. cristatum*, it is not as tolerant to livestock grazing or as competitive for soil resources (Eissenstat & Caldwell 1988a, 1988b). Although *P. sandbergii* is similar in phenology to *A. cristatum*, it is much smaller (approximately <25% biomass) and avoids much grazing pressure as a result. Thus, *A. cristatum* has been introduced to regions with patterns of precipitation (northern Great Plains) or grazing (Great Basin) that favour its survival relative to most native grasses. The observed loss of native plant community diversity following invasion appears to be most severe for C_3 species that phenologically develop a few weeks to a month later than *A. cristatum*, but has virtually no effect on *P. sandbergii* or the C_4 *B. gracilis* (Chapter 3). These observed patterns provide corroborating evidence for this hypothesis, but confirmation requires manipulated experiments.

In the case of competitive release due to seasonal differences in soil resource availability, a combination of greenhouse and field experiments are needed. In the greenhouse, temperature, light and precipitation patterns characteristic of the native and introduced ranges of one or several genotypes of *A. cristatum* could be simulated, and the production of roots, phytomass and seed could be compared to determine how phenology and environment affect plant size and reproductive output. In the field, reciprocal transplant experiments of *A. cristatum* germplasm from Asia and North America could be conducted to evaluate not only how the physical environment and phenology affect plant size and reproductive output, but also to test whether North American plants have "evolved increased competitive ability" (Blossey & Notzold 1995). In the case of differential competitive effects on native grasses varying in size and phenology, transplants of *A. cristatum* could be introduced to natural or synthetic communities and monocultures of native grasses, and measurements of module survival, cover, biomass and reproductive output of all species could be monitored (Goldberg & Barton 1992). To date, only Bakker & Wilson (2001) have attempted reciprocal field transplants of *A. cristatum* and *B. gracilis*.

CAN WE AND SHOULD WE RESTORE INVADED AREAS IN THE FUTURE?

Conceptually, it seems possible to eradicate *A. cristatum* seedbanks and vegetation, and to replace this species with a diverse mixture of native species. A sequenced combination of grazing to first reduce the seedbank, then glyphosate to kill adult plants, and native grass seed additions to overcome dispersal barriers may be effective (Chapter 5), but this sequence has yet to be practically tested. Plot and block designs suitable for these tests have been created (Chapter 5; Bakker et al. 1997), and the addition of subsequent grazing, herbicide and seeding treatments could be implemented.

An idea that emerged from Chapter 5 was the concept of native grass dispersal limitations in grassland restoration. Were the sequenced combination of grazing and glyphosate effective for selectively eradicating *A. cristatum*, the next question is which areas would be most efficiently restored? The area occupied along linear corridors is small relative to rectangular pastures, hayfields and wellpads (Appendix A), yet these corridors expose more edge to adjacent native grasslands. Narrow corridors also pose fewer dispersal limitations for native species to colonize from the matrix of adjacent native grassland communities. Thus, not only should linear corridors be easier to restore, but corridor removal could also reverse the trend of landscape fragmentation and potential for *A. cristatum* invasion.

Ideal experimental tests of how dispersal distance limits assembly and restoration of mixed-grass prairie requires controlled disturbance size, shape, intensity and timing. Preliminary sampling of soil seedbanks within these patches, and both vegetation and seedbanks adjacent to these patches, is necessary to provide a reference (Kalamees & Zobel 2002). Replicated disturbance sizes and shapes should be typical of those in the mixed-grass prairie ecoregion, and could potentially simulate one or more of the following: 100 x 100 m square petroleum drilling pads, 2 m diameter buffalo wallows, 0.5 m diameter fossorial mammal burrows, 30 m wide roadway rights-of-way, 10 to 5 m wide pipeline rights-of-way, and 0.5 m wide ungulate trails. Disturbance intensity in each case requires surface soil tillage and elimination of perennial vegetation cover for a minimum of one growing season. Compaction or harrowing to simulate differences in surface soil bulk density could also be attempted. Replication or repetition over several years could also help evaluate the role of climatic stochasticity in community assembly. Essential responses to measure over time in each patch type include the temporal sequence, spatial pattern and propagule source (soil seedbank, adjacent rhizomes, or adjacent seed production) of colonizing plants. There have been a few experiments that simulate some of the smaller disturbance types (Umbnahowar 1995) or tested the role of inter-annual climate variation on seed establishment (Bakker et al. 2003), and descriptive investigations involving the range of disturbance types (Platt 1975; Coffin & Lauenroth

1988; Umbanhowar 1992; Rogers & Hartnett 2001). Thus, future manipulated experiments should focus on the larger diameter disturbance types.

Whether tests involving a sequence of restoration treatments or disturbance of native grasslands represent an efficient use of resources can only be evaluated in terms of evolution and human values. This alien species has become established (naturalized?) in and adjacent to native plant communities on the northern Great Plains. Numerous interspecific interactions with plant competitors, microbial pathogens, invertebrate and vertebrate predators began the day *A. cristatum* arrived. Plants surviving in North America today are descendants of a founder population that passed and continues to pass through these natural and artificial filters. In fact the currently slow rates of invasion may be deceiving, since the regional population of long-lived plants may require time for particularly invasive, genetically-based advantages to manifest themselves (Lambrinos 2004). At some point, an arsenal of biotic enemies will suppress a formerly unchecked invader, and when this occurs the species will cease to be an invader; but what do we call it then? In the interim, how many formerly native species will become extinct as a result of the invasion, and how many are we willing to lose?

The complete eradication of *A. cristatum* would require enormous financial and energy inputs that would lead to conflicts with agricultural producers and right-of-way reclamationists, and may disrupt the ecosystem to a point that negates any environmental benefit. The widespread adoption of these control and restoration proposals requires acceptance of the problem and commitment to values of biodiversity conservation. It may be that only some jurisdictions (National Parks, Crown Lands) are willing to participate on a scale that is meaningful. Meanwhile, intensified economic utilization of private lands precludes an opportunity for participation without extensive land holdings, willing neighbours and land title caveats that prevent fragmenting developments.

LITERATURE CITED

Ambrose, L.G. & Wilson, S.D. (2003) Emergence of the introduced grass *Agropyron cristatum* and the native grass *Bouteloua gracilis* in a mixed-grass prairie restoration. *Restoration Ecology*, **11**, 110-115.

Bakker, J.D., Christian J., Wilson S.D. & Waddington J. (1997) Seeding blue grama in old crested wheatgrass fields in southwestern Saskatchewan. *Journal of Range Management*, **50**, 156-159.

Bakker, J.D. & Wilson, S.D. (2001) Competitive abilities of introduced and native grasses. *Plant Ecology*, **157**, 117-125.

Bakker, J.D., Wilson, S.D., Christian, J.M., Li, X., Ambrose, L.G. & Waddington, J. (2003) Contingency of grassland restoration on year, site, and competition from introduced grasses. *Ecological Applications*, **13**, 137-153.

Blossey, B. & Notzold, R. (1995) Evolution of increased competitive ability in invasive non-indigenous plants: a hypothesis. *Journal of Ecology*, **83**, 887-889.

Coffin, D.P. & Lauenroth, W.K. (1988) The effects of disturbance size and frequency on a shortgrass plant community. *Ecology*, **69**, 1609-1617.

Eissenstat, D.M. & Caldwell, M.M. (1988a) Competitive ability is linked to rates of water extraction: a field study of two aridland tussock grasses. *Oecologia*, **75**, 1-7.

Eissenstat, D.M. & Caldwell, M.M. (1988b) Seasonal timing of root growth in favorable microsites. *Ecology*, **69**, 870-873.

Elton, C.S. (1958) *The ecology of invasions by plants and animals*. University of Chicago Press, Chicago IL.

Goldberg, D.E. & Barton, A.M. (1992) Patterns and consequences of interspecific competition in natural communities: a review of field experiments with plants. *American Naturalist*, **139**, 771-801.

Grime, J.P. (1973) Competitive exclusion in herbaceous vegetation. *Nature*, **242**, 344-347.

Kalamees, R. & Zobel, M. (2002) The role of the seed bank in gap regeneration in a calcareous grassland community. *Ecology*, **83**, 1017-1025.

Lambrinos, J.G. (2004) How interactions between ecology and evolution influence contemporary invasion dynamics. *Ecology*, **85**, 2061-2070.

Platt, W.J. (1975) The colonization and formation of equilibrium plant associations on badger disturbances in tallgrass prairie. *Ecological Monographs*, **45**, 285-305.

Pyke, D.A. (1990) Comparative demography of co-occurring introduced and native tussock grasses: Persistence and potential expansion. *Oecologia*, **82**, 537-543.

Rogers, W.E. & Hartnett, D.C. (2001) Temporal vegetation dynamics and recolonization mechanisms on different-sized soil disturbances in tallgrass prairie. *American Journal of Botany*, **88**, 1634-1642.

Smoliak, S., Johnston, A. & McLean, A. (1980) *Management of crested wheatgrass pastures*. Publication 1473, Agriculture Canada, Research Branch, Ottawa.

Tilman, D. (1985) The resource-ratio hypothesis of plant succession. *American Naturalist*, **125**, 827-852.

Umbanhowar, C.E. (1992) Abundance, vegetation and environment of four patch types in a northern mixed prairie. *Canadian Journal of Botany*, **70**, 277-284.

Umbanhowar, C.E. (1995) Revegetation of earthen mounds along a topographic-productivity gradient in a northern mixed prairie. *Journal of Vegetation Science*, **6**, 637-646.

