

**PATTERNS AND PROCESSES OF EXOTIC PLANT INVASIONS IN RIDING
MOUNTAIN NATIONAL PARK, MANITOBA, CANADA**

by

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ABSTRACT

Invasive exotic species threaten the biodiversity and function of native ecosystems. Existing models, attempting to predict and control successful invaders, often emphasize isolated stages of in their life history and fail to formalize interactions between exotic species and recipient environments. In order to elucidate key mechanisms in the success of select invaders, I investigated the role of dispersal, establishment, proliferation, and persistence in their threat to natural areas. Focusing on Riding Mountain National Park, Manitoba, Canada, I integrated the native climatic range and biological traits of 251 exotic vascular plants reported inside and outside the park. Based on their climatic range in Europe, 155 among 174 exotic plant species absent from the Park were predicted to establish within its boundaries; among these, 40 clonal perennials were considered the highest threat to the Park's biodiversity. Focusing on smooth brome (*Bromus inermis* Leyss.), a Eurasian perennial, threatening the structure and function of native prairies throughout the Great Plains, I extended my research to investigate the role of dispersal, establishment, proliferation, and persistence in characterizing its threat to the endemic diversity of northern fescue prairies, protected within Riding Mountain National Park. Patterns of smooth brome invasions were contingent on the type of propagules dispersed. The shallow dispersal gradient of individual florets combined with the steeper gradient of panicles and spikelets suggested that smooth brome is capable of simultaneously invading along dense fronts as well as by establishing isolated foci. While low correlations between the number of dispersed seeds and their recruitment suggested post-dispersal transport, seedling establishment remained contingent on prairie diversity. Seedling biomass increased with declining plant diversity, however, its impact depended

on the availability of soil nitrogen. As a result, disturbed areas, preserving the root function of native plants, resisted smooth brome establishment. Even though low nitrogen contributed to a decline in seedling biomass, physiological integration between ramets facilitated their vegetative proliferation in low resource environments. Despite its rapid establishment and proliferation, smooth brome productivity declined at the center of invading clones. Although field and greenhouse observations failed to implicate soilborne pathogens, reasons for the observed decline remain unresolved. My research demonstrates that while Riding Mountain National Park and other natural areas in western Canada will continue to be impacted by exotic plants, integrating key stages in their life history provides an important conceptual framework in predicting their threat to natural areas and prioritizing management.

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To Anisia & My Parents

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Otfinowski, R., N. C. Kenkel, P. Dixon and J. F. Wilmschurst. 2007. Integrating climate and trait models to predict the invasiveness of exotic plants in Canada's Riding Mountain National Park. Canadian Journal of Plant Science 87: 1001-1012.

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Otfinowski, R. and N. C. Kenkel. 2008. Clonal integration facilitates the proliferation of smooth brome clones invading northern fescue prairies. Plant Ecology. DOI 10.1007/s11258-008-9428-8*

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CHAPTER 1: INTRODUCTION

1.1 The historical and ecological contexts of biological invasions

The cornerstone of biological invasions is the breakdown of natural biogeographical realms and their barriers, spurred by expanding economic and socio-cultural forces (Elton 1958). Exotic organisms, defined as those introduced intentionally or unintentionally by human agents (Usher 1988), have always been associated with human travelers (di Castri 1989). In central Europe, the temporal sequence of plant introductions reflects the historical scale of geographic exchange and includes cultivated plants, followed by ornamentals, and accidental exotics (Pyšek et al. 2003). More rapid introductions are more typical of recently colonized areas. In the new world, the higher number of exotic species is characteristic of the intense immigration of European species into newly explored areas (di Castri 1989, Lonsdale 1999).

In the last 100 years, the geographic scope, frequency, and number of exotic species involved in such introductions have grown enormously as a consequence of expanding transport and commerce (Mack et al. 2000). Annually, 3000 exotic plants quarantined by the Animal and Plant Health Inspection Service from cargo and baggage at ports of entry into the United States, and the vascular flora of North America consists of over 3,700 exotic species (> 17 % of the vascular flora; Kartesz 1999). The direct and indirect costs of exotic invasions on agriculture, forestry, and natural ecosystems in the United States exceed \$100 billion per year, including around \$35 billion from exotic plants alone (Pimentel et al. 2000). Economic costs often include an “invisible tax”, estimated as high as \$34.5 billion for 16 nuisance exotic species in Canada (Colautti et al. 2006).

Globally, few habitats remain free of exotic species, and a number of these pose serious threats to natural communities (Heywood 1989, Mack et al. 2000). In natural reserves, greater numbers of exotic species are often correlated with older settlement histories, higher numbers of visitors, and larger regional populations (Lonsdale 1999, McKinney 2002). However, compared with plant diseases and insect pests, the subtle losses caused by exotic plant infestations have traditionally attracted less attention, even in agriculture (Evans 2002). In natural areas, the most serious consequences of exotic plant invasions are seen in the compromised ecological variety (Usher 1986, 1988). As a result, the economic and experiential losses invoked by most definitions of weeds (Evans 2002) may be extended to exotic plants that establish outside cultivation, compromising the structure and function of native ecosystems.

The threat posed by exotic plants depends on their dispersal, establishment and proliferation and the nature of their impacts on native communities (Williamson and Fitter 1996). As a consequence of the population, community, and landscape-level interactions between exotic species and their novel habitats, introduced exotic species may become transient (eventually extirpated), naturalized (co-existing with native flora), or invasive (producing detrimental effects; Mack 1996). Often, introduced exotic species undergo a series of transitions before becoming invasive. This lag period may be the result of a delay required for hybridization between native and exotic species or between disparate source populations, which may serve as a stimulus for the evolution of traits (e.g. dispersal ability) coincident with invasiveness (Lewis and Kareiva 1993, Ellstrand and Schierenbeck 2000). In other cases, slow population growth may delay expansion

until a critical density required for dispersal is generated (Mack 1981, Lewis and Kareiva 1993).

Given the complex ecological contexts facilitating successful invasions, exotic species have become a tool with which to examine controls over community structure and ecosystem processes (D'Antonio and Kark 2002) and to study an array of contemporary ecological and evolutionary processes (Mack 1996). For example, the outcomes of exotic species introductions provide invaluable information about the assembly of biotic communities and the role of evolutionary adaptations in range expansions (Harper 1977, Mack et al. 2000).

1.2 Objectives

Successful invasions describe the dispersal, establishment and the proliferation of species in a new range such that their impacts on the environment are detrimental (Lee 2002, Mack 2003). Despite the large number of exotic species introduced into new environments, fewer than 10 % establish to cause ecological change, altering the character, condition, form or nature of ecosystems over substantial areas (Williamson and Fitter 1996, Colautti and MacIsaac 2004, Larson 2005). The main objective of my research includes the integration of ecological data to facilitate the prediction and management of exotic invaders in natural areas. Focusing on Riding Mountain National Park in Manitoba, Canada, a model area of high native biodiversity, I explore mechanisms of exotic plant invasions typical of prairie ecosystems in western Canada, characterized by the recent and intense impacts of settlement and a mosaic of natural and anthropogenic disturbances.

Within the northern fescue prairies, characteristic along the northern and northwestern fringes of the North American mixed prairie ((Blood 1966, Coupland 1992) and protected inside the boundaries of Riding Mountain National park, my experiments focused further on invasions of smooth brome (*Bromus inermis* Leyss.), a Eurasian perennial threatening the structure and function of prairie remnants throughout the Great Plains. I direct my research towards key stages in the life history of exotic invaders. Considering the dispersal, establishment, clonal proliferation, and long-term persistence of smooth brome invasions in northern fescue prairies, I aim to elucidate the ecological contexts that determine both the invasiveness of smooth brome, as well as the invasibility of northern fescue prairie communities. Despite the prevalence of exotic species in most regional floras, few studies have integrated multiple stages in their life history. It is my goal to demonstrate that such an understanding is critical to the prediction and management of biological invasion in natural areas.

1.3 Thesis structure

This thesis is comprised of six manuscripts, exploring first the potential threats posed by exotic vascular plants to natural areas in western Canada, and second, investigating the role of dispersal, disturbance, clonal reproduction, and soilborne pathogens in the dispersal, establishment, proliferation and persistence of smooth brome clones invading northern fescue prairies. All chapters have been compiled as manuscripts and all have been published or submitted for review.

The opening manuscript [Otfinowski, R., N. C. Kenkel, P. Dixon and J. F. Wilmschurst. 2007. Integrating climate and trait models to predict the invasiveness of

exotic plants in Canada's Riding Mountain National Park. Canadian Journal of Plant Science 87: 1001-1012] explores the role of climate and biological traits in the prediction of exotic plant invasiveness and the prioritization of exotic plant monitoring and management in western Canada. Providing a context for more detailed experiments, using smooth brome invasion of northern fescue prairies as a model for exotic invasions of natural areas, the following manuscript (Otfinowski, R., N. C. Kenkel and P. M. Catling. 2007. The biology of Canadian weeds. *Bromus inermis* Leyss. Canadian Journal of Plant Science 87: 183-198.), presents a comprehensive review of its biology, emphasizing the threats posed by smooth brome to prairie ecosystems across the Great Plains. The remaining four manuscripts explore the combined role of dispersal, disturbance, vegetative growth, and soilborne pathogens in the invasiveness of exotic plants and the invasibility of native communities. The first [Otfinowski, R., N. C. Kenkel and R. C. Van Acker. Reconciling seed dispersal and seedbank observations to predict the invasion patterns of smooth brome (*Bromus inermis*) in a northern prairie. Invasive Plant Science and Management DOI: 10.1614/IPSM-08-066.1], demonstrates the impact of seed dispersal on the patterns of smooth brome invasion. Exploring the role of disturbance on the invasiveness of northern fescue prairies, the following manuscript [Otfinowski, R. and N. C. Kenkel. Covariance between disturbance and soil resources dictates the invasibility of northern fescue prairies. Biological Invasions (*In review*)], provides an important context in the management and restoration of native prairies. The invasiveness of exotic plants is contingent on their proliferation. The third manuscript [Otfinowski, R and N. C. Kenkel. Clonal integration facilitates the proliferation of smooth brome clones invading northern fescue prairies. Plant Ecology DOI:

10.1007/s11258-008-9428-8], explores whether clonal growth, characteristic of the majority of successful invaders of natural areas, facilitates the proliferation of smooth brome invading northern fescue prairies. Finally, the long-term persistence of exotic invaders is considered in the last manuscript [Otfinowski, R., N. C. Kenkel and M. Tenuta. Lack of evidence for the role of soilborne pathogens in the decline of smooth brome invading northern fescue prairies. *Oecologia (In review)*].

The leading author developed the experimental designs, collected and analyzed all data, and wrote each manuscript. Thus, this thesis and the six related manuscripts are original contributions by Rafael Otfinowski. The comments, suggestions, and logistical help of the coauthors have been greatly appreciated and have significantly improved the quality of the research. The contribution of P. Dixon in mapping the potential ranges of exotic plants in North America and P. M. Catling in reviewing specimens of *Bromus inermis* and mapping their distribution in Canada (Figure 3.2) is gratefully acknowledged.

CHAPTER 2: INTEGRATING CLIMATE AND TRAIT MODELS TO PREDICT THE INVASIVENESS OF EXOTIC PLANTS IN CANADA'S RIDING MOUNTAIN NATIONAL PARK.

2.1 Abstract

Invasive exotic species threaten the biodiversity and function of native ecosystems. Existing models, attempting to predict successful invaders, often emphasize isolated stages of biological invasions and fail to formalize interactions between exotic species and recipient environments. By integrating the native climatic range and biological traits of exotic vascular plants reported inside and outside Riding Mountain National Park, Manitoba, Canada, I present a model where invasion risk is predicted using the likelihood of establishment and proliferation of exotic species. Exotic vascular plants constituted 11.5 % (77 / 669) of the total vascular flora of Riding Mountain National Park and approximately 14.2 % (202 / 1418) of the flora of Manitoba. Based on their climatic range in Europe, 155 among 174 exotic species absent from the Park, including those found in Manitoba and other natural areas in Canada, were predicted to establish within its boundaries. Among the biological traits of exotic plants, perenniality and vegetative growth correctly identified 61 % of documented invaders of natural areas in Canada and helped to further define a subset of 40 exotic plants with the highest potential to proliferate within the Park's natural areas. Among these, eleven are still absent from inside its boundaries and 17 are not yet reported in Manitoba. My results demonstrate that Riding Mountain National Park and natural areas in western Canada will continue to be impacted by exotic vascular plants. By integrating establishment and proliferation,

key stages in the progress of biological invasions, my model offers a synthetic approach to the prediction and management of biological invasions inside natural areas; such integration is critical to the protection of Canada's endemic biodiversity.

2.2 Introduction

The cornerstone of biological invasions is the breakdown of natural biogeographical regions (Elton 1958). Exotic organisms, defined as those introduced intentionally or unintentionally by human agents (Usher 1988), have always been associated with human travelers (di Castri 1989). In the last 100 years, the geographic scope, frequency, and number of exotic species have grown enormously as a consequence of expanding travel and commerce (MacIsaac et al. 2001). Globally, few habitats remain free of exotic species, and many pose serious threats to the biodiversity and function of native ecosystems (Mack et al. 2000, Ricciardi 2007). Exotic invaders, or those species whose introduction or spread threaten the environment, economy, or society (Environment Canada 2004), pose a particular threat to natural reserves, where protection of native biodiversity requires the prediction and control of a growing number of potential invaders (Palmer 2005).

Despite numerous attempts, predicting invaders has produced few generalizations (Henderson et al. 2006). Published models, predicting invasiveness can be broadly divided into those based on climate and plant traits. Climate models emphasize correlations between the native and introduced environments of exotic species. In many cases, applications of this approach have successfully defined regions threatened by the expanding range of exotic invaders (Peterson 2003). Climate, however, does not solely

dictate geographic distribution. Other biological constraints, such as dispersal vectors, habitat requirements, competition, mutualisms, and the genetic structure of invading populations often restrict the range of potential invaders (Thuiller et al. 2006). As a result, the presumption of climate models that species' geographic distributions correspond with their fundamental niches has often been criticized (Pearson and Dawson 2003).

Emphasizing the importance of biological interactions, the traits of exotic species have alternatively been used to predict their invasiveness. Among characters most correlated with invasiveness, self-compatibility, fruit size, short and long-range seed dispersal, wide germination and growth requirements, prolific and intermittent seed production, vegetative growth, a short vegetative period, competitiveness, and defense against herbivores are most often cited (Richardson and Pyšek 2006). Despite their appeal, trait models have proven poor predictors of invasion (but see Rejmánek and Richardson 1996, Herron et al. 2007). For example, even though exotic plants often possess traits that distinguish them from the native species they displace (Andersen 1995, Rejmánek 2000, Kolar and Lodge 2001), successful invaders represent a diversity of plant families and possess a wide range of life forms and breeding systems (Crawley 1987). As a result, other mechanisms, such as the biodiversity of the invaded community, absence of predators, physical disturbance and propagule pressure have been invoked to account for the success of exotic invaders (Colautti et al. 2006, Thuiller et al. 2006).

Despite their individual shortcomings, climate and trait models highlight important elements in the life history of exotic organisms. By integrating both

approaches, I conceptualized predicting potential invaders using a series of stages (*sensu* Williamson and Fitter 1996). I hypothesized that within natural areas, the threat of invasion corresponds to the potential of exotic species to establish and proliferate within recipient plant communities. Based on this approach, I sought to construct a predictive model to prioritize the monitoring and management of exotic plants in Riding Mountain National Park, Manitoba, Canada. My effort was motivated by the limited knowledge of the Park's exotic flora (but see Trottier 1986, Slogan 1997, Caners 1999) and by the increasing threat posed by exotic plants to Canada's endemic biodiversity (Canadian Endangered Species Conservation Council 2006).

2.3 Methods

2.3.1 Study area

Research was conducted in Riding Mountain National Park (50° 39' 00", - 99° 55' 48"), an area of 2,978 km² in Western Canada. Most of the Park lies in the Mixedwood Section of the Boreal Forest Region (Rowe 1972) and consists of large areas of rolling upland (550 – 640 m), underlain by glacial tills, as well a section of the Manitoba Escarpment, characterized by exposed Cretaceous shale (Lang 1974). Small areas of fescue and mixed prairies, as well as western extensions of bur oak (*Quercus macrocarpa* Michx.) forests are also protected within the Park's boundaries (Cody 1988). The region is characterized by mean annual precipitation of 450 – 500 mm and a growing season of 168 – 173 days; mean temperatures range between -18°C in January and 18°C during July (Leeson et al. 2005).

The exotic flora of Riding Mountain National Park reflects its long human history. Before its establishment in 1933, logging, cattle grazing, and haying were important to the local economy and created opportunities for the introduction of exotic species (Trottier 1986). Continued agricultural expansion along the Park's boundaries, increasing visitation, and the construction of roads have escalated this trend. Today, the most intensively used area of the Park centers on the town of Wasagaming (seasonal pop. 4,000), where campgrounds, accommodations, and services are offered to the 250,000 annual visitors (Parks Canada 1996). While preliminary surveys of the Park's exotic flora have focused on the fescue prairies (Trottier 1986, Slogan 1997, Caners 1999), its exotic species burden has not been reviewed prior to my study.

2.3.2 Model design

I based my model on a summary of exotic plants found in Riding Mountain National Park and areas outside its borders. Lists of exotic species were compiled using published literature and separated into three categories: (1) exotic species found in Riding Mountain National Park (Cody 1988); (2) exotic species found in the province of Manitoba but absent from the Park (Scoggan 1957, Leeson et al. 2005); (3) exotic species that are invasive species in natural areas in other regions of Canada (White et al. 1993, Haber 1996, Catling and Mitrow 2005). I confined, my analysis to Eurasian vascular species, the predominant element in Canada's exotic flora (Haber 2002, McClay et al. 2007). Using information about each species' climatic range, biological traits, and habitat preferences, exotic plants were assigned into five classes of invasion risk based on their potential to establish and proliferate within the Park's natural habitats (Fig. 2.1).

The risk of establishment of exotic plants in Riding Mountain National Park was predicted using the climatic range of each species in Europe, estimated using long-term environmental data from 79 climate stations (Walter et al. 1975), distributed across 39 geographic regions of Europe (Tutin et al. 1964-80). Depending on the physical area of each region I selected up to four evenly distributed stations to represent its climate (Fig. 2.2). Plants found in regions whose mean annual temperature and precipitation matched that of Riding Mountain National Park (Fig. 2.3) were considered more likely to establish within its boundaries and assigned to a higher class of invasion risk. I used principal component analysis (Legendre and Legendre 1998) to eliminate the multicollinearity inherent to large sets of climatic variables (Metzger et al. 2005, Thuiller et al. 2006). As a result, a more complex model, including the length of the growing and wet seasons and the number of frost-free and winter months produced similar results and is not presented here.

Predictions of my climate-matching model, based on regional means of annual temperature and precipitation, were validated using GARP, a genetic algorithm model integrated with global environmental databases that include summaries of climate, topography, solar radiation, and substrate (Elith et al. 2006). I confined my comparisons to a subset of 100 exotic plants, randomly selected among 251 species in my database, including those found in Riding Mountain National Park and areas outside its boundaries. For each species, I built 100 models predicting their potential range in North America using all rule types and default environmental variables (0.001 convergence, 70 % training data set; Stockwell and Peters 1999). I selected a subset of 20 best models for each species according to criteria proposed by Anderson et al. (2003) and used these to

compile single mean projections of each species' predicted North American range using ArcView 9.2 (ESRI). These, illustrating the potential climatic affinity of each species with Riding Mountain National Park, were used to predict their potential to establishment within the Park's boundaries. Finally, I used chi-squared analysis (Zar 1999) to test the hypothesis that the predictions of my climate-matching model were not significantly different from those generated using GARP.

The risk of proliferation of exotic plants within natural areas of Riding Mountain National Park was predicted using their biological traits (Fig. 2.1). Based on published floras, I collected information about the perenniality, woody habit, vegetative growth, flowering period, and fruit type of each species in my database (Scoggan 1957, Great Plains Flora Association 1986, Cody 1988, Gleason and Cronquist 1991). I eliminated redundancies among trait variables using principal component analysis (Legendre and Legendre 1998) and used the ordination scores of each species from the first three principal component axes in multiple logistic regression models to find independent sets of trait variables correlated with the invasiveness of exotic plants in Canada's natural areas. Using 251 species in my database, including 106 documented invaders (White et al. 1993, Haber 1996, Catling and Mitrow 2005), I tested the null hypothesis that the invasion of natural areas by exotic plants is independent of their biological traits.

The potential threat posed by exotic plants to the endemic diversity and structure of natural areas inside Riding Mountain National Park was further based on the habitat preferences of each species (Fig. 2.1). Exotic plants capable of proliferating within natural habitats, including prairies, wetlands, shorelines, and woodlands, were considered a higher management priority than those confined to ruderal habitats, including gardens,

lawns, roads, trails, and waste areas (Scoggan 1957, Great Plains Flora Association 1986, Cody 1988, Gleason and Cronquist 1991).

2.4 Results

2.4.1 Climate

Exotic vascular plant species constituted 11.5 % (77 / 669) of the total vascular flora of Riding Mountain National Park, and approximately 14.2 % (202 / 1418) of the flora of Manitoba. The Park's climate closely corresponded with that of central and northern Russia and northern Scandinavia (Fig. 2.3). As a result, all exotic plants whose European range included Sweden, Iceland, and areas of central and northern Russia, were considered capable of establishing inside the Park. This condition was met by all exotic species in its flora (Table 2.1).

Outside the Park's boundary, only twelve of the 125 exotic plants found in Manitoba did not match the Park's climate (Table 2.1). Many of these, including green pigweed (*Amaranthus hybridus* L.), yellow star thistle (*Centaurea solstitialis* L.), stink grass [*Eragrostis cilianensis* (All.) E. Mosher], and flower-of-an-hour (*Hibiscus trionum* L.), are confined to southern and central areas of Europe (Tutin et al. 1964-80). Only two species in this group, including spotted and Russian knapweed (*Centaurea biebersteinii* DC. and *C. repens* L.), are invasive in natural areas in Canada (Haber 1996). As predicted, their range in North America is confined to more arid regions of western Canada and the northern intermountain areas of the United States (Frankton and Mulligan 1970, DiTomaso 2000). Matching the climate of Riding Mountain National Park and geographic regions in Europe helped identify a high number of exotic plants, currently

absent from Manitoba, with the potential to establish within its boundaries. Among 49 species invasive within natural areas in other regions of Canada, only seven did not match the Park's climate (Table 2.1). Of the remaining 42 species still absent from Manitoba, many, including garlic mustard [*Alliaria petiolata* (M. Bieb.) Cavara & Grande], continue to expand their range in North America (Welk et al. 2002).

Compared with the genetic algorithm model (GARP), matching regional climates using the means of annual temperature and precipitation identified a greater number of exotic species with the potential to establish in Riding Mountain National Park. According to this method, only two among the 100 randomly selected exotics were not expected to establish within the Park. In contrast, 35 species were less than 50 % likely to establish inside the Park according to GARP (Table 2.2). Despite its conservative predictions, higher establishment risk categories frequently excluded exotic plants already reported inside the Park. For example, species with a risk of establishment less than 60 % included several invaders of the Park's natural areas such as smooth brome (*Bromus inermis* Leyss.; Table 2.2).

2.4.2 Traits

Logistic regression of principal component scores, separating along the first ordination axis clonal, perennial species from annuals (Table 2.3), correctly identified 76.6 % of non-invasive and 61 % of the invasive plants of natural areas in Canada, yielding an overall correct classification rate of 70 % ($X^2 = 58.361$, $P < 0.001$). Inside Riding Mountain National Park, a large number of clonal exotics consisted of escaped forage species. For example, crested wheatgrass [*Agropyron cristatum* (L.) Gaertn.], smooth

brome (*Bromus inermis*), and Canada and Kentucky bluegrass (*Poa compressa* L., *P. pratensis* L.) continue to be cultivated in areas surrounding the Park (Table 2.1). Also in this group were weeds of overgrazed rangelands such as Canada thistle [*Cirsium arvense* (L.) Scop.], leafy spurge (*Euphorbia esula* L.) and toadflax (*Linaria vulgaris* Hill.). Clonal perennials also included caragana (*Caragana arborescens* Lam.), which threatens the Park's woodlands.

The integration of climate and trait models helped identify the proliferation risk posed by exotic species currently absent from Riding Mountain National Park. For example, the Park's wetlands remain vulnerable to purple loosestrife (*Lythrum salicaria* L.), creeping yellow cress [*Rorippa sylvestris* (Crantz) Bess.], European milfoil (*Myriophyllum spicatum* L.) and flowering rush (*Butomus umbellatus* L.), clonal perennials that continue to expand their range in western Canada (Frankton and Mulligan 1970, Lindgren 2003, Olson 2004). According to my model, invaders of natural areas in other regions of Canada, including frog-bit (*Hydrocharis morsus-ranae* L.) and curly pondweed (*Potamogeton crispus* L.), are also capable of establishing and proliferating inside the Park (Table 2.1).

Distinguishing between natural and ruderal habitats also helped prioritize the monitoring and management of exotic plants found in Riding Mountain National Park. For example, escaped ornamentals confined to roads, gardens, or waste areas, including bouncing bet (*Saponaria officinalis* L.), sneezeweed (*Achillea ptarmica* L.), and goutweed (*Aegopodium podagraria* L.), were considered a lower threat to the Park's native diversity (Table 2.1). Also common in these habitats were weedy perennials, such as meadow buttercup (*Ranunculus acris* L.), ox-eye daisy (*Leucanthemum vulgare* Lam.),

quackgrass [*Elytrigia repens* (L.) Nevski], tansy (*Tanacetum vulgare* L.), as well as Dalmatian toadflax [*Linaria dalmatica* (L.) Miller] and creeping buttercup (*Ranunculus repens* L.) reported outside the Park boundary. Threats posed by these species likely depend on the extent and persistence of disturbances inside the Park (Olson and Wallander 1999, Rose and Hermanutz 2004, Hendrickson et al. 2005).

The majority of exotic species inside and outside Riding Mountain National Park were considered a moderate threat to its biodiversity. Among these, most were annuals, confined to disturbed areas (Table 2.1). In this category, sweet clovers [*Melilotus alba* Medic., *M. officinalis* (L.) Pallas], burdock (*Arctium minus* Schk., *A. tomentosum* Miller), and scentless false mayweed [*Tripleurospermum perforata* (Merat) M. Lainz] pose an ephemeral threat to prairies, stream banks, and open woodlands (Frankton and Mulligan 1970). Among species absent within its boundaries, this group includes red bartsia [*Odontites serotina* (Lam.) Dumort.], as well as diffuse knapweed (*Centaurea diffusa* Lam.), nodding thistle (*Carduus nutans* L.), and downy brome (*Bromus tectorum* L.), whose range in western Canada continues to expand (Frankton and Mulligan 1970, Douglas et al. 1990, Manitoba Agriculture Food and Rural Initiatives 2003). Moderately invasive species also included non-clonal perennials confined to ruderal habitats. Most species in this category, such as common dandelion (*Taraxacum officinale* Weber), timothy (*Phleum pratense* L.), and common purslane (*Portulaca oleracea* L.) are confined to trails, ditches, and campgrounds and pose little threat to the Park's natural areas (Cody 1988).

Low risks of proliferation were most often associated with weedy, agricultural species (Table 1). In the absence of soil disturbance, plants in this category, including

field pennycress (*Thlaspi arvense* L.), shepherd's purse [*Capsella bursa-pastoris* (L.) Medic.], and lamb's quarters (*Chenopodium album* L.) do not threaten native biodiversity. As expected, a high diversity of annual exotic species was found outside the Park (Table 2.1).

2.5 Discussion

2.5.1 Predictions

Climate matching provided a rapid method of predicting the potential establishment of exotic plant species absent from Riding Mountain National Park. Among 174 exotic plants absent from the Park, but found in Manitoba or natural areas in other regions of Canada, only 19 were not expected to establish in the Park. Several among these, including garlic mustard (*Alliaria petiolata*), purple loosestrife (*Lythrum salicaria*), creeping yellow cress (*Rorippa sylvestris*), European milfoil (*Myriophyllum spicatum*) and flowering rush (*Butomus umbellatus*) continue to expand their range in North America (Frankton and Mulligan 1970, Lindgren 2003, Olson 2004, Welk et al. 2002).

While climate matching based on regional means of temperature and precipitation offered a simple means of identifying potential invaders, predictions based on this method likely exaggerate the number of exotic species threatening the Park's natural areas. Despite the sophistication of competing approaches (Elith et al. 2006), climate models frequently over-predict potential species' distributions by identifying habitats to which they are unable to disperse (Dormann 2007). Other factors, including the strength of dispersal vectors, the importance of mutualisms, the resilience of native communities, and the availability of suitable establishment areas often constrain the geographic range

of species (Peterson and Vieglais 2001, Araújo and Guisan 2006, Colautti et al. 2006). While my model cannot predict these and other interactions, incorporating the biological traits of exotic species offered an effective method of anticipating potential biotic interactions relevant to the scale of native plant communities (Renne et al. 2006). My findings, emphasizing the role of perenniality and vegetative growth in the invasion of natural areas, are consistent with reports from other regions (Andersen 1995, Pyšek 1997, Reichard and Hamilton 1997, Acosta et al. 2006, Cadotte et al. 2006).

2.5.2 Limitations

Predictions of my climate-matching model depend on the accuracy of native range distributions. Poor accuracy of distributional data can lead to an under-representation of species limits and result in higher invasion risks from species that appear outside a climatic area (Peterson and Vieglais 2001, Welk et al. 2002). The underestimation of the fundamental niches of exotic species may help explain the conservative predictions of GARP (Anderson et al. 2003). Although more extensive species' distribution data, may have reduced the disparity between my climate-matching model and GARP, the choice of environmental variables may also account for the observed differences (Stockwell and Peterson 2002).

Equally important in predicting species' establishment risks may be the origins of founder populations (Wilson et al. 2007). Widespread species often show local adaptations and modeling these sub-populations together may overestimate their ecological breadth (Stockwell and Peterson 2002). For example, several exotic plants currently absent from Riding Mountain National Park, including European birch (*Betula*

pendula Roth), orchard grass (*Dactylis glomerata* L.) and scots pine (*Pinus sylvestris* L.), are characterized by regional adaptations (Sannikov et al. 1997, Li et al. 2002, Annese et al. 2006). It is possible that, despite their wide distribution in Europe, the introduced climatic ecotypes may not be well adapted to the environments of Riding Mountain National Park. In such cases, the plasticity, genetic diversity, and rapid adaptation of introduced populations may further determine their threat to natural areas (Sexton et al. 2002, Roy et al. 2000). Despite these and other potential limitations, including the potential impacts of global warming, climate models provide an important predictive tool, the results of which must be thoughtfully interpreted in the context of their application (Fielding and Bell 1997).

My findings must be considered in the context of natural areas. For example, the separation of native and human disturbed habitats in my model reflects a bias towards the conservation of “natural” habitats such as prairies, wetlands, and woodlands. While inside natural reserves, this focus places a justifiable emphasis on the preservation of native biodiversity, human as well as natural disturbances often fragment protected areas, providing staging points for the proliferation of exotic species into undisturbed habitats (Underwood et al. 2004, Rose and Hermanutz 2004, Mandryk and Wein 2006). Equally important in the management of exotic invasions may be considerations of their suppression (D’Antonio and Meyerson 2002). For example, MacDougall et al. (2006) warned against the impacts of disturbance during the removal of exotic invaders.

2.5.3 *A new integrative method*

The likelihood of invasion is a function of the environment, an exotic organism's traits, and the nature of its impacts on native communities (Smith et al. 1999). Despite the large number of exotic species in most regional floras, the majority fail to become invaders and many simply contribute to local species richness (Rosenzweig 2001). The challenge of managing exotic organisms rests in our ability to predict and contain species posing the greatest threat to endemic biodiversity and the function of native ecosystems (Usher 1988, Underwood et al. 2004). Current models, emphasizing isolated stages of biological invasions, often fail to formalize interactions between exotic organisms and recipient environments that frequently determine the outcome of introductions (Dietz and Edwards 2006, Thuiller et al. 2006). Using combinations of climate and the biological traits of exotic plants, my model offers a synthetic approach to the prediction of invasions and the prioritization of their management inside natural areas.

I suggest that the contingent nature of biological invasions (*sensu* Puth and Post 2005), consisting of transitions between stages in the invasion process, likely accounts for the poor performance of most predictive models and the lack of general principles attributed to invasion biology (Colautti et al. 2006, Dietz and Edwards 2006). In order to resolve this impasse, I propose an approach integrating the characteristics of exotic plants, which enable them to establish and proliferate within native communities. I suggest that, within the context of natural areas, only plants capable of successfully completing these two life-history stages should be considered a threat to native biodiversity and warrant the highest management concern. My model demonstrates that Riding Mountain National Park and other natural areas in western Canada will continue

to be impacted by exotic plants. By integrating the native climatic range, biological traits, and habitat preferences of exotic species, my model offers a synthetic approach to the prediction and management of biological invasions inside natural areas; such integration is critical to the protection of Canada's endemic biodiversity.

