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Smooth Brome (*Bromus inermis* Leyss.) in Foothills Fescue Grassland: Stand Characterization and the Effects of Cattle, Sheep, Mowing, Glyphosate and Fire

by

Debra Jean Brown ©

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the
requirements for the degree of Master of Science

in

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled SMOOTH BROME (*Bromus inermis* Leyss.) IN FOOTHILLS FESCUE GRASSLAND: STAND CHARACTERIZATION AND THE EFFECTS OF CATTLE, SHEEP, MOWING, GLYPHOSATE AND FIRE submitted by DEBRA JEAN BROWN in partial fulfillment of the requirements for the degree of MASTER OF SCIENCE in WATER AND LAND RESOURCES.

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ABSTRACT

Sheep and cattle grazing, mowing, glyphosate and fire were applied in combination to smooth brome (*Bromus inermis* Leyss.) stands over the 1994 and 1995 growing seasons. The purpose of the study was to attempt to reduce smooth brome which was invading foothills fescue grassland and displacing native species. Defoliation (to 5 to 10 cm, 2 to 4 times) did not reduce smooth brome tiller density, etiolated regrowth or total nonstructural carbohydrates, however, the three heaviest defoliation treatments (sheep 3x; cattle 3x; mowing 4x) reduced smooth brome composition by 1996. Repeated glyphosate wicking (1x in 1994; 2x in 1995) was the most effective treatment and reduced 1996 smooth brome tiller density by 50%. Early spring burning as smooth brome began to grow, stressed the plants and reduced tiller density. Kentucky bluegrass (*Poa pratensis* L.), the subdominant species, increased in all treatments except the reference; reducing smooth brome may result in another undesirable species becoming dominant.

ACKNOWLEGEMENTS

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Sacred Earth, Mother of us all, Blessed Be!

The mother of us all,
the oldest of all,
hard,
splendid as rock

Whatever there is that is of the land
is she
who nourishes it,
it is the Earth
that I sing

Whoever you are,
howsoever you come
across her sacred ground
you of the sea
you that fly,
it is she
who nourishes you
she,
out of her treasures
Beautiful children
Beautiful harvests
are achieved from you
The giving of life itself,
the taking of it back....

The Homeric Hymns
(c. 6500 B.C.)

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

1. INTRODUCTION

> *'The vast ocean of level prairie which lies to the west of Red River must be seen in its extraordinary aspects, before it can be rightly valued and understood in reference to its future occupation by an energetic and civilized race, able to improve its vast capabilities and appreciate its marvelous beauties. It must be seen at sunrise, when the cloudless plain suddenly flashes with rose-coloured light, as the first rays of the sun sparkle in the dew on the long rich grass, gently stirred by the unfailing morning breeze....It must be seen, too, by moonlight when the summits of the low green grass waves are tipped with sliver, and the stars in the west disappear suddenly as they touch the earth....These are some of the scenes which must be witnessed and felt before the mind forms a true conception on the Red River Prairies in that unrelieved immensity which belongs to them in common with the ocean, but which, unlike the ever-changing and unstable sea, seems to promise a bountiful recompense to millions of our fellow men.'*
>
> *– Henry Youle Hind (1858)*

BACKGROUND

Native grassland provides productive rangeland for cattle and valuable habitat for wildlife. However, in one hundred years of settlement, more than 80% of the Canadian prairie has been ploughed for agriculture, industry and urban development (World Wildlife Fund 1989). Ninety percent of the fescue grassland has been ploughed and the remaining fragments have been significantly modified by grazing and haying. In addition, grassland integrity is threatened by invasion of trees, shrubs and introduced competitive grasses and forbs. The loss of habitat has threatened several plant and animal species and some have become extinct. Maintaining the quality of the remaining prairie and restoring degraded grasslands have become important conservation issues.

Smooth brome (*Bromus inermis* Leyss.) has been considered the most important introduced forage grass in the Aspen Parkland (Looman 1976) and is widely used for hay and pasture due to its excellent production and nutritional characteristics (Casler and Carlson 1995). Aggressive growth by rhizomes and prolific seed production have facilitated its invasion of native grasslands, reducing plant biodiversity (Grilz 1992). This invasion may also impact fauna by modifying habitat structure and food supply. Smooth brome, Kentucky bluegrass (*Poa pratensis* L.) and leafy spurge (*Euphorbia* *esula* L.) which produce relatively tall, homogeneous cover significantly reduced native plant species in disturbed mixed-grass prairie and significantly changed species composition of the native bird community (Wilson and Belcher 1989; Romo et al. 1990).

Understanding the biology and ecology of smooth brome and foothills fescue grassland provides a context in which to develop management strategies to reduce smooth brome.

SMOOTH BROME

Biological Characteristics and Growth Cycle

In Eurasia, smooth brome is common on permanent grazing land in a landscape similar to the Canadian parklands (Looman 1969). Smooth brome was first introduced to Canada from northern Germany in 1888 (Casler and Carlson 1995). 'Northern stock', bred from selections from northern Europe, establishes slowly and has relatively open sod which allows good legume development and hay production. Smooth brome has been used to increase livestock production in prairie pastures by outyielding native species, by having greater palatability and nutrient content and by extending the grazing period earlier in the spring and later in the fall (Looman 1976). Beginning in the 1930s, smooth brome was planted in roadside ditches adjacent cultivated fields as a lure crop for the wheat stem sawfly (*Cephus cinctus* Norton) (Gray 1967). It is also used to control erosion (Casler and Carlson 1995).

Smooth brome is adapted to grow in temperate climates in Gray Luvisols, Black, Dark Brown and irrigated soils and grows best on deep fertile soils of well-drained silt loam or clay loam (Casler and Carlson 1995). It is fairly tolerant to alkalinity and somewhat tolerant of salinity and acidity. It is very responsive to nitrogen fertilization. Although it is favoured by moist conditions and irrigation is used to extend its useful range, it is drought tolerant and was one of the few imported species to survive the drought of the 1930s.