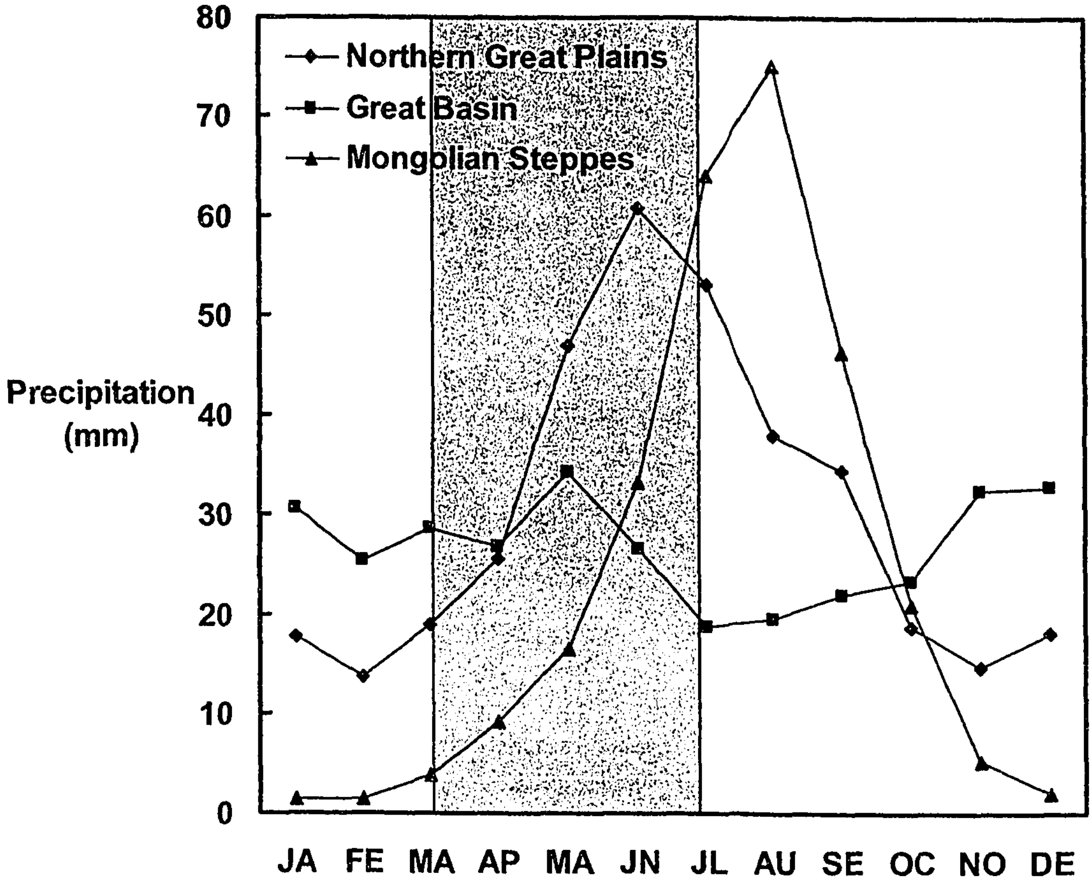

Figure 6.1 Monthly mean precipitation for three geographic regions where *A. cristatum* occurs (lines) and the period of maximum productivity (shaded area). Data for climate stations within these ecoregions in the USA, Mongolia and China were adapted from on-line monthly climate normals available from the National Oceanic and Atmospheric Administration (2004), and Canadian data were from on-line monthly climate normals available from Environment Canada (2004). Phenological data were adapted from Smoliak et al. (1980).

APPENDIX A. EXTENT OF CRESTED WHEATGRASS IN CANADIAN MIXED-GRASS PRAIRIE

To accurately estimate the area occupied by any one perennial forage species other than alfalfa (*Medicago sativa* L.) is difficult, because of aggregated land cover categories in the Canadian census (Statistics Canada 2002). As such, the rough estimate for the area of *A. cristatum* provided in this appendix was based on a number of assumptions. Of the "tame pasture" in the mixed-grass prairie region (Table A.1) at least 80% is *A. cristatum*, since it has proven to be the most drought tolerant, persistent and popular species. Of the "alfalfa and alfalfa mixture" approximately 50% is pure alfalfa under irrigation, and 25% is mixed with *A. cristatum* as dryland hay fields. The most difficult category to interpret is the "tame hay and other fodder or silage", because this could include a large area of annual grains. A conservative estimate of the proportion occupied by *A. cristatum* in this category may be 5%. When the reported area of *A. cristatum* on non-leased crown lands is also added, this single alien species dominates approximately 1.5 million ha, or 5.8% of the mixed-grass prairie region (Table A.2).

It is much more difficult to estimate the area occupied by *A. cristatum* on roadside ditches and petroleum disturbances. The area of ditches can be estimated using a simple formula using 10 m wide ditches either side of a road throughout the network of grid road allowances in the region. Assuming one third of the road allowances are developed, and all ditches were seeded to *A. cristatum*, this would cover approximately 10.7 ha per township. As of August 2004, Alberta had 293,350 operating petroleum wells (each 1 ha) and 293,812 km of licensed pipeline (Alberta Energy & Utilities Board 2004), and reported estimates from 1991 were 38,934 active and 17,287 abandoned wells within the mixed-grass prairie ecoregion (Kerr et al. 1993). Using this information and assuming it was common practice to use *A. cristatum* for reseeding lands disturbed by the petroleum industry from 1970 to 1990 (Alberta Environment 2003), that 75% of wells as of 1991 were drilled during that period, that 75% of wells were on low-rent rangelands, and that each 1 ha well pad is associated with 1 ha of pipeline (1 km * 10 m wide), it's possible to roughly estimate the area seeded to *A. cristatum*. For adjacent Saskatchewan, I will estimate the area was 10% of that in Alberta. Inclusion of these disturbances increases the total area of *A. cristatum* seeded in the mixed-grass prairie region, to 1.7 million ha or 6.7% of the region (Table A.2).

Alberta Energy & Utilities Board (2004) On-line statistics (http://www.eub.gov.ab.ca/bbs/energystats/default.htm). AEUB. Edmonton AB.

Alberta Environment (2003) *Problem introduced forages on prairie and parkland reclamation sites: Guidance for non-cultivated land.* Alberta Environment R&R/03-05. Edmonton AB.

Kerr, D.S., Morrison, L.J. & Wilkinson, K.E. (1993) *Reclamation of native grasslands in Alberta: A review of the literature.* Alberta Land Conservation and Reclamation Council, Report RRTAC 93-1. Edmonton AB.

Statistics Canada (2002) *2001 Census of Agriculture.* Catalogue No. 95F0301XIE. Statistics Canada, Ottawa ON.

Table A.1. The estimated area of land cover types in the mixed-grass prairie region of Alberta and Saskatchewan, Canada as of 2001.

Land Tenure	Total Area (ha)	Alfalfa (ha)	Other Hay (ha)	Tame Pasture (ha)	Native Pasture (ha)	Cultivated (ha)
Private & Leased, Farm & Ranch[a]	24,130,628	847,514	310,940	1,441,133	6,977,742	14,553,299
Federal & Provincial Community Pastures	1,065,906	2,630		134,947	928,329	
DND Suffield	269,000				269,000	
Grasslands Natl. Park	47,800			900	46,900	
Provincial Parks	13,000			300	12,700	
Total (ha)[b]	25,526,334	850,144	310,940	1,577,280	8,234,671	14,553,299
Total (% of area)	100	3.3	1.2	6.2	32.3	57.0

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[a] Private and Leased farm and ranch numbers and land use categories are from Statistics Canada (2002).

[b] These values exceed the ecoregion area because farm statistics[a] are based on census division boundaries that only approximate ecoregion boundaries and include the Cypress Hills upland. All other land tenure types were taken from federal and provincial sources for units known to occur wholly within the ecoregion boundary. Urban areas and transportation corridors were not included.

Table A.2. Estimated area of crested wheatgrass in the mixed-grass prairie region of Alberta and Saskatchewan, Canada. See text for rationale.

Land Cover Type	*A. cristatum* Dominant (ha)	*A. cristatum* Regional Population (%)	Regional Area (%)
Tame pasture	1,261,824	74.6	4.9
Alfalfa fields	212,536	12.6	0.8
Other hay fields	15,547	0.9	0.1
Roadside ditches	132,178	7.8	0.5
Petroleum disturbances	69,572	4.1	0.3
Total area	1,691,657	100.0	6.7

APPENDIX B. CRESTED WHEATGRASS HABITAT IN ASIA

Understanding how *A. cristatum* is capable of colonizing, dominating and persisting in an alien environment, the northern Great Plains, requires understanding the environmental conditions where the species evolved in Asia. Unfortunately for an English audience, much of the Asian literature on *A. cristatum* is written in Mandarin, Russian or German and this communication barrier limits accessibility. From the literature that is available, some distribution limits for *A. cristatum* can be estimated.

Environmentally, the distribution of *A. cristatum* coincides with temperate, semiarid "typical" and "montane steppe" where the mean annual precipitation ranges from 150 to 520 mm, and mean annual temperature ranges from -7 to 8 °C (Table B.1). On average, *A. cristatum* occurs where mean annual precipitation is 330 mm. In northern portions of the range, *A. cristatum* is distributed from the eastern border of Mongolia, through China and Siberia, west to the Volga River in Russia. In southern portions of the range, distribution is limited to upper elevations of foothills and mountains in Kazakhstan, Turkmenistan, Uzbekistan, Afghanistan, Iran and Turkey. This distribution is considerable, spanning 32 to 51 °N latitude and 38 to 121 °E longitude.

Ecologically, *A. cristatum* is common though subdominant on chernozemic and sandy regosolic soils where bunchgrasses of the genera *Stipa* and *Festuca*, and shrubs of the genus *Artemisia* are dominant. Conversely, *A. cristatum* is negatively associated with forests, shrublands and halophytic vegetation on moist or acidic soils (Jin-Tun 2002; Ni 2003; Wang et al. 2002b). The grazing response of *A. cristatum* varies from general recognition as a grazing tolerant species (Khasanova & Abramova 2000; Fernandez-Gimenez & Allen-Diaz 1999; Wang et al. 2002a; Xie & Wittig 2003), to instances of increasing with grazing pressure (Yunusbaev et al. 2003; Zhou et al. 2002), and other instances of disappearing from the most heavily grazed sites (Fernandez-Gimenez & Allen-Diaz 1999; Xie & Wittig 2003). On pastures cultivated and sown to *Bromus inermis*, *Medicago sativa* and *Elymus juncea* in Russia, *A. cristatum* was one of several indigenous species to colonize and increase over time (Khasanova & Abramova 2000).

Fernandez-Gimenez, M.E. & Allen-Diaz, B. (1999) Testing a non-equilibrium model of rangeland vegetation dynamics in Mongolia. *Journal of Applied Ecology*, **36**, 871-885.

Jin-Tun, Z. (2002) A study on relations of vegetation, climate and soils in Shanxi province, China. *Plant Ecology*, **162**, 23-31.

Khasanova, G.R. & Abramova, L.M. (2000) Prospects for restoring the biodiversity of steppe vegetation: sowing of perennial grasses. *Russian Journal of Ecology*, **31**, 439-441.

Ni, J. (2003) Plant functional types and climate along a precipitation gradient in temperate grasslands, north-east China and south-east Mongolia. *Journal of Arid Environments*, **53**, 501-516.

Titlyanova, A.A., Romanova, I.P., Kosykh, N.P. & Mironycheva-Tokareva, N.P. (1999) Pattern and process in above-ground and below-ground components of grassland ecosystems. *Journal of Vegetation Science*, **10**, 307-320.

Wang, Y., Shiyomi, M., Tsuiki, M., Tsutsumi, M., Yu, X. & Yi, R. (2002) Spatial heterogeneity of vegetation under different grazing intensities in the northwest Heilongjiang steppe of China. *Agriculture, Ecosystems and Environment*, **90**, 217-229.

Wang, G., Zhou, Q., Zhong, W., Sun, C. & Chen, Z. (2001) Species richness-primary productivity relationship of plants and small mammals in the inner Mongolian steppes, China. *Journal of Arid Environments*, **49**, 477-484.