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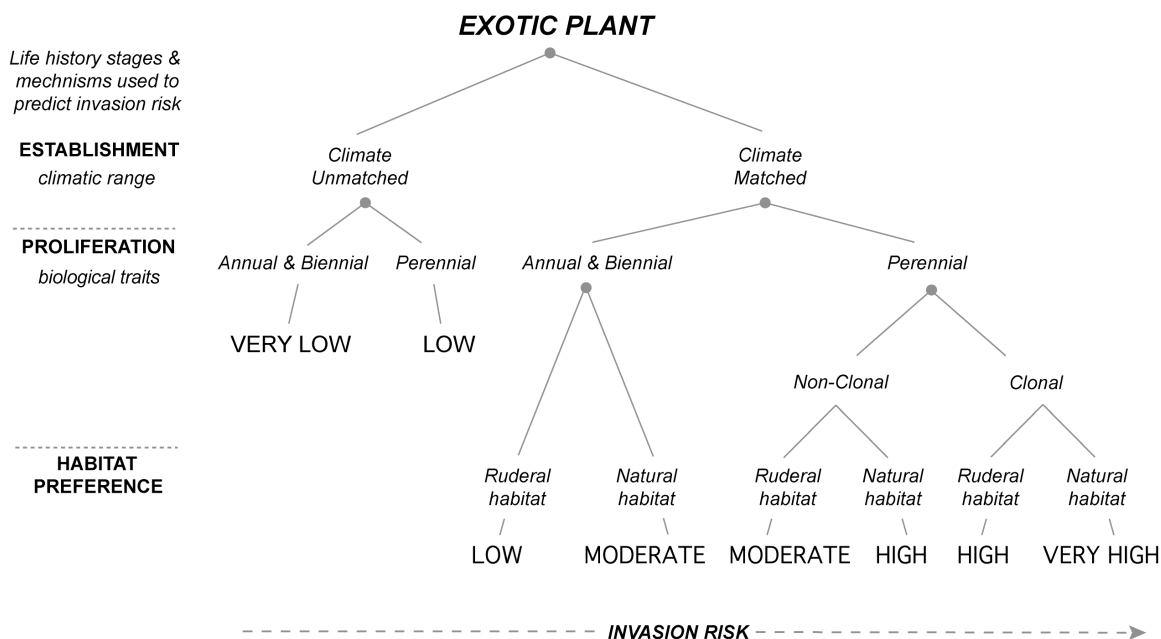


Figure 2.1 Conceptualized model for predicting the establishment and proliferation of exotic plants in natural areas and their threat to native biodiversity. Model was used to assign invasion risks to exotic vascular plant species found in Riding Mountain National Park and in areas outside its borders, including the province of Manitoba and natural areas in other regions of Canada. Risks of invasion were assigned using each species' climatic range, biological traits, and habitat preferences. Climatic range: higher invasion risks for exotic species whose geographic distribution matched the climate of Riding Mountain National Park; Biological traits: higher invasion risks for perennial exotic plants capable of vegetative growth; Habitat: higher invasion risks for exotic species capable of proliferating in the Park's natural habitats, including prairies, wetlands, shorelines, and woodlands; lower invasion risks for plants confined to ruderal habitats, including gardens, lawns, roads, trails, and waste areas, all of minor presence in the park.

Figure 2.2 The distribution of 79 climate stations across 39 geographic regions of Europe (Tutin et al. 1964-80) used to predict the climatic range of European exotic vascular plants threatening Riding Mountain National Park, Manitoba, Canada. Climate summaries according to Walter et al. (1975). Abbreviations: Al (Durazzo, Albania), Au (Wien, Austria), Az (Angra do Heroismo, Azores), Be (Brussel, Belgium), Bl (Palma de Mallorca, Balearic Islands), Br₁ (Cambridge, Britain), Br₂ (Liverpool, Britain), Br₃ (North Berwick, Scotland), Br₄ (Lerwick, Shetland Islands), Bu₁ (Sofia, Bulgaria), Bu₂ (Warna, Bulgaria), Co (Ajaccio, Corsica), Cr (Khania, Crete), Cz₁ (Praha, Czech Republic), Cz₂ (Arvavaralja, Czech Republic), Da (Vestervig, Denmark), Fa (Thorshavn, Faroe Islands), Fe₁ (Kuopio, Finland), Fe₂ (Sodankyla, Finland), Ga₁ (Rennes, France), Ga₂ (Dijon, France), Ga₃ (Toulouse, France), Ge₁ (München, Germany), Ge₂ (Frankfurt, Germany), Ge₃ (Hannover, Germany), Gr₁ (Athen, Greece), Gr₂ (Thessaloniki, Greece), Hb₁ (Cork, Ireland), Hb₂ (Valentia, Ireland), Hb₃ (Dublin, Ireland), He (Biel, Switzerland), Ho (Amsterdam, Netherlands), Hs₁ (Sevilla, Spain), Hs₂ (Zargoza, Spain), Hs₃ (Leon, Spain), Hu₁ (Budapest, Hungary), Hu₂ (Putnok, Hungary), Is₁ (Raufarhofn, Iceland), Is₂ (Reykjavik, Iceland), Is₃ (Teigahorn, Iceland), It₁ (Bologna, Italy), It₂ (Foggia, Italy), Ju₁ (Zagreb, Croatia), Ju₂ (Skopje, Macedonia), Ju₃ (Belgrade, Serbia and Montenegro), Lu (Evora, Portugal), No₁ (Oslo, Norway), No₂ (Trondheim, Norway), No₃ (Tromso, Norway), No₄ (Bronnysund, Norway), Pl₁ (Koszalin, Poland), Pl₂ (Racibòrz, Poland), Pl₃ (Radom, Poland), Rm₁ (Bukarest, Romania), Rm₂ (Cluj, Romania), Rm₃ (Iasi, Romania), RsB₁ (Tartu, Estonia), RsB₂ (Memel, Lithuania), RsC₁ (Moskva, Russian Federation),

RSC₂ (Minsk, Belarus), RSC₃ (Kursk, Russian Federation), RSC₄ (Pensa, Russian Federation), RSE₁ (Kharkov, Ukraine), RSE₂ (Maykop, Russian Federation), RSE₃ (Uralsk, Russian Federation), RSK (Yalta, Russian Federation), RSN₁ (Kologriv, Russian Federation), RSN₂ (Ust-Sysolsk, Russian Federation), RSN₃ (Ust-Sylma, Russian Federation), RSN₄ (Onega, Russian Federation), RSW₁ (Poltava, Ukraine), RSW₂ (Zdolbunov, Ukraine), RSW₃ (Uman, Ukraine), Sa (Sassari, Sardinia), Sb (Jan Mayen, Spitsbergen), Si (Agrigento, Sicily), Su₁ (Pitea, Sweden), Su₂ (Stockholm, Sweden), Tu (Istambul, Turkey). Map generated using Generic Mapping Tools v. 4.1.1 (Wessell and Smith 2006).

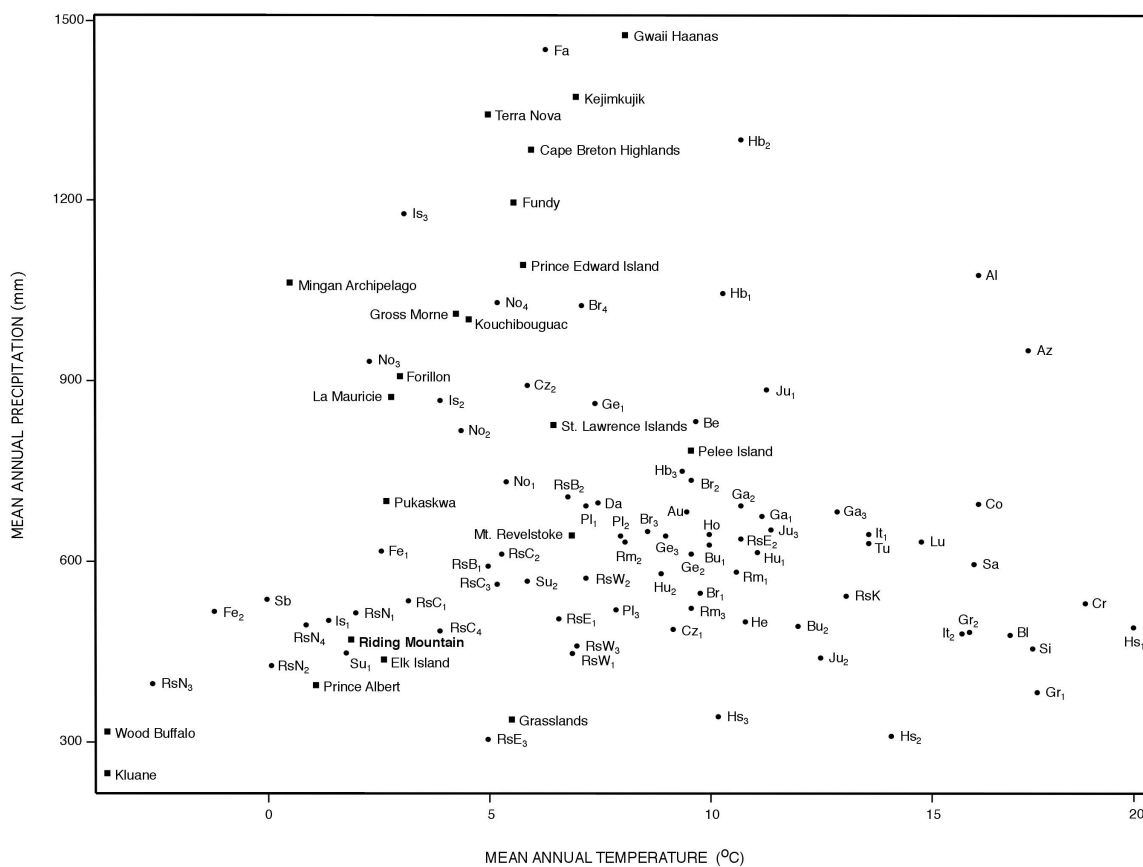


Figure 2.3 Using climate data to predict the establishment of exotic vascular plants in Riding Mountain National Park, Manitoba, Canada. Plants found in regions of Europe whose mean annual temperature (°C) and precipitation (mm) matched those of the Park were considered more likely to establish within its boundaries and assigned to a higher class of invasion risk. For climate station abbreviations refer to Fig. 2.2. Climate summaries according to Walter et al. (1975). The position of 21 national parks in Canada is provided for reference.

Table 2.1 Summary of exotic vascular plant species found in Riding Mountain National Park (Cody 1988) and in areas outside the Park boundary, including the province of Manitoba (Scoggan 1957) and natural areas in other regions of Canada (White et al. 1993, Haber 1996, Catling and Mitrow 2005). The increasing risks of establishment and proliferation of exotic plants inside the Park (Very Low – Very High) were predicted using their climatic ranges and biological traits, respectively. The potential threat of each species to the endemic diversity and structure of natural areas inside the Riding Mountain National Park was further based on its habitat preferences. Natural habitats include prairies, wetlands, shorelines, and woodlands; ruderal habitats include gardens, lawns, roads, trails, and waste areas. Nomenclature according to the Great Plains Flora Association (1986) and Gleason and Cronquist (1991). Bolded species are invasive in natural areas in Canada (White et al. 1993, Haber 1996, Catling and Mitrow 2005).

	VERY LOW	LOW	MODERATE				HIGH	VERY HIGH	Sum
	Climate unmatched annuals / biennials	Climate unmatched perennials	Annuals / biennials in ruderal habitats	Annuals / biennials in natural habitats	Non-clonal perennials in ruderal habitats	Non-clonal perennials in natural habitats	Clonal perennials in ruderal habitats	Clonal perennials in natural habitats	
RMNP			<i>Amaranthus retroflexus</i> <i>Avena fatua</i> <i>Brassica campestris</i> <i>Capsella bursa-pastoris</i> <i>Carum carvi</i> <i>Chenopodium album</i> <i>Crepis tectorum</i> <i>Erucastrum gallicum</i> <i>Galeopsis bifida</i> <i>Lappula echinata</i> <i>Malva rotundifolia</i> <i>Polygonum aviculare</i> <i>Polygonum convolvulus</i> <i>Senecio vulgaris</i> <i>Silene noctiflora</i> <i>Stellaria media</i> <i>Thlaspi arvense</i>	<i>Arctium minus</i> <i>Archium tomentosum</i> <i>Axyris amaranthoides</i> <i>Brassica kaber</i> <i>Chenopodium glaucum</i> <i>Descurainia sophia</i> <i>Dracoccephalum thymiflorum</i> <i>Erysimum cheiranthoides</i> <i>Hesperis matronalis</i> <i>Lolium perenne</i> <i>Tripleurospermum perforata</i> <i>Medicago lupulina</i> <i>Melilotus alba</i> <i>Melilotus officinalis</i> <i>Poa annua</i> <i>Polygonum lapathifolium</i> <i>Polygonum persicaria</i> <i>Setaria viridis</i> <i>Silene pratensis</i> <i>Sisymbrium altissimum</i>	<i>Artemisia absinthium</i> <i>Glechoma hederacea</i> <i>Humulus lupulus</i> <i>Lychnis chalcidonica</i> <i>Medicago sativa</i> <i>Phleum pratense</i> <i>Plantago major</i> <i>Portulaca oleracea</i> <i>Puccinella distans</i> <i>Silene latifolia</i> <i>Taraxacum officinale</i> <i>Tragopogon dubius</i> <i>Trifolium hybridum</i> <i>Trifolium pratense</i> <i>Vicia cracca</i>	<i>Lonicera tatarica</i> <i>Achillea ptarmica</i> <i>Aegopodium podagraria</i> <i>Dianthus deltoides</i> <i>Elytrigia repens</i> <i>Festuca rubra</i> <i>Gypsophila paniculata</i> <i>Leucanthemum vulgare</i> <i>Mentha spicata</i> <i>Ranunculus acris</i> <i>Saponaria officinalis</i> <i>Tanacetum vulgare</i> <i>Trifolium repens</i>	<i>Agropyron cristatum</i> <i>Agrostis stolonifera</i> <i>Bromus inermis</i> <i>Casragana arborescens</i> <i>Cirsium arvense</i> <i>Euphorbia esula</i> <i>Festuca pratensis</i> <i>Juncus compressus</i> <i>Linaria vulgaris</i> <i>Poa compressa</i> <i>Poa pratensis</i> <i>Sonchus arvensis</i>		
Sum	0	0	17	20	15	1	12	77	
MANITOBA	<i>Amaranthus hybridus</i> <i>Brassica juncea</i> <i>Centaurea solstitialis</i> <i>Delphinium ajacis</i> <i>Eragrostis cilianensis</i> <i>Hibiscus trionum</i> <i>Polygonum monspeliensis</i> <i>Silene cserei</i>	<i>Centaurea biebersteinii</i> <i>Centaurea repens</i> <i>Knautia arvensis</i> <i>Rumex patientia</i>	<i>Alyssum alyssoides</i> <i>Asperugo procumbens</i> <i>Berteroa incana</i> <i>Borago officinalis</i> <i>Brassica hirta</i> <i>Centaurea cyaneus</i> <i>Chaenorrhinum minus</i> <i>Daucus carota</i> <i>Elsholtzia ciliata</i> <i>Euphorbia peplus</i> <i>Fagopyrum tataricum</i> <i>Fumaria officinalis</i> <i>Lepidium ruderalis</i> <i>Lithospermum arvense</i> <i>Malva verticillata</i> <i>Matricaria chamomilla</i> <i>Papaver rhoeas</i> <i>Pastinaca sativa</i> <i>Phalaris canariensis</i> <i>Raphanus raphanistrum</i> <i>Setaria verticillata</i> <i>Tragopogon porrifolius</i> <i>Urtica urens</i> <i>Vaccaria pyramidata</i> <i>Veronica agrestis</i> <i>Veronica persica</i> <i>Vicia sativa</i> <i>Vicia villosa</i>	<i>Agrostemma githago</i> <i>Anethum graveolens</i> <i>Anthemis cotula</i> <i>Arctium lappa</i> <i>Atriplex hortensis</i> <i>Brassica nigra</i> <i>Bromus tectorum</i> <i>Bromus japonicus</i> <i>Camelina microcarpa</i> <i>Camelina sativa</i> <i>Carduus nutans</i> <i>Centaurea diffusa</i> <i>Cerastium glomeratum</i> <i>Conringia orientalis</i> <i>Cynoglossum officinale</i> <i>Digitaria ischaemum</i> <i>Echinochloa crusgalli</i> <i>Echium vulgare</i> <i>Erodium cicutarium</i> <i>Fagopyrum esculentum</i> <i>Geranium pusillum</i> <i>Hyoscyamus niger</i> <i>Kochia scoparia</i> <i>Lactuca serriola</i> <i>Lamium alexicaule</i> <i>Lapsana communis</i> <i>Myosotis arvensis</i> <i>Neslia paniculata</i> <i>Odontites serotina</i> <i>Panicum millaceum</i> <i>Reseda lutea</i> <i>Salsola iberica</i> <i>Senecio viscosus</i> <i>Setaria glauca</i> <i>Setaria italica</i> <i>Sisymbrium loeselii</i> <i>Sonchus asper</i> <i>Sonchus oleraceus</i> <i>Tragopogon pratensis</i> <i>Verbascum thapsus</i>	<i>Armoracia rusticana</i> <i>Artemisia abrotanum</i> <i>Cichorium intybus</i> <i>Dianthus barbatus</i> <i>Diplotaxis muralis</i> <i>Lotus corniculatus</i> <i>Nepeta cataria</i> <i>Plantago lanceolata</i> <i>Plantago media</i> <i>Potentilla argentea</i> <i>Rumex acetosa</i> <i>Sedum purpureum</i> <i>Stellaria graminea</i> <i>Taraxacum laevigatum</i>	<i>Alopecurus pratensis</i> <i>Betula pendula</i> <i>Cirsium vulgare</i> <i>Dactylis glomerata</i> <i>Frangula alnus</i> <i>Rhamnus cathartica</i> <i>Rumex crispus</i> <i>Geranium pratense</i> <i>Lathyrus tuberosus</i> <i>Linaria dalmatica</i> <i>Lithospermum officinale</i> <i>Ranunculus repens</i> <i>Rorippa austriaca</i>	<i>Butomus umbellatus</i> <i>Heracleum aurantiacum</i> <i>Hypericum perforatum</i> <i>Iris pseudacorus</i> <i>Leonurus cardiaca</i> <i>Lythrum salicaria</i> <i>Myriophyllum spicatum</i> <i>Populus alba</i> <i>Rorippa sylvestris</i> <i>Rumex acetosella</i> <i>Salvia nemorosa</i>		
Sum	8	4	28	40	14	7	13	125	
CANADA		<i>Buddleja davidii</i> <i>Cynanchum rossicum</i> <i>Morus alba</i> <i>Robinia pseudoacacia</i> <i>Robinia viscosa</i> <i>Rubus discolor</i> <i>Syringa vulgaris</i>	<i>Acinos arvensis</i> <i>Dipsacus sylvestris</i> <i>Malva neglecta</i> <i>Senecio jacobaea</i> <i>Tribulus terrestris</i>	<i>Alliaria petiolata</i> <i>Angelica sylvestris</i> <i>Anthriscus sylvestris</i> <i>Barbarea vulgaris</i> <i>Chelidonium majus</i> <i>Cirsium palustre</i> <i>Impatiens glandulifera</i>	<i>Hippophae rhamnoides</i> <i>Pimpinella saxifraga</i> <i>Quercus robur</i>	<i>Acer platanoides</i> <i>Alnus glutinosa</i> <i>Eleagnus angustifolia</i> <i>Euonymus europaeus</i> <i>Pinus sylvestris</i> <i>Potentilla recta</i> <i>Rorippa amphibia</i> <i>Viburnum opulus</i>	<i>Polygonum cuspidatum</i> <i>Polygonum sachalinense</i>	<i>Carex acutiformis</i> <i>Cytisus scoparius</i> <i>Gallium mollugo</i> <i>Geum urbanum</i> <i>Glyceria maxima</i> <i>Hedera helix</i> <i>Hydrocharis morsus-ranae</i> <i>Ligustrum vulgare</i> <i>Lysimachia nummularia</i> <i>Nymphoides peltata</i> <i>Origanum vulgare</i> <i>Phalaris arundinacea</i> <i>Phragmites australis</i> <i>Potamogeton crispus</i> <i>Tussilago farfara</i> <i>Ulex europaeus</i> <i>Vinca minor</i>	
Sum	0	7	5	7	3	8	2	17	

Table 2.2 Contingency between the predictions of a climate-matching model, based on regional means of annual temperature and precipitation, and GARP, a genetic algorithm model integrated with global environmental databases (Elith et al. 2006). Models were used to predict the establishment of 100 vascular exotic plants in Riding Mountain National Park, Manitoba (Canada). For each species, its potential to establish within the Park was predicted using its climatic range in Europe. Establishment risks represent the best 20 of 100 GARP models, selected according to criteria proposed by Anderson et al. (2003). Predictions of both models were compared using chi-squared analysis of contingency tables (Zar 1999). Probabilities of Type I error (P) illustrate the likelihood that predictions of the climate-matching model differ from those generated using GARP.

Number of species	Maximum establishment risk according to GARP	Contingency between climate-matching model and GARP	
		χ^2	P
7	> 80 %	-	-
13	70 - 80 %	0.15	0.6700
25	60 - 70 %	0.51	0.4750
20	50 - 60 %	1.67	0.1960
11	40 - 50 %	3.79	0.0516
11	20 - 40 %	8.16	0.0043
13	< 10 %	13.66	0.0002

Table 2.3 Principal component analysis of five plant traits describing 251 exotic vascular plants found in Riding Mountain National Park, Manitoba (Canada) and areas outside its borders, including the province of Manitoba and natural areas in other regions of Canada. Summaries of traits were compiled from the following sources: Scoggan (1957), Great Plains Flora Association (1986), Cody (1988), Gleason and Cronquist (1991).

Variable	Eigenvector elements		
	<i>Axis I</i>	<i>Axis II</i>	<i>Axis III</i>
Life history (annual/biennial;perennial)	0.8446	-0.2747	0.1528
Vegetative reproduction	0.7160	-0.5259	0.2295
Woody habit	0.5617	0.6074	-0.1224
Length of flowering period (months)	-0.5030	-0.2030	0.7286
Fruit type*	-0.2468	-0.6698	-0.5747
Eigen value	0.3711	0.2421	0.1904
Variance (%)	37.1	61.3	80.4

*fruit types were separated into four categories, each with an assigned dummy variable: indehiscent (11), fleshy (10), deshiscent (01), other (00); fruit categories summarized the following fruit types: indehiscent (achene, caryopsis, nut, nutlet, samara, schizocarp), fleshy (berry, drupe, druplet), deshiscent (capsule, follicle, pod, silicle, silique), other (catkin, cone, utricle).

CHAPTER 3: THE BIOLOGY OF CANADIAN WEEDS. *BROMUS INERMIS* LEYSS.

3.1 Abstract

Smooth brome (*Bromus inermis* Leyss.), a native of central Eurasia, was introduced to Canada as a forage and hay crop around 1888. Early reports of plants escaped from cultivation appear in 1903, however, based on the number of collections prior to 1920, smooth brome spread more rapidly in western Canada. Smooth brome is common along roadsides, forest margins, clearings, shorelines and disturbed areas, but its most detrimental impact is on the diversity of prairies and native grasslands. In Riding Mountain National Park, MB, plant diversity of fescue prairies recently invaded by smooth brome decreased by 70 %. Vegetative proliferation through underground rhizomes is key to the invasiveness of smooth brome, but long-range dispersal of seeds is facilitated by animals, wind and the transport of hay. Smooth brome is effectively controlled using selective applications of glyphosate and well-timed clipping. However, restoration of infested areas depends on the composition of native seed banks. Smooth brome remains valuable as a forage and cover crop in every province and territory in Canada.

3.2 Name

Bromus inermis Leyss. – smooth brome, awnless brome, Austrian brome, Austrian brome grass, Austrian brome hay, brome grass, Hungarian brome, Hungarian brome grass, Hungarian fodder grass, Russian brome, smooth brome, smooth brome grass (Clark and

Malte 1913, Newell and Keim 1943, Heinrichs 1969, Scoggan 1978; Darbyshire et al. 2000); brome inerme, brome sans arêtes, brome de Hongrie (Häfliger and Scholz 1981, Darbyshire et al. 2000). Poaceae, grass family, Poacées. The name *Bromus* is derived from the Greek *broma*, meaning food, and *bromos*, meaning oat (Zimdahl 1989).

3.3 Description and account of variation

3.3.1 Description

Rhizomatous perennial, 2-15 dm tall, the culms topped with open panicles 5-20 cm long with ascending or spreading branches. Rhizomes up to 1.5 m long without branching or producing stems, 2-5 mm wide, with pale scales. Culms smooth (rarely hairy), the nodes often with a purplish band, the sheaths most often smooth (rarely hairy), with auricles short or absent and ligules to 3 mm long and truncate. Leaf blades smooth, rarely with hair, but then the first two leaves are more often hairy, 8-40 cm long and 2-15 mm wide, flat, tapering and often marked with a wrinkled "W" near to the middle. Spikelets 1.5-4 cm long, born on 1-4 branches per node, each spikelet producing 7-10 florets. Glumes smooth, the first tapered from the base, 1-nerved or rarely obscurely 3-nerved, 4-5 mm long, the second 3-nerved, 6-8 mm long. Lemmas smooth, less often roughened (scabrous or puberulent), rounded on the back and flushed with purple toward the margins, 7-16 mm long, awnless or with awns less than 3 mm long. Anthers 3.5-6 mm long. Grains 5-8 mm long. The preceding description is based on Looman (1982), Looman and Best (1987), Alex (1998), Pavlick (1995).

No reports of chromosome numbers specific to Canada have been found, but those cited in the literature range between $2n = 28, 42, 49, 54-56-58, 70$ (Wagon 1952,

Mitchell 1967, Gleason and Cronquist 1991, Moss 1992, Pavlick 1995). A variable number of chromosome fragments found in addition to the normal complement of 56 may explain this wide range (Hill and Myers 1948). Cultivated varieties are auto-allo-octoploid ($2n = 8x = 56$) with a genomic formula of AAAAB1B1B2B2 derived from erect brome (*B. erectus* Hudson; A genome) and unknown ancestors (B genome; Casler et al. 2000, Delgado et al. 2000).

3.3.2 Distinguishing features

In most regions, smooth brome can be readily distinguished from other species of *Bromus* by the combination of perennial rhizomes and non-pilose lemmas (Pavlick 1995). Other useful characters include the first glume with 1 distinct nerve (instead of 3); lemmas rounded on the back, flushed with purple toward the margins, awnless or with awns up to 3 mm long; upper leaf surfaces mostly hairless; lower glume tapered from the base and auricles at summit of leaf sheath absent or rudimentary.

Smooth brome (*Bromus inermis*) can be distinguished from the native Pumpelly's brome (*B. pumpellianus* Scribn.), which is similar in its rhizomatous habit, by the glabrous or scabrous culms, lemmas and leaf blades, and rudimentary or absent auricles (Mitchell 1967, Voss 1972; Table 3.1). When present, the lemma awns of *B. inermis* do not exceed 3 mm (Scoggan 1978). The nodes, lemmas and blades of *B. pumpellianus* are pubescent with long, soft hairs (0.5 mm or longer), especially near the margins (Wagon 1952, Voss 1972). Also characteristic of the native species are its longer lemma awns (1.5-4 mm), a lower glume broadened above the base and better-developed auricles at the summit of each leaf sheath. Both taxa occur primarily as octoploids ($2n = 8x = 56$)

(Armstrong 1982). Meadow brome (*B. riparius* Rehmman), introduced for cultivation as a pasture grass in North America during the 1950s, differs from *B. inermis* and *B. pumpellianus* by its shorter culms, longer awns than *B. inermis*, and shorter rhizomes than *B. pumpellianus* (Barkworth et al. 2007).

Some authors have considered *B. pumpellianus* a subspecies of the introduced *B. inermis* (Scoggan 1978, Great Plains Flora Association 1986). The reduction of *B. pumpellianus* to subspecific rank is based primarily upon evidence of introgressive hybridization with *B. inermis* (Wagnon 1952). Although the distinction between these taxa requires further work, the vast majority of specimens are easily distinguished and most treatments recognize this taxon at the specific rank (Mitchell 1967, Voss 1972, Dore and McNeill 1980, Looman and Best 1987, Gleason and Cronquist 1991, Soreng et al. 2003).

3.3.3 Intra-specific variation

Bromus inermis (*sensu stricto*) is a highly variable taxon. Even in its native range in Europe, many forms have been recognized based on minor variation in pubescence and awn development (Tutin et al. 1980). In Canada, two varieties have been distinguished based on the aspect of their panicle branches. In contrast with the widely spreading to reflexed panicle branches of var. *divaricatus* Rohlena, those of var. *inermis* are spreading-ascending to erect (Fernald 1950, Scoggan 1978). Within var. *inermis*, three forms have been recognized. Awnless or blunt lemmas characterize f. *inermis* and f. *proliferus* Louis-Marie (Scoggan 1978), while short awns (< 3 mm) are typical of f. *aristatus* (Schur) Fern. (Scoggan 1978). Where present, pubescent types are not

geographically delimited (Mitchell 1967). In f. *proliferus*, the florets have the form of leafy propagules, the glumes normal but the lemma and palea leaf-like and 3-6 mm long (Louis-Marie 1940). Other variable traits include: stature, the extent of clonal growth and the fullness and colour of panicles (Dore and McNeill 1980). Recent treatments of the genus do not recognize the above infraspecific taxa and place all names in synonymy with *B. inermis* (Soreng et al. 2003, Barkworth et al. 2007).

A bright yellow variant of smooth brome is known from Matheson, Ontario and from Saskatoon (see DAO 54409, cultivated material). This strain proved useful for determining distances of pollen transport and appropriate isolation distances for maintaining varietal purity in seed-producing plots (Knowles 1964). When green plants were completely pollinated by yellow plants, 50 % of the seedlings were yellow and 50% were green.

Although not formally recognized, many agronomists distinguish two strains of smooth brome. Plants introduced indirectly into Canada from central Europe are considered of “southern origin” (Newell and Keim 1943). These begin growing earlier in the spring, remain greener through the fall and are taller, more creeping and produce fewer seeds (Leslie 1956, Knowles 1969). Seeds of plants from southern strains have wide, papery margins (Knowles 1969). Plants of “northern origin” were introduced directly into Canada from Russia (Anstey 1986). These produce more seeds and may resemble a “bunch-grass” due to their closely growing tillers (Parent 1947, Cormack 1961). Partly distinctive varieties introduced almost a century ago may persist along roadsides in some areas. For example a distinctive kind called “Hungarian” persists in the older parts of the town of The Pas, MB (DAO 5793272-5793275).

Recent breeding experiments have combined characters from smooth brome plants of southern and northern origins with those of other species. At the Agricultural Research Station in Brandon, Manitoba, plants of southern origin were combined with selections from the Research Station in Saskatoon, the University of Madison, Wisconsin and the USSR to reduce their creeping habit (Andrews 1963). In 1977, a hybrid of *B. inermis* and meadow brome grass (*B. riparius* Rehm.; a species native to south-eastern Europe; Tutin et al. 1980) was created at the Saskatoon Research Centre. Hybrid plants are characterized by improved fall regrowth and frost resistance (Knowles and Baron 1990, Anonymous 2003). Presently, 'Knowles' (*Bromus riparius* x *B. inermis*), a new variety, is under review (Anonymous 2003). Plants of 'Knowles' have narrower crowns, sparsely to moderately pubescent blades and less anthocyanin compared with existing commercial varieties (Anonymous 2003).

3.3.4 Illustrations

A single plant, its panicle and an individual spikelet are illustrated in Figure 3.1. Colour photographs and additional illustrations can be found on the United States Department of Agriculture's PLANTS database (<http://plants.usda.gov/index.html>) and other internet resources.

3.4 Economic importance

3.4.1 Detrimental

Smooth brome often escapes from cultivation to pose serious threats to the biodiversity of revegetated and natural areas, including prairies and native grasslands (Sather 1987, White et al. 1993, Stacy et al. 2005). In a mixed-grass prairie near Brandon, MB, invading smooth brome significantly reduced the abundance of native blue grama grass (*Bouteloua gracilis* (HBK.) Lag. ex Griffiths), *Carex obtusata* Lilj., creeping juniper (*Juniperus horizontalis* Moench), little bluestem (*Schizachyrium scoparium* (Michx.) Nash.) and porcupine grass (*Stipa spartea* Trin.; Wilson and Belcher 1989). In Riding Mountain National Park, MB, plant diversity of fescue prairies recently invaded by smooth brome decreased by 70 % (Otfinowski and Kenkel 2005). Similar declines in native plant diversity were reported from Yellowstone National Park by Frank and McNaughton (1992). In many protected areas of the Canadian prairies, smooth brome now dominates the once native plant communities and invading plants continue to colonize recently created openings. For example, in the Cypress Hills Interprovincial Park on the Saskatchewan-Alberta border, smooth brome now dominates forest clearings. In many regions of southwestern Saskatchewan, smooth brome has also colonized patches of prairie formerly occupied by native prairie roses (*Rosa acicularis* Lindley, *R. woodsii* Lindley and *R. arkansana* T. C. Porter; D. Larson, P. Catling, personal observation). These, destroyed by the alien rose stem girdler beetle (*Agrilus aurichalceus* Redtenbacher; Coleoptera: Buprestidae; Larson 2003), are unable to recover from injury as a result of the dense cover of smooth brome, which inhibits seed germination. The interaction between smooth brome and rose stem girdler beetle provides a unique

example of the combined impacts of two alien species on the function of native prairie ecosystems.