Smooth brome is a leafy sod-forming perennial with deep roots and many rhizomes (Casler and Carlson 1995). A cool-season grass, smooth brome begins vegetative growth early in the growing season. New spring shoots come primarily from below the soil surface (Reynolds and Smith 1962). Production of new tillers stops at jointing and resumes after anthesis or defoliation when soil moisture and fertility are not limiting (Easten et al. 1964). This second flush of new shoots which is rapid but never as vigorous as the first spring growth, arises from buds at the top of the proaxis and at the two nodes above this location (Reynolds and Smith 1962). Stems elongate but the apices remain vegetative and they do not emerge from the sheaths. In autumn, the uncut spring and summer growth dies and a few new tillers are produced which only grow a few centimeters (Reynolds and Smith 1962). Autumn growth of the new rhizomes and tillers is influenced by defoliation and nitrogen fertilization (Paulsen and Smith 1968).

Inflorescences are initiated in the cool short days of autumn and the mature seed is produced in the long days of early summer (Casler and Carlson 1995). Stubble removal increases seed production (Fulkerson 1980). Smooth brome germinates over a wide range of temperature, light and soil moisture conditions (Grilz et al. 1994) but its establishment is the most successful when competition is minimized or eliminated (Bowes and Zentner 1992). The optimal temperatures for seedling growth are 18 to 27 °C (Smoliak and Johnston 1968).

Total available carbohydrates (TAC) in the stem bases of smooth brome are largely comprised of fructosans; starch, sucrose, glucose and fructose also contribute to TAC (Smith and Grotelueschen 1966). TAC is generally lowest during vegetative growth, greatest at seed formation (Reynolds and Smith 1962; Paulsen and Smith 1969) and declines as second growth elongates in late summer and as new tillers form in autumn (Reynolds and Smith 1962).

Response to Defoliation

Defoliation frequency determines the length of the recovery period between defoliations and phenological stage of the plant at time of defoliation. Frequent cutting often does not destroy growing points because plant height is less than cutting height, allowing stems faster regrowth which is not dependent upon axillary buds or reserve carbohydrates (Reynolds and Smith 1962; Paulsen and Smith 1969). For example, in a three cut system, the first cut at early heading removed all shoot apices but the second 5 cm cut did not remove all of the shoot apices and leaf growth continued (Reynolds and Smith 1962). The third cut was primarily of plants that had not elongated at the second cut. Regrowth is important for capturing light, photosynthesizing, replenishing carbohydrate reserves and competing with other species in the canopy.

Phenological stage determines apical meristem height, tillering ability and ratio of fertile to vegetative stems which are all key factors influencing grass resistance to grazing (Branson 1953; Booysen et al. 1963). Morphological criteria are more effective in obtaining quality yield and effectively managing grassland than set time intervals which do not account for growth difference due to environmental conditions (Sheard and Winch 1966).

Height of defoliation determines removal of the terminal growing point, the amount of stubble available for food storage, the amount of leaf area for photosynthesis and water uptake (Knievel et al. 1971). Generally the lower the cutting height, the more plant material harvested and the greater the yield (Lawrence and Ashford 1969; Knievel et al. 1971). Regrowth and persistence may be reduced when plants are severely defoliated. A cutting height of 4 cm removed most of the apices from tillering smooth brome, reduced regrowth (Knievel et al. 1971), persistence (Smith et al. 1973) and spring vigour (Lawrence and Ashford 1969) compared to cutting at 10 or 15 cm.

Regrowth

The major disadvantage of smooth brome for forage is its slow regrowth after defoliation (Casler and Carlson 1995). Defoliation between initiation of internode elongation and ear emergence reduced yield and delayed appearance of new growth for ten days or more in Ontario (Sheard and Winch 1966). At these stages, carbohydrate reserves are lowest and there is no visible development of axillary buds so regrowth develops from belowground node buds (Sheard and Winch 1966). In grasses, new leaf primordia are not produced after the apical meristem enters the reproductive phase (Booysen et al. 1963), so harvest at post-elongation increases time without leaves and reduces yield.

Earlier cutting does not remove the apical meristem and results in growth from unelongated shoots; at later cutting, carbohydrate reserves are higher and the tiller system is much better developed (Paulsen and Smith 1968). Growth was sparse and short after a first cut at early heading which removed all shoot apices but recovery was better when first cut was at green seed when there was greater basal bud activity and higher levels of TAC (Reynolds and Smith 1962). Smooth brome stands harvested at mature stages had greater regrowth and larger tillers (Eastin et al. 1964). Regrowth seven weeks after cutting was greatest when the first cut was at tillering, lowest when cut soon after joints had elongated and then generally increased as plant maturity at cutting increased (Paulsen and Smith 1969). In contrast, Kunelius et al. (1974) found the stage of development at first harvest had limited influence on regrowth six to eight weeks later. A system of vegetative clipping in Ontario with the first cut before tiller elongation and second cut after axillary bud development began, repeated for four harvests, increased total yield, reduced the dormancy period and resulted in a strongly competitive stand which provided some weed control (Sheard and Winch 1966).

Activity of basal axillary buds may be more closely related to total nitrogen concentration of the storage organs than carbohydrate reserves and growth hormones (Paulsen and Smith 1969). Total nitrogen reserves and regrowth were greatest at tillering, decreased at jointing and then increased after heading as the plants matured.