Wang, G., Zhou, G., Yang, L. & Li, Z. (2002) Distribution, species diversity and life-form spectra of plant communities along an altitudinal gradient in the northern slopes of Qilianshan Mountains, Gansu, China. *Plant Ecology*, **165**, 169-181.

Xie, Y. & Wittig, R. (2003) Growth parameters of characteristic species of *Stipa* steppes in northern China as indicators of the grazing intensity. *Journal of Applied Botany*, **77**, 68-74.

Yunusbaev, U.B., Musina, L.B. & Suyundukov, Y.T. (2003) Dynamics of steppe vegetation under the effect of grazing by different farm animals. *Russian Journal of Ecology*, **34**, 43-46.

Zhou, G., Wang, Y. & Wang, S. (2002) Responses of grassland ecosystems to precipitation and land use along the northeast China transect. *Journal of Vegetation Science*, **13**, 361-368.

Table B.1 Selected environmental characteristics of Asian grasslands with *A. cristatum*.

Region	MAP (mm)	MAT (°C)	Elevation (m a.s.l.)	Reference
Mongolia	200-230	0		Fernandez-Gimenez & Allen-Diaz 1999
Shanxi	350	+8		Jin-Tun 2002
Bashkir	379	0		Khasanova & Abramova 2000
Inner Mongolia	320	-1	1300	Ni 2003
Tuva	130-150	-7	2000 to 2400	Titlyanova et al. 1999
Heilongjiang	410	+4	200 to 2000	Wang et al. 2002a
Inner Mongolia	350	0	1200 to 1400	Wang et al. 2001
Gansu	180-523	+3 to -4	2100 to 3500	Wang et al. 2002b
Inner Mongolia	412	+6		Xie & Wittig 2003
Bashkir	334	0		Yunusbaev et al. 2003
Inner Mongolia	343	0	1200	Zhou et al. 2002

APPENDIX C. DETAILED FIELD SITE LOCATOR MAPS

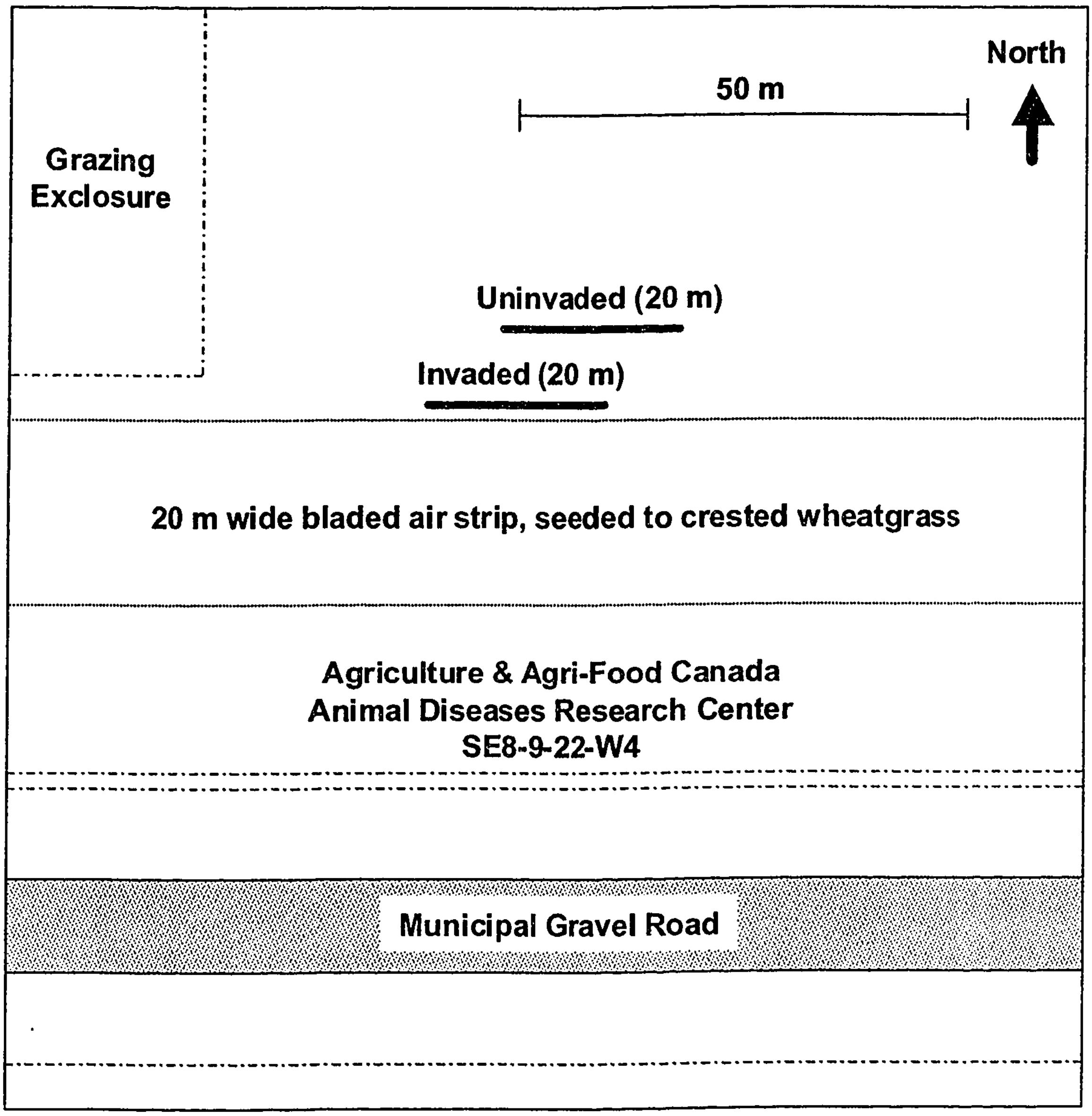

Figure C.1 Transect locations for site #1 (see Table 3.1).

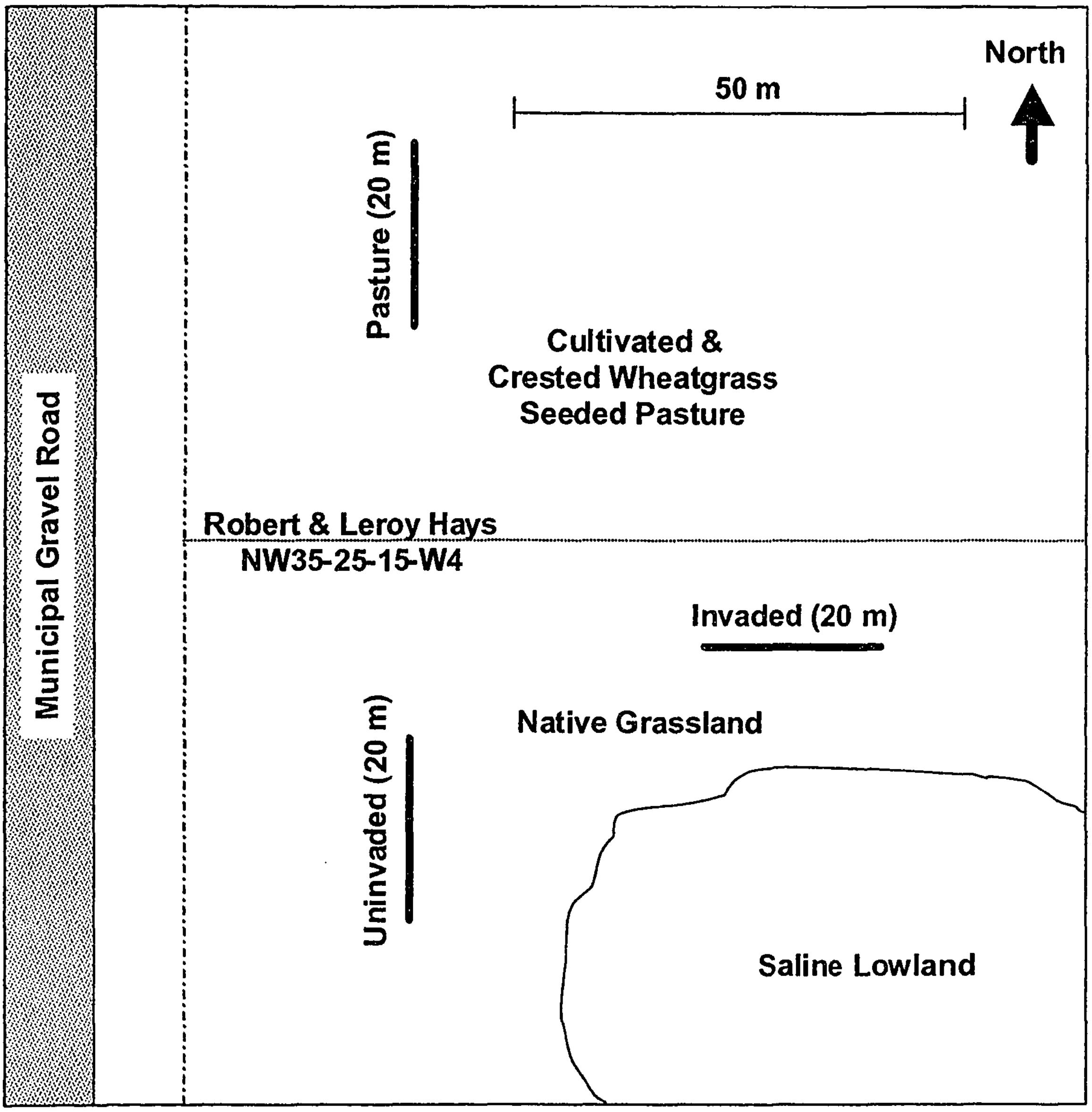

Figure C.2 Transect locations for site #2 (see Table 3.1).