Impacts of smooth brome invasions cascade to higher trophic levels. For example, Iowa roadsides dominated by smooth brome supported a lower richness of ground beetles compared to those revegetated with native species (Coleoptera: Carabidae; Varchola and Dunn 1999). Areas of smooth brome also support an impoverished fauna of leafhoppers (Homoptera: Cicadellidae). In Montana, conversion of mixed-grass prairies into smooth brome and alfalfa pastures reduced leafhopper diversity (Bess et al. 2004), and in Canada, only a few generalists, including the introduced silver leafhopper (*Athysanus argentarius* Metcalf) and species of *Psammotettix* and *Diplocolenus* were associated with smooth brome (A. Hamilton, personal communication, Biodiversity Section, Agriculture and Agri-Food Canada, ON). Invasions of smooth brome into a matrix of native prairie cordgrass (*Spartina pectinata* Link.) also altered the spatial and temporal dynamics of a planthopper (*Prokelisia crocea* Van Duzee; Hemiptera: Delphacidae) and its specialist egg parasitoid (*Anagris columbi* Perkins; Hymenoptera: Mymaridae; Cronin and Haynes 2004). This is one of the first experimental studies to demonstrate that matrix composition, influenced by an alien invader, can affect the population dynamics of a herbivore and its natural enemy.

Several reports illustrate the impacts of smooth brome invasions on communities of birds. At the Last Mountain Lake Refuge, an area of mixed-grass prairie in Saskatchewan, bird richness in infested areas declined from eight to two species (Romo and Grilz 1990). In Manitoba, upland sandpipers (*Bartramia longicauda* Bechstein) and Sprague's pipits (*Anthus spragueii* Audubon) were significantly more abundant in native

mixed-grass prairies than in areas dominated by smooth brome (Wilson and Belcher 1989). Decreased forb cover and increased visual obscurity in areas dominated by smooth brome lead to declined use of uplands by sage grouse (*Centrocercus urophasianus* Bonaparte), eastern meadowlarks (*Sturnella magna* Linnaeus) and grasshopper sparrows (*Ammodramus savannarum* Gmelin; Scott et al. 2002, Bunnell et al. 2004). Invasions of smooth brome may have other indirect effects. For example, low preference of native ungulates and cattle for smooth brome leads to overgrazing of uninfested areas and creates additional invasion foci (Frank and McNaughton 1992, Austin et al. 1994, Trammell and Butler 1995, Moisey et al. 2005).

Plants of smooth brome proliferating along ditches and field margins serve as pest and disease vectors. In Wyoming, smooth brome supported populations of the Russian wheat aphid (*Diuraphis noxia* Mordvilko; Homoptera: Aphididae), facilitating fall infestations of winter small grains (Brewer et al. 2000). Plants growing along field margins can also act as an alternative host to *Leptosphaeria nodorum* E. Muller, a fungal pathogen responsible for glume blotch in wheat (Krupinsky 1986). Smooth brome plants infected with the brome mosaic virus, leaf spot (*Pyrenophora tritici-repentis* (Died.) Drechs.) and ergot (*Claviceps purpurea* (Fr.:Fr.) Tut. can also infect adjacent cereal crops (Gussow 1938, Seaman 1980, Krupinsky 1987, Haber 1989). Pollen released from escaped populations can contaminate cultivated fields of certified smooth brome (Knowles and Ghosh 1968) and cause genetic introgression into the native Pumpelly's brome (Elliott 1949a).

Recently, smooth brome was ranked as the 8th most serious invasive alien plant threatening natural habitats in Canada (Catling and Mitrow 2005). In a national survey,

smooth brome was considered a species of “national concern” and regarded as a “serious invader of grasslands” by over half the respondents from the prairie region (Haber 1996). Romo and Grilz (1990) reported that western Canadian grasslands are seriously threatened by smooth brome and suggested that “a passive or hand-off approach to managing natural areas will eventually result in invasion.”

3.4.2 *Beneficial*

Smooth brome is widely cultivated for hay and pasture, and is one of the most valuable cover species used in the revegetation of mine tailings, roadside ditches, eroded slopes and canal banks (Carlson and Newall 1985, Hardy BBT Limited 1989). It has also been used to maintain firebreaks, suppress forest regrowth (Anderson 1966, Heinrichs 1969) and revegetate abandoned farmland in western Canada (Thomson 1937, Clarke and Heinrichs 1941, Palmer 1949). Smooth brome is very palatable to all classes of livestock (Looman 1983, Stubbendieck et al. 1997), and forage cultivars based on smooth brome hybrids have recently been produced (Ferdinandez and Coulman 2000, Coulman 2004, 2006).

Mixed pastures of smooth brome and alfalfa provide shelter for deer mice (*Peromyscus maniculatus* Wagner), montane voles (*Microtus montanus* Peale) and northern pocket gophers (*Thomomys talpoides* Richardson; Bechard 1982), as well as American bitterns (*Botaurus lentiginosus* Rackett), northern harriers (*Circus cyaneus* Linnaeus) and short-eared owls (*Asio flammeus* Pontoppidan; Duebbert and Lokemoen 1977). In Indiana, areas reclaimed with smooth brome were used by Henslow's and grasshopper sparrows (*Ammodramus henslowii* Audubon, *A. savannarum* Gmelin),

eastern meadowlarks, common yellowthroats (*Geothlypis trichas* Linnaeus), dickcissels (*Spiza americana* Gmelin) and red-winged blackbirds (*Agelaius tricolor* Audubon; Scott et al. 2002). Escaped and planted populations of smooth brome provide nesting cover for ducks and attract gray partridges (*Perdix perdix* Linnaeus), as well as vesper (*Pooecetes gramineus* Gmelin), clay-coloured (*Spizella pallida* Swainson) and grasshopper sparrows (Wilson and Belcher 1989, Lokemoen et al. 1990, Carroll and Crawford 1991). Although invasions by smooth brome reduce the biomass of native forages (Trammell and Butler 1995), brome can provide winter forage for elk (*Cervus elaphus* Linnaeus), mule deer (*Odocoileus hemionus* Rafinesque) and white-tailed deer (*O. virginianus* Zimmermann; Hobbs et al. 1981, Stubbendieck et al. 1997, Austin et al. 1994).

3.4.3 Legislation

Smooth brome is commercially distributed and not regulated under the Federal Seeds Act (Weed Seeds Order 2005) or any provincial noxious weeds acts.

3.5 Geographical distribution

Smooth brome is found growing without cultivation in every Canadian province and territory (Fig. 3.2). It appears to be best established in the eastern prairie and parkland region of Manitoba and Saskatchewan, in southern Ontario and southern Quebec and in the Okanagan and Thompson valleys of southern British Columbia.

Smooth brome is native across central Eurasia (Elliott 1949b). In continental Europe, its range extends westward to the Netherlands, Belgium, Luxemburg, France, Spain and NW Italy, and southward to the Balkans, Bulgaria, and Turkey. Introduced

populations are also found in Switzerland, Britain, Denmark, Sweden, Norway, Finland, and Iceland (Tutin et al. 1980). In the New World, smooth brome has been introduced to South America, including Argentina, Bolivia, Chile and Uruguay, as well as the Caribbean, Australia, New Zealand, areas of northern, tropical and southern Africa, temperate and tropical Asia, and islands in the Atlantic, Indian and Pacific Oceans; it is also found throughout the United States and Mexico (Häfliger and Scholz 1981, Soreng et al. 2003, Weber 2003).

3.6 Habitat

3.6.1 Climatic requirements

Smooth brome is a cool season grass. Its ability to tolerate dry conditions has made it a valuable forage and pasture crop in western Canada (Malte 1915). In greenhouse experiments, plants were more tolerant of moisture stress than the native green needle grass (*Stipa viridula* Trin.) and northern wheat grass (*Agropyron dasystacyum* (Hook.) Scribn.; Reekie and Redmann 1990). However, prolonged drought decreased shoot dry weight, induced dormancy (Dibbern 1947, Donkor and Bork 2002) and limited the establishment of smooth brome in southern Alberta (Thomson 1937, Palmer 1949) and central British Columbia (Willis 1965). The annual precipitation required for the establishment and proliferation of smooth brome is between 280 – 500 mm (Hardy BBT Limited 1989).

In Canada, smooth brome may be found in subalpine regions (Moss 1992), but does not reseed above 3,000 m (Dibbern 1947). The species tolerates severe winter

conditions (Gilbey 1954), including short periods of freezing (Rogler 1943), but does not survive flooding or water logging (Abbott 1954, Burns 1964).

In the northern Prairies and interior British Columbia, northern strains of smooth brome are more productive and hardy (Goulden 1957) as they require lower temperatures and shorter photoperiods to flower (Evans and Wilsie 1946). Southern strains are more tolerant of midsummer heat and drought (Newell and Keim 1943).

3.6.2 *Substratum*

The greatest encroachment of smooth brome is in rich, loamy soils (Knowles et al. 1969), and is lower in sandier (Malte 1915) and organic substrates (Myhr et al. 1966). In western Canada, smooth brome thrives in the loams and sandy loams of the Dark Brown and Black soil zones, well drained areas of the Black and Gray Luvisol zones, and in moist areas of the Brown zone (Knowles 1969, Alberta Agriculture Food and Rural Development 1981). In British Columbia, plants tolerated the high acidity (pH = 4.5) of coal spoils (Hardy BBT Limited 1989) and germinated in contaminated flare pit soils that were high in petroleum hydrocarbons and salts (Rutherford et al. 2005). In Iowa, smooth brome abundance in pastures declined above a soil electrical conductivity of 40.6 mS m⁻¹ (Guretzky et al. 2004).

The productivity of smooth brome, and its ability to displace native plants, increases with the availability of soil nitrogen (Harrison and Crawford 1941, Leyshon and Campbell 1995, Wilson and Gerry 1995). Even small patches of nutrients may increase its vigour. In central Minnesota, smooth brome plants growing on thatching ant mounds (*Formica obscuripes* Forel) were larger and produced more pollen compared to

those in undisturbed prairie (McKone 1989). However, additions of nitrogen may also reduce the vegetative encroachment. In fertilization experiments, nitrogen reduced the growth of roots and rhizomes of smooth brome and increased its aboveground biomass (Watkins 1940, Wilson and Gerry 1995).

3.6.3 *Communities in which the species occurs*

Smooth brome is common along roadsides, forest margins, clearings, shorelines and disturbed areas throughout Canada (Sather 1987, Dunster 1990, Pavlick 1995, Leeson et al. 2005; Table 3.2). In Manitoba, smooth brome invades mixed-grass prairies composed of *Bouteloua gracilis*, *Carex obtusata*, *Juniperus horizontalis*, *Schizachyrium scoparium* and *Stipa spartea* (Wilson and Belcher 1989). Also vulnerable are areas of fescue prairie, composed of slender wheat grass (*Elymus trachycaulus* (Link) Gould), rough fescue (*Festuca hallii* (Vasey) Piper), needle grasses (*Stipa* spp.), yarrow (*Achillea millefolium* L.), smooth aster (*Aster laevis* L.), northern bedstraw (*Galium boreale* L.) and other native grasses and forbs (Otfinowski and Kenkel 2005). Smooth brome is also common along shorelines and in the understory of open forests throughout western and eastern Canada (Moss 1992, Moreland and Promaine 2000, Lesica 2002; Table 3.2).

Impacts of smooth brome appear greatest in open prairie communities where invasions often produce large, monospecific stands (Sather 1987, Romo and Grilz 1990, White et al. 1993, Haber 1996). The size of invading patches ranges between 50 – 900 m² (Caners 1999) and large infestations in North Dakota can occupy as much as 20,000 m² of mixed-grass prairie (Trammell and Butler 1995).

3.7 History

Smooth brome was first introduced to North America from Hungary in 1884 by the California Agricultural Experiment Station (Newell and Keim 1943). By 1899, other stations in the United States, including those in North Dakota, Montana and Washington, were experimenting with smooth brome, and distributing shipments of Russian seed to Canada after 1898 (Newell and Keim 1943). The earliest mention of smooth brome in Canada appears in reports from experimental farms, established by Canada's Department of Agriculture in 1888 (Anstey 1986). One, from 1899, praises its ability to produce a profitable crop at Indian Head, Saskatchewan (Malte 1914). Another describes smooth brome as "a promising grass, possessing the necessary qualifications to the Prairie climate" (Malte 1915).

Some of the earliest collections of plants escaped from cultivation were from a Toronto dump in 1903, 1904 (Scott 54199, DAO; Scott 54200, DAO) and open woods in Ottawa in 1906 (Dore and McNeill 1980). Other early records include areas adjacent to grain elevators near Point Edward, Ontario in 1911 (Dore and McNeill 1980) and open areas in Outremont, Québec in 1915 (Malte 576852, DAO). Expanding settlement in the West extended the cultivated range of smooth brome, and judging by the numbers of collections prior to 1920, it spread through western Canada earlier and more rapidly than in the east.

In western Canada, agricultural immigration contributed to the introduction of exotic forages. In northern areas of the Prairie provinces, exotic forages were cultivated in forest clearings (Stacey 1949, McCartney 1993), and native meadows were supplemented with smooth brome to increase productivity (Lesica 2002). In southern

Alberta and Saskatchewan, farm settlement restricted the open wintering range of cattle ranches. By 1913, most ranchers resorted to exotic hay to compensate for the lost winter range of their animals (Potyondi 1995). Such purposeful introductions for hay likely contributed to the early establishment of smooth brome across Canada. For example, smooth brome was cultivated for hay on Sable Island, Nova Scotia in 1899 (Macoun 22680, CAN). Subsequently, it established but remained rare in this extreme environment (Catling et al. 1984). There are several collections from apparently natural habitats in the Yukon between 1887 and 1902 (before and during the gold rush), where smooth brome is now well established (Cody 2000). Additional introductions resulted from the construction of railroads. For example, disturbance of natural habitats along the mouth of the Moose River in Ontario likely led to the introduction of smooth brome into this area after 1935 (Riley 2003).

Following the droughts of the 1930s, the use of smooth brome for revegetation further increased its range in North America (Thomson 1937, Casler et al. 2000). Between 1937 and 1947, interest in the use of smooth brome increased in eastern Canada (Baird 1949), resulting in greater shipments of seed from the Great Plains to the eastern USA (Casler et al. 2000). The recent use of smooth brome in stabilizing roadsides, ditches and mine tailings also expanded its range in Canada (Parent 1957, Alberta Agriculture Food and Rural Development 1981).

Despite reference to apparently natural habitats on early collection labels, it is difficult to determine whether or not the collected plants established on their own. However, if present behaviour in newly colonized sites can be accepted as an indication of the past, then smooth brome in many areas likely spread rapidly from plantings by

seeds and rhizome fragments. Consequently many collections that are not clearly of cultivated plants are likely to have established naturally. The earliest dates of collection of non-cultivated plants for each Canadian province and territory are: Alberta in 1890 and 1898, British Columbia in 1887 and 1902, Manitoba in 1901 and 1906, New Brunswick in 1910 and 1927, Newfoundland in 1911 and 1927 (several collections from Goose Bay, Labrador in 1950), Northwest Territories in 1950 (several collections), Nova Scotia in 1939 and 1940, Ontario in 1890 and 1903, Prince Edward Island in 1945 and 1952, Quebec in 1914 and 1915, Saskatchewan in 1896 and 1903 and Yukon in 1899 and 1902.

Unlike a number of other invasive aliens of natural habitats in Canada, smooth brome appears to have spread with early settlement. To some extent, this very early timing of invasion probably contributed to its impact being less obvious. In some areas smooth brome may have already invaded native grasslands by the time botanists were documenting the occurrence and floristic composition of natural habitats.

3.8 Growth and development

3.8.1 Morphology

The invasiveness of smooth brome is enhanced by the proliferation of its rhizomes (Romo and Grilz 1990). Continued vegetative growth increases the density of older stands, intensifying both above- and below-ground competition (Engel et al. 1987, Gerry and Wilson 1995). For example, reduced establishment of alfalfa in pastures of smooth brome was attributed to strong competition for light (Groya and Sheaffer 1981). The roots of smooth brome are concentrated in the first 10 cm of soil (Gist and Smith 1948), but may penetrate to > 1.5 m (Campbell et al. 1966).

3.8.2 Perennation

Smooth brome is perennial, producing densely branching rhizomes (Dibbern 1947). Shoot meristems remain dormant at or below the ground surface, but may initiate regrowth even when spring temperatures remain below freezing (Lamp 1952). The emergence of new shoots from rhizome and basal stem nodes, or the penetration of rhizome branches aboveground, often represents regrowth from shoots arrested by low winter temperatures (Lamp 1952, Alex 1998).

3.8.3 Physiological data

The productivity of smooth brome declines by late summer (Tinline 1937). In Melfort, Saskatchewan, the leaf conductance of plants inside rain shelters decreased between July 4 and August 22 (Bittman and Simpson 1989). In contrast, shading resulted in a decrease in the number of shoots, rhizomes and inflorescences, and shorter day lengths produced denser stands of shorter, decumbent shoots (Watkins 1940).

3.8.4 Phenology

Smooth brome grows most rapidly in the spring, remaining green through the summer months, during which time it makes little additional growth (Dibbern 1947). On the Canadian prairies, growth commences in early May (Looman 1983), and in Saskatoon, irrigated plants produced only 8 % of their total annual yield after August 8 (Knowles and Sonmore 1985). Similar results were reported from Nebraska, where maximum

yields were harvested as early as May 25 (Engel et al. 1987). In Wisconsin, cultivated plants began growth ahead of alfalfa (*Medicago sativa* L.) and timothy (*Phleum pratense* L.), with tillering starting in late March and anthesis and seed maturing by the middle of June and July, respectively (Reynolds and Smith 1962).

In Ontario, smooth brome plants flower from June to September (Alex 1998), but in Wisconsin, plants repeated flowering in the late fall (Reynolds and Smith 1962, Great Plains Flora Association 1986). In western Canada, seed crops of smooth brome are harvested between late July and early August (Knowles et al. 1969), or as late as mid-September (May et al. 1999). Provided adequate moisture and fertility, tillering resumes following anthesis (Lamp 1952, Eastin et al. 1964), but tillers emerging in late summer and fall do not elongate until the following season (Lamp 1952). The majority of floral primordia are initiated during the spring, and apices initiated in the fall do not survive the winter (Lawrence and Ashford 1964).

3.8.5 *Mycorrhiza*

In greenhouse experiments, seedlings of smooth brome infected with *Glomus etunicatum* Becker & Gerd. produced more biomass and root stele tissue (Miller et al. 1997). However, plants infected with *G. intraradix* Schenck & Smith were competitively inferior to alfalfa (Hamel et al. 1992) and accumulated less phosphorus at higher temperatures (Hetrick and Wilson 1994).

3.9 Reproduction

3.9.1 *Floral biology*

Synchronous flowering in smooth brome is common (McKone 1985). While most pollen is wind dispersed within 50 m, plants may be cross-pollinated for up to 300 m (Knowles 1964, Knowles and Ghosh 1968). Smooth brome is generally self-sterile (McKone 1985), and outcrossed plants yield up to 62.5 % more seeds per panicle than those selfed (Domingo 1941). Smooth brome pollen loses viability within 24 h and delays in pollination reduce the number of produced seeds (Domingo 1941). In the greenhouse, flowering at 16°C was less than at 27°C and did not occur on cloudy days (Evans and Wilsie 1946). Cold vernalization and short photoperiods are required for flowering (Newell 1951).

3.9.2 *Seed production and dispersal*

Seeds of smooth brome are wind dispersed and dispersal is greatest when seed moisture falls below 25 % (Knowles et al. 1969). In Riding Mountain National Park, seeds did not disperse beyond 3.5 m from invading clones (Otfinowski et al. 2008), but may travel much farther by wind transport over encrusted snow (Hume and Archibold 1986, Morton and Hogg 1989, Romo and Grilz 1990). Seeds may also be dispersed by attachment to animal fur, by ants and small rodents developing food caches, transported with hay and mulch and distributed by seed companies (Sather 1987).

Among 30 self-sterile clones of smooth brome, fertility ranged between 2.6 and 75.8 %, and open-pollinated plants produced 156 – 10,080 viable seeds (Lowe and

Murphy 1955). Cormack (1961) found that seed production was higher in northern strains of smooth brome where only 30 % of florets were sterile, compared to over 50 % for plants of southern origins. On average, commercial crops of smooth brome yield 100 kg seed ha⁻¹, but may exceed 1100 kg (Campbell et al. 1966, Knowles et al. 1969). Applications of nitrogen had no effect on the number of spikelets per panicle, but heavily fertilized plants produced more florets per spikelet (Harrison and Crawford 1941).

3.9.3 Seed banks, seed viability and seed germination

In a fescue prairie near Saskatoon, SK, seedlings of smooth brome emerged only from soil cores collected inside patches of smooth brome and not from those collected in the adjacent native prairie (Grilz and Romo 1995). However, in Riding Mountain National Park, seedlings of smooth brome germinated from cores collected as far as 4.0 m away from established clones (Otfinowski et al. 2008). Seeds of ‘Manchar’, a commercial variety of smooth brome, retained viability of more than 70 % for six years when stored under cool, dry conditions (Hafenrichter et al. 1968).

The germination and emergence of smooth brome may exceed that of native prairie grasses, including *Bouteloua gracilis*, Parry oat grass (*Danthonia parryi* Scribn.), *Festuca hallii*, June grass (*Koeleria macrantha* (Lebed.) J.A. Schultes.), *Schizachyrium scoparium* and needle and thread grass (*Stipa comata* Trin. & Rupr.; Smoliak and Johnston 1968). Germination occurs at low temperatures (exceeding 80 % at 7°C), but rates of seedling growth are highest at 18°C (Smoliak and Johnston 1968). Germination may occur under a broad range of osmotic potentials, light and dark conditions (Grilz et al. 1994) and under snow cover (Bleak 1959).

Seeds of smooth brome are susceptible to fungal pathogens. In Ontario, seeds buried in upland soils did not germinate unless treated with fungicide, and no seeds germinated in wetland soils (Blaney and Kotanen 2001). Seeding depths below 26 mm reduced emergence and delayed seedling maturity, but seedlings emerged from a soil depth of 50 mm by elongating their true leaves (Ries and Hofmann 1995).

3.9.4 Vegetative reproduction

Smooth brome spreads by underground rhizomes (Campbell et al. 1966). Early forage scientists noted that smooth brome was often aggressive when added to forage mixtures. For example, in Manitoba, smooth brome crowded out alfalfa within a year of seeding (Sigfusson 1925), and became difficult to eradicate in experimental plots (Malte 1915). In the greenhouse, rhizomes are initiated at the four-leaf stage (R. Otfnowski, personal observation) and may spread up to 83 cm into an adjacent native prairie over two growing seasons (R. Otfnowski and N. C. Kenkel, unpublished data). Vegetative reproduction in smooth brome depends on nutrient availability and interspecific competition. In cultivated plots, application of nitrogen decreased rhizome production (Paulsen and Smith 1968) and the presence of a companion crop reduced the number of tillers (Hertz 1962).

3.10 Hybrids

The absence of reproductive barriers between *Bromus inermis* and *B. pumpellianus* has prompted questions regarding species validity (Elliott 1949a, Wagon 1952). In greenhouse experiments, the average fertility of crosses was approximately half of

intraspecific matings of both parents (Elliott 1949a). Although both taxa occur primarily as octoploids, hybrids of naturally occurring tetraploids may also produce seeds (Armstrong 1982).

Hybrid plants possess intergrading forms of pubescence of the lemmas, nodes and upper leaf sheath (Mitchell 1967, Voss 1972, Armstrong 1982). However, plants of *B. pumpellianus* with glabrous nodes retain villous lemmas and may possess hairy glumes (Voss 1972). Recently, hybrid populations of *B. inermis* and *B. riparius* were created at the Saskatoon Research Centre (Knowles and Baron 1990), and various cultivars have been described (Ferdinandez and Coulman 2000, Coulman 2004, 2006).

3.11 Population dynamics

Plantings of smooth brome may persist for over 60 years (Plummer et al. 1968), and in Nebraska, fields established in 1897 and 1898 still produced seeds in the 1940s (Newell and Keim 1943). Immobilization of nutrients in plant litter (Lardner et al. 2000) and increasing stand density often reduce the productivity of older populations (Alberta Agriculture Food and Rural Development 1981). Decline in plant vigour leads to an increase in self-sterility (Kirk 1934), and older plantings of smooth brome produce fewer flowering panicles (Newell 1951).

Smooth brome is a strong competitor. In greenhouse experiments, lower establishment and yield of alfalfa grown with smooth brome were attributed to shading (Groya and Sheaffer 1981). However, the establishment of grass and broadleaf seedlings was unaffected by the removal of smooth brome shoots, suggesting strong belowground competition (Gerry and Wilson 1995). In other experiments, the low emergence of

Canada goldenrod (*Solidago canadensis* L.) transplants was attributed to the deep litter deposited by smooth brome (Goldberg 1987).

3.12 Response to herbicides and other chemicals

Smooth brome is effectively controlled using selective applications of glyphosate [*N*-(phosphonomethyl)glycine; Grilz and Romo 1995] and Sather (1987) recommended treatment at 0.5 to 1.1 kg glyphosate ha⁻¹, applied before flowering. In overgrazed tall-grass prairie in southeastern Nebraska, spring application of atrazine (6-Chloro-N²-ethyl-N⁴-isopropyl-1,3,5-triazine-2,4-diamine) or glyphosate (*N*-(Phosphonomethyl)glycine) shifted community dominance from smooth brome and Kentucky bluegrass (*Poa pratensis* L.) toward native warm-season grasses (Waller and Schmidt 1983). However, the restoration of native prairie infested with smooth brome depends on the ability of the native seedbank and rhizome bank to compete with the regrowth of brome tillers (Willson and Stubbendieck 1996).

In Minnesota, May applications of glyphosate and dalapon (2,2-dichloropropionic acid) were also effective in suppressing smooth brome prior to seeding alfalfa (Martin et al. 1983). Applications of glyphosate were most effective in May, when the grasses were 15 cm tall and beyond the three-leaf stage. In rangelands, applications of imazapic ((±)-2-(4,5-dihydro-4-methyl-4-(1-methylethyl)-5-oxo-1*H*-imidazol-2-yl)-5-methyl-3-pyridinecarboxylic acid) at rates above 70 g ha⁻¹ caused visible injury to smooth brome (Shinn and Thill 2004), but the biomass of plants was not affected by applications of picloram (4-amino-3,5,6-trichloro-pyridine-2-carboxylic acid; Shinn and Thill 2002). Within a year of application, smooth brome was also susceptible to diallate (*S*-(2,3-

Dichloroallyl) diisopropyl-thiocarbamate) and trillate (*S*-(2,3,3-Trichloroallyl) diisopropyl-thiocarbamate; Knowles et al. 1969) and not affected by paraquat (1,1'-Dimethyl-4,4'-bipyridinium dichloride; Martin et al. 1983).

3.13 Response to other human manipulations

The most effective means of controlling smooth brome is through cutting (Sather 1987). Intensive defoliation, following tiller elongation, decreases root dry matter (Donkor and Bork 2002), total available carbohydrates (Reynolds and Smith 1962) and increases winter injury of plants (Lawrence and Ashford 1964). The frequency and timing of cutting are important to the success of the operation. For example, the yield of smooth brome following five cuts was lower compared to plants cut only three times (Paulsen and Smith 1968). Plants were most easily damaged by intensive defoliation during internode elongation (Eastin et al. 1964) or during the early stages of panicle development (Sather 1987). Cutting is most effective when the growing apices of plants or their tillers are removed and when the regenerating plants are subjected to competition from native species (Willson and Stubbendieck 1996). Tillering in smooth brome is suppressed by the developing shoots (Eastin et al. 1964), and rhizome and basal axillary buds at the lower nodes of stems may not expand until early fruit development (Reynolds and Smith 1962). As a result, cutting of plants during stem elongation may also accelerate vegetative growth (Reynolds and Smith 1962, Eastin et al. 1964).

Fire can also be used to suppress smooth brome. However, timing of the burn, community composition and environmental conditions are critical in determining its success (Sather 1987, Blankenspoor and Larson 1994). In eastern Nebraska, Willson

(1991) found a 50 % reduction in smooth brome tiller density following a prescribed burn during tiller elongation, and Old (1969) reported decreases in July dry matter production following an April fire in Illinois. Community composition is crucial to the success of the burn. In tall-grass prairies, early spring burning suppress smooth brome at a time when the native, warm-season grasses are dormant (Hover and Bragg 1981). However, in fescue prairies in Manitoba and Saskatchewan, spring burning may adversely affect the dominant native cool-season grasses (Anderson and Bailey 1979, Redmann et al. 1993) and increase the abundance of smooth brome (Grilz and Romo 1994). Burning is less effective where the recovering plants are not subject to competition from native species (Willson and Stubbendiek 1996). As a result, Willson and Stubbendiek (2000) recommend avoiding burning areas where native warm-season grasses contribute less than 20 % to the community. Regrowth of smooth brome following defoliation is reduced in dry years (Harrison and Romo 1994).

Smooth brome survives burning by sprouting from rhizomes and early spring or fall burning may actually promote smooth brome by removing litter and increasing tillering (Howard 1987, Willson and Stubbendiek 2000). By reducing the interception of snow and decreasing soil moisture, fall burns may also compromise the vigour of native species (Grilz and Romo 1994). Care must be taken during mowing or burning of smooth brome to avoid fragmenting rhizomes, which readily germinate in disturbed soil (Albrecht et al. 2005).

In production, yields of smooth brome hay decline after three to four years (Lowe 1950), but may recover following applications of fertilizer or by mixed seeding with

alfalfa (Alberta Agriculture Food and Rural Development 1981). Stands are also rejuvenated by plowing (Cormack 1961), burning, or mowing (Knowles et al. 1969).

One of the difficulties in managing smooth brome invasions in native prairies is its frequent co-occurrence with Kentucky bluegrass (*Poa pratensis*), another cool-season invader (Sather 1987). As a result, the timing and frequency of defoliation treatments must be carefully administered to prevent an increase in Kentucky bluegrass abundance (Murphy and Grant 2005).

3.14 Response to herbivory, disease and higher plant parasites

3.14.1 Herbivory

3.14.1.1 Mammals

Smooth brome is palatable to all classes of livestock, as well as native ungulates (Campbell et al. 1966, Hobbs et al. 1981, Austin et al. 1994, Trammell and Butler 1995), and its seeds are palatable to deer mice (*Peromyscus maniculatus* Wagner; Everett et al. 1978). However, in experiments with common rangeland plants, the preference of mule deer for smooth brome was very low (Austin et al. 1994). Plants are most palatable before heading (Looman 1983, Falkner and Casler 1998). Compared to other common forages, smooth brome is high in fibre and total phenols (Gauthier and Bedard 1991) and better suited for hay than pasture production (Van Esbroeck et al. 1995). Its decline in digestibility, from 60 % in the early stages of growth to less than 40 % at maturity, is attributable to decreased protein and increased fibre content (Campbell et al. 1966).

The regrowth of smooth brome is affected by harvest frequency. Following eight years of annual sheep grazing, plants became shorter and more vigorous (Falkner and

Casler 2000). However, above ground biomass was inversely proportional to the frequency of clipping and regrowth occurred at the expense of roots (Harrison and Hodgson 1939, Dibbern 1947, Reynolds and Smith 1962). Frequent clipping also reduced the crude protein yield and increased fibre concentration and root dieback (Robertson 1933, Donkor and Bork 2002). Severe defoliation may delay regrowth by removing the growing points of tillers and activating rhizome buds (Carlson and Newall 1985, Van Esbroeck et al. 1995), and lead to the infestation of smooth brome pastures by shepherd's purse (*Capsella bursa-pastoris* (L.) Medic.) and dandelion (*Taraxacum officinale* Weber; Harker et al. 2000, Lardner et al. 2000). Defoliation may also decrease the pollen yield and the number of florets per spikelet (McKone 1989).

3.14.1.2 Birds and/or other vertebrates

Smooth brome is palatable to Canada and blue geese (*Branta canadensis* Linnaeus, *Chen caerulescens* Linnaeus; Burgess 1969, Gauthier and Bedard 1991).

3.14.1.3 Insects

In Alberta, insects in the genera *Irbisia* and *Capsus* were reported to damage forage grasses (Alberta Agriculture Food and Rural Development 1981). Seed production of smooth brome is reduced by seed midges (*Stenodiplosis bromicola* Marikovskiy & Agafonova) and thrips (Neiman and Manglitz 1973, Carlson and Newall 1985). In Wisconsin, an insect infestation that caused a shortage in the supply of smooth brome seed during 1956 may have been caused by midges (Itinididae, *Phytophaga*; Nielson and Burks 1958). Escape holes of chalcid flies (Eulophidae, *Tetrastichus*), a likely parasite of

the midge, have been observed on mature caryopses of native fringed brome (*Bromus ciliatus* L.), arctic brome (*B. kalmii* A. Gray) and *B. pumpellianus* (Nielson and Burks 1958).

Seedlings of smooth brome are susceptible to several species of cereal aphids, including the Russian wheat aphid (*Diuraphis noxia* Mordvilko), greenbug (*Schizaphis graminum* Rondani), English grain aphid (*Macrosiphum avenae* F.) and the oat-birdcherry aphid (*Rhopalosiphum padi* L.; Stoner and Kieckhefer 1979, Springer et al. 1992, Brewer et al. 2000) The planthopper *Prokelisia crocea* (Hemiptera: Delphacidae) and species of leafhoppers (Homoptera: Cicadellidae), including *Endria inimica* Say, *Doratura stylata* Boheman and *Psammotettix alienus* Dahlbom, are also abundant in fields of smooth brome (Whitmore et al. 1981, Bess et al. 2004, Cronin and Haynes 2004).