Yield

Total seasonal yield generally increased with plant maturity at time of first cut (Paulsen and Smith 1969; Kunelius et al. 1974) and declined when cutting frequency was three or more times per season (Paulsen and Smith 1969; Marten and Hovin 1980). Smooth brome cut three times in the season produced a greater total yield than brome cut five times (Paulsen and Smith 1969). Smooth brome cut four times had yields lower than those cut two or three times in Minnesota (Marten and Hovin 1980). In Ontario, yield increased as time interval between cuts increased from two to four to six weeks (Sheard and Winch 1966). Yield declined as clipping frequency increased from three to five to eight times per season in West Virginia (Jung et al. 1974). Harrison and Romo (1994) concluded that the best time to harvest smooth brome to maximize forage production in Saskatchewan depended on growth conditions, especially precipitation, rather than physiological stage.

Carbohydrate Reserves

Carbohydrate reserves decreased dramatically after shoot apices were removed (Reynolds and Smith 1962; Smith 1967; Paulsen and Smith 1968). When cut only two or three times in a season in Wisconsin, smooth brome usually regained the precutting level of reserves by the time of next cut (Reynolds and Smith 1962). Paulsen and Smith (1968) found that the rebounding of TAC after cutting three times at head emergence or elongation was somewhat variable in Wisconsin. Cutting at elongation five times in the summer reduced TAC levels throughout the growing season (Paulsen and Smith 1968). Whether cut two, three or five times, carbohydrate levels were once again high by the end of the fall (Reynolds and Smith 1962; Paulsen and Smith 1968).

Carbohydrate reserves at harvest may have little bearing on future productivity and may only be important to support early regrowth (May 1960). Photosynthesis may be the major source of carbon for regrowth after defoliation (Richards 1984). Stage of first cut had little consistent effect on autumn reserves as measured by TAC (Reynolds and Smith 1962; Paulsen and Smith 1968) or etiolated regrowth (Wright et al. 1967, cited by Paulsen and Smith 1969). Paulsen and Smith (1969) concluded that carbohydrates had no apparent effect on bud activity since there was little association between TAC and stem base weight at the time of spring cutting and regrowth produced in the following seven weeks. Raese and Decker (1966) noted that grasses producing the greatest regrowth had the lowest levels of fructose and suggested that fructose levels may be an index of plant growth. Declining TAC have also been associated with rapid growth during tillering and stem elongation in spring and regrowth after defoliation (Reynolds and Smith 1962; Smith 1967; Paulsen and Smith 1969).

Residual Effects on Growth

Defoliaton may continue to impact smooth brome growth one year after treatment implementation. Spring growth in Wisconsin, following two years of cutting two times per year, was lowest in stands of smooth brome first cut at jointing, boot and heading (Paulsen and Smith 1969). Smooth brome frequently clipped at short and elongated vegetative stages to simulate grazing produced less residual growth the following year than smooth brome first cut at beginning of bloom (Bird 1943). Lawrence and Ashford (1969) in Saskatchewan, rated the overall spring vigour of smooth brome first cut at flowering the previous year to be much greater than the stands cut at shot-blade. Growth the year following two cuts per growing season was greater than where smooth brome had been cut three or four times for two to three years (Sheaffer et al. 1990).

Persistence

Smooth brome has generally good winter hardiness and stand persistence (Casler and Carlson 1995). Timing of first cut alone does not affect stand persistence (Lawrence and Ashford 1969; McElgunn et al. 1972; Kunelius et al. 1974; Kunelius 1979).

Less frequent cutting generally favours smooth brome (Jung et al. 1974; Marten and Hovin 1980). Smooth brome had relatively poor persistence under three and four cut schedules in Minnesota and Wisconsin (Smith et al. 1973; Marten and Hovin 1980;

Sheaffer et al. 1990). Three years of cutting in Minnesota reduced smooth brome persistence as annual cutting frequency increased from two times with the first cut at green seed (100% ground cover) to three times with the first cut at anthesis (72%) and four times with the first cut at vegetative, early boot or boot (40%) (Marten and Hovin 1980). When the four cut regime was followed by two years of cutting three times per year, stands improved to 69%. It was noted that damage was greatest when plants were cut at boot or early boot. Also in Minnesota, Sheaffer et al. (1990) found percent ground cover by smooth brome within seeded rows decreased much more when cut three or four times than when cut two times per summer for a period of two or three years. Ground cover by smooth brome which was cut three times, beginning at pre-anthesis tended to be lower than where four cuts beginning at late stem elongation or inflorescence emergence were conducted. Weed invasion increased as cutting frequency increased and ground cover decreased (Sheaffer et al. 1990). Smith et al. (1973) in Wisconsin nearly eliminated smooth brome within three years by cutting three times annually at 4 cm with the first cut being at pre-anthesis. Persistence was higher under regimes of cutting four times per season with the first cut being at boot or late stem elongation (36%) or cutting two times per season with the first cut being at green seed (99%). In contrast, persistence of smooth brome grown with alfalfa under irrigation in Saskatchewan was not influenced by the stage of first cutting when cut four times in the summer (McElgunn et al. 1972).

Smooth brome did not decline as clipping frequency increased from once to two or three times per summer south of the Parkland in Saskatchewan (Knowles 1987), however, smooth brome ground cover decreased significantly over four years in Saskatchewan Parkland when intensively grazed (to 2-5 cm) two, three and five times (McCartney and Bittman 1994).

Recommended Grazing Practices

Although smooth brome is fairly resistant to overgrazing due to vigorous rhizome growth (Alberta Agriculture, Food and Rural Development 1981), smooth brome ground cover decreased as grazing intensities increased (McCartney and Bittman 1994). Early spring grazing should be of light intensity to allow growth to accumulate for later use (Alberta Agriculture, Food and Rural Development 1981; Casler and Carlson 1995). During tillering, crude protein and carbohydrates reserves are high, nitrogen is available in the crown and grazing does not slow tiller development. Stocking rates may be increased after reserves have been restored and before seed formation (Casler and Carlson 1995). At least 20 to 30 cm of growth is required before grazing and at least 8 to 12 cm should be left after grazing to ensure recovery (Casler and Carlson 1995). Allowing one quarter of the tillers to form seed heads before the next grazing will ensure sufficient time for regrowth and high yields in Alberta (Bjorge 1994). Rest periods should be longer in midsummer when growth is slower (Casler and Carlson 1995). Heavy use late in the growing season reduced stored energy reserves and reduced vigour and productivity the following season (Casler and Carlson 1995); spring grazing following heavy fall grazing is not recommended in central Alberta (Bjorge 1994). These considerations are more easily accommodated with rotational grazing than continuous grazing (Casler and Carlson 1995). In the Dark Brown soil zone of Saskatchewan, where conditions are drier, it is recommended that smooth brome be grazed only once per year in mid-May or later with stocking rates adjusted to ensure regrowth is not grazed (Harrison and Romo 1994).