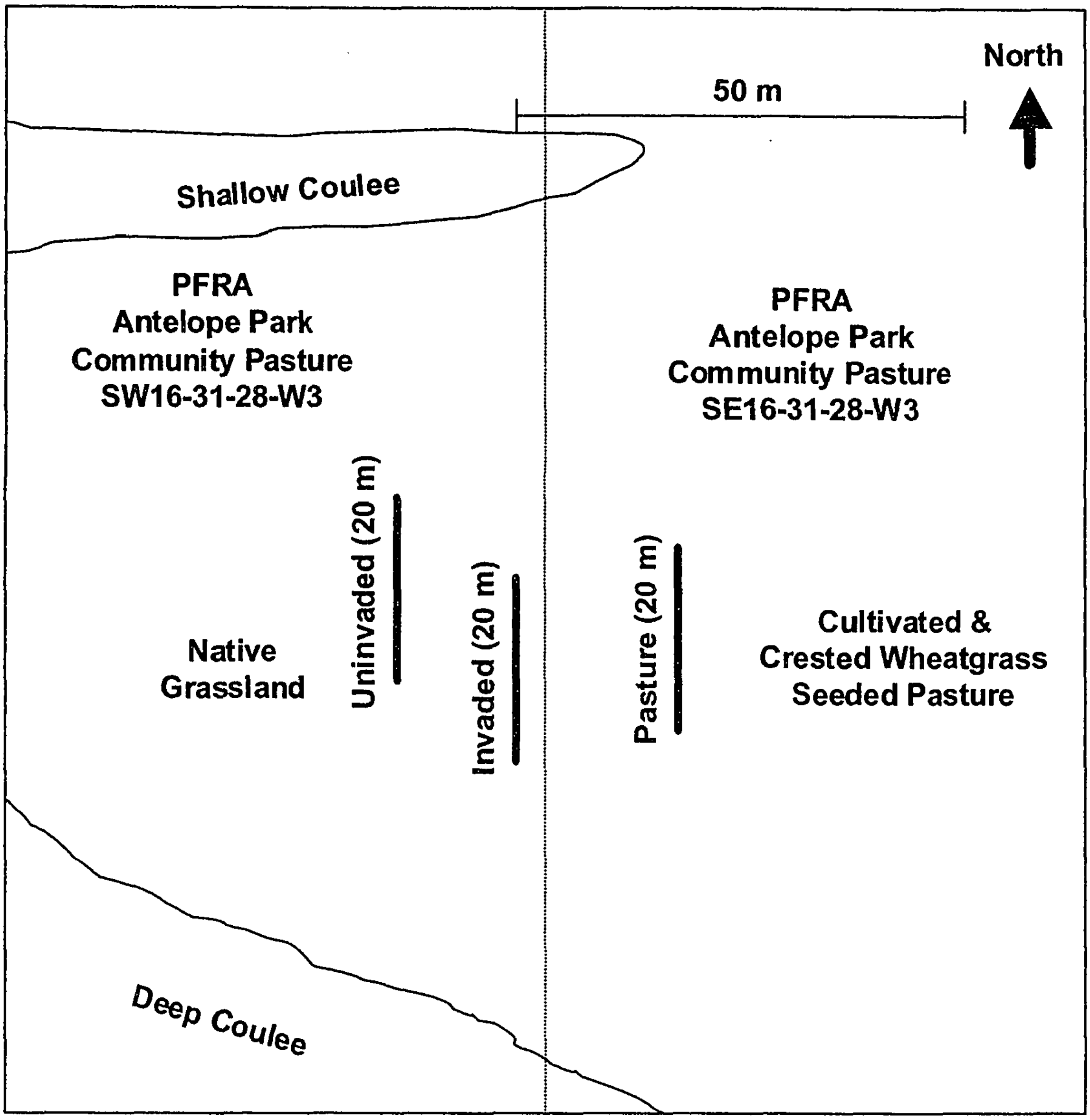

Figure C.3 Transect locations for site #3 (see Table 3.1).

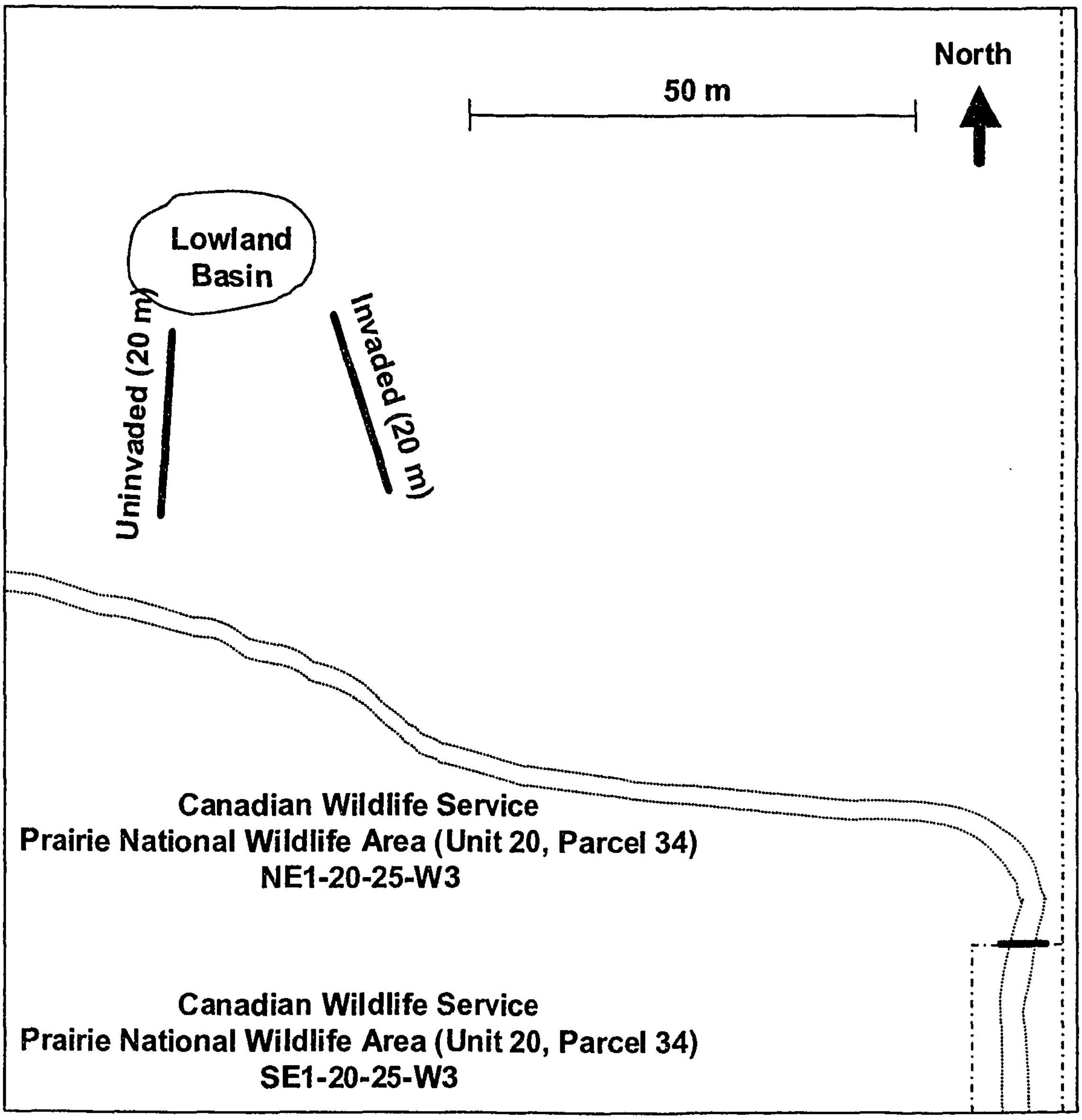

Figure C.4 Transect locations for site #4 (see Table 3.1).

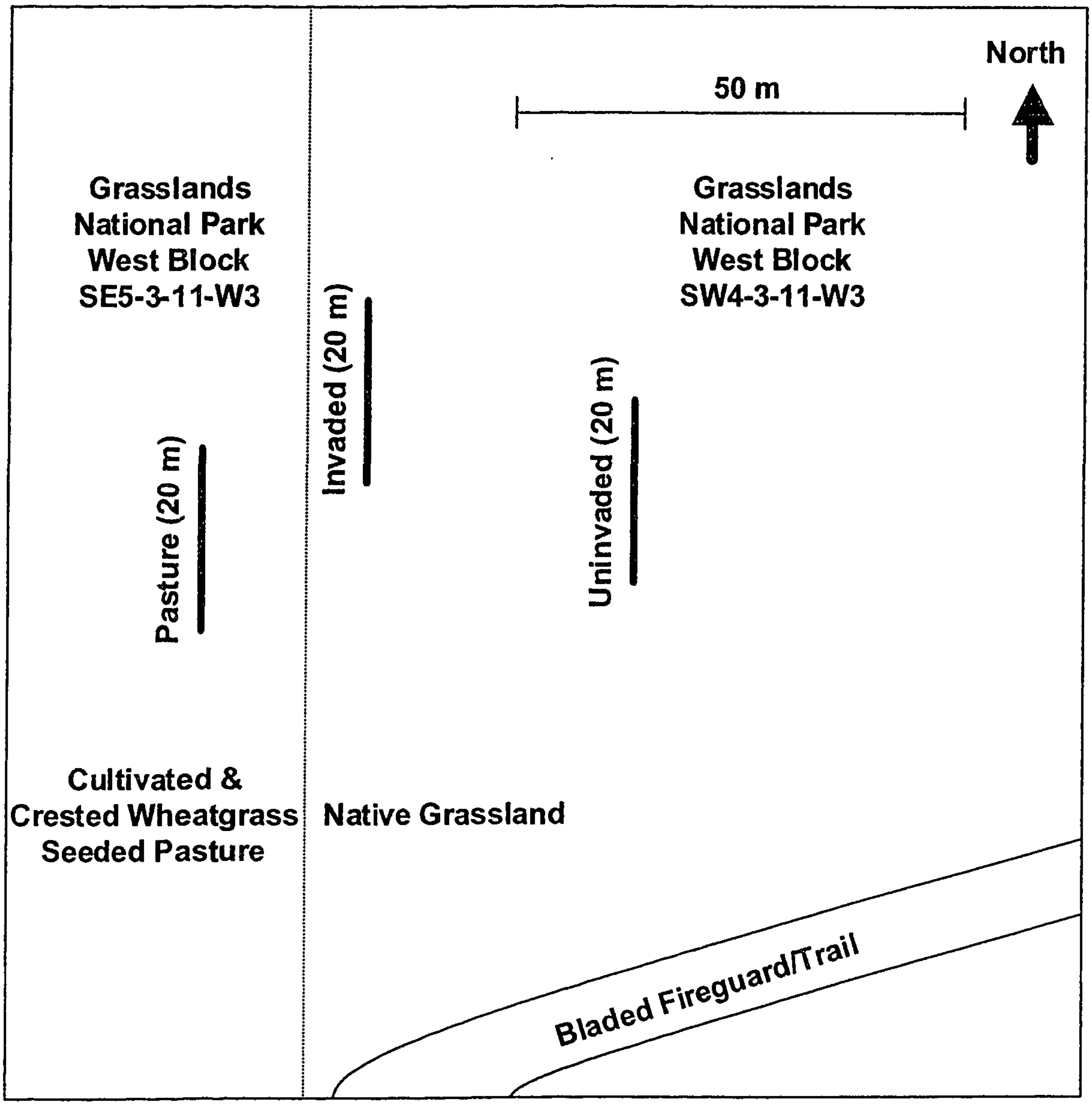

Figure C.5 Transect locations for site #5 (see Table 3.1).