3.14.1.4 Nematodes and/or other non-vertebrates

Smooth brome is susceptible to the root-lesion nematodes *Pratylenchus penetrans* (Cobb) Filipjev & Schur-Stekhoven (Petersen et al. 1991) and *P. neglectus* (Rensch) Filipjev & Schur-Stekhoven (Société de protection des plantes du Québec 1992). In Quebec, the following genera of soilborne plant-parasitic nematodes were recovered from soil samples collected from cultivated fields of smooth brome: *Pratylenchus* spp., *Meloidogyne* spp., *Helicotylenchus* spp., *Heterodera* spp., *Tylenchorhynchus* spp. (Santerre and Lévesque 1982). In greenhouse trials, seedlings of smooth brome became infected with the ectoparasitic nematodes *Paratylenchus projectus* Jenkins and

Helicotylenchus digonicus Perry, as well as the migratory endoparasites *Pratylenchus neglectus* Rensch and *P. penetrans* Cobb (Townshend and Potter 1976).

3.14.2 Disease

3.14.2.1 Fungi

In cultivation, the leaves and culms of smooth brome may become infected with leaf blotches (*Drechslera bromi* (Died.) Shoem, *Pyrenophora bromi* (Died.) Drechs., *Selenophoma bromigena* (Sacc.) Sprague and Johnson), rusts (*Puccinia coronata* Corda, *P. recondita* Roberge ex Desmaz.), scald (*Rhynchosporium secalis* (Oudem.) J.J. Davis), spots (*Ascochyta sorghi* Sacc., *Bipolaris sorokiniana* (Sacc.) Shoemaker, *Pseudoseptoria bromigena* (Sacc.) Sutton, *Phyllachora graminis* (Pers.) Fuckel, *Pyrenophora tritici-repentis* (Died.) Drechs., *Septoria bromi* Sacc., *S. bromigena* Sacc., *Stagonospora bromi* A.L. Sm. & Ramsb.) and stripes (*Cercosporidium graminis* (Fuckel) Deighton; Crowell and Lavalee 1942, Berkenkamp 1973, Krupinsky 1987, Société de protection des plantes du Québec 1992). Infections are most prevalent under humid conditions (Greenshields 1967). Because poor soil nutrition may contribute to leaf spot infestation, control includes the maintenance of soil fertility and stubble burning (Alberta Agriculture Food and Rural Development 1981). Recently, a new morphotype of the crown rust *Puccinia coronata* Corda was discovered independently in Wisconsin, South Dakota and Minnesota (Delgado et al. 2001, Anikster et al. 2003). This morphotype, described as *Puccinia coronata* var. *bromi* sensu Mühlethaler (Anikster et al. 2003), is uniquely pathogenic to smooth brome in North America and produces aecia on common buckthorn

(*Rhamnus cathartica* L.), an alternate host that is also an invasive alien (Anikster et al. 2003).

Smooth brome is also susceptible to winter crown rot (*Coprinus psychromorbidus* Redhead & J.A. Traquair) and snow molds (*Myriosclerotinia borealis* (Bubak & Vleugel) L.M. Kohn.), but in the parkland region of the Canadian prairies, its tolerance of snow molds exceeds that of other common forages (Hwang et al. 2002). Other pathogens of roots and stems include: root rots (*Fusarium culmorum* (Wm. G. Sm.) Sacc., *F. equiseti* (Corda) Sacc., *Pythium graminicola* Subramanian and *P. arrhenomanes* Drechs.), silvertop (*F. poae* (Peck) Wollenweb.), dry root (*Nigrospora sphaerica* (Sacc.) Mason) and take all (*Gaeumannomyces graminis* (Sacc.) Arx & D. Olivier; Crowell and Lavalee 1942, Société de protection des plantes du Québec 1992). The root rots *Fusarium spp.* and *Pythium spp.* are especially prevalent in moist soils and may cause the decline of irrigated stands (Myhr et al. 1966).

Other pathogens of smooth brome include: powdery mildew (*Erysiphe graminis* DC.), downy mildew (*Sclerophthora macrospora* (Sacc.) Thirumalachar, C.G. Shaw & Narasimhan), halo blight (*Pseudomonas syringae* pv. *atropurpurea* (Reddy & Godkin) Young, Dye & Wilkie) and ergot (*Claviceps purpurea* (Fr.:Fr.) Tul.). Flower stalks of smooth brome were susceptible to *Alternaria alternata* (Fr.) Keissler (Smith and Knowles 1974). Collections of brome stubble at the Forestry Farm in Saskatoon, SK yielded the following plant parasitic fungi: *Leptosphaeria herpotrichoides* De Notaris, *L. luctuosa* Niessl in Sacc., *Ophiobolus herpotrichus* (Fries) Sacc., *Pyrenophora bromi* (Died.) Drechsler, *Myxormia atroviridis* Berk. & Br., *Hendersonia culmicola* Sacc, *H.*

crastophila Sacc., *Septoria bromi* Sacc., *Stagonospora foliicola* (Bres.) Bubak, *Pithomyces chartarum* (Berk. & Curt.) M. B. Ellis (Shoemaker and LeClair 1974).

3.14.2.2 Bacteria

Bacterial streak caused by *Xanthomonas campestris* pv. *cerealis* (Hagborg) Dye has been reported from plants of smooth brome growing in Japan (Miyajima and Tsuboki 1980).

3.14.2.3 Viruses

Smooth brome is susceptible to the barley yellow dwarf virus and the brome mosaic virus (Société de protection des plantes du Québec 1992). The latter was isolated from plots of spring wheat, barley and smooth brome in Portage la Prairie and Glenlea, Manitoba (Haber 1989).

3.14.3 Higher plant parasites

There are no reported higher plant parasites of smooth brome.

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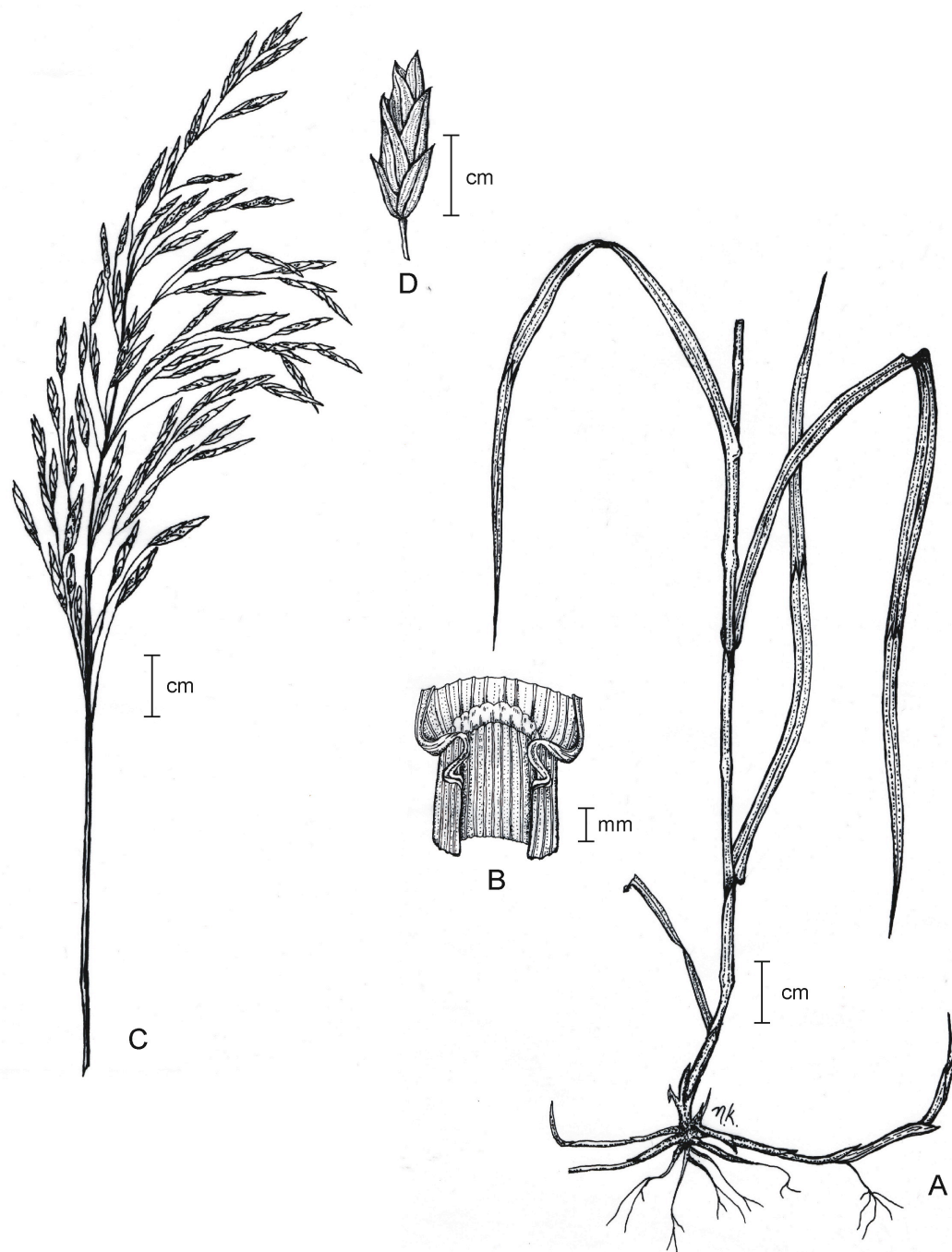


Figure 3.1 *Bromus inermis* Leyss. a, habit sketch of a culm illustrating the proliferating rhizome; b, detail of leaf illustrating the rudimentary auricles; c, inflorescence of a mature plant; d, detail of a single spikelet illustrating the glabrous glumes and the glabrous, awnless lemmas.

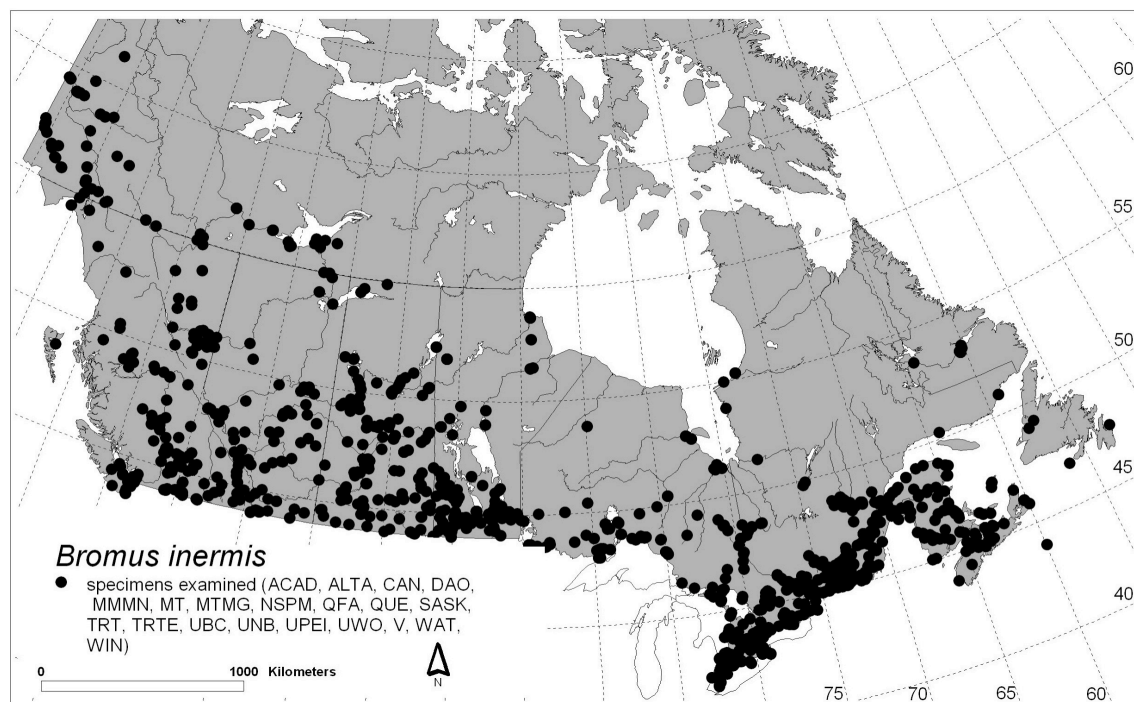


Figure 3.2 Distribution of smooth brome (*Bromus inermis* Leyss.) growing without cultivation in Canada. Map is based on 2344 specimens examined and verified in 20 herbaria across Canada, including ACAD, ALTA, CAN, DAO, MMMN, MT, NSPM, OAC, QFA, QUE, SASK, TRT, TRTE, UAC, UBC, UNB, UWO, V, WAT, and WIN (acronyms according to Holmgren et al. 1990).

Table 3.1 Features distinguishing introduced *Bromus inermis* Leyss. and native *B. pumpellianus* Scribn. The summarized characters were compiled from the following sources: Elliott (1949a); Wagnon (1952); Mitchell (1967); Voss (1972); Scoggan (1978); Looman and Best (1979); Dore and McNeill (1980); Gleason and Cronquist (1991); Pavlick (1995). Meadow brome (*B. riparius* Rehmman) differs from *B. inermis* and *B. pumpellianus* by its shorter culms, longer awns than *B. inermis*, and shorter rhizomes than *B. pumpellianus* (Barkworth et al. 2007).

	<i>Bromus inermis</i> Leyss.	<i>Bromus pumpellianus</i> Scribner
<i>Lemmas:</i>	glabrous or scabrous, finely appressed puberulent, short-hispid or shortly hirsute across the base or on the nerves; awns absent or up to 2.5 (3.1) mm long	pubescent with distinct long hairs (0.5 mm or more) to villous at least toward the margins and keel; awns mostly (1) 1.5-4 (5.5) mm long (Voss 1972); 2-3 mm (Dore and McNeill 1980); 1.5-6.0 mm (Mitchell 1967)
<i>Glumes:</i>	glabrous	pubescent to glabrous
<i>Culms:</i>	culms glabrous or somewhat scabrous to finely pubescent at the nodes	culms usually pubescent (0.5 mm or more) to densely hairy with long hairs at or immediately adjacent to the nodes (occasionally glabrous)
<i>Leaf blades:</i>	usually glabrous or somewhat scabrous (rarely ± pilose on both surfaces or at least on lower surface)	pubescent to pilose on upper surface, glabrous or sparsely pubescent below
<i>Auricles:</i>	rudimentary or absent	well developed
<i>Habit:</i>	strongly rhizomatous	rhizomatous to tufted

Table 3.2 Examples of plant species associated with *Bromus inermis* Leyss. growing without cultivation in Canada. Summary is based on a review of 448 specimens from the Agriculture and Agri-Food Canada herbarium in Ottawa, ON (DAO). Nomenclature according to Gleason and Cronquist (1991).

Community Type	Community composition
roadside	<i>Agropyron</i> spp., <i>A. cristatum</i> (L.) Gaertn., <i>Carex</i> sp., <i>Cornus</i> spp., <i>Linaria vulgaris</i> Miller, <i>Matricaria</i> sp., <i>Phleum pratense</i> L., <i>Picea glauca</i> (Moench) Voss, <i>Poa pratensis</i> L., <i>Populus</i> spp., <i>P. tremuloides</i> Michx., <i>P. deltoides</i> Marshall, <i>Thalictrum</i> sp.
disturbance/clearing	<i>Agrostis</i> sp., <i>Dactylus glomerata</i> L., <i>Equisetum arvense</i> L., <i>Phleum</i> sp., <i>Poa pratensis</i> L., <i>Populus balsamifera</i> L., <i>P. tremuloides</i> Michx., <i>Prunus pensylvanica</i> L.
prairie/meadow*	<i>Agropyron smithii</i> Rudb., <i>Andropogon gerardii</i> Vitman, <i>Bouteloua gracilis</i> (HBK.) Lag., <i>Carex bebbii</i> (L. H. Bailey) Fern., <i>C. muhlenbergii</i> Schk., <i>Elymus trachucaulus</i> (Link) Gould., <i>Festuca hallii</i> (Vasey) Piper, <i>Hieracium piloselloides</i> Villars., <i>Koeleria pyramidata</i> (Lam.) P. Beauv., <i>Poa compressa</i> L., <i>P. pratensis</i> L., <i>Rubus idaeus</i> L., <i>Salix</i> spp., <i>Schizachyrium scoparium</i> (Michx.) Nash., <i>Solidago canadensis</i> L., <i>Stipa spartea</i> Trin.
forest	<i>Acer negundo</i> L., <i>Alliaria petiolata</i> (Bieb.) Cavara & Grande., <i>Betula</i> sp., <i>Calystegia sepium</i> (L.) R. Br., <i>Impatiens capensis</i> Meerb., <i>I. pallida</i> Nutt., <i>Juglans cinerea</i> L., <i>J. nigra</i> L., <i>Platanus occidentalis</i> L., <i>Picea glauca</i> (Moench) Voss, <i>Populus tremuloides</i> Michx., <i>Salix nigra</i> Marshall, <i>Solidago gigantea</i> Aiton., <i>Ulmus americana</i> L.
open forest	<i>Acer saccharum</i> Marshall, <i>Carya ovata</i> (Miller) K. Koch., <i>Equisetum</i> spp., <i>Juniperus horizontalis</i> Moench., <i>J. communis</i> L., <i>Kohleria</i> sp., <i>Lilium philadelphicum</i> L., <i>Picea</i> spp., <i>Poa compressa</i> L., <i>Prunus serotina</i> Ehrh., <i>P. virginiana</i> L., <i>Quercus rubra</i> L., <i>Shepherdia</i> sp., <i>Solidago nemoralis</i> Aiton., <i>Symphoricarpos occidentalis</i> Hook.
forest margin	<i>Phalaris arundinacea</i> L., <i>Populus tremuloides</i> Michx., <i>Ulmus americana</i> L.
shoreline	<i>Acer saccharinum</i> L., <i>Carex</i> spp., <i>Celtis occidentalis</i> L., <i>Picea glauca</i> (Moench) Voss, <i>Populus</i> spp., <i>P. balsamifera</i> L., <i>P. tremuloides</i> Michx., <i>Rubus odoratus</i> L., <i>Tilia americana</i> L.

*reports based on reviewed DAO specimens and the following sources: Anderson and Bailey (1980); Pylypec (1986); Wilson and Belcher (1989); Otfinowski and Kenkel (2005).

**CHAPTER 4: RECONCILING SEED DISPERSAL AND SEEDBANK
OBSERVATIONS TO PREDICT THE INVASION PATTERNS OF SMOOTH
BROME (*BROMUS INERMIS*) IN A NORTHERN PRAIRIE.**

4.1 Abstract

The importance of dispersal in the initiation, spatial distribution and proliferation of exotic populations make this life history stage critical in the prediction and management of biological invasions. I observed the dispersal of seeds by clones of smooth brome (*Bromus inermis*) invading northern fescue prairies and explored models to predict its invasion patterns. Based on my observations from two prairies in Riding Mountain National Park, MB, Canada, patterns of smooth brome invasion were contingent on the type of propagules dispersed. While 85 % of brome seeds were intercepted within the first meter of invading clones, the slopes of the log-log plots of seed number against their distance from clone margins were steeper for spikelets than individual florets. Despite the aggregation of propagules along the margins of invading clones, seed rain was a poor predictor of seed bank density and the number of recruited seedlings was independent of the number of seeds dispersed. The shallow dispersal gradient of individual florets combined with the steeper gradient of panicles and spikelets suggest that smooth brome is capable of simultaneously invading along dense fronts and by establishing isolated foci. Although low correlations between the number of dispersed seeds and their recruitment from the seed bank may suggest post-dispersal transport of seeds, other mechanisms, including seed predation and pathogens remain unexplored. Conservation

and restoration of northern fescue prairies must include efforts to control the dispersal of smooth brome seeds as well as explore mechanisms facilitating their establishment.

4.2 Introduction

Impacts of exotic plants on natural habitats are contingent upon discrete stages in their life history (Williamson and Fitter 1996, Kolar and Lodge 2001). Each among these, including dispersal, establishment and proliferation illustrates the critical interplay between exotic plants and recipient environments (Williamson and Fitter 1996, Kolar and Lodge 2001, Puth and Post 2005, Richardson and Pyšek 2006, Dietz and Edwards 2006). Despite the large number of exotic species in most regional floras, the majority fail to become invaders and many simply contribute to local species richness (Rosenzweig 2001). Consequently, the main challenge in invasion biology rests in resolving the mechanisms that facilitate the invasiveness of a small number of exotic organisms (Richardson et al. 2000).

The contingent nature of biological invasions renders the initial dispersal of exotic organisms fundamental to all consecutive stages (Puth and Post 2005). By definition, all exotic species are initially dispersal limited (Richardson et al. 2000) and depend on human activities, including cultivation, commerce and recreation to overcome natural geographic barriers (Elton 1958, Mack 2003, Lockwood et al. 2005, Lodge et al. 2006). Once established, the invasiveness of exotic organisms often depends on their ability to spread away from sites of introduction (Richardson et al. 2000). The importance of dispersal in the initiation, spatial distribution and proliferation of exotic populations

(Harper 1977, Higgins and Richardson 1999, DiVittorio et al. 2007) also makes this stage key in the prediction and management of biological invasions (MacIssac et al. 2001, Tassin et al. 2007).

Dispersal frequently determines the progress and extent of biological invasions (Higgins and Richardson 1999, Levine and D'Antonio 1999, Buckling et al. 2000, Cassey et al. 2004). For example, the proliferation of exotic populations is often directly proportional to the time since establishment and inversely related to the distance from the site of introduction (MacIssac et al. 2001). As a result, propagule pressure, or the frequency and intensity of introductions (Wilson et al. 2007), often determines the impact of biological invaders (Williamson and Fitter 1996, Lockwood et al. 2005, Colautti et al. 2006, Blackburn and Cassey 2007). Among plants, dispersal often combines primary mechanisms that move propagules away from parent plants and secondary mechanisms that move them away from subsequent locations (Nathan and Muller-Landau 2000). As a result, the distribution of dispersed propagules is often directly related to spatial patterns of recruitment (Willson 1993). For example, Harper (1977), extending a model for the dispersal of pathogens (van der Plank 1960), proposed that plants limited to local dispersal tend to advance as a dense wave, while those dispersing across greater distances expand by establishing isolated populations (Willson 1993).

The objective of my study was to examine the dispersal dynamics of smooth brome, a Eurasian perennial threatening the structure and function of prairie remnants throughout the Great Plains (Otfinowski et al. 2007). Widely planted for hay, forage and to revegetate disturbances, smooth brome often escapes to invade native prairies throughout the Great Plains (Wilson and Belcher 1989, Frank and McNaughton 1992).

While vegetative growth facilitates the encroachment of established clones (Otfinowski and Kenkel 2008), little is known about the contribution of seeds to the proliferation of this exotic invader. I directed my observations towards quantifying the production and dispersal of seeds by clones of smooth brome invading northern fescue prairies. Using a combination of field and greenhouse observations, I focused on resolving whether patterns of seed dispersal could predict future invasions.

4.3 Materials and methods

4.3.1 Study area

Research was conducted in Riding Mountain National Park, Manitoba, Canada (50° 39' 00", - 99° 55' 48"). The park occupies an area of 2,978 km² in western Canada and consists of large areas of rolling upland (550 – 640 m), underlain by glacial tills (Lang 1974). The region is characterized by mean annual precipitation of 450 – 500 mm and a growing season of 168 – 173 days; mean temperatures range between -18°C in January and 18°C during July (Leeson et al. 2005). The Park lies in the Mixedwood Section of the Boreal Forest Region (Rowe 1972) and protects areas of northern fescue prairie (Cody 1988). In North America, fescue prairies form an arc around the northern and northwestern perimeter of the mixed prairie (Coupland 1961), occupying a transition between the warmer and drier grasslands and the cooler, moister aspen parkland (Coupland and Brayshaw 1953). Fescue prairies, dominated by rough fescue (*Festuca hallii* (Vasey) Piper) and species of *Agropyron* and *Carex*, are threatened in western Canada by the impacts of grazing, cultivation and exotic species invasions (Trottier 1986).

4.3.2 Observations of seed dispersal

I examined the impacts of seed dispersal on smooth brome invasions using a combination of field and greenhouse observations. In the field, I used strips of landscape fabric to quantify seed dispersal away from invading clones. During August 2003, strips of landscape fabric (0.15 x 5 m; Easy Gardener Inc., Waco TX) were installed in two fescue prairies representative of Riding Mountain National Park (Blood 1966). At each site, four strips were positioned around nine smooth brome clones (Fig. 4.1) and in four locations along the margins of recreational trails (52 strips / site = 39 m² sampling area). Selected clones and trail margins were located away from animal trails, forest margins and neighboring smooth brome clones to reduce error and overlap among seed shadows.

Each strip was pinned 1 m inside each clone or trail fringe using aluminum fabric staples (Easy Gardener Inc., Waco TX) and extended 4 m into the adjacent prairie (Fig. 4.1). Strips were coated with Tree Tanglefoot Paste (The Tanglefoot Company, Grand Rapids MI) to intercept dispersing seeds, and re-coated as required. On three occasions between August and September 2003, I measured the distance of all smooth brome seeds adhered to the strips. Seeds were identified in the field using diagnostic morphological characters (Otfinowski et al. 2007). Caryopses (seeds), the dry, indehiscent fruit of grasses, can disperse alone; as florets (subtended by a palea and lemma); or aggregated within parts of an inflorescence. Among these, I distinguished spikelets (clusters of several florets attached to a rachilla) and panicles (branches of several spikelets, attached to a rachis; Harris and Wolf Harris 1994). Only five individual caryopses were found adhered to the strips, so I combined their numbers with those of florets. Fertility among

populations of smooth brome ranges between 2.6 and 75.8 % (Otfinowski et al. 2007). As a result, I also counted the number of mature seeds inside each dispersed floret, spikelet, and panicle. I terminated my observations in October, when dispersing seeds became scarce.

I compared the yield and viability of dispersing seeds at the start and end of my observations. Ten panicles, collected randomly from each of eight clones at each study site, were cleaned using a belt-thresher and an air-screen separator (Blount/Ferrell-Ross, Bluffton IN) and winnowed by hand. Collected panicles represented less than 1 % of those produced by each patch of smooth brome and were harvested more than 4 m away from each strip of landscape cloth. Cleaned seeds were stored in the dark (5°C) for seven months prior to germination trials. I used germination to examine seed viability. Twenty-five seeds from each clone were transferred into 9 cm Petri dishes, lined with filter paper and placed inside a plant growth chamber (25/15°C, 12/12 h light/dark, 107 $\mu\text{mol}/\text{m}^2/\text{s}^1$ PPFD; Conviron Controlled Environments Limited, Winnipeg MB). De-ionized water was added to the plates as required. Germinated seeds, whose radicle penetrated the seed coat, were counted weekly and removed. After one month, seed coats of ungerminated seeds were nicked at the embryo end using tweezers and returned to the growth chamber for an additional week. These, as well as any remaining seeds which contained a firm embryo, were considered dormant (Cavers et al. 1995). Stratification was not required for germination and seeds collected during October 2004 were 89 % viable.

4.3.3 Soil seedbank analysis

Measurements of smooth brome dispersal were complemented with observations of its soil seed bank. At each study site, seed bank samples were collected during October 2003, at the end of my dispersal observations. I selected two representative clones at each site and collected two cores of soil (0–10 cm, 98 cm³) at 10 cm intervals along the S and N strips of landscape cloth (400 cores / study site; Fig. 4.1). Cores were stored inside plastic Ziploc bags, air dried in the field, and placed in a cool room (4°C) for six weeks to break seed dormancy (Bewley and Black 1982).

Samples were transferred to the greenhouse in November 2003, spread thinly (< 1 cm) inside 12 cm x 16 cm pots, over a base of moistened, sterilized, soilless mix (Metro-Mix 220, Scotts Co. Maryville OH), and watered as required. Greenhouse conditions were maintained using artificial and natural lighting (day: 16 h / 21°C; night: 8h / 15°C). Eight pots filled with peat-moss mix served as controls for seed contamination inside the greenhouse. Emerging seedlings of smooth brome were counted and removed and several were transplanted into separate pots to verify my identification. The first phase of the experiment was terminated after no additional seedlings germinated for two weeks, at which time all pots were returned to the cool room for an additional six weeks. The experiment was terminated after four months, when no additional seedlings emerged. Although prone to errors arising from specific germination requirements of individual species, germination offers a reliable estimate of the viability and composition of plant seed banks (Gross 1990) and has been successfully used to examine the persistence of smooth brome seeds in prairie seed banks (Grilz and Romo 1995). In separate trials, 91

% of seeds collected from Riding Mountain National Park germinated under similar greenhouse conditions (Otfinowski, unpubl.).

4.3.4 Statistical analysis

Data from all clones and trail margins at both study sites were pooled. I divided each dispersal transect into ten, 50 cm intervals and used the inverse power function to model smooth brome seed dispersal as a function of distance from clone margins (Okubo and Levin 1989). The slope of the log transformed inverse power function provides an estimate of the spatial pattern of population recruitment (Willson 1993); slopes steeper than that of the inverse square law (-2 on a log-log scale) characterize populations recruiting along a sharply defined front, while those greater than two characterize populations establishing as isolated foci (van der Plank 1960).

I used a subset of four clones to explore the correlation between the number of smooth brome seeds dispersed and those found in the seed bank. Based on a linear regression model, I tested the null hypothesis that the number of seeds in the seed bank was independent of that dispersed in the seed rain. The frequencies of dispersed and recruited seeds were log transformed to improve the homogeneity of variance among observations (Zar 1999). Linear regression analyses were implemented using Data Desk 6.2 (Data Description Inc. Ithaca NY).

4.4 Results and discussion

4.4.1 *Patterns of seed dispersal*

The majority of seeds dispersed by smooth brome clones invading fescue prairies were intercepted inside the clones or within 1 m of their margins (Table 4.1). Panicles and spikelets comprised 94 % (3842 / 4082) of dispersed propagules (Table 4.1) and accounted for the steep dispersal gradient of invading clones. Among a subset of seeds captured outside the clones, slopes of the log-log plots of seed number against their distance from clone margins were steeper for spikelets than individual florets (Figure 4.2). The viability of dispersing seeds increased between the initiation of their dispersal in August 2003 (78 %) and its termination in October (84 %; $F_{1, 29} = 5.54$, $P = 0.0255$), however neither the mass nor the number of seeds per panicle changed significantly (Table 4.2). Among 4082 seeds of smooth brome examined, fewer than 15 % (599) contained a conspicuous caryopsis and were considered mature. Seed viability remained high (84 %) for over-wintered seeds collected in May 2004.

The observed aggregation of smooth brome seeds in the vicinity of parents is characteristic of most plants, independent of their dispersal mode (Cook 1980, Willson 1993, Heidinga and Wilson 2002, Czarnecka 2004). My observations confirm that this pattern is even more pronounced where propagules contain multiple seeds, whose greater weight likely contributes to their short dispersal distance (Thompson 1986, Kjellsson 1992, Czarnecka 2004). While potentially supporting dense “invasion fronts” (Harper 1977) and intensifying interactions with adjacent communities (Kjellsson 1992), short distance dispersal may also contribute to a lag between the regional and local dominance of exotic invaders (MacDougall and Turkington 2006). As a result, the establishment of

small, isolated foci, facilitated by longer distance dispersal, may pose a more serious threat to the biodiversity of natural areas (Moody and Mack 1988). In addition to evading early detection, the greater edge inherent to smaller foci increases their propagule pressure on adjacent native communities, which may facilitate their rapid consolidation into larger infestations (Moody and Mack 1988). My observations illustrate that the shallow dispersal gradient of smooth brome florets, characteristic of species adapted to longer distance dispersal (Harper 1977), may contribute to this pattern of invasion within fescue prairies.

4.4.2 Persistence in the seed bank

Despite the observed aggregation of seeds around the margins of invading clones, recruitment of smooth brome seedlings from the seed bank was more diffuse. Less than 38 % of dispersed seeds were represented in the seed bank (33 / 87) and only 48 % (16 / 33) of these germinated within the first meter of the clone margin (Table 4.3). As a result, seed rain was a poor predictor of seed bank density and the number of recruited seedlings was independent of the number of seeds dispersed ($F_{1,3} = 1.96$, $P = 0.2563$, $R^2 = 39.5$).

The abundance of dispersed seeds in the soil seed bank is a function of many factors. Previous correlations between the number of dispersed and recruited seeds have been attributed to short distance dispersal (Czarnecka 2004, Jakobsson et al. 2006), the persistence of seeds in the soil (Dessaint et al. 1991, Kjellsson 1992), and plant density (Dessaint et al. 1991). Although characteristic of many plant populations (Thompson 1986, Matlack and Good 1990, Kjellsson 1992, Czarnecka 2004), post-dispersal transport

and predation often account for discrepancies between patterns of seed dispersal and deposition (Schupp and Fuentes 1995, Derksen and Watson 1998, Blaney and Kotanen 2001, Jakobsson et al. 2006). My own observations suggest that winter dispersal of viable “aerial seed banks”, consisting of mature panicles (Csontos 2007), could also contribute to the low correlations between the seed rain and seed bank of invading clones. In other areas of the Great Plains, post dispersal transport of seeds by water, from smooth brome populations established along riparian areas (Potyondi 1995), could further contribute to discrepancies between local seed dispersal and recruitment, and facilitate invasions of new areas of native prairie.

4.4.3 Implementing dispersal models to predict invasion patterns

While biological invasions are contingent upon the dispersal of propagules, their arrival does not guarantee establishment (Nathan and Muller-Landau 2000). As a result, the availability of suitable recruitment sites, seedling mortality, and the demographic viability of establishing populations may restrict the ability of dispersal models to predict invasions patterns (Schupp and Fuentes 1995, Vander Wall and Joyner 1998, Eriksson and Kiviniemi 1999, Higgins and Richardson 1999). For example, Bergelson et al. (1993) emphasized that “realized dispersal” and seedling establishment are constrained by landscape fragmentation and the spatial distribution of recruitment sites.