ECOLOGY OF FOOTHILLS FESCUE GRASSLAND

The Foothills Fescue Grassland Association includes approximately 150 species of higher plants (Moss and Campbell 1947). Rough fescue (*Festuca campestris* Rydb.) is the dominant climax species and may form nearly pure stands but Parry oat grass (*Danthonia parryi* Scribn.) is usually present and may dominate on shallow soils (Moss and Campbell 1947; Looman 1969). Foothills fescue grassland evolved with winter grazing by bison when fescue was dormant (Johnston and Macdonald 1967) and is now primarily grazed by cattle and elk (Bailey 1976). Cattle and wildlife activity is greater in areas where excessive litter buildup is prevented by grazing or burning (Willms et al. 1980; Jourdonnais and Bedunah 1990). Control of fire has allowed willows, aspen and balsam poplar to encroach into fescue grassland (Bailey 1976).

Protection from grazing favours fescue dominance, possibly due to large amounts of litter which accumulate (Johnston 1961; Willms et al. 1985). Under light grazing, rough fescue decreases and Parry oat grass, which is most productive with multiple growing season harvests (Willms 1991), increases (Moss and Campbell 1947; Johnson 1961; Looman 1969). Species diversity also increases (Johnston 1961; Trottier 1986). Moderate to heavy grazing decreases Parry oat grass; sedges (*Carex* L. spp.) increase on dry sites and Kentucky blue grass increases on wet sites (Looman 1969). Fescue becomes patchy, persisting in more moist situations and where protected by shrubs from grazing; it may be greatly reduced or eliminated under very heavy grazing (Moss and Campbell 1947; Willms et al. 1985; Trottier 1986). Smooth brome, Kentucky bluegrass, timothy (*Phleum pratense* L.), white clover (*Trifolium repens* L.) and dandelion (*Taraxacum officinale* Weber) are common invaders, especially under poor management and on subirrigated lowlands (Looman 1969; Bailey 1976; Willms 1988).

Mowing decreases fescue tussock size and other species become more prominent (Moss and Campbell 1947). Forbs are favoured over grasses and sedges.

Fire may enhance or depress plant growth due to direct effects of burning and changes in environmental conditions, competitive relationships, and allocation of resources to growth. Fire reduced rough fescue for one to three years, however, drought may delay production recovery (Bailey and Anderson 1978; Jourdonnais and Bedunah 1990). Spring burns immediately after snowmelt are recommended by Jourdonnais and Bedunah (1990) because fall burns reduce snow trapment, increase soil erosion potential and frost damage, and leave no winter forage for elk. In contrast, Romo (1997) recommends burns in foothills fescue grassland be of various sizes and types, throughout the entire year, to imitate natural variability and ecological processes.

Foothills Rough Fescue

Biological Characteristics and Growth Cycle

Foothills rough fescue is the most productive species on good condition range in the foothills (Willms et al. 1985) and grows best on deep well drained soils with ample moisture (Willms et al. 1992). It cures well in the field, maintaining a crude protein content of about 6% in September, which is sufficient for providing maintenance nutritional requirements for cows (Willms et al. 1992). Rough fescue is the preferred winter forage for elk in the foothills of Montana (Jourdonnais and Bedunah 1990).

Foothills rough fescue is a large tufted, deep rooted plant with vegetative growing points remaining near ground level throughout most of the year and with relatively few reproductive tillers (Johnston 1961). Growth starts in early May when soil temperature reaches 2.6 to 2.9 °C at 10 cm depth (Stout et al. 1981) or approximately 2 °C at 20 cm depth (Johnston and Macdonald 1967). Soil temperature is more important than air temperature or soil moisture for initiating spring growth of foothills rough fescue (Stout et al. 1981). The cumulative yield of rough fescue reaches a maximum by end of July with cessation of summer growth appearing to be related to soil moisture (Stout et al. 1981). Dead culms are persistent and are thought to protect the perennating buds from fire (Johnston and Macdonald 1967).

Initiation of floral primordia appears to occur in late August to early September but the determining environmental conditions are not known (Johnston and Macdonald 1967). Spring management does not influence initiation. Initiated growing points are elevated gradually through the winter and then elongate rapidly during May and early June. Heading generally begins in late June (soil temperature 12.7 °C and daylength 16 hours) and is completed by mid July (Johnston and Macdonald 1967; Willms 1991). Seed set is erratic. Seed ripens by early August and shatters, foliage cures and plants enter winter dormancy by early October. Foothills rough fescue seed germinates readily (Johnston and Macdonald 1967) and there appears to be no after-ripening requirement for plains rough fescue (*Festuca altaica* ssp. *hallii*), a closely related species which will germinate in summer as long as it reaches a suitable safe site with sufficient moisture

(Romo et al. 1991). Descending temperatures reduce germination which is presumably a mechanism to reduce germination in autumn when there is insufficient time for seedlings to become sufficiently established (Romo et al. 1991). Stands are slow to develop with the establishment period being three to four years compared to one to two years for cultivated grasses such as smooth brome (Johnston and Macdonald 1967).