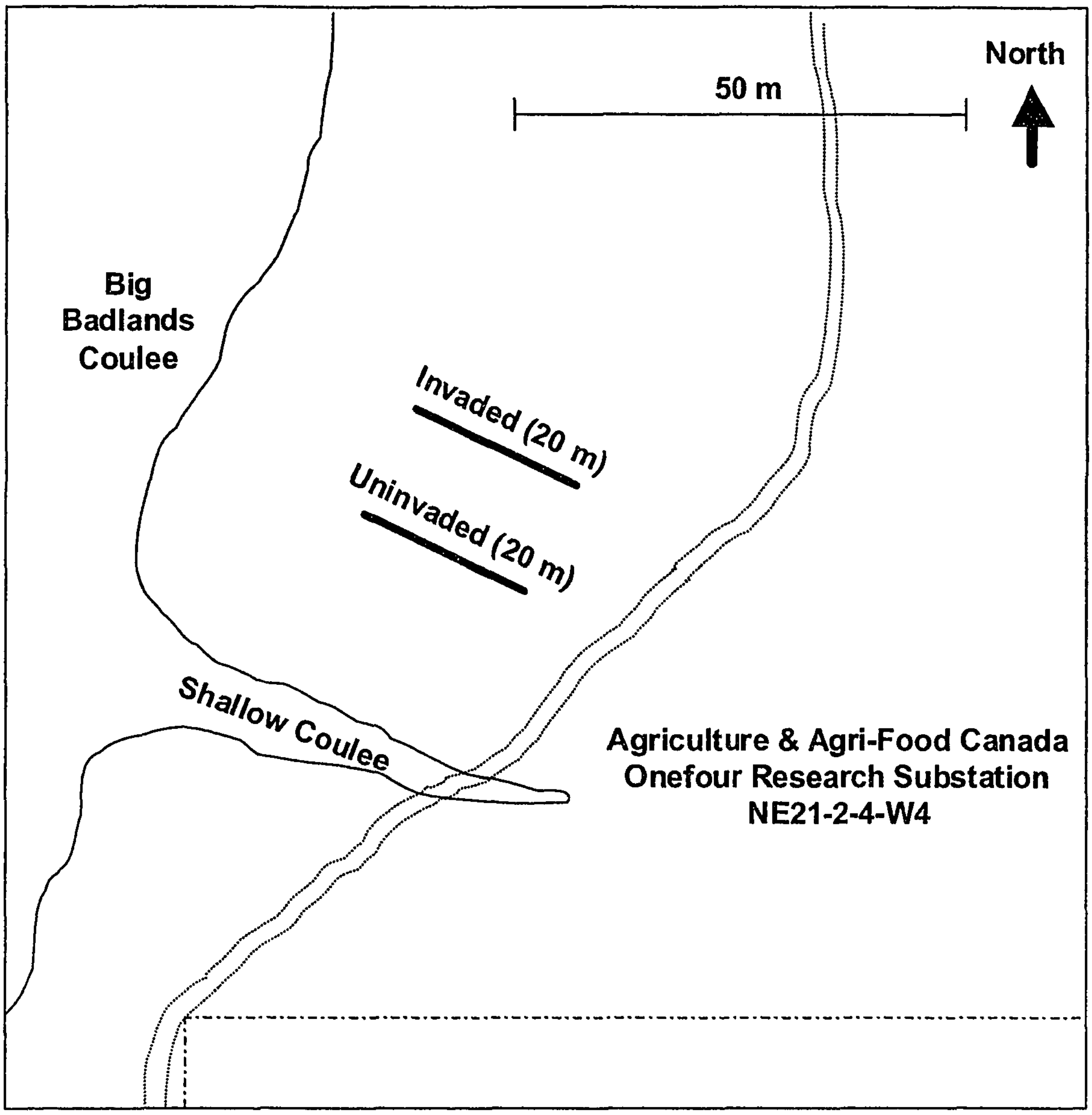

Figure C.6 Transect locations for site #6 (see Table 3.1).

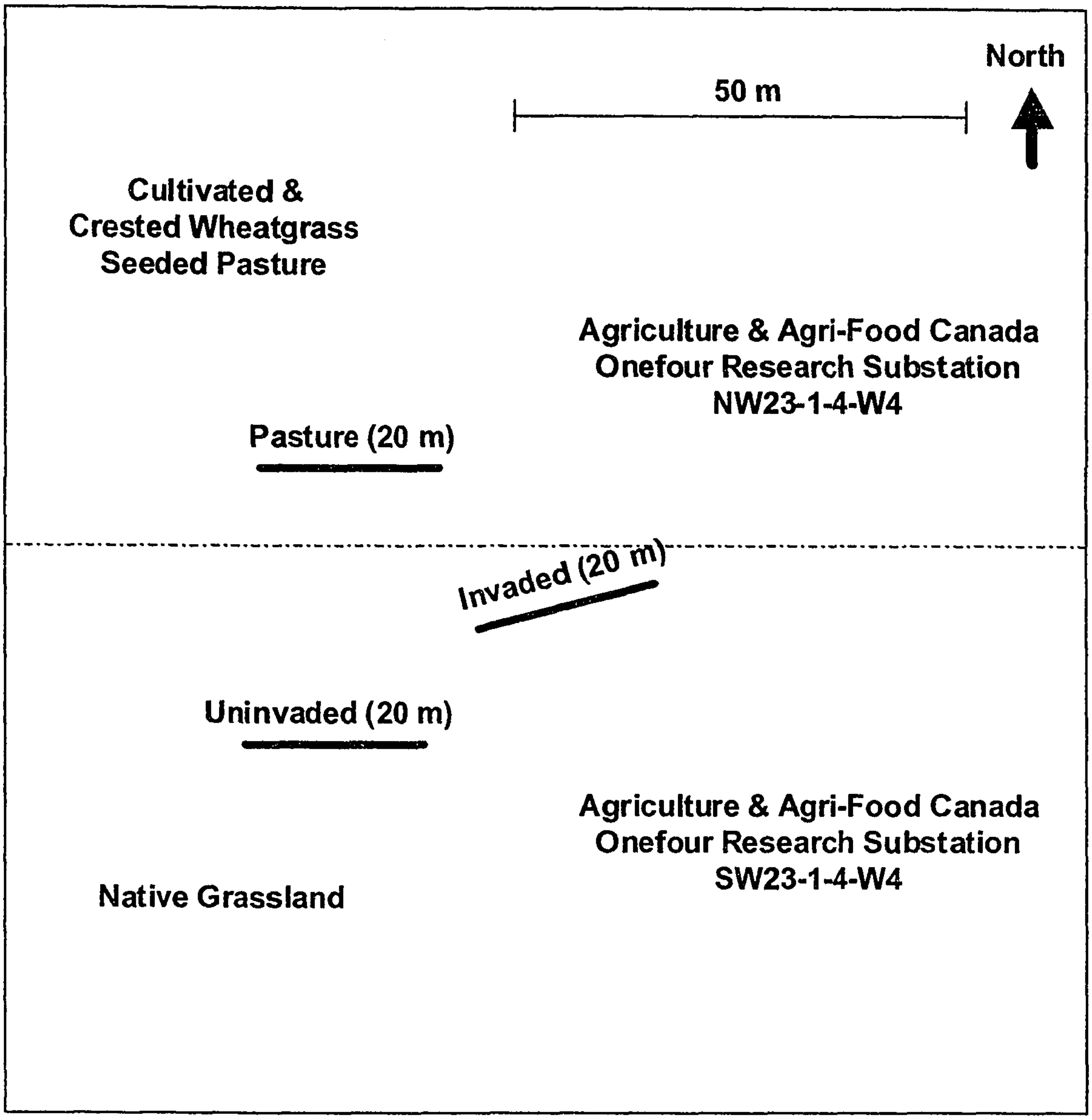

Figure C.7 Transect locations for site #7 (see Table 3.1).

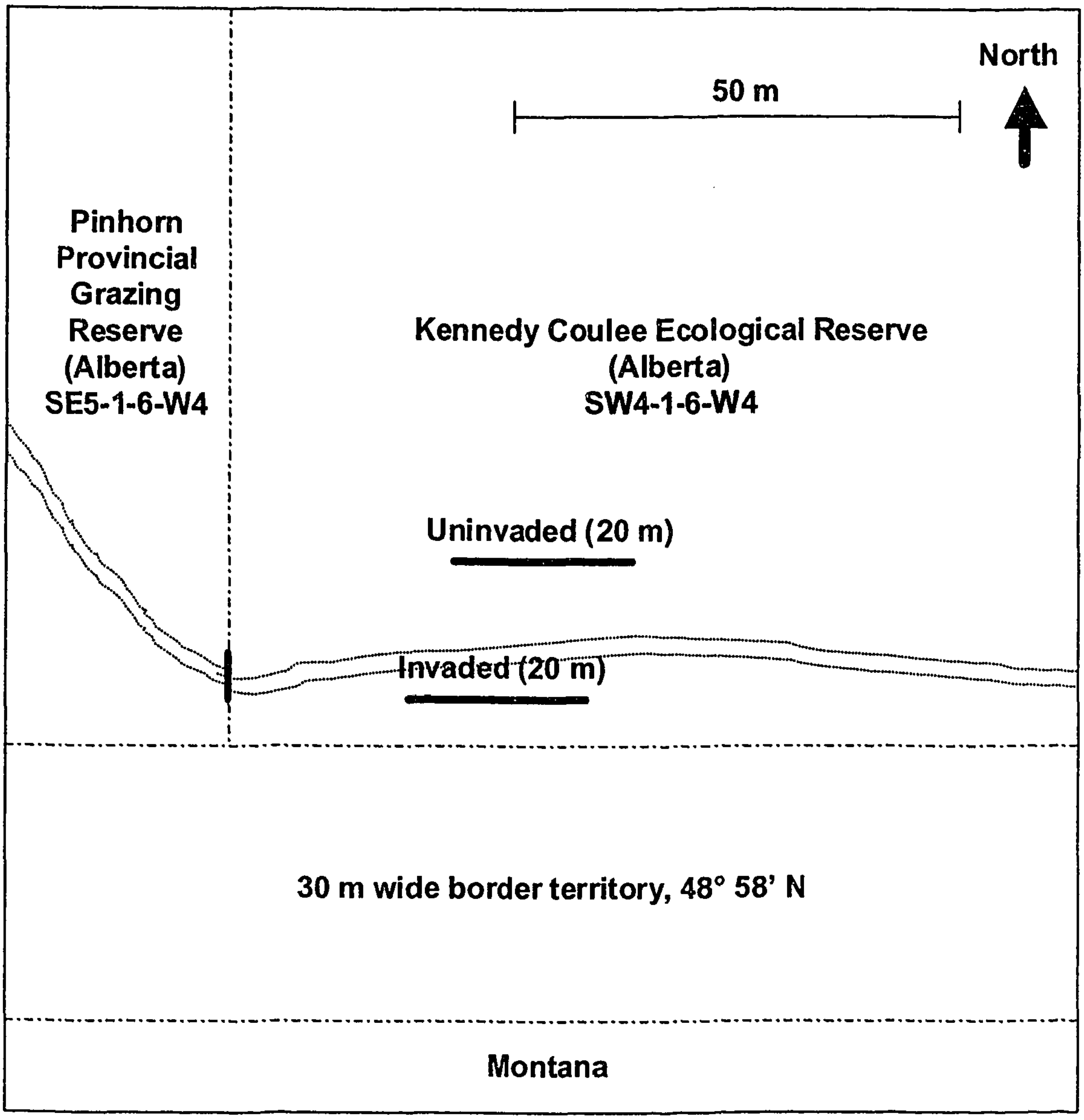

Figure C.8 Transect locations for site #8 (see Table 3.1).