Consequently, the potential of individual smooth brome florets to generate dense invasion fronts remains highly contingent on local disturbances, facilitating their establishment. Although small, scattered animal-generated disturbances could provide ideal recruitment areas within native prairies, however, their dense, competition-induced edges could

restrict the establishment and proliferation of potential invaders (Reichman et al. 1993). As a result, the invasiveness of exotics such as smooth brome may depend on their ability to optimize sexual and vegetative forms of reproduction during their colonization of perennial plant communities (Huenneke and Vitousek 1990). Consequently, trade-offs between the dispersibility and competitiveness of propagules could help elucidate important differences among the potential impacts of exotic species (Jakobsson et al. 2006, Duyck et al. 2007). Such context dependence among different stages in an invader's life history deserves further research and may account for important discrepancies in the ability of dispersal models to predict patterns of biological invasions (Dietz and Edwards 2006).

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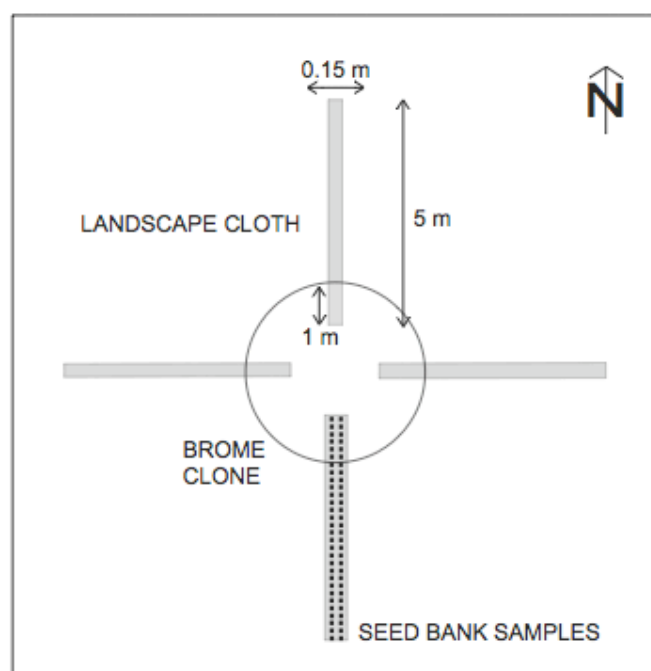


Figure 4.1 Measurement of seed dispersal away from smooth brome clones invading fescue prairies in Riding Mountain National Park, Canada. Strips of landscape cloth (0.15 x 5 m) were pinned 1 m inside each clone using lawn staples, extended 4 m into the adjacent prairie, and treated with Tanglefoot paste to facilitate the capture of dispersing seeds. For selected clones, seed bank samples were collected along the north and south dispersal transects.

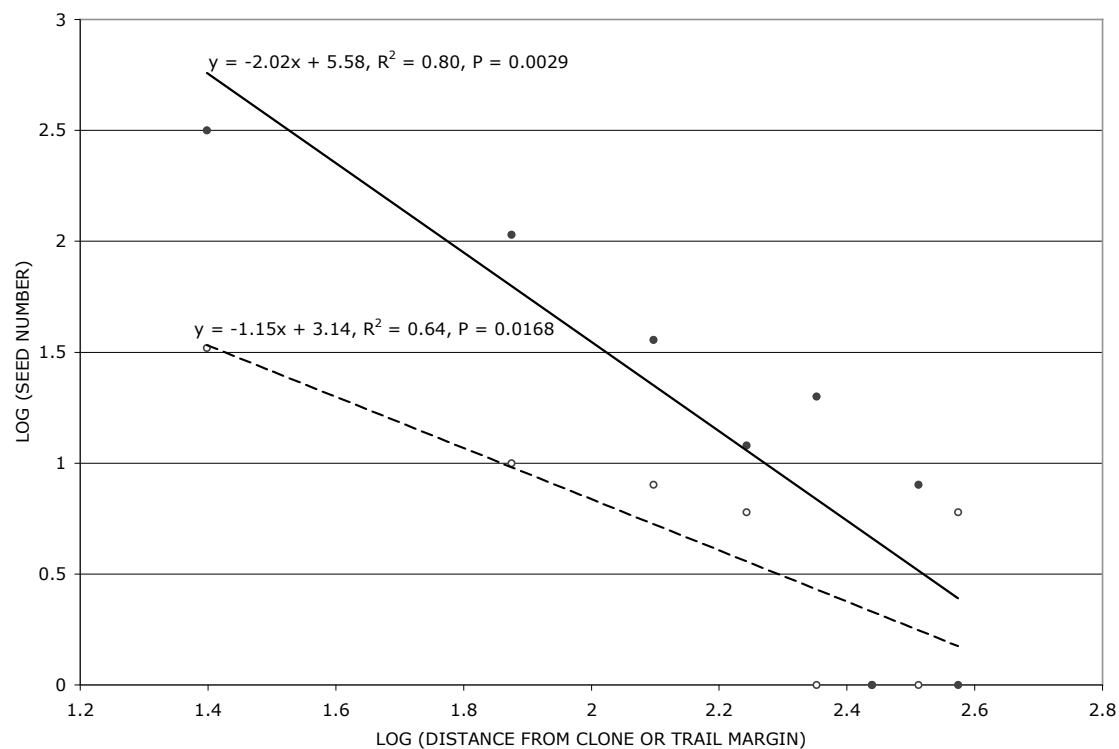


Figure 4.2 Relationship between the number of dispersed seeds and distance from the margins of smooth brome clones invading fescue prairies in Riding Mountain National Park, Canada. Open circles (dashed line) represent florets ($n = 58$); closed circles (solid line) represent spikelets ($n = 494$). Up to seven florets were found within a spikelet. Distances from the clone margin represent the mid-points of 50 cm intervals.

Table 4.1 Cumulative percentage of seeds dispersed by smooth brome clones invading fescue prairies in Riding Mountain National Park, Canada (absolute seed numbers in brackets). Each column represents the cumulative percentage of seeds dispersed as individual florets (subtended by a palea and lemma) or aggregated within parts of the inflorescence, including spikelets (clusters of several florets attached to a rachilla) and panicles (branches of several spikelets, attached to a rachis). Seeds were captured along 5 m strips of landscape cloth, pinned 1 m inside the fringe of invading clones (indicated by a dashed line). Up to seven florets were found within a spikelet; panicles represented two or more attached spikelets. Mean \pm 1 S.E.

	Distance	Panicles	Spikelets	Florets	Mean (m ⁻²)
INSIDE CLONE	0-50	57.5 (1099)	45.2 (872)	23.8 (57)	260 \pm 47
	51-100	63.8 (120)	74.4 (565)	75.8 (125)	104 \pm 19
	101-150	95.4 (605)	90.8 (316)	89.2 (32)	122 \pm 39
	151-200	100 (87)	96.3 (106)	92.9 (9)	26 \pm 12
OUTSIDE CLONE	201-250		98.1 (35)	95.8 (7)	5 \pm 2
	251-300		98.7 (11)	97.9 (5)	2 \pm 1
	301-350		99.6 (19)	97.9 (0)	2 \pm 1
	351-400		99.6 (0)	97.9 (0)	0 \pm 0
	401-450		100 (7)	97.9 (0)	1 \pm 1
	451-500			100 (5)	1 \pm 1
SUM		1911	1931	240	52 \pm 27

Table 4.2 Comparisons of the yield and viability of smooth brome seeds collected from clones invading fescue prairies in Riding Mountain National Park, Canada. Data were collected at the beginning and end of seed dispersal and represent the pooled results from 16 clones, randomly selected from two prairies. Cleaned seeds from ten panicles, randomly selected from each clone, were germinated in a growth chamber. Seed data were blocked by site to reduce between site variability within the ANOVA test. Means \pm 1 S.E.

	August	October	F	df	P
Seeds / pannicle	23.9 \pm 4.2	15.6 \pm 3.5	1.33	1, 29	0.2569
Seed mass (mg)	3.0 \pm 0.08	3.2 \pm 0.12	1.38	1, 29	0.2501
Germination (%)	78.8 \pm 2.4	84.8 \pm 2.3	5.54	1, 29	0.0255

Table 4.3 Comparisons between the numbers of smooth brome seeds dispersed and recruited from the seed bank surrounding four clones invading two fescue prairies in Riding Mountain National Park, Canada. Seeds were captured along 5 m strips of landscape cloth, pinned 1 m inside the fringe of invading clones (indicated by a dashed line). Germinable seeds account for the mean viability (84 %) and proportion of dispersed seeds containing a conspicuous caryopsis (15 %). Means \pm 1 S.E.

Distance		Seed rain			Seed bank	
		Total	Germinable	Mean (m ⁻²)	Total	Mean (m ⁻²)
INSIDE CLONE	0-50	263	33	55 \pm 21	8	13 \pm 5
	51-100	154	19	32 \pm 20	3	5 \pm 4
	101-150	253	32	53 \pm 44	2	3 \pm 2
	151-200	16	2	3 \pm 3	3	5 \pm 4
	201-250	6	1	1 \pm 1	1	2 \pm 2
OUTSIDE CLONE	251-300	-	-	-	2	3 \pm 2
	301-350	-	-	-	3	5 \pm 2
	351-400	-	-	-	2	3 \pm 2
	401-450	-	-	-	5	8 \pm 8
	451-500	-	-	-	4	7 \pm 4
SUM		692	87	15 \pm 7	33	6 \pm 1

CHAPTER 5: COVARIANCE BETWEEN DISTURBANCE AND SOIL RESOURCES DICTATES THE INVASIBILITY OF NORTHERN FESCUE PRAIRIES.

5.1 Abstract

The loss of global biodiversity, exacerbated by the increasing environmental impacts of exotic organisms, continues to stimulate debate into its role in ecosystem function. Despite the relevance of the diversity-stability hypothesis for the conservation and restoration of natural communities, experimental results have been mixed. Although, resource availability, often related to natural and anthropogenic disturbances, appears central to the invasibility of biological communities, few studies have considered the impacts of disturbance intensity on the community invasibility. To test the hypothesis that community invasibility is contingent on impact of disturbance on the above and belowground function of resident species, I designed an experiment testing the invasibility of northern fescue prairies by smooth brome (*Bromus inermis* Leyss.), a Eurasian perennial, threatening the structure and function of prairie remnants throughout the Great Plains. Using soil disturbances and herbicide I imposed treatments manipulating the above and belowground structure and composition of prairie communities. My observations demonstrate that the vulnerability of northern fescue prairies to exotic plant invasions remains contingent on plant community function and composition. While the establishment of smooth brome seedlings increased with decreasing plant diversity, its impact depended on nitrogen availability. As a result, soil

disturbances that maintained the belowground function of prairie communities, decreasing nutrient levels, remained resistant to the establishment of smooth brome seedlings. Emphasizing the functional role of above- and belowground biomass, my findings illustrate the importance of disturbance type in the invasibility of prairie communities. Such a consideration is critical in the conservation and restoration of natural areas.

5.2 Introduction

The relentless and unprecedented loss of global biodiversity continues to stimulate an intense polemic regarding its role in ecosystem function (Chapin et al. 1998, McCann 2000, Mattingly et al. 2007). Recent work, motivated by the increasing environmental and social impacts of exotic organisms (Mack et al. 2000, Ricciardi 2007), has centered on the ability of diverse communities to resist biological invaders (Kennedy et al. 2002). Although the mechanisms contributing to their invasion resistance remain unclear (Levine and D'Antonio 1999; McCann 2000), decreasing the destabilizing oscillations in population and consumer-resource dynamics, remain fundamental to the persistence of diverse ecosystems (MacArthur 1955; Elton 1958; Odum 1971; Levine and D'Antonio 1999; Rooney et al. 2006).

Despite the relevance of the diversity-stability hypothesis to the conservation and restoration of natural communities, experimental results have been mixed (Levine and D'Antonio 1999, Wardle 2001). Recent studies, exploring links between diversity and invasibility, have revealed both positive (Lonsdale 1999, Stohlgren et al. 1999, McKinney 2002, White and Houlahan 2007) and negative (Tilman 1997, Knops et al. 1999, Levine 2000, Naeem et al. 2000, Kennedy et al. 2002, Biondini 2007)

relationships, while others have been inconclusive (Crawley et al. 1999, Collins et al. 2001, Mattingly et al. 2007). Despite these inconsistencies, the majority of studies consider resource availability central to the invasibility of biological communities (Levine and D'Antonio 1999, Davis and Thompson 2000). While species richness often increases the utilization of resources and decreases community invasibility (Tilman et al. 1997, Shea and Chesson 2002), the establishment of potential invaders may depend more on spatial and temporal fluctuations in the availability of resources than on community diversity (Burke and Grime 1996, Wardle 2001, Kolb et al. 2002, Melbourne et al. 2007). These, often exacerbated by natural and anthropogenic disturbances, likely act as important catalysts for invasion (Fox and Fox 1986, Hobbs and Huenneke 1992, Wardle 2001, McCann 2007).

Understanding the links between diversity and invasibility is often confounded by the covariance among key variables (Levine and D'Antonio 1999, Lamb 2008). For example, disturbances that alter community diversity and biomass, including fire and herbivory, also frequently alter the availability of resources (Mack 1989, D'Antonio and Vitousek 1992). As a result, their impacts on community architecture and trophic structure (Mack et al. 2000, McCann 2007), functional complementarity (Prieur-Richard 2002, Shipley et al. 2006, Biondini 2007), and the physical and chemical elements of environments (Lake and Leishman 2004), all can create establishment opportunities for potential invaders.

In the Great Plains, natural disturbances, including fire, grazing, and the burrowing of fossorial mammals are integral to the structure and function of prairie ecosystems (Biondini et al. 1989, Martinsen et al. 1990, Collins and Steinauer 1998). In

addition to their role in creating potential niche opportunities for exotic invaders (Parker et al. 1993), changes in the type and intensity of disturbance suggest important differences in their contribution to community invasibility (Vujnovic et al. 2002, Gibson 1989). For example, the large belowground biomass of most prairie plants (Tilman et al. 1996, Rice et al. 1998) suggests that plant communities characterized by the loss of aboveground biomass should continue to resist invasion, provided that their roots and rhizomes remain active. While continuing to compete for soil resources during regrowth, belowground biomass of resident species should also limit the niche opportunities available to potential invaders (Crowley et al. 2005).

To test this hypothesis, I explored the impacts of several types of disturbance on the establishment of smooth brome (*Bromus inermis* Leyss.), a Eurasian perennial threatening the structure and function of prairie remnants throughout the Great Plains (Otfinowski et al. 2007). Widely planted for hay, forage and to revegetate disturbances, smooth brome often escapes to invade native prairies. Using soil disturbances, designed to simulate the impacts of northern pocket gophers (*Thomomys talpoides*), and herbicide I tested the impact of plant community function and composition on their invasibility. Unlike the burial of prairie plants by pocket gophers, which often sustains the function of roots and rhizomes (Laycock 1958, Foster and Stubbendieck 1980, Gibson 1989), applications of herbicide eliminate both the above- and belowground biomass of resident plants. Based on these manipulations, I tested the hypothesis that while the establishment of smooth brome within northern fescue prairies increases with decreasing diversity, community invasibility remains contingent on the persistence and function of belowground plant biomass.

5.3 Methods

Research was conducted in Riding Mountain National Park, Manitoba, Canada (50° 39' 00", - 99° 55' 48"). The park occupies an area of 2,978 km² in western Canada and consists of large areas of rolling upland (550 – 640 m), underlain by glacial tills (Lang 1974). The region is characterized by mean annual precipitation of 450 – 500 mm and a growing season of 168 – 173 days; mean temperatures range between -18°C in January and 18°C during July (Leeson et al. 2005). The park lies in the Mixedwood Section of the Boreal Forest Region (Rowe 1972) and protects areas of northern fescue prairie, threatened in western Canada by grazing, cultivation, and invasions of exotic species (Trottier 1986).

To examine the impact of disturbance type on smooth brome establishment, I selected three experimental blocks (8 x 5 m) in each of two fescue prairies located in the Park. The two study areas were situated approximately 50 km apart; soils at the more western Bob Hill prairie were more xeric and lower in mineral nitrogen than the centrally located Strathclair prairie [volumetric water content (0-20 cm, July 2005) $7.5 \pm 3.7\%$ vs. $9.5 \pm 4.2\%$, $F_{1,100} = 9.2$, $P = 0.0031$; mineral nitrogen (0-15 cm; July 2005): $\text{NH}_4\text{-N}$, 5.3 ± 0.4 mg/kg vs. 9.1 ± 0.4 mg/kg, $F_{1,38} = 37.4$, $P < 0.0001$; $\text{NO}_3\text{-N}$, 0.60 ± 0.1 mg/kg vs. 2.1 ± 0.2 mg/kg, $F_{1,38} = 40.7$, $P < 0.0001$].

I examined the impacts of disturbance on smooth brome establishment by manipulating the structure and composition of prairie communities. Based on a simple randomized block design, I divided each experimental block into six quadrats (each 2 x 2 m) and randomly assigned treatments to the four 1 x 1 m cells within each quadrat (Fig.

5.1). Starting in July 2003, one moderate and two low plant diversity treatments were applied to 60 x 60 cm areas at the center of each cell. Inside the moderate diversity treatments, I used foam brushes to apply a 33 % glyphosate:water solution (Vantage Plus, Dow AgroSciences Canada, Calgary AB) to the leaf surfaces of forbs only. In the first low diversity treatment, I used non-selective, brush applications of this systemic herbicide to target both the above- and belowground biomass of all resident forbs; in the second, I targeted only the aboveground biomass by burying all plants with loose soil, used to simulate disturbances caused by northern pocket gophers. Loose soil (24 L) was collected from pocket gopher mounds adjacent to each experimental block. The fourth cell was left untreated as a control.

Starting in May 2004, I transplanted four seedlings of smooth brome (Carlton; Brett-Young seeds, Winnipeg MB) inside a 20 x 20 cm area at the center of each treatment area (Fig. 5.1). Seedlings were germinated and raised in root trainers in a greenhouse (day: 16 h / 21°C; night: 8h / 15°C) and cold hardened at the five-leaf stage (height < 9 cm, < 1 tiller), one week prior to transplanting. I used a hand auger to extract cores of prairie soil (0-15 cm deep, 5 cm wide, 74 cm³), replacing each with a plug of greenhouse soil containing one seedling. Previous attempts to germinate seeds directly inside the treatments failed. Transplanted seedlings were harvested in August 2004, at the end of one growing season. I clipped all seedlings at the soil surface and used a small spade to excavate their roots and rhizomes to a depth of 10 cm. All samples were oven dried (48 h, 60°C) before weighing; roots and rhizomes of smooth brome were washed using a mechanical root washer and separated by hand from those of other species.

Although some of the transplanted seedlings were heavily browsed by animals, fewer than one percent (5/576) died during the experiment.

I monitored the impacts of community disturbance on soil moisture, temperature, and mineral nitrogen. Prior to harvest, I measured volumetric soil moisture inside each treatment cell using a time domain reflectometer (0-10 cm; HydroSense, Campbell Scientific Inc., Logan UT), and used a digital stem thermometer to measure surface soil temperature. Measurements of soil mineral nitrogen were based on in-situ incubation of mineral soil (Binkley and Hart 1989). Cores of soil, extracted using a hand auger (0-15 cm, 74 cm³), were placed in plastic Ziplock bags and returned to the auger excavations between July and August 2004. Along with reference samples, collected at the start of the incubation, all samples were air dried, milled, extracted with 2.0 M KCl, and analyzed for ammonium and nitrate using a Technicon Autoanalyzer II (Maynard and Karla 1993). As a result of rodent damage to the incubation bags, only the results from Strathclair prairie are presented here.

Differences in the structure and composition of plant communities following disturbance were compared using foliar cover data collected inside 1 x 1 m quadrats, centered inside each treatment cell. Foliar cover for each species was estimated using five percent intervals and isolated individuals were assigned a cover of 0.5 %. Plant communities were inventoried during August 2004, prior to the harvest of smooth brome transplants.

5.3.1 Data analysis

I used a blocked, one-way analysis of variance (ANOVA) to examine the impacts of community diversity and disturbance on the establishment of smooth brome seedlings. Using the mean above- and below-ground biomass and the maximum rhizome length of seedlings I tested the null hypothesis that brome establishment was independent of disturbance type. Total plant cover, species and effective richness, as well as diversity and evenness were used to compare the response of plant communities to herbicide and burial manipulations. Effective richness [$N2 = (\sum p_i^2)^{-1}$] and evenness $\{E3 = [(\sum p_i^2)^{-1} - 1] / [\exp(-\sum p_i \log p_i) - 1]\}$ describe plant communities based on the proportional abundance of species and the shape of their frequency distributions (Kvalseth 1991) and are helpful in examining species responses to environmental manipulations (Legendre and Legendre 1998). One-way comparisons of the physical environments complemented those describing plant communities. These, including available and mineralized nitrogen, were log transformed to improve the homogeneity of variance among treatment groups, while measurements of volumetric soil moisture, recorded as percentages, were arcsine transformed to approximate a normal distribution (Zar 1999). Where no significant differences were found between the two study sites, data were pooled and the combined results presented.

I further examined the impact of the physical environments of disturbed communities on smooth brome establishment using multiple regression models. I used principal component analysis to eliminate the multicollinearity among environmental variables (Graham 2003), and used scores along the first three component axes as predictors of the above- and below-ground biomass of smooth brome seedlings. Best

models were selected using backward elimination of successive variables (Zar 1999). Based on eigenanalysis of a square, symmetric dispersion matrix, principal component analysis finds linear combinations of variables that maximize the dispersion among samples along linearly independent axes (Legendre and Legendre 1998).

Lastly, I used canonical variate analysis to compare the recovery of prairie communities following burial and manipulations with herbicide. Related to principal components analysis, canonical variate analysis defines linearly uncorrelated axes, maximizing the dispersion among *a priori* groupings of objects (Legendre and Legendre 1998). The discriminant weights, assigned to species along each discriminant axis, can be interpreted as measures of their relative power in separating treatment groups (Kenkel et al. 2002). I log transformed the abundances of each species prior to analysis in order to improve the within-group normality of each descriptor (Legendre and Legendre 1998). Univariate and multivariate statistical analyses were performed using SPSS 11.0.0 (SPSS Inc., Chicago, IL) and SYNTAX 2000 (Podani 2001), respectively.

5.4 Results

Undisturbed prairies resisted the establishment of smooth brome. Compared to other treatments, brome seedlings transplanted into native fescue prairies accumulated little above- and belowground biomass and were characterized by short rhizomes (Fig. 5.2). Smooth brome establishment was more successful in plots with low plant diversity. As a result, seedlings transplanted into areas treated selectively with herbicide, characterized by lower plant cover, effective richness and evenness (Table 5.1), accumulated more biomass and produced longer rhizomes (Fig. 5.2). This response was most pronounced

where the above- and belowground biomass of resident species had been removed with non-selective applications of herbicide (Fig. 5.2).

The impact of plant community composition on smooth brome establishment was related to the availability of soil resources. Compared with undisturbed controls, both available and mineralized nitrogen increased following a decline in prairie diversity (Table 5.1). The negative covariance between soil nitrogen and plant diversity accounted for a high proportion of variance among quadrats (Fig. 5.3). The first principal component axis accounted for 52.2 % ($\lambda = 5.74$) of variability among community variables, with total and graminoid cover and all indices of diversity covarying positively (all loadings ≥ 0.788) and opposite to mineral nitrogen, soil moisture, and the proportion of forbs (all loadings ≤ 0.428 ; Fig. 5.3). The second axis (15.8 %, $\lambda = 1.74$) separated treatments characterized by higher soil temperatures (loading = - 0.804) and lower moisture (loading = 0.631; Fig. 5.3). Differences in mineral nitrogen were also emphasized along the third component axis. Accounting for 9.7 % of variance among samples ($\lambda = 1.06$), this axis separated treatments characterized by high evenness (loading = 0.451) and elevated levels of incubated nitrogen (0.660).

Ordination scores along the first and third principal component axes accounted for a large proportion of variance in the aboveground biomass of smooth brome seedlings ($r^2 = 0.593$, $F_{2, 67} = 51.2$, $P < 0.001$). Seedling biomass was correlated negatively with plant diversity, increasing along the first component axis ($\beta = - 0.088$, $t = - 9.2$, $P < 0.001$), and positively with soil nitrogen, decreasing along the first and increasing along the third component axes ($\beta = 0.091$, $t = 4.1$, $P < 0.001$; Table 2). Similar responses were observed in the belowground biomass of seedlings (Table 5.2).

While increased levels of soil nitrogen facilitated smooth brome establishment, nitrogen availability was higher where the disturbance was greater and where the native community was less diverse. As a result, the rapid recovery of prairie communities following burial, combined with the lower soil nitrogen and moisture characteristic of simulated pocket gopher mounds (Table 5.1), led to lower biomass of brome seedlings in these treatments (Fig. 5.2). Buried plant communities were easily distinguished from those treated with herbicide, and the first canonical variate axis, summarizing 85.8 % of variance among treatment groups ($\lambda = 18.73$; $X^2_{210} = 499.93$, $P < 0.0001$), was strongly correlated with native perennials, including smooth aster (*Aster laevis* L.), northern bedstraw (*Gallium boreale* L.), and rough fescue (*Festuca hallii* (Vasey) Piper; Fig. 5.4). Although distinct from those treated with herbicide, buried communities also differed from those of undisturbed, control treatments. The second canonical variate axis summarized 11.3 % of variance among treatment groups ($\lambda = 2.47$; $X^2_{138} = 183.82$, $P = 0.0055$) and was correlated with ruderal species, including pygmyflower (*Androsace septentrionalis* L.), Canada blue grass (*Poa compressa* L.), and chickweed (*Stellaria longifolia* Muhl.), persisting after soil disturbance (Fig. 5.4).

5.5 Discussion

My observations of northern fescue prairies demonstrate that their vulnerability to exotic plant invasions is contingent on community function and composition. While the establishment of smooth brome seedlings increased with decreasing plant diversity, its impact depended on the availability of soil nitrogen. Above and below-ground, brome biomass increased in response to greater nitrogen mineralization, characteristic of low

diversity communities, however, establishment of brome seedlings remained contingent on diversity. As a result, burial treatments, simulating the disturbance caused by northern pocket gophers, provided poor recruitment areas for smooth brome. Their low levels of soil moisture and nitrogen, combined with the rapid recovery of the prairie community, compromised seedling establishment.

5.5.1 Impacts of diversity

Understanding the role of community diversity in invasions is imperative to the conservation and restoration of natural ecosystems (Chapin et al. 1998). Although the potential mechanisms responsible for the stability of diverse communities remain elusive (Levine and D'Antonio 1999), the ability of species to reduce fluctuations in available resources is likely a key element (McCann 2000). The importance of diversity in community invasibility suggests that invasions are most likely when one or more species are fluctuating or are under-represented at a given moment (Hutchinson 1959). My results, demonstrating the functional role of community diversity in invasibility of northern fescue prairies, support these observations.

Even though diverse communities are more likely to include competitive species that resist potential invaders (Wardle 2001), compensation and greater variance of responses by a small number of species may also enable the maintenance of community productivity and continued resistance to potential invaders (Chapin et al. 1998). As a result, even low diversity patches may resist invaders given their dominance by one or few highly competitive species (Levine and D'Antonio 1999). This raises important

questions about the direction of character displacement in communities subjected to the loss of species. To my knowledge, these questions remain unanswered.

5.5.2 Covariance with resources

Understanding the impacts of diversity on community resistance to exotic invasions is complicated by the fact that changes in diversity covary with factors known to influence invasibility (Levine and D'Antonio 1999). While aboveground changes in the structure and composition of native communities also affect their invasibility (Crawley 1987), the impacts of plant diversity on the niche opportunities available to potential invaders can be equally acute belowground. My results demonstrate that decreasing prairie diversity corresponds with higher rates of nitrogen mineralization, a likely response to higher soil moisture and temperature of low diversity communities as well as the increased mineralization of plant biomass killed by herbicide. Increasing soil nitrogen following a decline in plant diversity has been observed in other studies. For example, Tilman et al. (1996) correlated the number of species in experimental prairie plots with lower concentrations of inorganic soil nitrogen. While the mechanisms underlying the inverse relationship between diversity and resource availability remain unclear (Chapin et al. 1998), the efficiency of resource use is central to both the niche complementarity and sampling effect hypotheses invoked to explain these observations (Tilman 1999).

Although my results demonstrate the impact of community diversity on soil resources and the invasibility of prairie communities, disturbance is not pre-requisite for successful invasions (Usher 1988, Lodge 1993). For example, the degree of niche overlap between the native and exotic species may determine the pattern and extent of

invasion (Hoopes and Hall 2002). As a result, exotic species with broad ecological niches or wide dispersal may become prolific invaders regardless of disturbance (Lodge 1993, Silvertown et al. 1999, Buckling et al. 2000). Equally important may be the extent of environmental heterogeneity and its ability to facilitate the coexistence of a higher number of resident species (Melbourne et al. 2007).

5.5.3 Community recovery

Simulated pocket gopher mounds provided poor recruitment areas for the establishment of smooth brome seedlings. While several authors have demonstrated successful recruitment of exotic plants on gopher mounds as well as areas of bare ground (Hobbs and Mooney 1985, D'Antonio 1993, Symstad 2000), the observed discrepancies may be attributable to differences in environmental conditions (Koide et al. 1987). For example, Laycock (1958) reported low germination of plants colonizing gopher mounds in areas of low soil moisture and emphasized the importance of mound thickness in the regeneration of buried plants. Among others, thickness of the deposit as well as its origin in the soil profile may also impact plant regrowth and establishment through their influence on moisture and nutrient concentrations (Weaver and Fitzpatrick 1934, Koide et al. 1987). While my observations of community recovery following burial are corroborated by other studies (Sherrod et al. 2005), my results also stress the importance of disturbance type on community invasibility. As a result, disturbances that preserve the root and rhizome function of native species, including burial by pocket gophers, may be less vulnerable to exotic invaders than those where the root function has been compromised. The integrity of belowground biomass may constitute an important and often overlooked

component of community diversity, the maintenance and restoration of which may be key in the ability of ecosystems to resist biological invaders.

Impacts of diversity and resources on community invasibility depend on the life history of potential invaders (Renne et al. 2006). While I demonstrate the impacts of community function and composition on the establishment of smooth brome, factors that determine the dispersal and proliferation of established populations remain key in the prediction and management of potential invasions (Davis et al. 2000, Larson 2003). For example, the rapid initiation of rhizomes by seedlings established on simulated pocket gopher mounds illustrates their continued threat to adjacent prairie communities. Despite their low biomass, clonal expansion by seedlings established in burial treatments could facilitate their proliferation into adjacent communities (Moody and Mack 1988). Equally important in predicting biological invasions may be impacts of multi-trophic interactions (Klironomos 2002, Callaway et al. 2004) and the important role of dispersal in compensating the potential inverse density dependence among invading populations (Crawley 1986, Sakai et al. 2001). Such factors emphasize the importance of considering several stages in the life history of potential invaders (Dietz and Edwards 2006) as well as a clear definition of their invasion success (Levine and D'Antonio 1999).

Globally, few habitats remain free of exotic species, and many pose serious threats to the biodiversity and function of native ecosystems (Ricciardi 2007). My results confirm that niche opportunities afforded to potential invaders, may be central to the frequently conflicting results of studies examining the role of diversity in community invasibility (Levine and D'Antonio 1999, Davis and Thompson 2000). Emphasizing the functional role of both the above- and belowground biomass, my findings illustrate the

importance of disturbance type in the invasibility of prairie communities. Such a consideration is critical in the conservation and restoration of natural areas and maintaining their resistance to exotic invaders (MacDougall and Turkington 2007).

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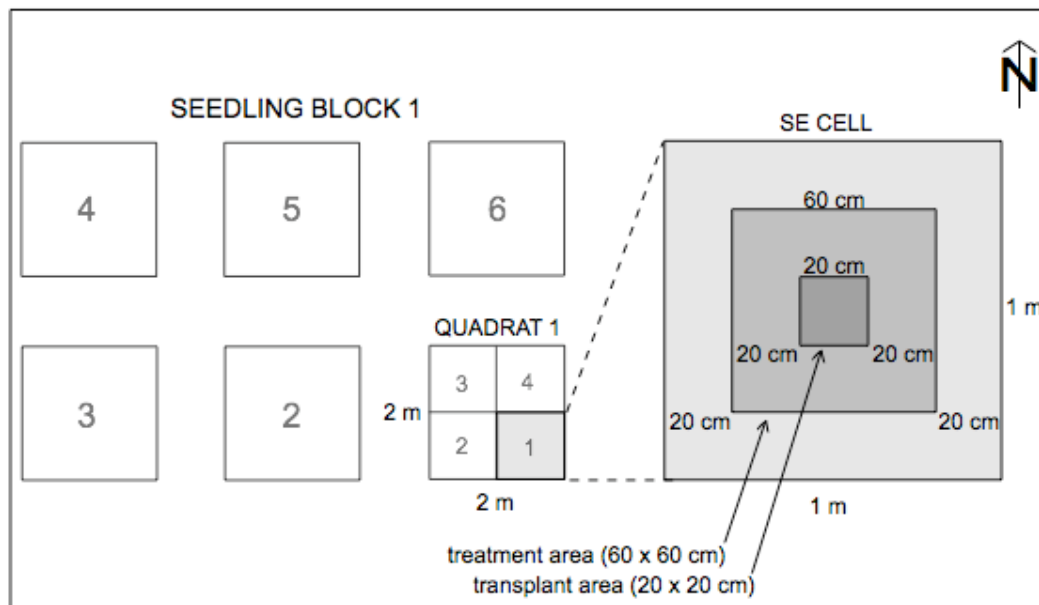


Figure 5.1 Experimental design used to measure the impact of plant community function and composition on the establishment of smooth brome (*Bromus inermis* Leyss.) seedlings within northern fescue prairies in Riding Mountain National Park, Manitoba, Canada. Four seedlings of smooth brome were transplanted into treatment areas at the center of 1 x 1 m quadrats used to manipulate the function and composition of prairie communities.