Surviving tillers are the basis for regeneration in the recovery of overgrazed rough fescue grasslands (Johnston and Macdonald 1967; Willms 1991). Seed set is important only when pasture condition is fair or poor, plants have been killed by overuse and grasses must reinvade by seed. One year of rest from grazing will not improve range by natural reseeding because seed production is so low, particularly in heavily grazed rangelands (Stout et al. 1981).

Response to Defoliation

Defoliation during the growing season reduces yield of foothills rough fescue regardless of cutting frequency or height (Willms 1991). When a series of clippings ceased before fescue became dormant rather than continuing throughout the summer, injury was reduced and plants produced more regrowth (McLean and Wikeem 1985). Johnston and Macdonald (1967) suggested fescue's intolerance to summer grazing may be due to a limited ability to produce lateral tillers from axillary meristems or removal of large amounts of photosynthetic material by close grazing due to its erect growth.

Dormant season defoliation does not decrease survival or vigour of foothills rough fescue (McLean and Wikeem 1985; Willms et al. 1986a), perhaps because it evolved with winter grazing by bison (Johnston and Macdonald 1967). Foothills rough fescue yields were greatest with a single harvest near the end of August when plants had completed growth and were dormant (Willms 1991). Three consecutive years of this clipping regime did not affect production potential and yields were similar to plants with no previous disturbance (Willms and Fraser 1992). Standing litter removal and associated reduction in shading may even enhance plant vigour by stimulating tillering in grasses (Willms et al. 1986a). The more standing litter removed, the shorter the tillers, perhaps due to soil moisture deficit, higher soil temperature and greater light intensity at the crown.

Cutting frequency had a greater impact on fescue than cutting height (Willms 1991; Willms and Fraser 1992). Fescue plants cut twice in the season had less than half of the number of tillers than the plants cut once in late August and tillers were smaller (Willms 1991). Plants cut more frequently had even fewer and smaller tillers, lower yields and reduced etiolated regrowth (Willms 1991). McLean and Wikeem (1985) found that clipping treatments with higher plant mortality had fewer tillers, shorter leaves and lower yields. Lower growth rate and shorter tillers may be due to reduced carbohydrate reserves, smaller root mass and hence reduced nutrient uptake. The small tufted form of the surviving tillers may be a survival strategy that ensures reduction or avoidance of grazing pressure (Willms and Fraser 1992).

Fescue mortality increased as clipping height decreases from 15 cm to 5 cm (McLean and Wikeem 1985; Willms 1991). Cutting frequency increased the effect of these cutting heights (Willms 1991). Mortality rates for fescue plants clipped weekly at 20 cm all season long were not significantly different from the unclipped control (McLean and Wikeem 1985). Close harvesting (5 cm clipping height) over several years reduced forage yield, plant height, tiller numbers and competitiveness (Willms and Fraser 1992).

Parry Oat Grass

Parry oat grass occurs in association with rough fescue and other grasses in relatively forb free stands on coarse textured shallow soils and dominates on exposed south and west facing slopes (Johnston and Dormaar 1970). During the growing season, Parry oat grass has softer textured foliage with higher crude protein content than rough fescue and is readily used by cattle (Willms et al. 1992). Parry oat grass starts growing about two weeks later than rough fescue, is shorter (20 cm), produces about half of the forage and is more subject to nutritional losses by weathering in fall and winter (Willms et al. 1992).

Parry oat grass is more resistant to grazing than rough fescue and yields more when grazed two or three times during the growing season than only once in late summer (Willms et al. 1992). Whereas a modest increase in stocking rate decreased basal area of rough fescue from 38% (1.2 AUM/ha grazing pressure) to 21% (1.6 AUM/ha) over 32 years, Parry oat grass increased from 24% to 48% (Willms et al. 1985). Very heavy grazing (4.8 AUM/ha) reduced Parry oat grass to 35% basal cover, nearly eliminated rough fescue (3%) and severely deteriorated the range condition. Stocking rate had to be adjusted annually to avoid animal losses. Stocking at a light rate (1.2 AUM/ha) for 32 years did not affect range condition (Willms et al. 1985).

Recommended Grazing Practices

Fall and winter grazing maximized yields of dry matter, nutrients and digestible dry matter but forage quality may be limiting for some classes of livestock (Willms and Beauchemin 1991). Alternatively, continuous summer grazing ensured forage quality is adequate for all classes of cattle, however, rough fescue is likely to decline (Willms 1991). Generally, a stocking rate of 1.6 AUM/ha is recommended for continuous summer grazing of foothill fescue grasslands (Willms et al. 1986b; Willms et al. 1992). This relatively light stocking rate produces lower cattle yields but maintains the productivity of the vegetation and sustains habitat value (Willms et al. 1986b). Light or moderate summer-long grazing (1.2 to 1.6 AUM/ha) is best for maintaining the litter and organic matter required for good hydrologic conditions (Naeth et al. 1991); however, overgrazed and undergrazed patches may develop (Willms et al. 1988). Although patches represent unused production, they also provide more diverse habitat for animals, ensure the presence of climax species for recolonizing and provide emergency forage during drought years. Sustained heavy grazing will eliminate grazed patches and produce beef more efficiently (Willms et al. 1986b) but soil and watershed properties may deteriorate (Willms 1991).

Summer grazing is most effective if the timing of grazing of topographic zones can be controlled (Willms 1988). It is best to graze the subirrigated lowlands first in the spring. These areas are dominated by timothy, Kentucky blue grass, white clover and dandelion which are grazing resistant. This delays grazing of the native species on the upland zone which are sensitive to defoliation during the growing season. The south aspect of the upland area should be grazed first because it develops faster than the other aspects. It is important to leave some litter, particularly in the upland areas because litter helps stabilize annual production by enhancing soil moisture and protecting soil integrity and also provides emergency forage during a drought if the stocking rate is fixed (Willms et al. 1988).