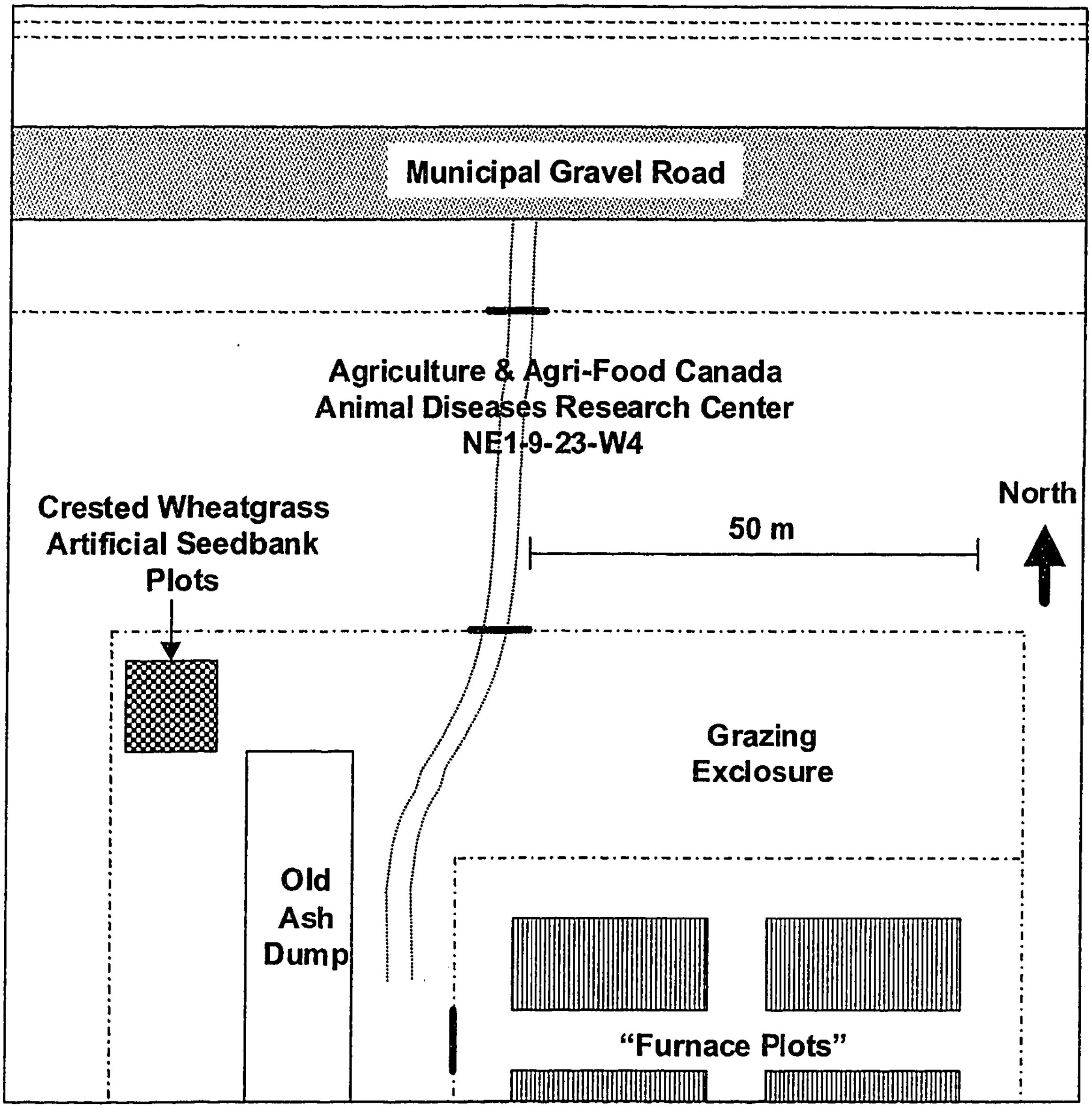

Figure C.9 Experimental plot location for Chapter 4.

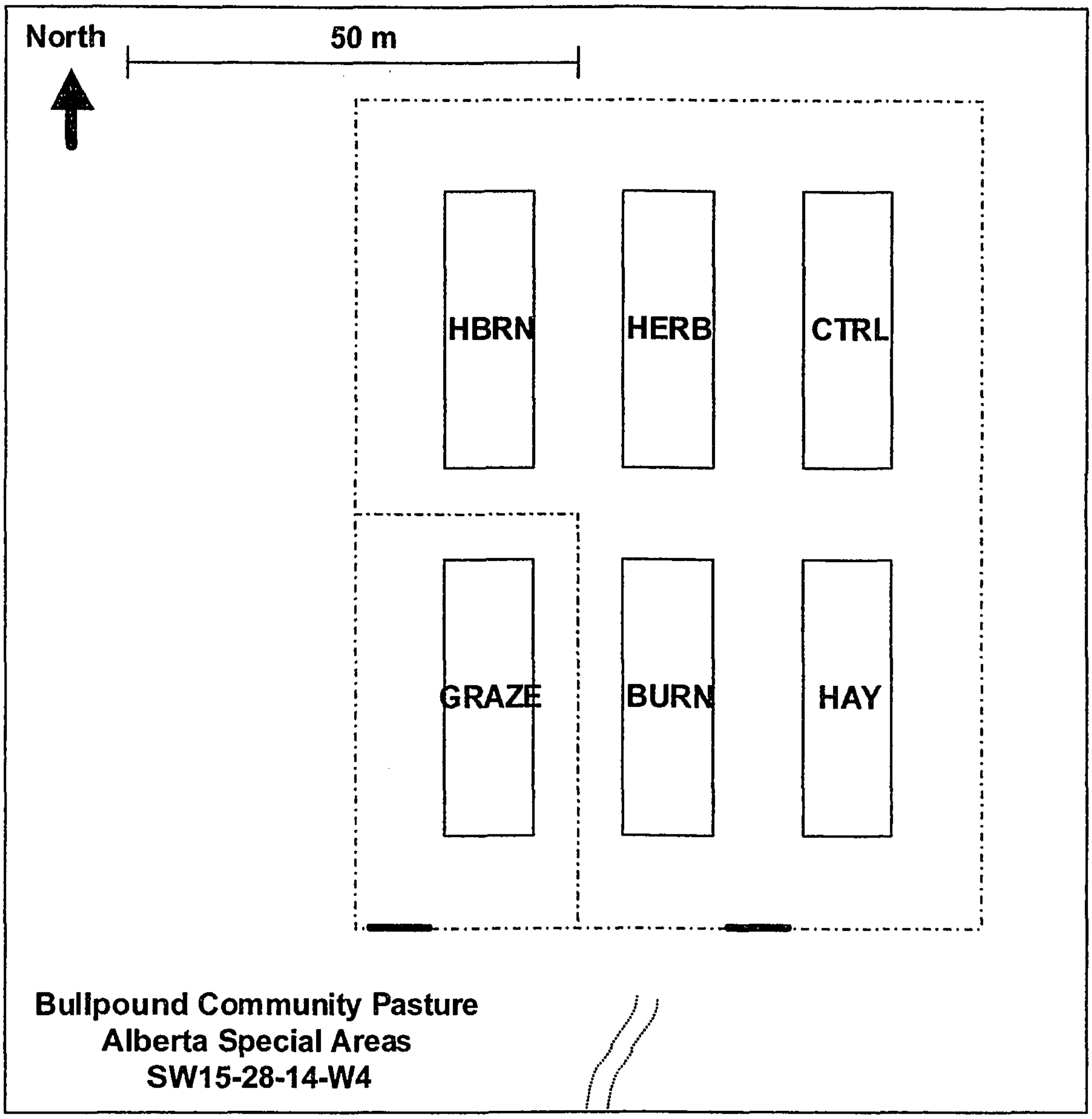

Figure C.10 Experimental block location for Hanna (see Table 5.1).

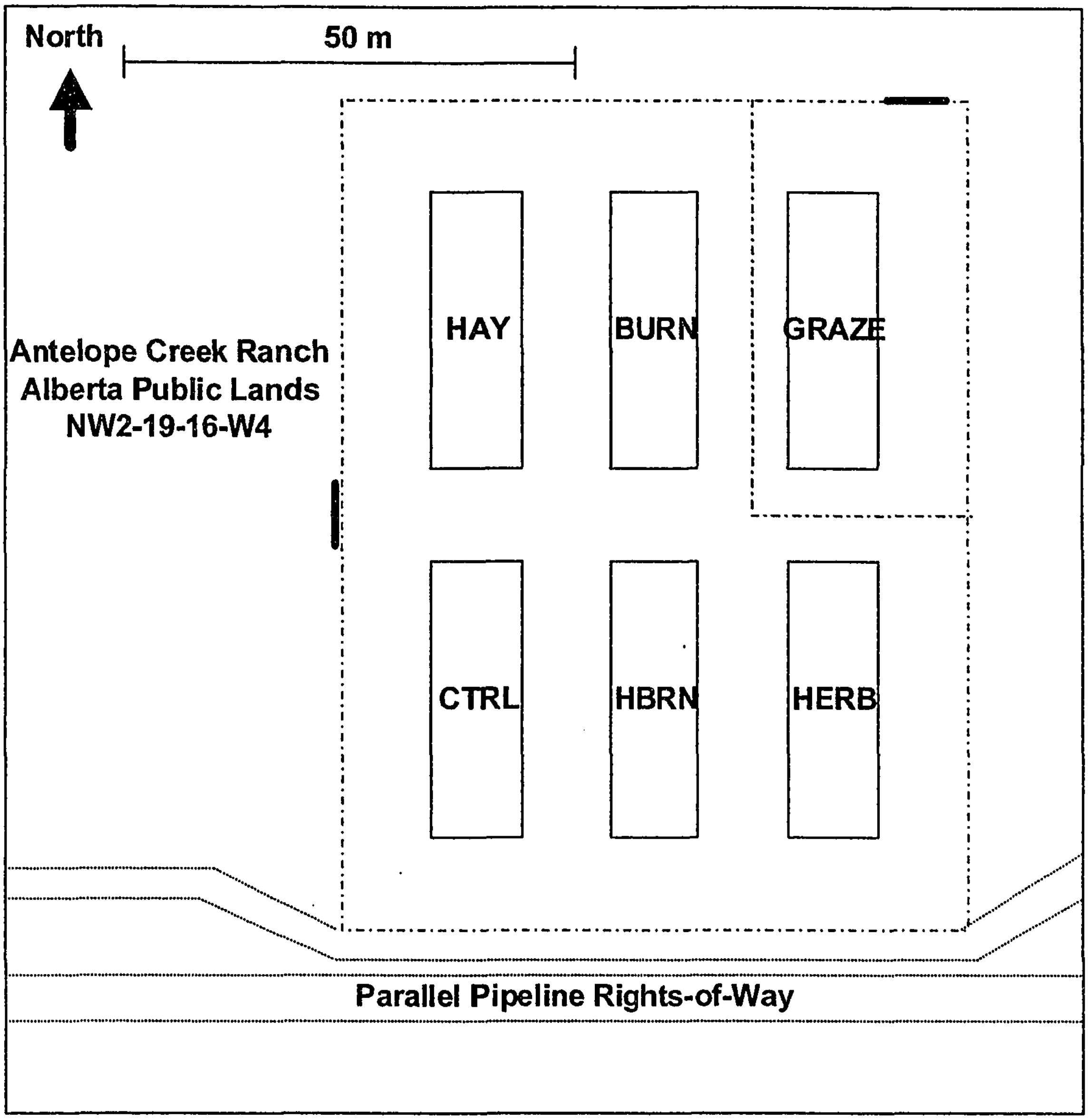

Figure C.11 Experimental block location for Brooks (see Table 5.1).