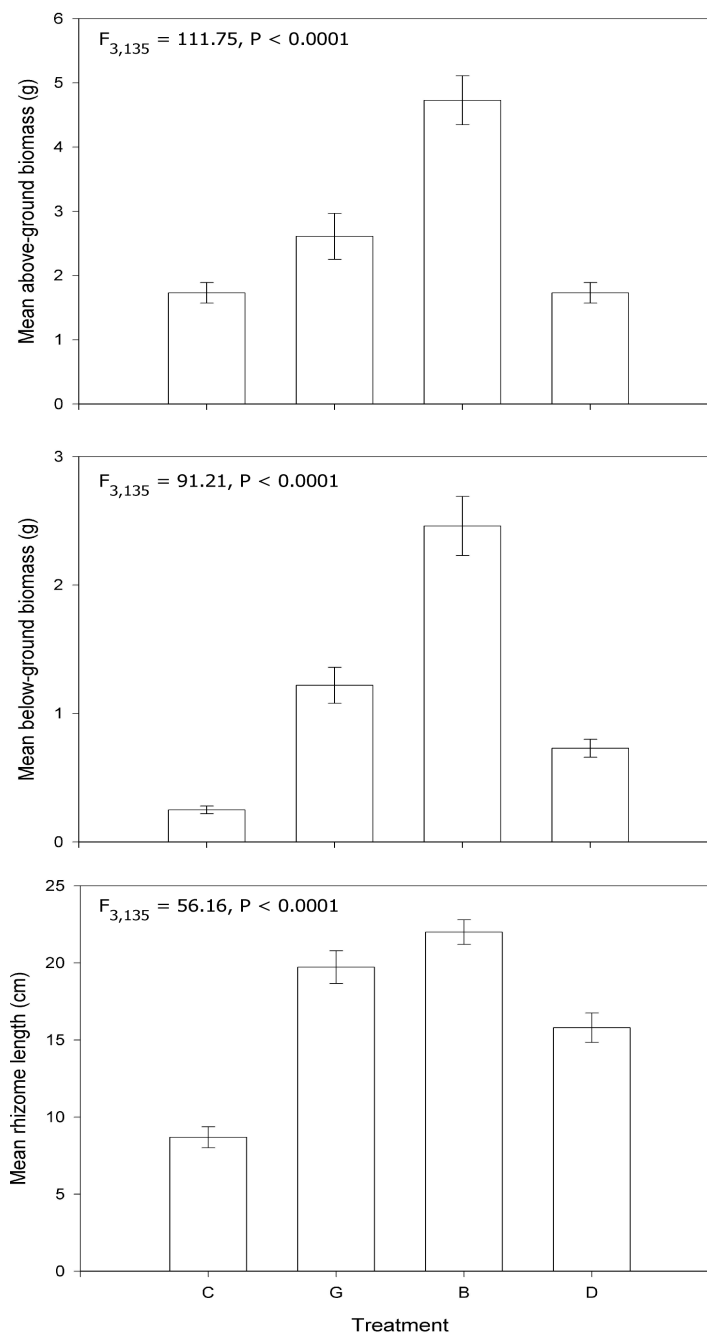


Figure 5.2 Impacts of plant community function and composition on the establishment of smooth brome (*Bromus inermis* Leyss.) seedlings, transplanted into northern fescue prairies in Riding Mountain National Park, Manitoba, Canada. The treatments, control (C), selective application of herbicide (G), non-selective application of herbicide (B), and simulated pocket gopher (*Thomomys talpoides*) disturbance (D) represent a gradient of above- and belowground community diversity. Data represent the mean biomass and maximum rhizome length of four seedlings at the end of one growing season, and were blocked to reduce variability between experimental plots within the one-way ANOVA model.

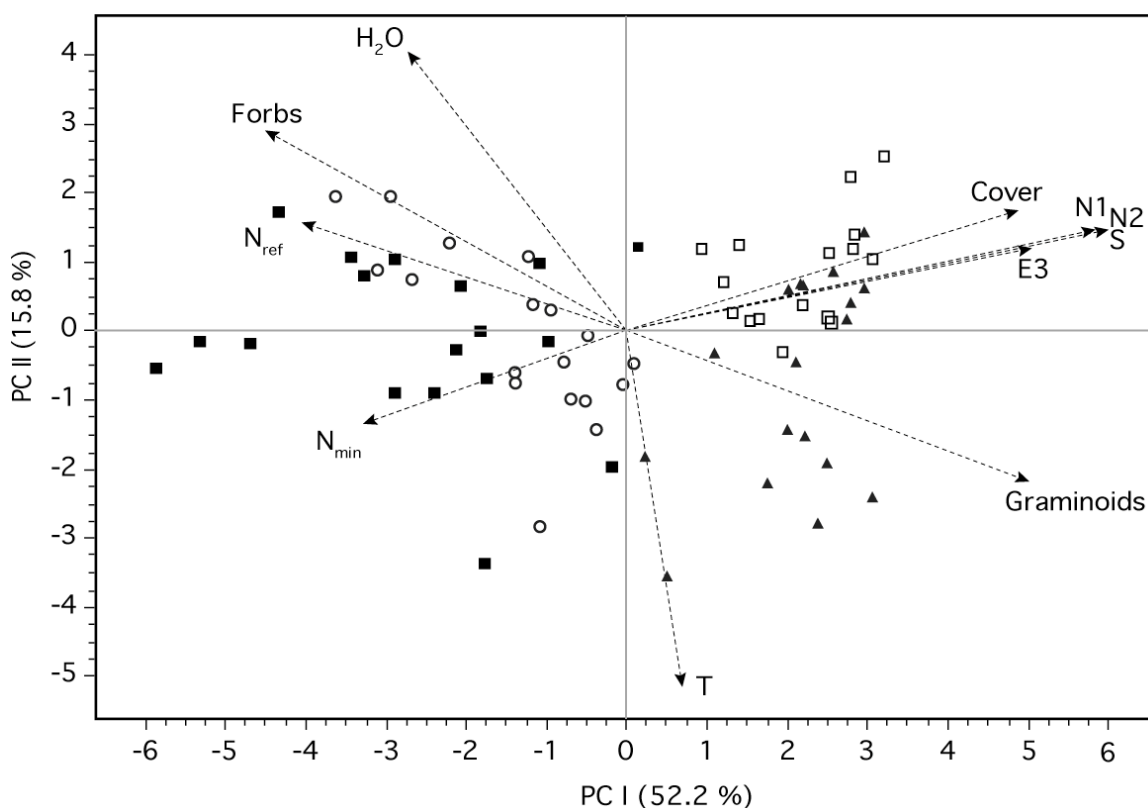


Figure 5.3 Covariance between the impacts of disturbance and plant diversity manipulations and the function of northern fescue prairies in Riding Mountain National Park, Manitoba, Canada. The magnitude and direction of arrows illustrates the contribution of each variable to the maximizing of dispersion among samples along principal component axes. The treatments, control (\square), selective application of herbicide (\circ), non-selective application of herbicide (\blacksquare), and simulated pocket gopher (*Thomomys talpoides*) disturbance (\blacktriangle) represent a gradient of above- and belowground community diversity. Graminoids and forbs represent their proportional contribution to total plant community cover. Community richness (S), Shannon's diversity (N1), Effective richness (N2), and evenness (E3) summarize differences in plant community composition among treatment groups, while volumetric soil moisture (H₂O), temperature (T), mineral (N_{ref}) and incubated nitrogen (N_{min}) describe the covariance between changes in plant community composition and soil environments. All variables were log transformed.

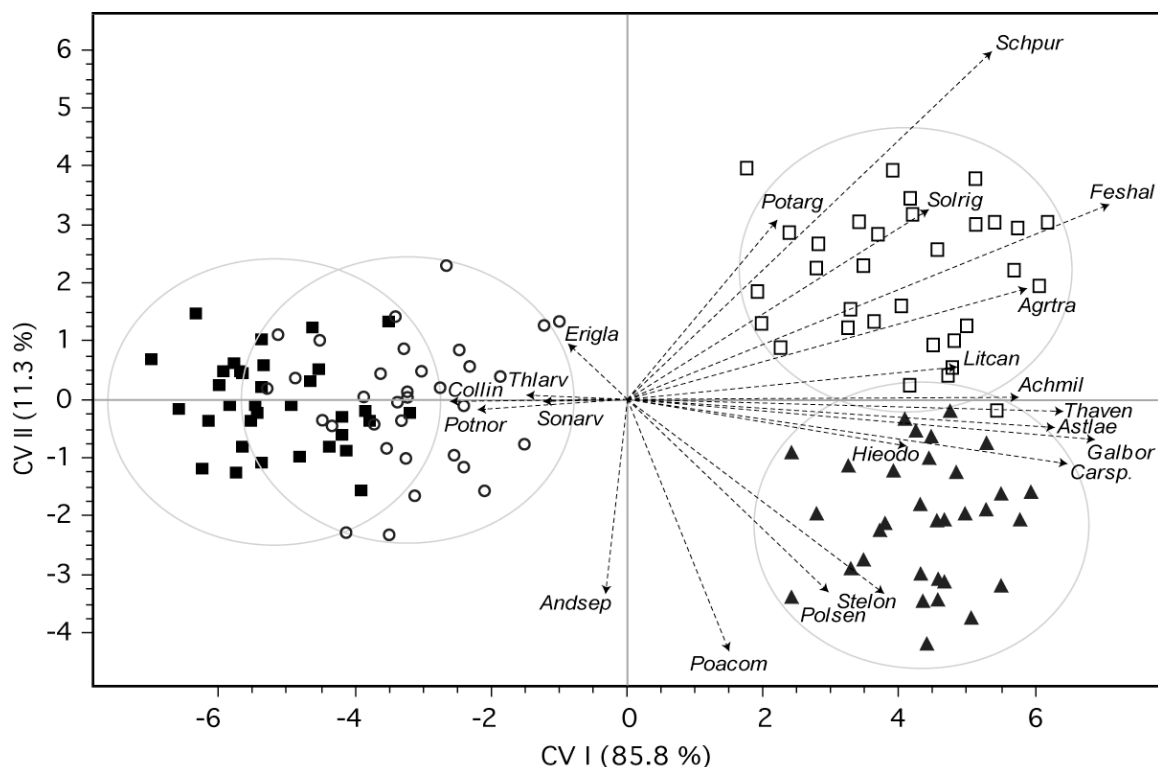


Figure 5.4 Impacts of disturbance and plant diversity manipulations on the recovery of northern fescue prairies in Riding Mountain National Park, Manitoba, Canada. The discriminant weights of each species along each canonical variate axis represent their relative power to separate treatment groups. Eigenvectors have been normalized to unit length resulting in spherical dispersions of group objects; the illustrated isodensity circles contain 95 % of the individuals belonging to each group (Podani 2001). The treatments, control (\square), selective application of herbicide (\circ), non-selective application of herbicide (\blacksquare), and simulated pocket gopher (*Thomomys talpoides*) disturbance (\blacktriangle) represent a gradient of above- and belowground community diversity. For clarity, only those species contributing substantially to each axis were included. Abbreviations: Achmil (*Achillea millefolium* L., yarrow), Agrtra (*Agropyron trachycaulum* (Link.) Malte; slender wheatgrass), Andsep (*Andosace septentrionalis* L.; pygmyflower), Astlae (*Aster laevis* L.; smooth blue aster), Carsp. (*Carex* sp.; sedge), Collin (*Collomia linearis* Nutt.; collomia), Erigla (*Erigeron glabellus* Nutt.; fleabane), Feshal (*Festuca hali* (Vasey) Piper; rough fescue), Galbor (*Galium boreale* L.; northern bedstraw), Hieodo (*Hierochloe odorata* (L.) Beauv.; sweet grass), Litcan (*Lithospermum canescens* (Michx.) Lehm.; puccoon), Polsen (*Polygala senega* L.; seneca snakeroot), Potarg (*Potentilla arguta* Pursh.; white cinquefoil), Potnor (*P. norvegica* L.; rough cinquefoil), Schpur (*Schizachne purpurascens* (Torr.) Swallen; purple oat grass), Solrig (*Solidago rigida* L.; goldenrod), Sonarv (*Sonchus arvensis* L.; sow-thistle), Thaven (*Thalictrum venulosum* Trel.; meadow-rue), Thlarv (*Thlaspi arvense* L.; pennycress). Nomenclature according to Cody (1988).

Table 5.1 Impacts of disturbance and plant diversity manipulations on the function and composition of northern fescue prairies in Riding Mountain National Park, Manitoba, Canada. The treatments, control (C), selective application of herbicide (G), non-selective application of herbicide (B), and simulated pocket gopher (*Thomomys talpoides*) disturbance (D), representing a gradient of above- and belowground community diversity, were applied one year prior to the survey. Measurements of volumetric soil moisture (0-10 cm; HydroSense, Campbell Scientific Inc., Logan UT) were collected during August 2004. Available and mineralized nitrogen were based on samples of soil (0-15 cm), air dried, milled and extracted using 2.0 M KCl. Mineralized nitrogen describes samples of mineral soil (0-15 cm), incubated in-situ between July and August 2004 (see text for details). Only the results from a single study site are presented here and two incubation bags were not recovered at the end of the experiment. Data were log transformed and the means of treatment groups blocked to reduce variability between experimental blocks within the one-way ANOVA model. Means \pm 1 S.E.

	Treatment				F	df	p
	Control	Graminoid	Bare	Disturbed			
Graminoids (%)	44.7 \pm 3.5	7.6 \pm 1.1	2.8 \pm 0.6	40.2 \pm 4.1	116.3	3, 135	\leq 0.0001
Forbs (%)	83.0 \pm 5.4	37.2 \pm 5.2	21.7 \pm 2.9	79.4 \pm 5.1	93.8	3, 135	\leq 0.0001
Total cover (%)	127.9 \pm 8.01	44.8 \pm 5.2	24.5 \pm 3.2	119.7 \pm 7.7	168.8	3, 135	\leq 0.0001
Richness (S)	14.9 \pm 0.5	7.7 \pm 0.3	5.2 \pm 0.4	13.9 \pm 0.4	129.5	3, 135	\leq 0.0001
Shannon's index [$N1 = \exp(-\sum p_i \log p_i)$]	2.87 \pm 0.05	2.22 \pm 0.04	1.90 \pm 0.06	2.78 \pm 0.05	88.5	3, 135	\leq 0.0001
Effective richness [$N2 = (\sum p_i^2)^{-1}$]	9.46 \pm 0.37	5.52 \pm 0.32	4.22 \pm 0.32	8.89 \pm 0.38	57.6	3, 135	\leq 0.0001
Evenness [$E3 = (N2-1)/(N1-1)$]	4.45 \pm 0.1	3.58 \pm 0.13	3.36 \pm 0.12	4.31 \pm 0.12	20.8	3, 135	\leq 0.0001
Soil moisture (%)	16.6 \pm 0.7	16.9 \pm 0.8	18.3 \pm 0.7	14.6 \pm 0.6	7.7	3, 135	\leq 0.0001
Soil temperature ($^{\circ}$ C)	12.8 \pm 0.1	13.4 \pm 0.2	13.3 \pm 0.2	13.8 \pm 0.3	10.8	3, 135	\leq 0.0001
Available nitrogen (mg kg $^{-1}$)*	17.65 \pm 1.49	25.25 \pm 1.81	24.95 \pm 2.18	14.63 \pm 0.67	15.2	3, 69	\leq 0.0001
Mineralized nitrogen (mg kg $^{-1}$)*	14.02 \pm 4.06	32.33 \pm 5.05	52.51 \pm 10.78	21.77 \pm 5.50	1.51	3, 64	\leq 0.0001

*[NH $_4^+$ N] + [NO $_3^-$ N]

Table 5.2 Impacts of disturbance and manipulations of community diversity on the above- and belowground biomass of smooth brome (*Bromus inermis* Leyss.), invading northern fescue prairies in Riding Mountain National Park, Manitoba, Canada. Model variables were selected using backward elimination and represent principal component scores from an ordination of plant community and soil descriptors. See the text for details.

Model	F	df	P	r ²	Variables	β	SE	t	P
Above-ground biomass	51.2	2,67	< 0.001	0.593	Constant	0.484	0.023	21.4	< 0.001
					PC 1	-0.088	0.010	-9.2	< 0.001
					PC 3	0.091	0.022	4.1	< 0.001
Below-ground biomass	30.9	2,67	< 0.001	0.479	Constant	0.310	0.021	15.0	< 0.001
					PC 1	-0.061	0.009	-7.0	< 0.001
					PC 3	0.072	0.020	3.6	0.001

**CHAPTER 6: CLONAL INTEGRATION FACILITATES THE
PROLIFERATION OF SMOOTH BROME INVADING NORTHERN FESCUE
PRAIRIES.**

6.1 Abstract

Predicting exotic invaders and reducing their impacts on the biodiversity and function of native ecosystems requires an understanding of the mechanisms that facilitate their success during key stages of invasion. I determined whether clonal growth, characteristic of the majority of successful invaders of natural areas, facilitates the proliferation of *Bromus inermis* (smooth brome), an exotic grass invading ecosystems across the Great Plains. By manipulating the below-ground connections of proliferating rhizomes as well as the levels of soil nitrogen along the margins of invading clones I hypothesized that physiological integration would most benefit ramets invading low resource environments. Severing clonal connections reduced the mass of smooth brome shoots invading native prairies and was exacerbated by the immobilization of soil nutrients with glucose. Clonal connections were equally important in the maintenance of smooth brome density and the horizontal proliferation of ramets. My results demonstrate the role of physiological integration in the proliferation of a clonal exotic invader and may help explain the success of clonal invaders in other regions. Although integration among invading ramets suggests several possibilities for successful management, future research must continue to elucidate differences in the invasiveness of native versus exotic species as well as the persistence of clonal connections among exotic invaders.

6.2 Introduction

Exotic plant invasions pose a growing threat to the endemic biodiversity and function of ecosystems around the world (D'Antonio and Vitousek 1992, Davis 2003, Yurkonis et al. 2006). The success of exotic species is contingent upon their transition between several stages of invasion (Puth and Post 2005). For example, while the proliferation of exotic invaders is contingent on their interaction with native communities (Kolar and Lodge 2001), their establishment often depends on propagule pressure, disturbance, and the diversity and structure of invaded habitats (Lockwood et al. 2005, Pokorny et al. 2005, Hierro et al. 2006). Despite the large number of exotic species in most regional floras, few among them have become serious invaders and many simply contribute to local species richness (Rosenzweig 2001). Consequently, predicting exotic invaders and reducing their impacts on native communities requires an understanding of the mechanisms that facilitate their success at each stage of invasion (Smith et al. 1999). Here, I determine whether clonal growth, characteristic of the majority of successful invaders of natural areas (Andersen 1995, Pyšek 1997, Reichard and Hamilton 1997, Acosta et al. 2006, Cadotte et al. 2006, Otfinowski and Kenkel 2008), facilitates the proliferation of an exotic grass invading northern fescue prairies.

Clonal plants, described as genetic individuals comprised of potentially independent modules (Kelly 1995), dominate most regional floras. In central Europe, clonal species comprise as much as 69 % of the native flora and over 90 % of alpine and arctic communities (Kelly 1995, Pyšek 1997). The success of clonal species is often attributed to their capacity to share resources among individual subunits. Translocation of resources, including water, carbohydrates, and minerals (Alpert and Mooney 1986,

Lau and Young 1988, Tissue and Nobel 1988, Stuefer and Hutchings 1994, Alpert 1996, Wijesinghe and Hutchings 1997, Kembell and Marshall 1995) enables clonal species to exploit patchy resources (Alpert and Mooney 1986; Wijesinghe and Hutchings 1997), ameliorate environmental stress (Amsberry et al. 2000, Pennings and Callaway 2000), and reduce the impacts of competition and herbivory (Hartnett and Bazzaz 1985, Schmid et al. 1988).

Despite the preponderance of clonal growth among successful invaders, few experimental studies have explored the functional role of clonality in the course of exotic invasions (Puth and Post 2005; but see Meyer and Schmid 1999, Maurer and Zedler 2002, Price et al. 2002). Where examined, clonal growth most often facilitated the proliferation of exotic species invading stressful environments, including wetlands (Amsberry et al. 2000) but its role in supporting invasions of other plant communities is less clear (Pennings and Callaway 2000).

I focused my experiments on examining the role of clonal growth in exotic plants invasions of native prairies. Using smooth brome (*Bromus inermis* Leyss.), a Eurasian perennial that has successfully invaded ecosystems across the Great Plains (Otfinowski et al. 2007), I designed a field experiment to examine the importance and environmental contexts of clonal integration among invading plants. I focused my experiment along the margins of invading clones, where inter-specific interactions between the invader and the native prairie community most likely contribute to resource heterogeneity (Caraco and Kelly 1991) and hypothesized that physiological integration would most benefit ramets invading low resource environments.

6.3 Methods

Research was conducted in Riding Mountain National Park, Manitoba, Canada (50° 39' 00", - 99° 55' 48"). The park occupies an area of 2,978 km² in western Canada and consists of large areas of rolling upland (550 – 640 m), underlain by glacial tills (Lang 1974). The region is characterized by mean annual precipitation of 450 – 500 mm and a growing season of 168 – 173 days; mean temperatures range between -18°C in January and 18°C in July (Leeson *et al.* 2005). The park lies in the Mixedwood Section of the Boreal Forest Region (Rowe 1972) and protects areas of rough fescue prairie, threatened in western Canada as a result of grazing, cultivation, and invasions by exotic species (Trottier 1986).

To examine the role of physiological integration in the proliferation of smooth brome, I randomly selected 20 clones invading prairies in each of two areas of Riding Mountain National Park. The two study areas were situated approximately 50 km apart; soils at the more western Bob Hill prairie were more xeric and lower in mineral nitrogen than the centrally located Strathclair prairie [volumetric water content (0-20 cm, July 2005) $7.5 \pm 3.7\%$ vs. $9.5 \pm 4.2\%$, $F_{1,100} = 9.2$, $P = 0.0031$; mineral nitrogen (0-15 cm; July 2005): $\text{NH}_4\text{-N}$, 5.3 ± 0.4 mg/kg vs. 9.1 ± 0.4 mg/kg, $F_{1,38} = 37.4$, $P < 0.0001$; $\text{NO}_3\text{-N}$, 0.60 ± 0.1 mg/kg vs. 2.1 ± 0.2 mg/kg, $F_{1,38} = 40.7$, $P < 0.0001$].

I examined the importance and the environmental contexts that favour physiological integration among smooth brome ramets invading prairies by manipulating belowground rhizomes and the levels of soil nitrogen. Based on a factorial design, I divided each clone into three pie-shaped sections and randomly assigned one of two rhizome treatments, three nitrogen treatments and a control to each (Fig. 6.1). Rhizomes,

located 5-15 cm below the soil surface (pers. obs.), were left intact or severed using plastic lawn edging (0.15 x 1.6 m), installed into narrow, semi-circular trenches along the margins of invading clones. Severing connections is a standard method of investigating the importance of clonal integration (Kelly 1995). Despite its potential to traumatize plants and allow entry of pathogens (Kelly 1995), many field studies have found no effect of severing on plants, suggesting that potential artifacts are limited (Hartnett and Bazzaz 1983, Alpert 1991, Evans 1992, Pennings and Callaway 2000, Peltzer 2002). I did not observe any sudden death of ramets or increased incidence of disease following severing.

Starting in May 2004, glucose (40 % C) and ammonium nitrate fertilizer (34-0-0) were broadcast inside the treatment areas in order to manipulate levels of soil nitrogen available to invading ramets. The annual rate of glucose ($300 \text{ gCm}^{-2}\text{y}^{-1}$) was split among three applications (May, June, July; 2004, 2005) and corresponded to the calculated amount of carbon required to immobilize most mineral nitrogen within 10 cm of the soil surface; applications of fertilizer ($11 \text{ gNm}^{-2}\text{y}^{-1}$) were also split (May, June, 2004, 2005) and corresponded with the amount of mineral nitrogen immobilized in the glucose treatments. Carbon amendments to soils stimulate microbial immobilization of available nitrogen (Recous and Mary 1990) and can reduce the competitiveness of exotic invaders (Blumenthal et al. 2003, Perry et al. 2004). In separate trials, additions of glucose ($300 \text{ gCm}^{-2}\text{y}^{-1}$) decreased soil concentrations of nitrate more than ammonium. In 2005, soil nitrate (0-15 cm) declined 25 – 59 % ($2.4 \pm 0.2 \text{ mg/kg}$ (control; annual mean $\pm 1 \text{ S.E.}$) vs. $1.4 \pm 0.1 \text{ mg/kg}$, $F_{1,99} = 33.1$, $P < 0.0001$), compared with 4 – 9 % for ammonium (9.7 ± 0.5 vs. 9.1 ± 0.5 , $F_{1,99} = 1.5$, $P = 0.2275$).

Impacts of rhizome and nitrogen manipulations on smooth brome invasion were measured following two growing seasons. The density and mass of all ramets were measured inside 50 x 50 cm quadrats centered inside each treatment area. Ramets were clipped at the soil surface, air dried (48 h, 60°C) and weighed. I determined the encroachment of clones by comparing the position of invading ramets at the beginning and end of the experiment (May 2004, July 2005).

6.3.1 Statistical analysis

I used two-way analysis of variance (ANOVA), blocked by individual clones, to examine the response of smooth brome to rhizome and nitrogen manipulations. All data were log transformed to improve the homogeneity of variance (Zar 1999). Data were pooled where no significant differences were found between the study sites.

6.4 Results

Severing clonal connections reduced the mass of smooth brome shoots invading native prairies and was exacerbated by the immobilization of soil nutrients with glucose. Reducing soil nitrogen decreased the biomass of shoots disconnected from parent plants, but had no effect on those with intact rhizomes (Fig. 6.2a; Table 6.1). Clonal connections were equally important in the maintenance of smooth brome density, and for all levels of nitrogen, the density of brome shoots declined following the severing of rhizomes (Fig. 6.2b; Table 6.1). Physiological integration remained important in the horizontal proliferation of smooth brome clones, but its effect was site specific. Among the two study areas, sharing of resources with mother clones inhibited the encroachment of

ramets invading Bob Hill prairie in the western part of the Park, an area lower in mineral soil nitrogen (Fig. 6.2c-d, Table 6.1).

6.5 Discussion

My observations demonstrate the importance of physiological integration in the proliferation of smooth brome clones invading native prairies. Underground rhizomes, connecting ramets with mother clones, maintained the biomass and density of invading ramets and were, as predicted, key to the proliferation of smooth brome into resource poor environments. Physiological integration between vegetatively connected ramets often facilitates the colonization of environments where parts of the clone experience contrasting conditions. Coastal dunes, deserts, and wetlands are often dominated by clonal perennials, whose vegetative connections permit the “homogenization” of patchy resources and the amelioration of environmental stress (Alpert 1996, Pennings and Callaway 2000). Translocation between ramets supported the encroachment of smooth brome into adjacent prairies, however, sharing of resources with the mother clone inhibited the proliferation of ramets invading nutrient enriched patches. While integration among ramets most often entails transport of resources towards younger ramets (Alpert 1991), competition among ramets can reduce recovery following herbivory (Hellstrom et al. 2006). Others have suggested that suppression of proliferation in low nutrient environments may reduce intra-ramet competition for scarce resources and facilitate the formation of monoclonal patches (Schmid and Bazzaz 1987).

Despite previous reports, my observations illustrate the importance of vegetative connections in the proliferation of clonal plants invading neighbouring plant

communities. Although several previous authors have accorded greater importance to clonal integration in resource limited environments, its role in interspecific interactions remains unresolved. For example, Amsberry et al. (2000) and Pennings and Callaway (2000) reported that clonal connections did not affect the growth of plants penetrating dense marsh communities, and Peltzer (2002) did not observe a significant decrease in the growth of severed *Populus tremuloides* ramets invading a native prairie. In contrast, by manipulating the composition of plant communities neighbouring *Solidago canadensis*, Hartnett and Bazzaz (1985) demonstrated the importance of physiological integration in ameliorating impacts of interspecific interactions. It remains unresolved whether more intense interactions between smooth brome and its neighbours could inhibit or reverse the observed integration (Kelly 1995, Hellstrom et al. 2006) and how other factors, including intraspecific competition between ramets (Bullock et al. 1994), the spatio-temporal heterogeneity of resources (Gough et al. 2002) and the age and length of clonal connections (Schmid and Bazzaz 1987, Bullock et al. 1994) affect its importance during invasions. These questions deserve further investigation.

The persistence of clonal connections remains key to understanding the impact of physiological integration on the invasiveness of exotic plants. My observations illustrate that smooth brome ramets remain physiologically integrated along clone edges, a distance of at least 0.5 m from the clone margin, and, based on the observed rate of clonal advance (~ 24 cm/year), those 2-3 years old remain active in supporting the vegetative advance of invading clones. In other herbaceous species, physiological integration often encompasses at least 4 or 5 rooted ramets (Noble and Marshall 1983, Headley et al. 1988, Birch and Hutchings 1999), but its maintenance may be contingent on the net

contribution of connected ramets to the genet's growth (Kelly 1995). As a result, disintegration of clonal connections is predicted whenever the growth of daughter ramets does not compensate for the physiological demands of the older parts of the clone (Caraco and Kelly 1991).

Conceptual models of exotic plant invasion are characterized by several discrete steps, including dispersal, establishment and proliferation (Kolar and Lodge, Puth and Post 2005). Successful invasion requires that an exotic species be superior to the native species it displaces in at least one or all these stages. Even though exotic plants often possess traits that distinguish them from the native species they displace (Andersen 1995, Rejmánek and Richardson 1996, Kolar and Lodge 2001; but see Thompson et al. 1995, Acosta et al. 2006), successful invaders represent a variety of plant families and possess a wide range of life forms and breeding systems (Crawley 1987). Although my results demonstrate that clonal growth facilitates the proliferation of smooth brome invading native prairies and may help explain the success of clonal invaders in other regions (Andersen 1995, Pyšek 1997, Reichard and Hamilton 1997, Acosta et al. 2006, Cadotte et al. 2006), many questions related to the success of clonal invaders remain unanswered. For example, clonal growth remains a common trait among native species in many plant communities (Kelly 1995, Pyšek 1997), and other factors, including ramet longevity, the persistence of clonal connections, and the spatio-temporal extent of physiological integration (Schmid and Bazzaz 1987, Jónsdóttir and Watson 1997, Tamm et al. 2002) deserve further investigation. To my knowledge, no studies have explored these hypotheses in the context of differences between exotic invaders and the native plants they displace.

The preponderance of vegetative growth among successful invaders suggests that clonal growth facilitates exotic plant invasions and increases their threat to native plant communities (Pyšek 1997, Reichard and Hamilton 1997, Cadotte et al. 2006). This suggests that management of clonal invaders will require an understanding of the ecological contexts and the extent of physiological integration among invading ramets. My results demonstrate that physiological integration maintains the biomass and density of smooth brome ramets invading native prairies and that its importance is greatest in low resource environments. The observed integration suggests several methods of managing clonal invaders. For example, applications of herbicide along the margins of invading clones could capitalize on the translocation of resources between the mother clone and establishing ramets and help slow or stop their proliferation (Brey 2001), while mowing the margins of invading clones could facilitate the potential disintegration of connections between the damaged ramets and the mother clone (Caraco and Kelly 1991, Meyer and Schmid 1999, Hellstrom et al. 2006). My results suggest that due to their increased dependence on clonal subsidy, ramets in resource poor environments would be most vulnerable to such manipulations.

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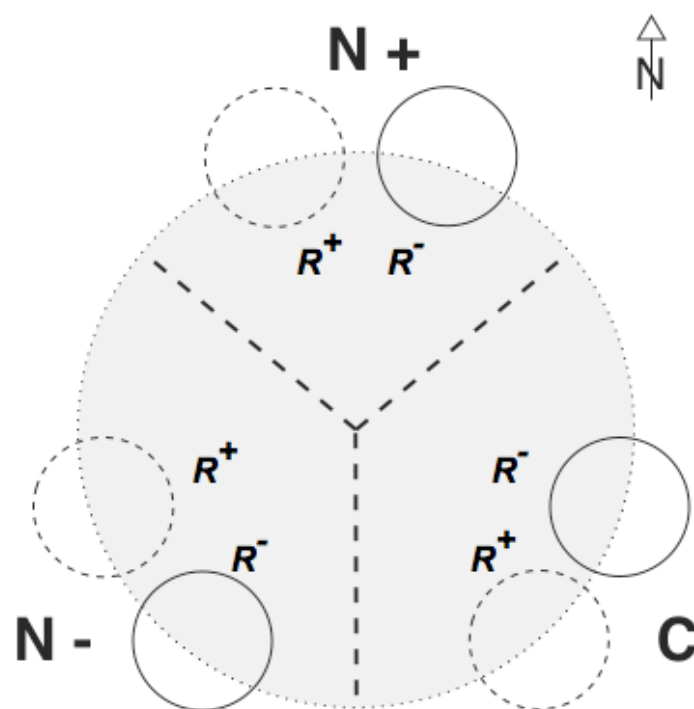


Figure 6.1 Manipulation of nitrogen and rhizomes along the margins of smooth brome (*Bromus inermis*) clones invading fescue prairies in Riding Mountain National Park, Manitoba, Canada. Each clone was divided into three sections and each randomly assigned the following treatments along the clone margins: intact rhizome (R^+), severed rhizome (R^-), nitrogen immobilized (N^-), nitrogen unmanipulated (C), nitrogen added (N^+). Circles represent treatment areas (diameter = 0.91 cm).