RESEARCH OBJECTIVES

Although the agronomic characteristics of smooth brome have been widely studied from a hayland management persepective, relatively little research has been conducted on the ecology of smooth brome stands and techniques to eliminate smooth brome or reduce its competitiveness in native grasslands.

The objectives of this research were to:

1. Document the vegetation and litter of smooth brome stands in foothills fescue grassland,
2. Conduct a preliminary study of seed bank potential of smooth brome stands and adjacent native grassland, and
3. Determine the effect of combinations of grazing, mowing, glyphosate wicking and prescribed spring burning on smooth brome, as assessed by tiller density, plant species composition, carbohydrate reserves and etiolated regrowth.

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2. CHARACTERIZATION OF SMOOTH BROME (BROMUS INERMIS LEYSS.) STANDS IN FOOTHILLS FESCUE GRASSLAND

> *'In one human lifetime, the prairies have passed from wilderness to become the most altered habitat in this country and one of the most disturbed, ecologically simplified and over-exploited regions in the world.'*
>
> *–Adrian Forsyth (1983)*

INTRODUCTION

Smooth brome (*Bromus inermis* Leyss.) has been considered the most important introduced forage in the Canadian aspen parkland (Looman 1976). Its rapid spring growth, prolific rhizome production and seed development enable it to compete intensely for light and moisture and invade native grassland (Pearon et al. 1995). Smooth brome invades as an advancing front and as nearby patches which become established in disturbances created by pocket gophers and other animals (Grilz 1992). These patches then become foci for further invasion.

Litter (dead plant material) accumulation, which is greatest in highly productive ungrazed stands, influences microclimate, soils, hydrology, flora and fauna. Litter reduces soil temperature and evaporation, intercepts precipitation, traps snow and increases water infiltration, thereby influencing overall soil moisture, stabilizing grassland productivity and preventing erosion (Weaver and Rowland 1952; Hopkins 1954; Willms et al. 1988). Litter buildup increases pore space, organic matter and nitrogen content of surface soil and improves habitat for soil organisms (Weaver and Rowland 1952). Although grazers (domestic and wild) preferentially select forage without litter (Willms et al. 1980; Jourdonnais and Bedunah 1990), litter may provide emergency forage during drought (Willms 1988). Spring plant growth may be delayed because of colder soils (Hopkins 1954) or reduced light penetration to the soil (Weaver and Rowland 1952). Accumulation of litter also reduces tiller density, basal area, forage yield, grass flowering and plant species biodiversity (resulting in nearly pure stands of the dominant species with only a few of the taller forbs persisting from the understory) (Weaver and Rowland 1952). Although litter may reduce seed germination by allelopathy, changing the microclimate and presenting a physical barrier to emergence (Bosy and Reader 1995), it may also enhance seed preservation by maintaining seed dormancy (Williams 1983 cited by Willms and Quinton 1995) or reducing exposure of seed to predation and environmental hazards. Emergence by large seeded species is less affected by litter than small seeded species likely because larger seeds have more food reserves and more vertical thrust (Bosy and Reader 1995).

In well managed grassland, most species are maintained by vegetative reproduction, rather than by seed (Johnston and Macdonald 1967). However, where species are depleted by soil disturbance, species invasion or inappropriate grazing, regeneration from seed rain or from seed and other propagules in the seed bank becomes important. Analysis of the seed bank provides an indication of what species may become established when disturbance creates new 'safe sites' for germination (Rosburg et al. 1992).

Seed production and germinability vary with plant species, season and environmental conditions (Johnston et al. 1969; Lagroix-McLean 1990; Willms and Quinton 1995). The autumn seed bank represents the carry-over from previous years plus the seed rain from the current year minus all losses to dispersal, predation and dormancy (Willms and Quinton 1995). Seed numbers would be expected to decrease from autumn to the following spring due to induced dormancy, disease or predation. An increase could only occur if there was an import from other areas. Willms and Quinton (1995) reported seed densities of Kentucky bluegrass (*Poa pratensis* L.) and whitlow grass (*Draba* L. spp.) decreased 50% from autumn to spring, however, the germinability of other species did not essentially change.

Grazing influences seed bank composition by changing vegetation composition and seed production and by reducing litter accumulation which influences dormancy (Willms and Quinton 1995). As grazing intensity increases, seed bank contribution by graminoids decreases and forbs and shrubs increase (Johnston et al. 1969). Kentucky bluegrass seed density was greatest under light grazing while whitlow grass, an annual native forb, increased exponentially under heavy grazing (Willms and Quinton 1995).

Although the climax condition of fescue grassland and its response to grazing and mowing have been described by Moss and Campbell (1947), Looman (1969) and Willms et al. (1985), less is known about fescue grassland which has been invaded by smooth brome (Grilz 1992) or seeded to smooth brome for many years (Looman 1976). The objectives of this study were to document the vegetation and litter of smooth brome stands in foothills fescue grassland and to conduct a preliminary study of seed bank potential of smooth brome stands and adjacent native grassland.

STUDY AREA DESCRIPTION

Location and Land Use

Research was conducted at the Ann and Sandy Cross Conservation Area (the Conservation Area) approximately 3 km southwest of Calgary, Alberta. This three section parcel of land (Section 7E, 8W, 8NE, 8SE, 17, 18E Township 22 Range 2 W5) was donated to the Fish and Wildlife Division of Alberta Forestry, Lands and Wildlife in 1987 and is managed by the Nature Conservancy of Canada.

Since agricultural settlement of western Canada by Europeans, this land has been variously used for cattle grazing and, more recently, crop and hay production on the plateaus, hilltops and gentler slopes. Land use changes were documented by Steeves (1993) using air photos taken in 1926, 1944, 1962 and 1993 (Appendix A, Table 1). In 1926, only 6% of the land was under cultivation, however, by 1944, 22% of the area was cultivated and native grassland had declined from 40 to 14% of the area. Further losses of native grassland since 1962 have been due to encroachment by agronomic species. Tree and shrub covered area also expanded throughout the documented time period, due in part to fire suppression.