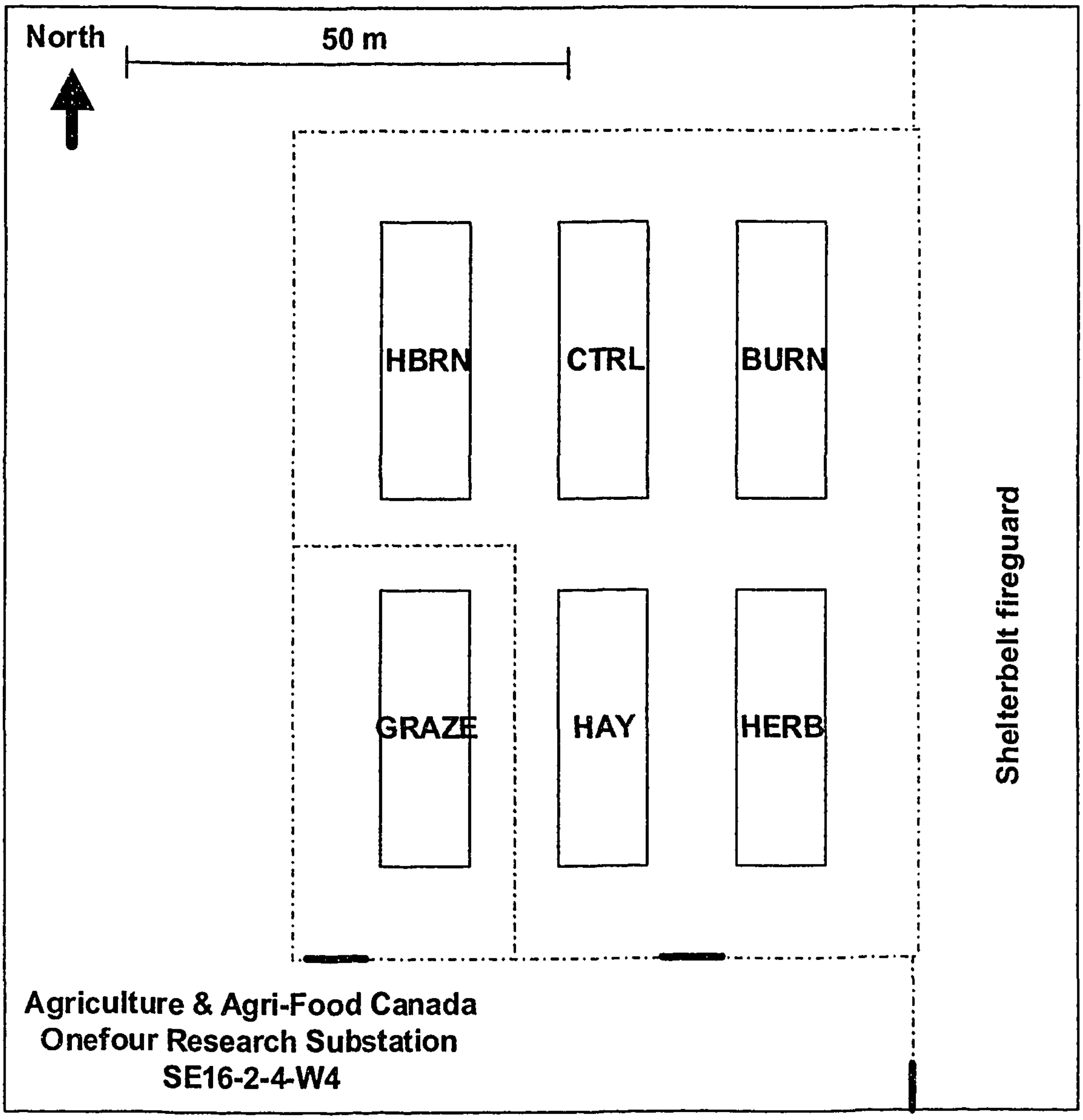

Figure C.12 Experimental block location for Onefour (see Table 5.1).

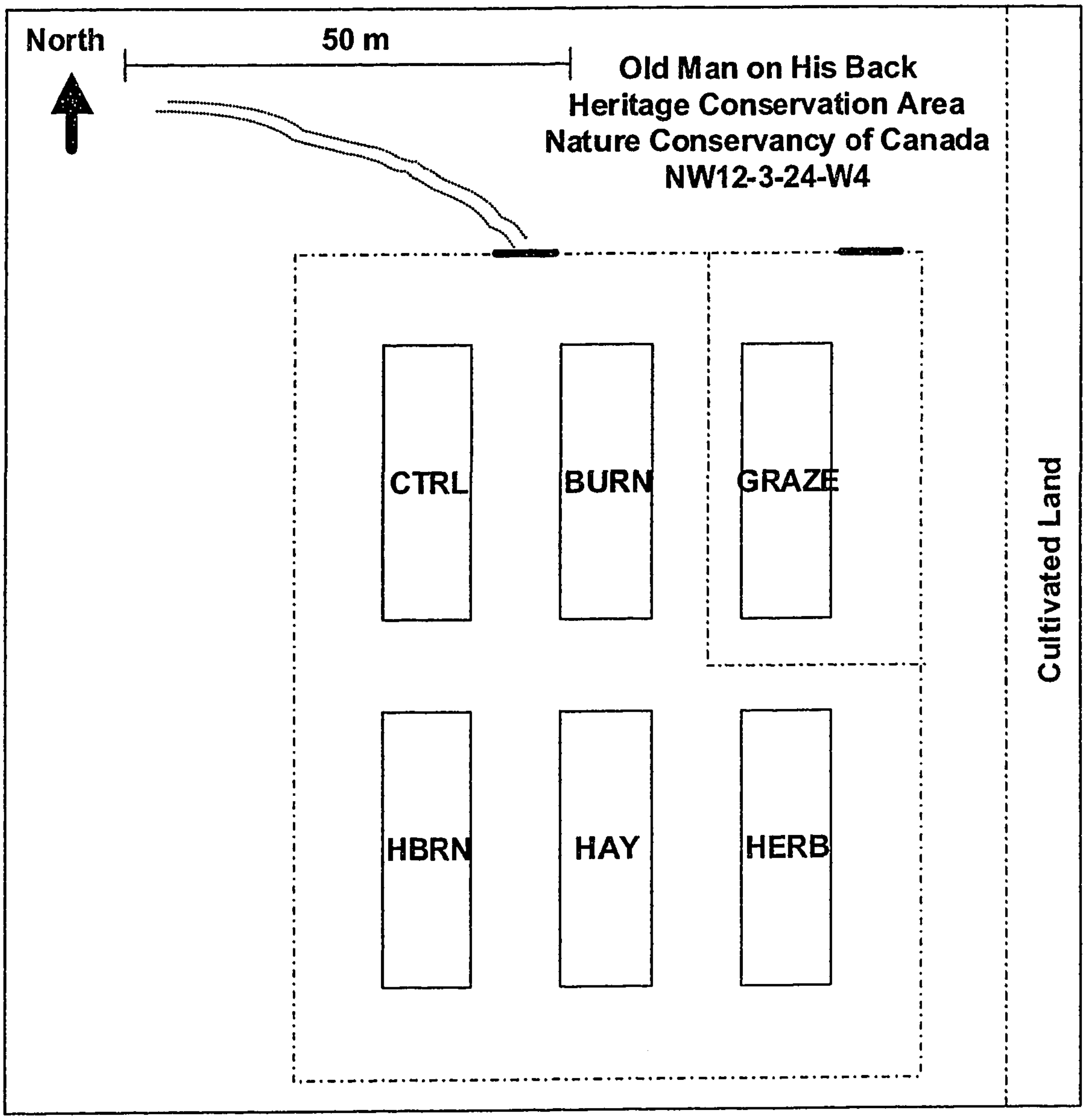

Figure C.13 Experimental block location for Eastend (see Table 5.1).

APPENDIX D. FUNCTIONAL GROUP ASSOCIATIONS FOR CHAPTER 3

Annual & Biennial Forbs (seedbank group only, aggregated with forbs in vegetation group)

Amaranthus retroflexus
Androsace septentrionalis
Arabis retroflexus
Chenopodium album
Chenopodium leptophyllum
Erigeron candadensis
Descurainia sophia
Draba nemorosa
Euphoribia glyptosperma
Lapulla squarrosa
Lepidium densiflorum
Monolepis nuttaliana
Oenothera nuttalii
Plantago patagonica
Rumex crispus
Taraxacum officinale
Thlaspi arvense
Tragopogon dubius

Perennial Forbs (seedbank group only, aggregated with forbs in vegetation group)

Achillea millefolium
Allium textile
Antennaria aprica
Antennaria dimorpha
Artemisia frigida
Artemisia ludoviciana
Astragalus missouriensis
Cirsium arvense
Cirsium flodmannii
Erigeron caespitosus
Eurotia lanata
Geum triflorum
Gutierreza sarothrae
Heterotheca villosa
Liatris punctata
Linum lewisii
Lygodesmia juncea
Opuntia polyacantha
Oxytropis sericea
Phlox hoodii
Potentilla pensyllvanica
Psoralea lanceolata
Ratibida columnifera
Rosa acicularis
Solidago missouriensis
Sphaeralcea coccinea
Verbena bracteata.
Vicia americana
Unknown (seedling)

C4 Perennial Grasses

Bouteloua gracilis
Sporobolus cryptandrus

C3 Perennial Grasses (*Carex* included)

Agropyron cristatum
Agropyron dasystachyum
Agropyron smithii
Carex eleocharis
Carex pensyllvanica
Festuca scabrella
Koeleria macrantha
Poa juncifolia
Poa sandbergii
Stipa comata
Stipa viridula

Cryptogams (vegetation group only)

Cladonia gracilis
Cladonia pocillum
Cladonia pyxidata
Coelocaulon aculeatum
Collemia
Diploschistes scruposus
Selaginella densa
Tortula ruralis
Xanthoparmelia chlorochroa

Nomenclature of vascular plants follows Moss, E.H. (1994) *The flora of Alberta*. University of Toronto Press, Toronto ON., and cryptogams follow Vitt, D.H., Marsh, J.E. & Bovey, R.B. (1988) *Mosses, lichens and ferns of northwestern North America*. Lone Pine Publishing, Edmonton AB.