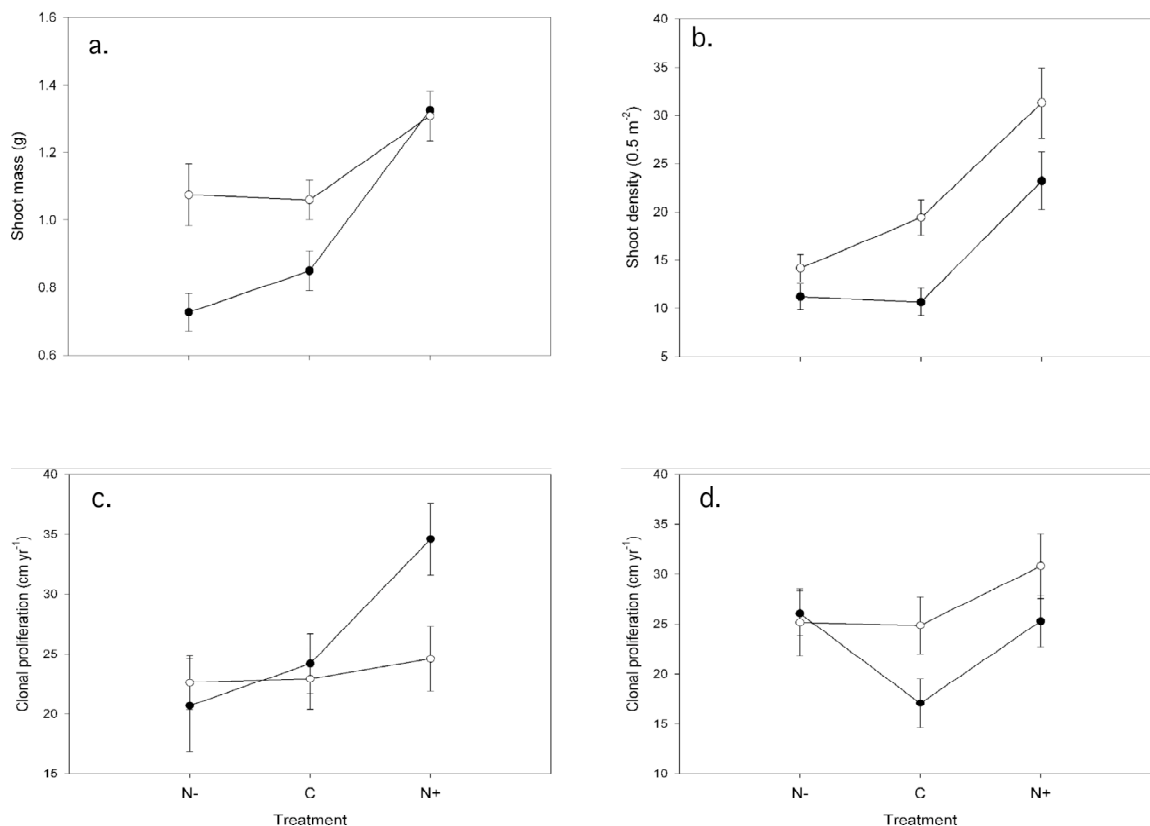


Figure 6.2 Impacts of nitrogen addition (N+) and immobilization (N-) on the biomass, density, and horizontal proliferation of smooth brome (*Bromus inermis*) invading two prairies in Riding Mountain National Park, Manitoba, Canada. Ramets along the margins of invading clones were either left intact (open symbols) or severed from parent clones (closed symbols; $n = 40$, error bars = ± 1 S.E.). Illustrations of shoot mass (a.) and density (b.) represent the combined measurements from two study areas; those of clonal proliferation represent separate measurements from Bob Hill (c.) and Strathclair (d.) prairies, located in the western and central areas of the Park, respectively (see text for details). Control treatments (C) represent areas where levels of soil nitrogen were left unmanipulated.

Table 6.1 Two-way ANOVA testing the effect of soil nitrogen addition and immobilization on the biomass, density, and horizontal proliferation of smooth brome (*Bromus inermis*) invading a fescue prairie in Riding Mountain National Park, MB. Ramets along the margins of invading clones were either left intact or severed from parent clones.

Effect	Shoot mass			Shoot density			Encroachment (Bob Hill)			Encroachment (Strathclair)		
	<i>F</i>	<i>df</i>	<i>P</i>	<i>F</i>	<i>df</i>	<i>P</i>	<i>F</i>	<i>df</i>	<i>P</i>	<i>F</i>	<i>df</i>	<i>P</i>
Sever	18.18	1, 195	< 0.0001	21.90	1, 195	< 0.0001	0.08	1, 95	0.7729	0.90	1, 95	0.3461
Nitrogen	37.58	2, 195	< 0.0001	27.52	2, 195	< 0.0001	3.25	2, 95	0.0432	3.12	2, 95	0.0488
Sever x nitrogen	6.57	2, 195	< 0.0017	1.87	2, 195	0.1563	4.53	2, 95	0.0132	0.65	2, 95	0.5264

CHAPTER 7: LACK OF EVIDENCE FOR THE ROLE OF SOILBORNE PATHOGENS IN THE DECLINE OF SMOOTH BROME INVADING NORTHERN FESCUE PRAIRIES.

7.1 Abstract

The modeling of exotic species' impacts on native ecosystems requires an understanding of the ecological processes that regulate their invasions. Despite the accumulating evidence that biotic interactions occurring belowground play a significant role in determining the outcome of plant interactions, few studies have examined the role of soilborne pathogens in invasion dynamics. The strength of feedback between plants and soilborne pathogens is often a function of time and the size and density of host populations. Although exotic plants may have escaped their enemies, long-term persistence of their dense monocultures may still depend on the accumulation of soilborne pathogens. To test the hypothesis that declines in the productivity of perennial invaders are attributable to negative plant-soil feedbacks, I designed a study investigating the impact of soilborne pathogens on the productivity of smooth brome (*Bromus inermis* Leyss.) clones invading northern fescue prairies. I examined the productivity of smooth brome in the center, middle and along prairie margins of invading clones and measured nutrient availability, plant diversity, and the accumulation of plant litter in each area. I partitioned my observations of soilborne pathogens among soilborne and rootborne plant parasitic nematodes and used soil pasteurization to examine the impacts of other soilborne pathogens. Despite a decrease in the productivity of smooth brome at the

center of invading clones, its decline was not attributable to soilborne pathogens. Accumulation of litter at the center of invading clones, combined with an increase in soil nutrient availability suggests that declining plants may be senescing. My findings illustrate that, despite its declining productivity, restoration of northern fescue prairies invaded by smooth brome may be complicated by the accumulation of thatch and litter following invasion and their persistent impacts on plant diversity.

7.2 Introduction

Scientific justification for controlling exotic organisms requires an understanding of both their impacts on native ecosystems and the ecological processes that regulate their invasions (Hager and McCoy 1998). Accumulating evidence that biotic interactions occurring belowground play a significant role in determining the outcome of plant interactions (Bever 2003) promises important insights into the mechanisms determining the ultimate success of biological invasions. Among complex, multi-trophic interactions between plants and soilborne organisms, soilborne pathogens remain a poorly studied element in invasion dynamics (Klironomos 2002, Eppinga et al. 2006).

Pathogens affect host populations and plant communities through direct effects on the survival, growth and fecundity of individual plants (Gilbert 2002). Losses of carbon and nutrients to natural enemies result in lower growth rates and decreased primary productivity (Mitchell 2003). Negative plant-soil feedbacks also help maintain local community diversity by preventing individual species from increasing to complete dominance (Chesson 2000). Negative feedback loops are favored in natural systems where pathogen and host dispersal is limited (Gilbert 2002). For example, at the interface

of plant roots and soil, host-specific microorganisms, including root feeding nematodes and plant pathogenic fungi, may accumulate over time, increasing their biological effects on the host (Bever 2003).

Declines in the vigor of perennial plants are well documented in both natural and agroecosystems. Along the Great Lakes, reductions in the height and density of American beachgrass (*Ammophila breviligulata* Fern.) have been attributed to the gradual accumulation of pathogenic nematodes (Eldred and Maun 1982, Little and Maun 1996). Nematodes and pathogenic fungi were also responsible for declines in patches of red fescue (*Festuca rubra* L.) and sand sedge (*Carex arenaria* L.) in the Netherlands (D'Hertefeldt and van der Putten 1998, Olff et al. 2000), and the successional dynamics of foredune and temperate forest vegetation (Van der Putten 1993, Packer and Clay 2003). Perennial crops are also victims of accumulating populations of pathogens. For example, the management of crop residues and specific elements of soil communities remains key to the suppression of the Take-all Patch fungus (*Gaeumannomyces graminis* (Sacc.) Arx & D. Oliver) and other soilborne pathogens (Mazzola 1998, Cox et al. 2005).

The strength of the feedback between plants and soilborne pathogens is a function of time and the size and density of host populations (Carlsson et al. 1990, Packer and Clay 2003). In crop monocultures, cumulative losses of productivity are often linked to qualitative and quantitative changes in pathogen communities (Shipton 1977). Often, yields can only be recovered by rotating crops and interrupting cycles of disease (Krupinsky et al. 2004). In native communities, negative feedbacks between soilborne pathogens and plants are thought to increase species turnover and maintain plant biodiversity (Callaway et al. 2004). Although untested, the accumulation of soilborne

pathogens in plant monocultures could provide important mechanistic insights into recent models linking reduced productivity with the loss of plant biodiversity (Fukami and Morin 2003). For example, the observed disproportional mortality near parent plants (Howe and Smallwood 1982) forms the basis of the enemy escape hypothesis, which proposes the selective advantage of dispersal and predicts increased rates of infection of common species (Schupp 1992).

The link between disease incidence and the spatial structure of plant populations poses a unique problem for species forming dense, perennial populations, including those capable of vegetative growth. For example, compared with annual species, rhizomatous perennials are often associated with a greater number of fungal pathogens (Clay 1995). Higher parasite pressures have also been reported among perennial species in the Caryophyllaceae (Thrall et al. 1993) and larger, morphologically complex hosts, such as shrubs and trees (Strong and Levin 1979). Although exotic plants may have escaped native enemies, their long-term persistence may still depend on the build-up of pathogens (Olf et al. 2000). Especially vulnerable may be exotics capable of rapidly displacing native species and forming dense monocultures (Carlsson et al. 1990). Among the large number of exotic species in most regional floras (Rosenzweig 2001), the ability to reproduce vegetatively, shared by the majority of successful invaders (Pyšek 1997) might be expected to contribute to their vulnerability to plant pathogens. For example, given that clonal growth can result in substantial lateral spread, large clones may provide a bigger target for pathogen colonization than smaller, individual plants (Clay and van der Putten 1999).

The objective of my study was to examine the persistence of smooth brome (*Bromus inermis* Leyss.), a Eurasian perennial threatening the structure and function of prairie remnants throughout the Great Plains (Otfinowski et al. 2007). Widely planted for hay, forage, and to revegetate disturbances, smooth brome often escapes to invade native prairies. The centrifugal organization of invading clones and their gradual transformation of diverse prairie communities into virtual, smooth brome monocultures (Otfinowski et al. 2007) create a convenient model system for the study of interactions between plant diversity and the negative feedbacks of soilborne plant pathogens. Despite its susceptibility to several root pathogens, including species of *Fusarium*, *Pythium*, and the root-lesion nematode *Pratylenchus penetrans* (Cobb) Filipjev & Schur-Stekhoven (Otfinowski et al. 2007), existing research has failed to elucidate fundamental questions regarding the long-term persistence of smooth brome monocultures in both native and cultivated communities (Lardner et al. 2000). Based on earlier observations of declining productivity of smooth brome at the center of invading clones, I used a combination of field and greenhouse experiments, to quantify the productivity of invading clones and test the hypotheses that their declines are attributable to negative plant-soil feedbacks.

7.3 Methods

7.3.1 Study area

Research was conducted in Riding Mountain National Park, Manitoba, Canada (50° 39' 00", - 99° 55' 48"). The park occupies an area of 2,978 km² in western Canada and consists of large areas of rolling upland (550 – 640 m), underlain by glacial tills (Lang 1974). The region is characterized by a mean annual precipitation of 450 – 500 mm and

a growing season of 168 – 173 days; mean temperatures range between -18°C in January and 18°C during July (Leeson et al. 2005). Riding Mountain National Park lies in the Mixedwood Section of the Boreal Forest Region (Rowe 1972) and protects areas of fescue prairie (Cody 1988). In North America, fescue prairies form an arc around the northern and northwestern perimeters of the mixed prairie (Coupland 1961) and occupy a transition between the warmer and drier grasslands to the south and the cooler, moister aspen parkland to the north (Coupland and Brayshaw 1953). Dominated by rough fescue (*Festuca hallii* (Vasey) Piper), species of *Agropyron* and *Carex*, and a high diversity of forbs (Cody 1988), fescue prairies in western Canada are threatened by the impacts of grazing, cultivation, and exotic species (Trottier 1986).

7.3.2 Surveys of smooth brome productivity.

I quantified the observed decline of smooth brome at the center of invading clones in two areas of northern fescue prairie, situated in Riding Mountain National Park. I randomly selected 17 clones of smooth brome at each site. The two study areas were situated approximately 50 km apart; soils at the more western Bob Hill prairie were more xeric and lower in mineral nitrogen than the centrally located Strathclair prairie [volumetric water content (0-20 cm, July 2005) $7.5 \pm 3.7\%$ vs. $9.5 \pm 4.2\%$, $F_{1,100} = 9.2$, $P = 0.0031$; mineral nitrogen (0-15 cm; July 2005): $\text{NH}_4\text{-N}$, 5.3 ± 0.4 mg/kg vs. 9.1 ± 0.4 mg/kg, $F_{1,38} = 37.4$, $P < 0.0001$; $\text{NO}_3\text{-N}$, 0.60 ± 0.1 mg/kg vs. 2.1 ± 0.2 mg/kg, $F_{1,38} = 40.7$, $P < 0.0001$].

I used transects extended between the center and margins of invading clones (bearing: 135°) to measure the above-ground density, biomass, and vegetative cover of

smooth brome, record the accumulation of litter and thatch, and compare root biomass. Based on a factorial design, I divided each clone into three areas (center, middle, and prairie fringe) and used 50 x 50 cm quadrats to collect samples of brome biomass, thatch and litter during July 2005. These, defined as standing, fallen, and variously disintegrated residues of plants (Agriculture Canada 1987), were not distinguished by species. Ramets of smooth brome were clipped at the soil surface, and all samples were air dried (48 h, 60°C) before weighing. Quadrats were also used to collect samples of root biomass. Based on a subset of six clones per study site, I combined three root cores (0-10 cm, 10-30 cm) inside each 50 x 50 cm quadrat using a hand auger (diameter: 5 cm). All root samples were cleaned using a root washer, air dried (48 h, 60°C), and weighed. No distinction was made between the roots of smooth brome and other species.

Observations of smooth brome productivity were complemented with measurements of soil minerals and the structure and composition of prairie plant communities at the center, middle, and along the prairie margins of invading clones. I used *in situ* incubations to monitor changes in mineral nitrogen (Binkley and Hart 1989). Cores of soil, extracted using a hand auger (0-15 cm, 74 cm³), were placed in plastic Ziploc bags and incubated by burying them in the auger excavations between July and August 2004. Along with reference samples, collected at the time of installation, all samples were air dried, milled, extracted with 2.0 M KCl and analyzed for ammonium and nitrate using a Technicon Autoanalyzer II (Maynard and Karla 1993). As a result of rodent damage to incubation bags installed at Bob Hill prairie, only the results from Strathclair prairie are presented here. I repeated my measurements of soil mineral nitrogen during July 2005. Although I did not install incubation bags during the second

season, each sample of air dried soil was also extracted with NaHCO_3 and analyzed for available phosphorus (Olsen et al. 1954).

Differences in the structure and composition of invaded prairie communities were based on surveys conducted in August 2004. I used 1 x 1 m quadrats to evaluate the proportional cover (0-100 %) of species in each area of the invading clones. As a consequence of the late timing of the inventory, species of *Carex* were only identified to genus level. Earlier in the season, at least five sedge species were identified from the two prairie study areas, including *Carex torreyi* Tuck., *C. sprengelii* Dewey., *C. richardsonii* R. Br., *C. pennsylvanica* Lam., and *C. obusata* Lilj.

7.3.3 Impacts of soilborne pathogens.

The hypothesis that decline in the productivity of smooth brome is attributable to negative plant-soil feedbacks was tested using observations of soilborne and rootborne pathogens. I partitioned my observations of soilborne pathogens into two components: soilborne and rootborne plant parasitic nematodes and other soilborne pathogens. Samples of nematodes were extracted from the soil and roots collected in the center, middle, and at the margins of six clones invading native prairies in each study area. Selected clones were characterized by a measurable decline in brome cover at the center. During August 2004, I collected the soil samples using a hand auger (0-15 cm, ~ 1200 cm^3 composite of four cores) and excavated the roots of four smooth brome ramets (0-10 cm). Collected samples were stored at 5°C and analyzed within three weeks of collection.

Extractions of soilborne nematodes were based on the Cobb sieving and flotation method (Shurtleff et al. 2000). Nematodes were suspended from 100 g of field soil (mean gravimetric water content: 4.8 %) using a sucrose solution, sieved, counted, and identified. Nematodes were also extracted from samples of roots, however, no effort was made to separate the roots of smooth brome from those of other species. Based on the Baermann technique (Shurtleff et al. 2000), root samples were immersed in water, and the extracted nematodes counted and identified at 48 h and 96 h intervals. Identification of plant parasitic nematodes from soil and root extracts followed Mai and Mullin (1996) and Yeates et al. (1993).

The impact of soilborne pathogens on the productivity of smooth brome was further tested in the greenhouse. Based on the above-described six clones at two study sites, I used a hand auger to collect samples of soil (0-15 cm, $\sim 900 \text{ cm}^3$ composite of three cores) in the center, middle, and at the prairie fringe of the each clone. Soil samples were cleaned of rocks and all roots cut into 1 cm pieces. I split each soil sample in half and pasteurized one portion to isolate the potential impacts of soilborne pathogens on smooth brome productivity. Samples were pasteurized using an automatic soil pasteurizer ($< 99^\circ\text{C}$, 1h; Dillion Industries Inc., Melrose, MA). Pasteurized and non-pasteurized (live) soils were potted into eight (4.5") pots, surface sterilized with 70 % ethanol and lined with paper towels. All pots were at least half full but I did not control for the weight and volume of soil. Leaving potted soil idle for one week before transplanting reduced effects of the initial nutrient flush following pasteurization.

I used plastic Petri dishes (9 cm), lined with filter paper, to germinate seeds, and watered each with de-ionized water, as required. Seeds with an emerging cotyledon were

considered germinated. These, germinated in a growth chamber (25°C / 15°C, 12/12 h light/dark, 107 $\mu\text{mol m}^{-2} \text{s}^{-1}$) from seeds collected at each study sites, were transplanted into each pot using tweezers. Three seedlings of smooth brome were transplanted into pots of live and pasteurized soil. Greenhouse conditions were maintained between 20 – 25°C (16/8 h), and supplemented with sodium lights. Between December 2004 and July 2005, five consecutive generations of brome seedlings were raised in each pot and harvested at the end of a five-week cycle. Live pots were fertilized with 20-20-20 N-P-K fertilizer during the third week of the second and third growth cycles. The rate of nitrogen addition (53.26 mg N / kg soil) corresponded with the amount of nitrogen mineralized following pasteurization and was reduced by half during the third growth cycle. Nutrient mineralization is characteristic of soil sterilization treatments (Troelstra et al. 2001). At the end of each growth cycle, all seedlings were clipped at the root crown, 1 cm below the soil surface, dried (48 h, 60°C), and weighed, and a fresh seedling was replanted into the same soil.

7.3.4 Data analysis.

I used a blocked, one-way analysis of variance (ANOVA) to compare the mean density and biomass of smooth brome ramets in the center, middle, and along the prairie fringe of invading clones. For each replicate, mean density and biomass were log transformed to improve the homogeneity of variance among treatments (Zar 1999). One-way comparisons of the physical environments of clones complemented those describing brome productivity. These, including available and mineralized nitrogen were log transformed to improve the homogeneity of variance among treatment groups, while

measurements of volumetric soil moisture, recorded as percentages, were arcsine transformed to approximate a normal distribution (Zar 1999). Where no significant differences were found between the two study sites, data were pooled and the combined results presented.

I examined the impacts of smooth brome invasions on the diversity of northern fescue prairies using indices of community diversity and equitability. Effective richness [$N_2 = (\sum p_i^2)^{-1}$] and evenness $\{E3 = [(\sum p_i^2)^{-1} - 1] / [\exp(-\sum p_i \log p_i) - 1]\}$ describe plant communities based on the proportional abundance of species and the shape of their frequency distributions (Kvalseth 1991) and can be used to examine species responses to environmental manipulations and the intensity of interspecific interactions (Legendre and Legendre 1998). Lastly, I used redundancy analysis to compare the composition of prairie communities in among areas inside the clones and the adjacent native prairies. Related to principal component analysis, redundancy analysis (RDA) constrains an ordination of objects in such a way that the resulting ordination vectors are also linear combinations of treatment or other environmental variables (Legendre and Legendre 1998). I log transformed the abundance of each species prior to analysis in order to improve the within-group normality of each descriptor (Legendre and Legendre 1998), and determined the significance of the RDA ordination using a Monte Carlo permutation (full model, 999 permutations). Univariate and multivariate statistical analyses were performed using Data Desk 6.2 (Data Description Inc., Ithaca NY) and Canoco 4.53 (Biometrics Plant Research International, Wageningen, The Netherlands), respectively.

7.4 Results

The productivity of smooth brome declined towards the center of invading clones. Although more dense, ramets of smooth brome at the center of clones accumulated less biomass (Fig. 7.1) and contributed less to the vegetative cover of the plant community (Fig. 7.2). Despite their decline, soil concentrations of available nitrogen, phosphorus, and moisture increased in the center of invading clones (Table 7.1). Although the biomass of thatch, litter, and shallow roots increased inside the clone, I observed no significant increases in nitrogen mineralization (Table 7.1).

Decreased productivity of smooth brome at the center of invading clones was not attributable to the impacts of soilborne pathogens. Fewer soilborne plant parasitic nematodes were found at the center of clones ($F_{2,22} = 1.26$, $P = 0.3025$; Fig. 7.3 A.) and their roots contained few potential parasites ($F_{2,22} = 3.56$, $P = 0.0455$; Fig. 7.3 B.). Representatives of the genus *Helicotylenchus* were most abundant in all areas of invading clones, however, their decline toward the center of invading clones contributed to more even communities of plant parasitic nematodes in this area (Table 7.2). Soil pasteurization had no effect on seedlings raised in soil collected from the center of invading clones. Following five growth cycles, the biomass of seedlings raised in unpasteurized soil did not decline ($F_{1,89} = 1.34$, $P = 0.2501$), and I found no difference in the mass of seedlings raised in live and pasteurized soil at the end of the experiment ($F_{1,89} = 0.02$, $P = 0.8776$; Fig. 7.4). Sharp differences in the biomass of seedlings between cycles were attributable to the release of nutrients following pasteurization and the fertilization of unpasteurized pots.

Despite its decline, the impacts of smooth brome on the composition of northern fescue prairies persisted inside the clones. Compared to native prairies, clone centers were characterized by significantly lower community richness, diversity, and evenness, and lower aboveground cover of native forbs and graminoids (Table 7.3). The first axis of the redundancy analysis ordination illustrated the impact of smooth brome invasion on the abundance of native species. While the abundance of most species declined inside the clones, clone centers were characterized by increased cover of dwarf thistle (*Cirsium drummondii* T. & G.), wild pea (*Lathyrus ochroleucus* Hook.) and shrubby cinquefoil (*Potentilla fruticosa* L.; Fig. 7.5).

7.5 Discussion

My observations demonstrate that the productivity of smooth brome invading northern fescue prairies declines towards the center of invading clones. Despite the observed increase in mineral nitrogen and available phosphorus at the center of clones, both the mean biomass and vegetative cover of smooth brome ramets declined in this area. The observed loss of brome productivity was not attributable to the impacts of soilborne pathogens. For example, fewer soilborne plant parasitic nematodes were found at the center of clones and their roots contained few potential parasites. Compared to those raised in prairie soil, the mass of smooth brome seedlings grown in soil collected from the center of declining clones was not affected by pasteurization. Despite the observed decline, smooth brome had a persistent impact on the diversity of northern fescue prairies. Compared to the fringes of invading clones and their adjacent native prairies,

clone centers were characterized by significantly lower community richness and diversity, and a decline in the abundance of native species.

7.5.1 Mechanisms of smooth brome decline

The observed decline of smooth brome is characteristic of other clonal species. Watt (1947) first reported a similar, ring-like morphology in tussocks of sheep fescue (*Festuca ovina* L.) and bent-grass (*Agrostis tenuis* Sibthorp) and Weaver (1968) described deterioration in the center of big bluestem clumps (*Adropogon gerardii* Vitman.). While my observations are also supported by several recent studies (Soukupova 1992, Bonanomi et al. 2005), to my knowledge, no studies have previously observed this growth pattern among exotic invaders.

Despite the observed decline among clones of smooth brome invading northern fescue prairies, I was unable to attribute their loss of productivity to soilborne plant pathogens. On the contrary, the decline in the abundance of soil- and rootborne plant parasitic nematodes at the center of invading clones, could signal a decrease in the vigour of plant roots in this area (Deydn et al. 2004). The impact of pathogens on disease incidence remains a function of community diversity and pathogen dispersal (Harper 1977). While invasions of smooth brome resulted in a clear decrease in the diversity of northern fescue prairies, it remains possible that its declines are attributable to other groups of pathogens. For example, airborne pathogens, such as the splash dispersed rusts and mildews, impact dense stands of perennial crops and low diversity prairies (Mitchell et al. 2002, Cox et al. 2005) and have been attributed to the declines of cultivated stands of smooth brome (Otfinowski et al. 2007). Also possible is the residual effect of a

historic community of soilborne pathogens, whose “ghost” is the observed decline in the productivity of smooth brome ramets at the center of invading clones (Harper 1990).

Despite my focus on soilborne pathogens, negative feedbacks in the rhizosphere following invasion, could also include changes in populations of host-specific rhizosphere bacteria and mycorrhizal fungi (Bever 2003). These questions remain unanswered.

In the absence of a demonstrated impact of soilborne pathogens on the observed decline of smooth brome clones a number of hypotheses remain untested. Several authors have attributed the loss of vigour of clonal species to their senescence. For example, both Watt (1947) and Weaver (1968) attributed a similar, ring-like growth of clonal grasses to the aging of ramets, and Tamm et al. (2002) reported higher rates of ramet turnover among perennial species characteristic of meadow communities. Similar observations of self-thinning among other clonal species, including trembling aspen (*Populus tremuloides* Michx.; Krasny and Johnson 1992), suggest that potentially weak physiological integration among their ramets could increase intra-clonal competition, resulting in stand thinning (de Kroon 1993, Peltzer 2002). Although I observed an increase in the density of ramets at the center of declining clones, the corresponding decrease in ramet biomass suggests an equally intriguing hypothesis that older ramets could become resource sources for the younger, flourishing ramets, given the persistence of their clonal connections (Bullock et al. 1994). The predominance of acropetal translocation among clonal species (Ashmun et al. 1982, Noble and Marshall 1983, Slade and Hutchings 1987) could prevent the reversal of this mechanism and the recovery of

the declining centers of invading clones. To my knowledge, these hypotheses remain unexplored.

Equally important in the persistence of invading clones may be their impact on nutrient cycling. Although, several authors have suggested that the immobilization of nitrogen in the litter of exotic invaders, including smooth brome, could lead to their gradual decline (Christian and Wilson 1999, Lardner 2000), feedbacks between litter quality, environmental factors, and soil microbial communities are likely key to the outcome of litter deposition (Pastor et al. 1987, Matson 1990, Facelli and Pickett 1991, Cragg and Bardgett 2001). For example, Wedin and Tilman (1990) reported an increase in the mineralization of nitrogen associated with the nitrogen rich litter of Kentucky bluegrass (*Poa pratensis* L.) and quack-grass (*Agropyron repens* (L.) Beauv.) invading native prairies. While my observations, demonstrating an increase in available nitrogen and phosphorus at the center of invading clones, do not support the immobilization hypothesis, I found no significant differences in the rates of nitrogen mineralization inside the invading clones. While the decline of smooth brome, despite the increased availability of soil resources at the center of invading clones, further supports the senescence hypothesis, other mechanisms remain untested. For example, the accumulation of litter or the formation of dense root mats at the center of clones could inhibit their access to moisture and nutrient uptake, leading to their decline (Weaver and Rowland 1952).

7.5.2 *The persistent impacts of smooth brome invasions*

Despite the observed impacts of pathogens on species turnover in plant communities (van der Putten et al. 1993, Bever et al. 1997), most studies of biological invasions fail to incorporate sufficiently long temporal scales to evaluate long-term changes in ecological communities that determine the persistence of exotic organisms (Dietz and Edwards 2006). My results, measuring the productivity of smooth brome from the fringes to the declining centers of invading clones, illustrate that exotic populations can gradually lose their initial vigour (Hager and McCoy 1998, Simberloff 2002). Despite its decline, the impacts of smooth brome on the diversity of northern fescue prairies were more persistent. The accumulating thatch and litter inside the clones is likely to continue to hinder the recovery of prairie communities (Weaver and Rowland 1952). Restoration of invaded areas is also likely to remain complicated by the accumulation of seed and rhizome banks, and the potential chemical alteration of prairie habitats (D'Antonio and Meyerson 2002). Alteration of soil conditions in the center of declining clones could also facilitate the establishment of other exotic species (Soukopova 1992, Bonanomi et al. 2005, Jordan et al. 2008). Although I observed a steep decline in the diversity of invaded communities, the persistence of dwarf thistle (*Cirsium drummondii* T. & G.), wild pea (*Lathyrus ochroleucus* Hook.) and shrubby cinquefoil (*Potentilla fruticosa* L.) in the center of clones, suggests that the restoration of invaded communities may be possible based on the complementarity of species traits (Shipley et al. 2006). These and other questions regarding the rejuvenation of invaded communities remain unanswered.

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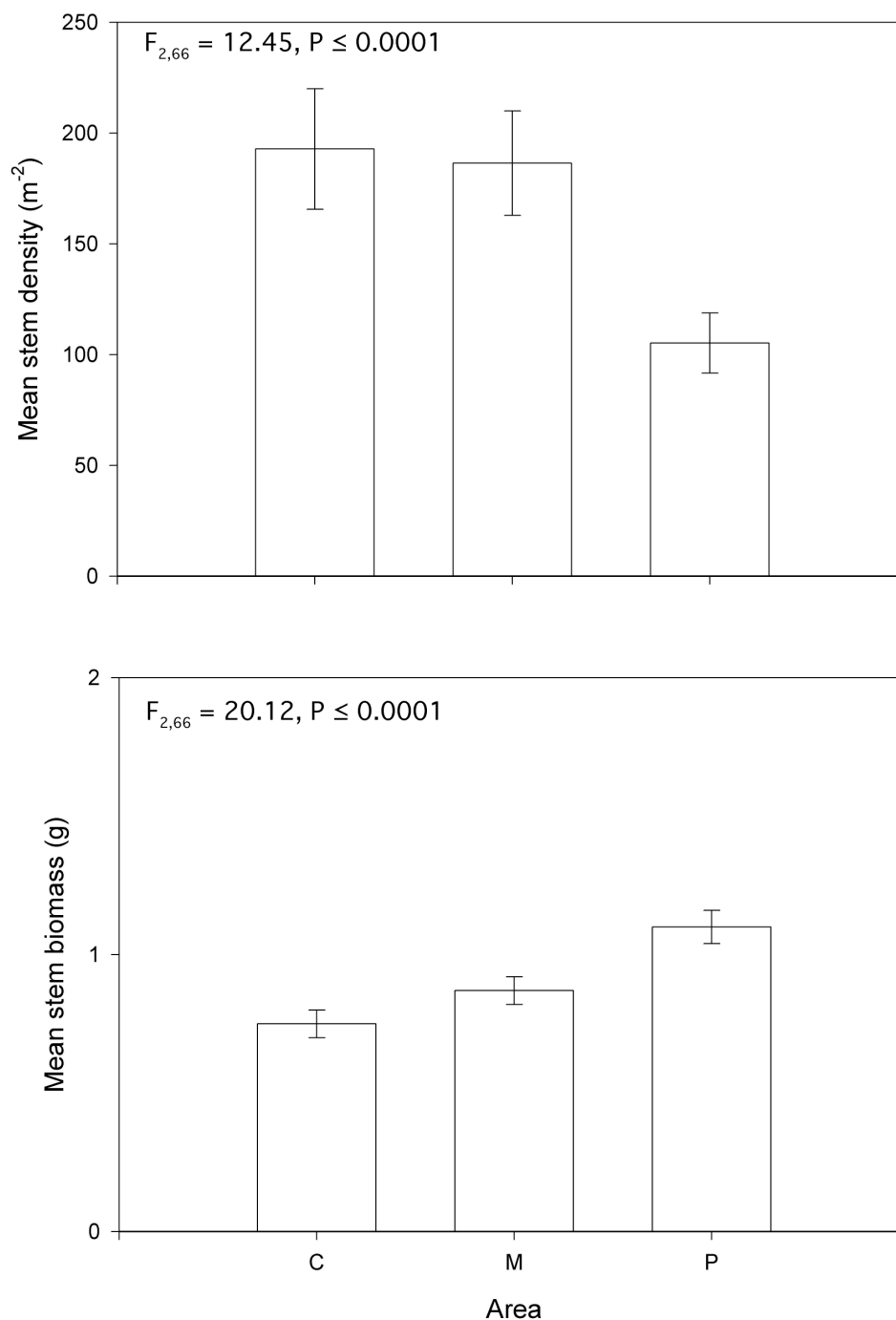


Figure 7.1 Summary of the density and dry biomass of smooth brome (*Bromus inermis* Leyss.) invading two northern fescue prairies in Riding Mountain National Park, Manitoba, Canada. Data were collected inside 50 x 50 cm quadrats, placed at the center (C), middle (M), and the prairie margins (P) of invading clones. Means of treatment groups were blocked to reduce variability between individual clones within the one-way ANOVA. Means \pm 1 S.E.