Physiography and Soils

The study site is located within the Leighton Centre Upland Subdivision of the Alberta Plains Division, immediately east of the Rocky Mountain Foothills Division

(MacMillan 1987). The rolling topography of the area is underlain by sandstone bedrock. One tributary of Fish Creek and two tributaries of Pine Creek drain the area. Elevation ranges from approximately 1190 m in the tributary valleys to at least 1310 m (MacMillan 1987).

Soils have formed over a blanket of fine loamy till which is moderately to strongly calcareous with moderate amounts of coarse fragments. Well drained Dark Gray and Gray Luvisols (and occasionally Eutric Brunisols) (Leighton Centre Soil Group) are found primarily on the north and east facing slopes and on the till plateaus where cooler, moister conditions have supported forest development (MacMillan 1987). Orthic Black Chernozemic soils (Dunvargan Soil Group) have developed on the moderately to strongly sloping south and west facing hillsides under fescue grassland and periodic aspen forest cover.

Climate

The Humid Microthermal climate of the area is characterized by warm summers and relatively cool winters which are generally moderated by Chinook winds (MacMillan 1987). July is the warmest month with a mean temperature of 13.4 to 16.6 °C and January is the coldest month with a mean temperature of -10.0 to -12.7 °C. The mean annual precipitation is approximately 470 mm with 67% occurring within the May to September growing season. The short frost free period (60 to 75 days) is considered a moderate limitation to most plant growth. The growing season may be extended on the long smooth south facing slopes because these slopes receive more sunlight and cold air moves down the slope at night. Microclimates are cooler on north and east facing slopes which receive less sunshine and on valley bottoms which trap cold air.

In 1994, annual and growing season (April to September) air temperature was warmer than the 30 year normals; annual and growing season precipitation was less than the 30 year normals (Appendix B, Table 1). Precipitation of 219 mm was recorded for the period June to September, inclusive, at the Conservation Area.

Vegetation

The study area is located in the Rocky Mountain Foothill Ecodistrict of the Aspen Parkland Ecoregion, which is comprised of a mosaic of aspen clones, shrub communities and fescue grassland (Strong and Leggat 1992). Soil moisture is adequate for aspen (*Populus tremuloides* Michx.) on the north facing slopes, seepage areas, depressions and creek banks (Strong and Leggat 1992). Shrubs such as saskatoon (*Amelanchier alnifolia* Nutt.), prickly rose (*Rosa acicularis* Lindl.), buckbrush (*Symphoricarpos occidentalis* Hook.), snowberry (*Symphoricarpos albus* (L.) Blake) and silverberry (*Elaeagnus commutata* Bernh. *ex* Rydb.) frequently are found on the north facing slopes, ravines and in the areas that accumulate snow (Strong and Leggat 1992). Foothills rough fescue (*Festuca campestris* Rydb.) is the dominant species in the undisturbed fescue grasslands (Moss and Campbell 1947; Looman 1969). Parry oat grass (*Danthonia* parryi Scribn.) is the codominant species in the lower southern foothills of the Rocky Mountains and may dominate the exposed south and west facing slopes (Johnston and Dormaar 1970). Kentucky bluegrass, sedges (*Carex* L. spp.), bluebunch fescue (*Festuca idahoensis* Elmer), June grass (*Koeleria macrantha* (Ledeb.) J.A. Schultes f.), needle grasses (*Stipa* L. spp.), old man's whiskers (*Geum triflorum* Pursh), sticky purple geranium (*Geranium viscosissimum* Fisch. & Trautv.) and northern bedstraw (*Galium boreale* L.) are also common in natural aspen parkland grassland (Strong and Leggat 1992).

In the Conservation Area, native grassland is found only on the steepest, driest portions of south facing slopes. Other areas are often invaded by smooth brome and Kentucky bluegrass. The majority of the till plain plateau is covered with timothy (*Phleum pratense* L.), alfalfa (*Medicago sativa* L.) and clover (*Trifolium* L. spp.) hayland (Steeves 1993). The valley bottoms are dominated by smooth brome and Canada thistle (*Cirsium arvense* (L.) Scop.). The dominant species of the native grasslands immediately adjacent to the study blocks were Parry oat grass, Kentucky bluegrass, western wheatgrass (*Agropyron smithii* Rydb.), foothills rough fescue, June grass and Columbia needle grass (*Stipa columbiana* Macoun) (Steeves 1993).

MATERIALS AND METHODS

Site Description and History

Study blocks were situated in smooth brome stands on mid (Blocks 1 and 3) to upper (Blocks 2 and 4) portions of south facing hillsides in proximity to areas of native vegetation. Slopes ranged from 10 to 19%.

The history of the areas encompassing the study blocks was interpolated from aerial photographs. The blocks were in their natural state in 1920, but by 1944, fields were established in the vicinity of Block 1, immediately adjacent Block 2 and on Blocks 3 and 4. Blocks 3 and 4 were seeded to smooth brome, frequently mowed (and/or grazed in the case of Block 3) and likely reseeded, with the most recent reseeding occurring prior to 1985 (Rempel 1995). Smooth brome in Blocks 1 and 2 may have established by natural invasion as well as cultivation and seeding, however, it is likely that these areas were cultivated and seeded much less frequently than Blocks 3 and 4 (for more details, refer to Appendix A). The grazing regime in the 1980s was fall grazing in Block 1, mid-summer grazing in Blocks 2 and 3 and haying in Block 4 (Rempel 1995). Cattle grazing was not conducted for seven years prior to this study.