APPENDIX E. FUNCTIONAL GROUP ASSOCIATIONS FOR CHAPTER 5

eaf - Alien Annual & Biennial Forbs

Amaranthus retroflexus
Capsella bursa-pastoris
Chenopodium album
Descurainia sophia
Galeopsis tetrahit
Kochia scoparia
Lappula squarrosa
Melilotus officinale
Plantago major
Polygonum aviculare
Polygonum convolvulus
Rumex crispus
Salsola kali
Silene noctiflora
Taraxacum officinale
Thlaspi arvense
Tragopogon dubius
Urtica dioica

epf - Alien Perennial Forbs

Cirsium arvense
Medicago sativa
Sonchus arvensis

cwg - Alien Perennial Grasses (only traces of *Elymus* and *Poa* at 1 block, and thus grouped)

Agropyron cristatum
Elymus junceus
Poa pratensis

naf - Native Annual & Biennial Forbs

Androsace septentrionalis
Arabis retroflexus
Cerastium arvense
Chenopodium leptophyllum
Crepis tectorum
Draba nemorosa
Epilobium paniculatus
Erigeron canadensis
Erucastrum gallicum
Euphorbia glyptosperma
Lappula occidentalis
Lepidium densiflorum
Monolepis nuttaliana
Orthocarpus luteus
Plantago patagonica
Polygonum lapathifolium
Solanum triflorum
Stellaria media
Unknown 1 (seedling)
Unknown 2 (seedling)

npf - Native Perennial Forbs (includes some suffratescent and woody shrubs)

Achillea millefolium
Allium textile
Anemone patens
Antennaria aprica
Arnica fulgens
Artemisia cana
Artemisia frigida
Artemisia ludoviciana
Aster ericoides
Aster laevis
Astragalus bisulcatus
Astragalus missouriensis
Campanula rotundifolia
Epilobium angustifolium
Erigeron caespitosus
Geum triflorum
Grindelia squarrosa
Guitiereza sarothrae
Heterotheca villosa
Liatris punctata
Mammilaria vivipara
Opuntia fragilis
Penstemon procerus
Potentilla pensyllvanica
Ratibida columnifera
Rosa acicularis
Solidago missouriensis
Sphaeralcea coccinea
Symphoricarpos occidentalis
Thermopsis rhombifolia
Vicia americana
Unknown 1 (seedling)

npg - Native Perennial Grasses (*Carex* included for vegetation functional group only)

Agropyron smithii
Agropyron subsecundum
Agrostis scabra
Bouteloua gracilis
Calamagrostis montanensis
Deschampsia caespitosa
Festuca saximontana
Helicotrichon hookeri
Hordeum jubatum
Koeleria macrantha
Muhlenbergia cuspidata
Poa sandbergii
Schedonardus paniculatus
Stipa comata
Stipa viridula
Unknown 1 (seedling)

car - Sedges (seedbank functional group only)

Carex eleocharis
Carex pensyllvanica
Carex spp.

cry - Cryptogams (vegetation functional group only)

Selaginella densa
Xanthoparmelia chlorochroa
Cladonia spp.

Nomenclature follows Moss, E.H. (1994) *The flora of Alberta.* University of Toronto Press, Toronto ON.

APPENDIX F. COMPLETE LIST OF VASCULAR SPECIES AND AUTHORITIES

Scientific Name	Authority	Common Name
Achillea millefolium	L.	Yarrow
Agropyron cristatum	(L.) Gaertn.	Crested wheatgrass
Agropyron subsecundum	(Link) A.S. Hitchc.	Awned wheatgrass
Agrostis scabra	Willd.	Tickle grass
Allium textile	Nels. & Macbr.	Prairie onion
Amaranthus retroflexus	L.	Red-root pigweed
Androsace septentrionalis	L.	Fairy candelabra
Anemone patens	L.	Prairie crocus
Antennaria aprica	Greene	Pussy toes
Antennaria dimorpha	(Nutt.) T. & G.	Pussy toes
Arabis retroflexus	(Graham) Rydb.	Reflexed rock-cress
Arnica fulgens	Pursh	Arnica
Artemisia cana	Pursh	Silver sagebrush
Artemisia frigida	Willd.	Fringed sage
Artemisia ludoviciana	Nutt.	Prairie sage
Aster ericoides	L.	Tufted white prairie aster
Aster laevis	L.	Smooth aster
Astragalus bisulcatus	(Hook.) A. Gray	Two-grooved milk vetch
Astragalus missouriensis	Nutt.	Purple milk vetch
Bouteloua gracilis	(HBK) Lag.	Blue grama
Bromus tectorum	L.	Cheatgrass
Calamagrostis montanensis	Scribn.	Prairie reed grass
Campanula rotundifolia	L.	Harebell
Capsella bursa-pastoris	(L.) Medic.	Shepherd's purse
Carex eleocharis	Bailey	Low sedge
Carex pensyllvanica	Lam.	Sun-loving sedge
Centaurea spp.	L.	Knapweed
Cerastium arvense	L.	Mouse ear chickweed
Chenopodium album	L.	Lamb's quarters
Chenopodium leptophyllum	(Nutt. ex. Moq.) S. Wats.	Narrow-leaved goosefoot
Cirsium arvense	(L.) Scop.	Canada thistle
Cirsium flodmannii	(Rydb.) Arthur	Flodman's thistle
Crepis tectorum	L.	Annual hawk's beard
Deschampsia caespitosa	(L.) Beauv.	Tufted hair grass
Descurainia sophia	(L.) Webb	Flixweed
Draba nemorosa	L.	Low whitlow grass
Elymus junceus	Fisch.	Russian wild rye
Elymus lanceolatus	(Hook.) Scribn.	Northern wheatgrass
Epilobium angustifolium	L.	Fire weed
Epilobium paniculatus	Nutt. ex. T. & G.	Willow herb
Erigeron caespitosus	Nutt.	Tufted fleabane
Erigeron candadensis	L.	Horseweed
Erucastrum gallicum	(Willd.) Schulz	Yellow dog mustard
Euphorbia esula	L.	Leafy spurge
Euphoribia glyptosperma	Engelm.	Thyme-leaved spurge
Eurotia lanata	(Pursh) Moq.	Winterfat
Festuca scabrella	Torr.	Plains rough fescue

Scientific Name	Authority	Common Name
Festuca saximontana	Rydb.	Sheep's fescue
Galeopsis tetrahit	L.	Hemp nettle
Geum triflorum	Pursh	Three flowered avens
Grindelia squarrosa	(Pursh) Dunal	Gumweed
Gutierreza sarothrae	(Pursh) Britt. & Rusby	Broomweed
Helicotrichon hookeri	(Scribn.) Henr.	Hooker's oat grass
Heterotheca villosa	(Pursh) Shinners	Hairy golden aster
Hordeum jubatum	L.	Foxtail barley
Kochia scoparia	(L.) Schrad.	Summer cypress
Koeleria macrantha	(Ledeb.) J.A. Schultes	June grass
Lapulla occidentalis	(S. Wats.) Greene	Beggar ticks
Lappula squarrosa	(Retz.) Dumort	Blue bur
Lepidium densiflorum	Schrad.	Lemon peppergrass
Liatris punctata	Hook.	Dotted blazing star
Linum lewisii	Pursh	Wild blue flax
Lygodesmia juncea	(Pursh) D. Don	Skeleton weed
Mammilaria vivipara	(Nutt.) Haw.	Ball cactus
Melilotus officinale	(L.) Lam.	Yellow sweet clover
Medicago sativa	L.	Alfalfa
Monolepis nuttaliana	(Schultes) Greene	Spear-leaved goosefoot
Muhlenbergia cuspidata	(Torr.) Rydb.	Prairie muhly
Oenothera nuttalii	Sweet	White evening primrose
Opuntia fragilis	(Nutt.) Haw.	Brittle prickly pear
Opuntia polyacantha	Haw.	Prickly pear
Orthocarpus luteus	Nutt.	Owl's clover
Oxytropis sericea	Nutt.	Early yellow loco weed
Pascopyrum smithii	Rydb.	Western wheatgrass
Penstemon procerus	Dougl. ex. Grah.	Slender blue beard tongue
Phlox hoodii	Richards.	Moss phlox
Plantago major	L.	Common plantain
Plantago patagonica	Jacq.	Wooly plantain
Poa juncifolia	Scribn.	Alkali bluegrass
Poa pratensis	L.	Kentucky bluegrass
Poa sandbergii	Vasey	Sandberg's bluegrass
Polygonum aviculare	L.	Prostrate knotweed
Polygonum convolvulus	L.	Wild buckwheat
Polygonum lapathifolium	L.	Pale smart weed
Potentilla pensyllvanica	L.	Prairie cinquefoil
Psoralea lanceolata	Pursh	Scurf pea
Pseudoregneria spicata	(Pursh) Scribn. & Smith	Bluebunch wheatgrass
Ratibida columnifera	(Nutt.) Wooton & Standl.	Prairie coneflower
Rosa acicularis	Lindl.	Prickly rose
Rumex crispus	L.	Curled dock
Salsola kali	L.	Russian thistle
Schedonardus paniculatus	(Nutt.) Trel.	Tumble Grass
Selaginella densa	Rydb.	Little clubmoss
Silene noctiflora	L.	Night-flowering catch-fly
Solanum triflorum	Nutt.	Wild tomato
Solidago missouriensis	Nutt.	Low goldenrod

Scientific Name	Authority	Common Name
Sonchus arvensis	L.	Perennial sow thistle
Sphaeralcea coccinea	(Pursh) Rydb.	Scarlet mallow
Sporobolus cryptandrus	(Torr.) A. Gray	Sand dropseed
Stellaria media	(L.) Cyrill.	Common chickweed
Stipa comata	Trin. & Rupr.	Needle and thread
Stipa curtiseta		Porcupine grass
Stipa viridula	Trin.	Green needle grass
Symphoricarpos occidentalis	Hook.	Western snowberry
Taraxacum officinale	Weber	Dandelion
Thermopsis rhombifolia	(Nutt.) Richards	Golden bean
Thlaspi arvense	L.	Stinkweed
Tragopogon dubius	Scop.	Goat's beard
Urtica dioica	L.	Stinging nettle
Verbena bracteata	Lag. & Rodr.	Sand bladderpod
Vicia americana	Muhl.	American vetch