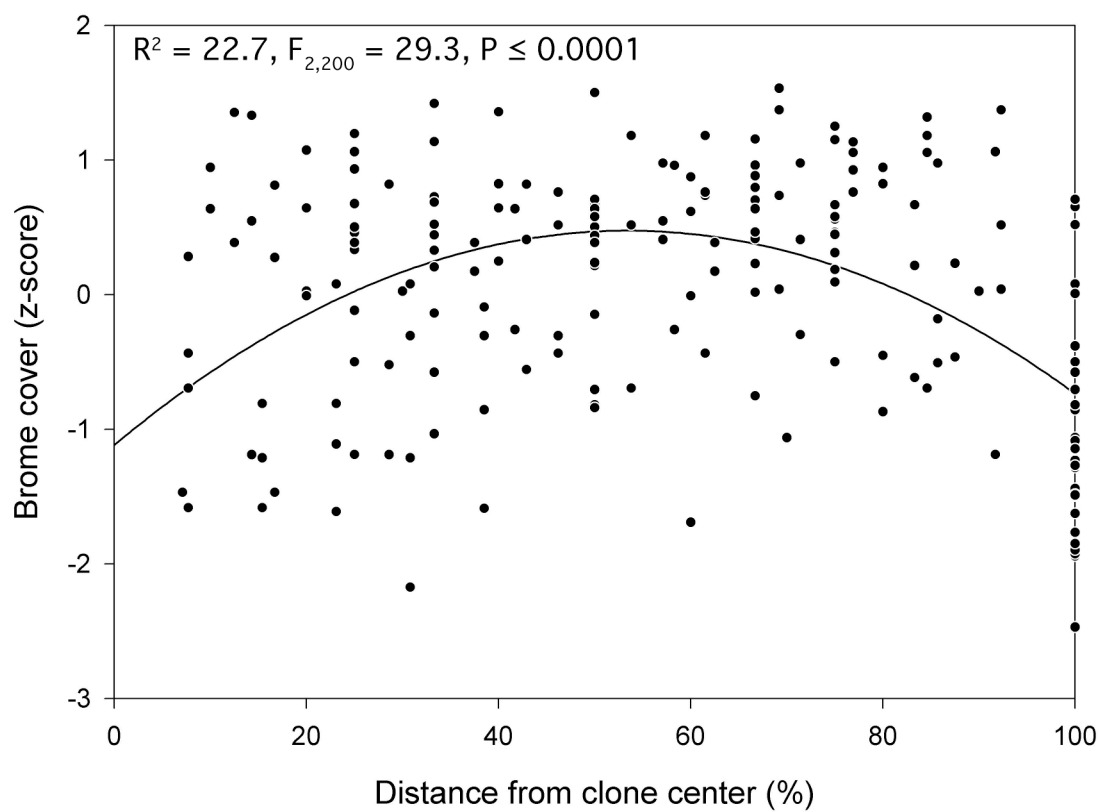


Figure 7.2 Change in the absolute vegetative cover of smooth brome (*Bromus inermis* Leyss.) invading two northern fescue prairies in Riding Mountain National Park, Manitoba, Canada. Data were collected inside 1 x 1 m quadrats, placed at the center, middle, and the prairie margins of invading clones. For each transect, the standardized change in brome cover [$z_i = (x_i - \mu) \sigma^{-1}$] along each transect was plotted against the proportional distance between each quadrat and the centers of clones.

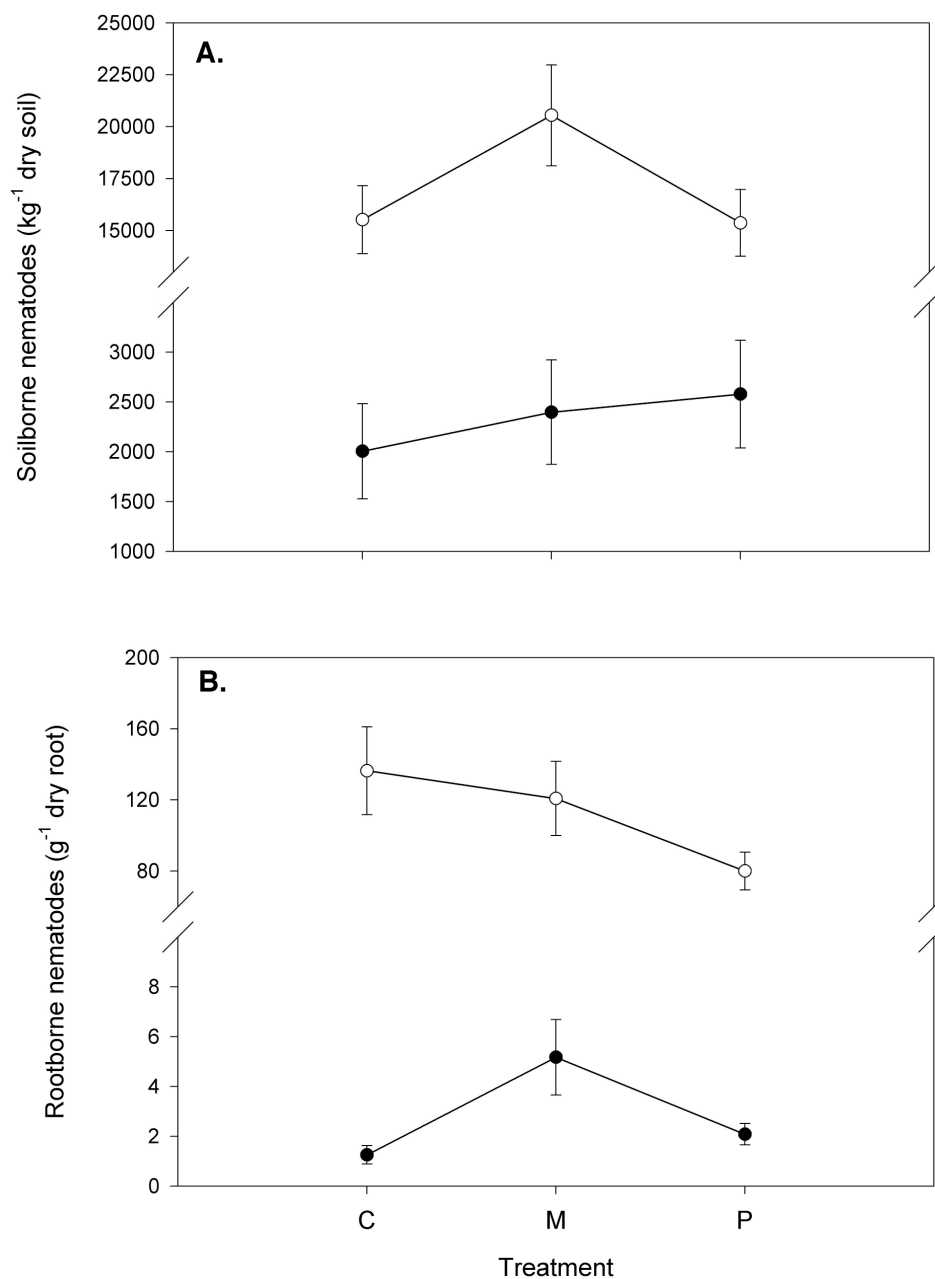


Figure 7.3 Mean abundance of soilborne (A.) and rootborne nematodes (B.) in samples of soil collected from twelve clones of smooth brome (*Bromus inermis* Leyss.) invading two northern fescue prairies in Riding Mountain National Park, Manitoba, Canada. The three samples: center (C), middle (M), and prairie (P) represent a transect from the center of invading clones to their prairie margins. Closed and open symbols illustrate plant parasitic and non-parasitic nematodes, respectively. Rootborne nematodes represent the combined counts following 48 h and 96 h of immersion in water (Shurtleff et al. 2000). Nematode identifications according to Mai and Mullin (1996). Means ± 1 S.E.

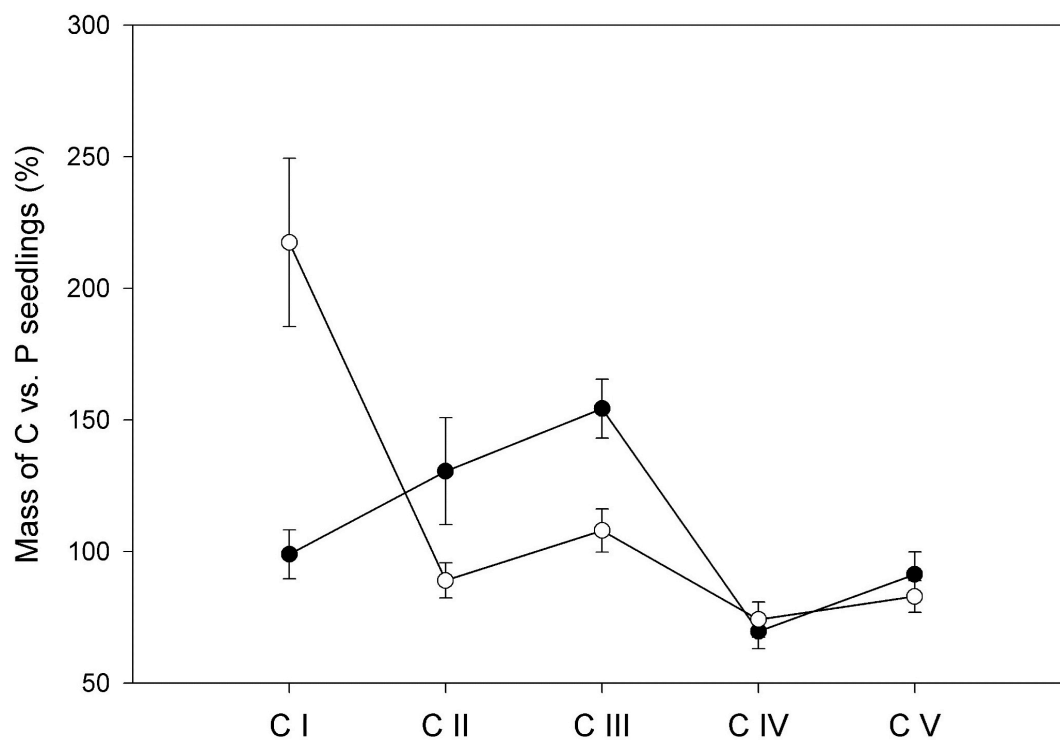


Figure 7.4 Biomass of smooth brome (*Bromus inermis* Leyss.) seedlings raised in soil collected from the centre and native prairie adjacent to smooth brome clones invading northern fescue prairies in Riding Mountain National Park, Manitoba, Canada. Seedlings were raised in the greenhouse, in live (closed symbols) and pasteurized soil (open symbols), and harvested at the end of each five week cycle. Within each cycle (C I – V), results represent the proportional difference in mass between seedlings raised in soil collected from the center and native prairie. Means ± 1 S.E.

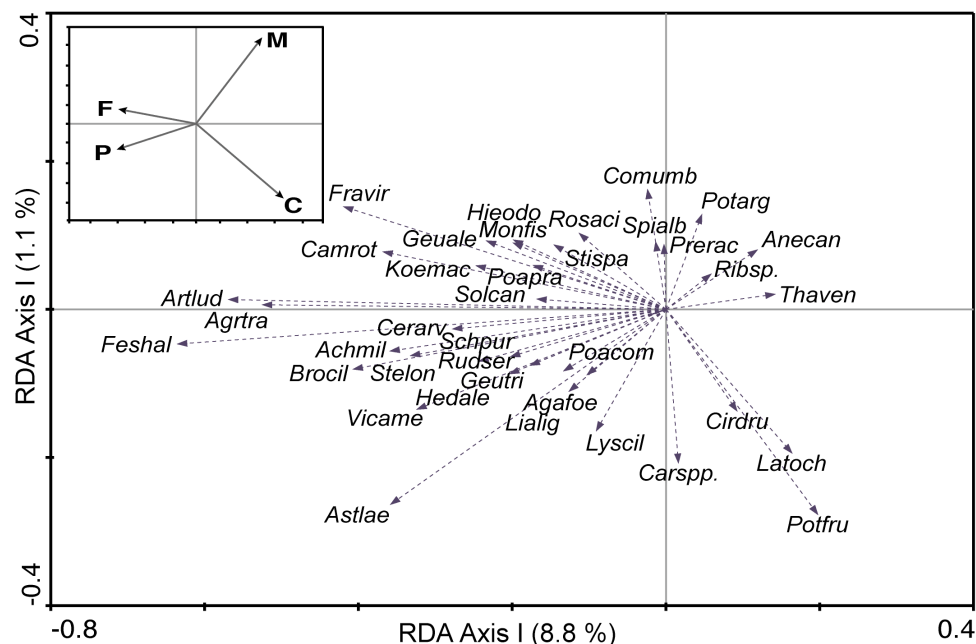


Figure 7.5 Redundancy analysis ordination (RDA) of northern fescue grasslands in Riding Mountain National Park, Manitoba, Canada, invaded by smooth brome (*Bromus inermis* Leyss.). The ordination of quadrats and species was constrained by four pseudo-variables, center (C), middle (M), fringe (F), and prairie (P), representing a gradient from the center of invading clones to the adjacent native prairies (inset). The first two component axes accounted for 9.9 % of variance in the plant community and 93.9 % of the species-environment correlation. Some species with a low proportion of variance explained by the environmental variables were removed for clarity. Abbreviations: Achmil (*Achillea millefolium* L., yarrow); Agafae (*Agastache foeniculum* (Pursh) Ktze., giant-hyssop); Agrtra (*Agropyron trachycaulum* (Link) Malte, slender wheat grass); Anecan (*Anemone canadensis* L., Canada anemone); Artlud (*Artemisia ludoviciana* Nutt., white sage); Astlae (*Aster laevis* L., smooth blue aster); Brocil (*Bromus ciliatus* L., fringed brome); Camrot (*Campanula rotundifolia* L., bluebell); Carspp. (*Carex* spp.); Cerarv (*Cerastium arvense* L., field chickweed); Cirdru (*Cirsium drummondii* T. & G., thistle); Comumb (*Comandra umbellata* (L.) Nutt., comandra); Feshal (*Festuca halii* (Vasey) Piper; rough fescue); Fravir (*Fragaria virginiana* Dcne. ssp. *glauca* (Wats.) Staudt, strawberry); Geuale (*Geum aleppicum* Jacq., yellow avens); Geutri (*Geum triflorum* Pursh, three-flowered avens); Hedale (*Hedysarum alpinum* L., liquorice-root); Hieodo (*Hierochloe odorata* (L.) Beauv., sweet grass); Koemac (*Koeleria macrantha* (Led.) Schultes, June grass); Latoch (*Lathyrus ochroleucus* Hook., wild pea); Lialig (*Liatris ligulistylis* (A. Nels.) K. Schum., blazingstar); Lyscil (*Lysimachia ciliata* L., fringed loosestrife); Monfis (*Monarda fistulosa* L., wild bergamot); Poacom (*Poa compressa* L., Canada blue grass); Poapra (*Poa pratensis* L., Kentucky bluegrass); Potarg (*Potentilla arguta* Pursh., white cinquefoil); Potfru (*Potentilla fruticosa* L., shrubby cinquefoil); Prerac (*Prenanthes racemosa* Michx., rattlesnakeroot); Ribsp. (*Ribes* sp., currant); Rosaci (*Rosa acicularis* Lindl., prickly rose); Rudser (*Rudbeckia serotina* Nutt.,

black-eyed Susan); Solcan (*Solidago canadensis* L., goldenrod); Stelon (*Stellaria longipes* Goldie, chickweed); Stispa (*Stipa spartea* Trin. var. *curtiseta* Hitchc., western porcupine grass); Thaven (*Thalictrum venulosum* Trel., meadow-rue); Vicame (*Vicia americana* Muhl, vetch). Nomenclature according to Cody (1988). Significance of all canonical axes following Monte Carlo permutation: $F = 2.511$, $P = 0.002$.

Table 7.1 Impacts of smooth brome (*Bromus inermis* Leyss.) invasion on the structure and belowground environments of northern fescue prairies in Riding Mountain National Park, Manitoba, Canada. The treatments, center, middle, and prairie, represent a transect from the center of invading clones to their prairie margins. Means of treatment groups were blocked to reduce variability between individual clones within the one-way ANOVA. Means \pm 1 S.E.

		Area			F	df	p
		Center	Middle	Prairie			
Thatch	depth (cm)	68.8 \pm 20.2	85.4 \pm 23.6	53.2 \pm 21.9	23.4	2, 66	\leq 0.0001
	mass (g/m ²)	124.7 \pm 10.4	160.3 \pm 14.9	125.3 \pm 12.0	3.2	2, 66	0.0490
Litter	depth (cm)	14.1 \pm 6.1	15.2 \pm 6.5	10.7 \pm 4.0	4.5	2, 66	0.0143
	mass (g/m ²)	175.2 \pm 17.3	198.5 \pm 19.9	135.0 \pm 16.9	3.6	2, 66	0.0325
Root mass (g)	0-10 cm	12.5 \pm 1.3	12.7 \pm 1.3	8.9 \pm 0.6	4.0	2, 22	0.0328
	10-30 cm	2.5 \pm 0.3	4.0 \pm 0.7	3.4 \pm 0.7	1.7	2, 22	0.2054
Moisture (%)	August 2004	5.2 \pm 0.5	4.4 \pm 0.3	3.6 \pm 0.2	7.0	2, 66	0.0018
	July 2005	9.5 \pm 0.8	8.5 \pm 0.6	7.5 \pm 0.6	4.2	2, 66	0.0195
Available N (mg/kg)*	July 2004	19.20 \pm 1.71	21.24 \pm 2.07	19.90 \pm 2.43	1.3	2, 66	0.2816
	July 2005	33.40 \pm 2.61	28.79 \pm 2.16	27.12 \pm 1.85	7.3	2, 66	0.0014
Mineralized N (mg/kg)*	Jul-Aug 2004	9.03 \pm 1.57	14.98 \pm 2.65	10.77 \pm 3.38	1.8	2, 30	0.1912
Olsen P (mg/kg)		0.99 \pm 0.09	0.64 \pm 0.06	0.66 \pm 0.05	16.8	2, 66	\leq 0.0001

*[NH₄⁺ N] + [NO₃⁻ N]

Table 7.2 Summary of the mean abundance of soilborne (kg^{-1} dry soil) and rootborne (g^{-1} dry root) plant parasitic nematodes in samples collected from twelve clones of smooth brome (*Bromus inermis* Leyss.) invading two northern fescue prairies in Riding Mountain National Park, Manitoba, Canada. The treatments, center, middle, and prairie, represent a transect from the center of invading clones to their prairie margins. Nomenclature according to Mai and Mullin (1996). Feeding habits according to Yeates et al. (1993). Numbers in brackets refer to single sample occurrences. Means \pm 1 S.E.

Genus	Feeding Habit	Soil			Roots		
		Center	Middle	Prairie	Center	Middle	Prairie
<i>Criconebella</i>	ecotparasite	345 \pm 108	320 \pm 28	422 \pm 76	7 (1)	-	-
<i>Helicotylenchus</i>	semi-endoparasite	884 \pm 217	1130 \pm 392	1348 \pm 357	13 \pm 4	36 \pm 14	11 \pm 1
<i>Hemicriconemoides</i>	ectoparasite	903 \pm 467	387 \pm 98	346 \pm 109	12 (1)	10 \pm 3	-
<i>Hemicyclophora</i>	ecotparasite	614 \pm 296	1448 \pm 693	577 \pm 267	-	-	-
<i>Heterodera</i>	sedentary parasite	147 (1)	243 \pm 94	318 \pm 8	-	36 (1)	5 \pm 3
<i>Hoplolaimus</i>	semi-endoparasite	165 \pm 13	328 \pm 109	131 \pm 24	23 (1)	-	-
<i>Paratylenchus</i>	ectoparasite	-	324 \pm 1	217 (1)	8 (1)	-	-
<i>Pratylenchus</i>	migratory endoparasite	197 (1)	323 (1)	151 \pm 48	-	6 (1)	7 (1)
<i>Unidentified (juvenile)</i>	-	-	134 (1)	109 (1)	-	12 \pm 5	-
Richness (S)		3.1 \pm 0.4	3.0 \pm 0.3	4.1 \pm 0.3	1.3 \pm 0.2	1.4 \pm 0.2	1.4 \pm 0.2
Shannon's index [$N1 = \exp(-\sum p_i \log p_i)$]		1.5 \pm 0.1	1.4 \pm 0.1	1.6 \pm 0.1	1.1 \pm 0.1	1.1 \pm 0.1	1.1 \pm 0.1
Effective richness [$N2 = (\sum p_i^2)^{-1}$]		2.5 \pm 0.4	2.1 \pm 0.2	2.7 \pm 0.3	1.3 \pm 0.2	1.3 \pm 0.2	1.3 \pm 0.1
Evenness [$E3 = (N2-1)/(N1-1)$]		2.8 \pm 0.2	2.3 \pm 0.2	2.5 \pm 0.2	2.8 \pm 0	1.9 \pm 0.9	1.9 \pm 0.6

Table 7.3 Impacts of smooth brome (*Bromus inermis* Leyss.) invasion on the composition and diversity of northern fescue prairies in Riding Mountain National Park, Manitoba, Canada. The treatments, center, middle, and fringe contrast the diversity and structure inside the invading clones with those in the adjacent native prairies. Means of treatment groups were blocked to reduce variability between individual clones within the one-way ANOVA. Means \pm 1 S.E.

	Area				F	df	p
	Center	Middle	Fringe	Prairie			
Total cover (%)	138.6 \pm 4.8	142.9 \pm 5.7	157.3 \pm 7.4	132.1 \pm 6.0	4.9	3, 99	0.0032
% forbs	34.0 \pm 2.5	35.8 \pm 2.4	43.3 \pm 2.0	53.0 \pm 2.6	21.8	3, 99	\leq 0.0001
% graminoids	22.7 \pm 2.2	23.5 \pm 1.9	36.7 \pm 1.8	45.8 \pm 2.6	36.9	3, 99	\leq 0.0001
% smooth brome	41.7 \pm 3.2	39.7 \pm 3.6	18.6 \pm 2.0	-	44.5	2, 66	\leq 0.0001
Richness (S)	4.1 \pm 0.7	13.4 \pm 0.8	17.3 \pm 0.6	17.4 \pm 0.6	23.3	3, 99	\leq 0.0001
Shannon's index [$N1 = \exp(-\sum p_i \log p_i)$]	2.2 \pm 0.1	2.3 \pm 0.1	2.8 \pm 0.1	2.8 \pm 0.1	20.4	3, 99	\leq 0.0001
Effective richness [$N2 = (\sum p_i^2)^{-1}$]	4.6 \pm 0.4	5.3 \pm 0.4	7.7 \pm 0.4	7.6 \pm 0.5	15.9	3, 99	\leq 0.0001
Evenness [$E3 = (N2-1)/(N1-1)$]	2.7 \pm 0.1	2.9 \pm 0.2	3.6 \pm 0.1	3.5 \pm 0.2	9.8	3, 99	\leq 0.0001

CHAPTER 8: CONCLUSIONS

8.1 Ecological contexts in the prediction and management of exotic invaders

Incorporating ecological contexts into the prediction and management of exotic invaders is essential to reducing their impacts on native biodiversity and ecosystem function.

Critical to this challenge is the determination of the relative importance of multiple factors influencing the success of potential invaders (Howe and Smallwood 1982).

Unfortunately, many studies, emphasizing isolated elements in the interaction between exotic organisms and recipient environments, are unable to predict the consequences of their introduction (Dietz and Edwards 2006, Thuiller et al. 2006). By integrating key stages in the life history of exotic species, including dispersal, establishment, proliferation, and persistence (Fig. 8.1), my research presents a conceptual framework to evaluate the threats posed by exotic species, as well as facilitate their monitoring and management. Critical to this framework is its potential application in the conservation and restoration of natural areas.

The consideration of key stages in the life history of exotic species in my research emphasizes interactions between exotic plants and recipient environments that often determine their impacts on natural areas. For example, observations of dispersal suggest that patterns of smooth brome (*Bromus inermis* Leyss.) invasion within northern fescue prairies, including its encroachment along dense fronts or as isolated foci, remains contingent on the types of propagules released, as well as the potential impact of animals in their post-secondary dispersal (Otfinowski et al. 2008). Based on these results, as well as those recently demonstrating the importance of human activities in the dispersal of

exotic organisms (Lockwood et al. 2005, Lodge et al. 2006), managers of natural areas must carefully consider the dispersal pathways and the viability of exotic propagules. Considering the large pool of exotic species absent from protected areas in western Canada, including Riding Mountain National Park (Otfinowski et al. 2007), controlling their dispersal should be evaluated in context of potential costs associated with managing exotic plants permitted to establish and proliferate inside protected areas (Fig. 8.1).

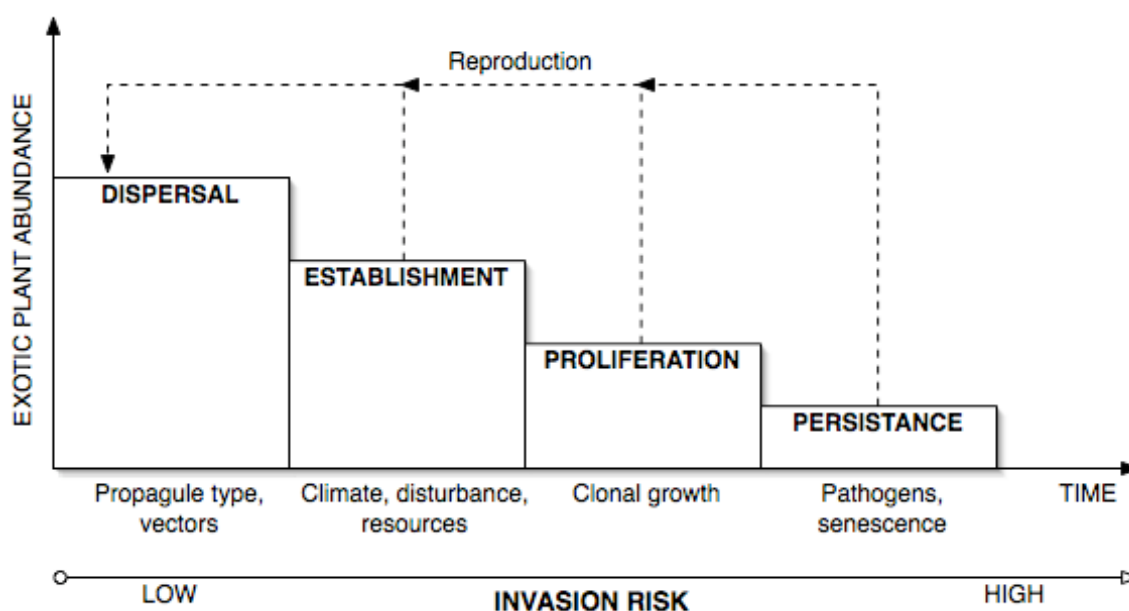


Fig. 8.1. Integrating key stages in the life history of exotic plants to predict their threat to the native biodiversity of natural areas (*sensu* Williamson and Fitter 1996).

The ultimate goal of management rests in simultaneously controlling exotic invaders as well as reducing the invasibility of native communities (DiTomaso 2000). By emphasizing the functional role of above- and belowground diversity in prairie communities, my research demonstrates that resources play a critical role in the

invasibility of disturbed communities. The resistance of disturbed prairies, preserving the root function of resident plants, illustrates the importance of considering the type of disturbance in estimating the invasibility of natural areas. Even though other studies support the role of resources in the establishment of exotic plants (Levine and D'Antonio 1999, Kennedy et al. 2002), their threat to native communities remains contingent on their proliferation (Ricciardi and Cohen 2007). As a result, the demonstration that vegetative growth facilitates the proliferation of smooth brome clones provides an important functional link between its establishment and invasiveness of northern fescue prairies (Ostrowski and Kenkel 2008). Severing physiological connections between invading ramets may provide a viable method in the management of smooth brome as well as other clonal exotic species successfully established within natural areas.

Existing research has principally focused on the evolutionary potential of successful invaders rather than the invaded communities. For example, the invasiveness of exotic organisms can also emerge in the absence of co-evolution between native and introduced organisms (Hanfling and Kollmann 2002). Equally important may be the long-term interactions between populations of exotic invaders and resident communities. My observations of smooth brome clones invading northern fescue prairies demonstrate that, although not attributable to soilborne pathogens, their long-term productivity declines over time. Consideration of this phenomenon among exotic invaders may help prioritize their management and the assessment of their long-term impacts on endemic biodiversity.

8.2 Restoring the integrity of natural areas invaded by exotic species

If we look far enough ahead, the eventual state of the biological world will become more depauperate (Elton 1958). Increasing commerce, transport, and travel will continue to disintegrate natural barriers that isolate continental realms of life, and disperse species to the limits set by their adaptability (Elton 1958, Mooney and Drake 1989, Mack 2003). My research, characterizing the climatic range of exotic plants illustrates that natural areas in western Canada will continue to be impacted by invaders currently absent from this region. As a result, conservation of endemic biodiversity will require not only an understanding of the biology of potential invaders and their interactions with native ecosystems, but an awareness of the changing patterns of commerce and transport, key to the introduction of new exotic species (Lodge et al. 2006). Despite these trends, potential threats posed by exotic species must be assessed within the ecological context of each environment (Crawley 1987, Mooney and Drake 1989, Lodge 1993). For example, the recent decline in the populations of many exotic species in central Europe is the result of urbanization and improvements in agricultural methods, which lead to the extinction of ruderal floras (Kornas 1990). Changes in regional patterns of land use and commerce can have noticeable impacts on the local exotic diversity (Dahen-Schmutz 1998) and should be an important element in the planning of monitoring and management programs in natural areas.

The restoration of native communities invaded by exotic species remains a formidable challenge. Nature reserves, often surrounded and dissected by disturbances, remain prone to re-invasion by exotic propagules (Usher 1988, Tyser and Worley 1992, Gelbard and Harrison 2005), compromising the ability of native species to re-establish

(Primack and Miao 1992). My experiments with smooth brome illustrate that viable propagules, capable of short and long range dispersal, may continue to pose a threat to native prairies, establishing new foci of invasion or retreating into the seedbank. The limited recruitment of native species and the restricted viability of seeds among fragmented populations (Eriksson and Ehrlén 1992, Primack and Miao 1992, Tilman 1997) may also pose important barriers to restoration efforts (Pywell et al. 2002). As a result, while impacts of human disturbance at the larger scale of landscapes, justifies the urgency to control exotic species, effective conservation measures must also reduce the less obvious impacts of dispersal (MacDougall and Turkington 2006). These, combined with careful management of disturbances and soil resources must remain an important element in the management of exotic invaders, including smooth brome.

Globally, little is known about ecosystem-level consequences of biological invasions. For example, the “ecosystem services” of altered ecosystems, such as regional climates, soil conservation and genesis, nutrient cycling, and controlling pests are rarely considered, yet likely have substantial social and economic costs (Ehrlich and Wilson 1991, National Research Council 2002). Experiments considering local introductions or transplants of exotic species outside of their range may offer small-scale models for such broad-scale dynamics (Mack et al. 2000). Also promising and under-utilized are comparisons of the performance of congeners, especially through field trials in the new range (Mack 1996). My investigations also emphasize the important role of examining the long-term persistence of exotic invaders. Their interactions with native environments, including potential changes in soil fauna and accumulations of thatch and litter are likely to have profound impacts on the potential restoration of impacted areas.

My research demonstrates that natural areas in western Canada will continue to be impacted by exotic plants. By integrating the stages of life history key in the progress of biological invasions, my work proposes a conceptual model in the investigation, monitoring, and management of exotic invaders threatening natural areas. Such approaches are critical in elucidating the context dependence of biological invasions. In addition to understanding the impacts of exotic species on native ecosystems and the ecological processes which regulate their invasions, the study and management of exotic species remains deeply rooted in our ability to adjudicate among conflicting constituencies with respect to the benefits and harm of exotic species (Lodge and Shrader-Frechette 2003). Thus, combining disparate social, political, legal, economic, cultural, spiritual, and educational dimensions of exotic species remains an important future direction in the study of plant invasions (Wittenberg and Cock 2001).

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