Soil Sampling and Analysis

To characterize soil diversity across each block, one core was collected randomly from each plot with a dutch auger (7.5 cm diameter) in June 1994. Samples were taken in 15 cm increments to the B horizon at 45 cm for Block 2, 60 cm for Block 4 and 75 cm for Blocks 1 and 3. Soil samples were air dried and ground to 2 mm prior to analysis.

Particle-size analysis using the hydrometer method with pretreatment for organic matter (Gee and Bauder 1986) was carried out for each depth increment of three randomly selected plots from each block. Total soil carbon was determined by oxidation with a Leco carbon determinator. Analysis was conducted on all 0 to 15 and 15 to 30 cm samples, and three randomly chosen samples at 30 to 45 cm from each block. Water holding capacity (WHC) was measured for all samples and depths using pressure chambers with ceramic plates set at 1/3 bar and 15 bar representing field capacity and permanent wilting percentage, respectively. Available water holding capacity (AWHC) was calculated by subtracting the 15 bar reading from the 1/3 bar reading.

For all samples and depths, electrical conductivity (EC) and pH of a saturated soil extract (20 g soil per 40 ml deionized water) were measured using an EC meter and pH meter, respectively.

Litter Assessment

Litter, defined as dead plant material not incorporated with mineral soil and occurring above the soil mineral horizon (Naeth et al. 1991), was separated into three categories: standing, fallen and partially or totally decomposed. Five 0.05 m^2 samples were collected in June 1994 from each plot at regular intervals to prevent resampling. Samples were oven dried at 65 °C to constant weight and weighed. Litter depth to mineral soil was measured at each litter sampling location.

Vegetation Assessment

Ground cover (live vegetation, litter, bare ground, manure and rocks) and species composition of live vegetation were assessed in July 1994 in ten 0.1 m^2 quadrats randomly located in each plot. An additional assessment of ground cover and plant species composition of native areas adjacent each block was conducted using 15 randomly located 0.1 m^2 quadrats in September 1996. Plot species richness was calculated as the total number of species occurring in the ten quadrats of each plot. Species frequency was calculated as the percentage of quadrats in a plot in which a species occurred. Density of grass tillers and other plants were counted in five 0.1 m^2 quadrats randomly located in areas of high smooth brome density in each plot on July 9 to 11, 1994. Scientific and common names follow Moss (1983), with some additional common names being sourced from Looman (1982). *Festuca campestris* Rydb. is according to the taxonomic revision by Pavlick and Looman (1984).

Live plant material was clipped in July 1994 to 5 cm above the litter layer from five 0.1 m^2 quadrats randomly located in each plot. Samples were oven dried at 65 °C to constant weight. Biomass was sorted into smooth brome, other grasses, forbs and shrubs and separately weighed.

Seed Bank Assessment

A seed bank germination study was conducted to assess the potential contribution of seed in the soil and litter to grassland regeneration. In late Autumn 1994, 10 soil and litter samples (each approximately 100 cm^2) were collected in a randomly stratified manner using a spade from the smooth brome stand surrounding each study block and the adjacent native stand. Plants were clipped near the ground surface and discarded. Litter and loose material were separated from the top 2.5 cm of soil.

Samples were kept cool and dark until placed in the refrigerator for stratification (5 °C) for three months. Each soil sample was crumbled and stones, roots, rhizomes and stems removed. One soil subsample, of approximately 200 ml volume, was placed over perlite to a depth of 2 cm in a container 12 cm long x 9.5 cm wide x 5 cm deep. Each litter sample was mixed with approximately 125 ml of autoclaved clay loam soil and placed over perlite in similar containers. Samples of autoclaved soil were also placed over perlite to verify lack of viable seed. No seedlings emerged within 28 days from the autoclaved samples.

Samples were placed in a randomized complete block design in a 21 °C greenhouse and natural daylight was supplemented with 16 hours of high intensity discharge (HID) light. When mist covers were removed after the first two weeks, Metromix (peat and vermiculite), was added to samples having coarse litter and uneven surfaces to reduce their rate of drying and eliminate additional watering. Damp Off fungicide was applied once, three weeks after beginning the experiment.

Documentation of seedling emergence commenced one week after potting, continued twice a week for four weeks, and then once a week as germination rate slowed. Emergence was counted over a period of 56 days. Once identifiable, plants were removed to prevent tillering and potential double counting. Examples of unknown seedlings were planted in separate containers until identification was confirmed.

Composition of the seed bank was compared to the vegetation composition of smooth brome and native stands assessed in July 1994 and September 1996, respectively (as described above).

Experimental Design and Statistical Analyses

Four blocks, each containing twelve 10 by 30 m plots, were arranged in a complete randomized block oriented parallel to the slope.

Species richness and soil data and plot means for species composition, ground cover, biomass, tiller density and litter were analyzed with a SAS analysis of variance program. Fisher's protected LSD was used to separate means. Proc Univariate was used to test for random, independent, normal distribution of experimental error. Homogeneity of variance of experimental error was evaluated with Bartlett's test.

Results based on untransformed data are reported. The majority of categories of any dataset met the statistical assumptions using the untransformed data. Preliminary transformation of count and percentage data detected similar levels of statistical significance and suitability in terms of meeting statistical assumptions. Harris (1975, cited in Green 1979) noted that most univariate normal distribution-based statistical tests are ''extremely robust'' under violations of the assumptions of normality and homogeneity of within-group variation. Bartlett's and Hartley's tests are more sensitive to departures from normality than the Anova F-test and may detect nonnormality rather than heterogeneity of variance (Steel and Torrie 1980). When samples sizes are nearly equal, as they were in this study, the variances can be markedly different and the p-values for analysis of variance will only be mildly distorted (Steel and Torrie 1980).

The only datasets for which statistics are not reported are species composition and seedling emergence of other introduced grasses and richness of introduced grasses because timothy, the key species in both groups, was present in only a few samples and did not occur in all blocks. Datasets for which statistics are reported but which did not pass the Wilcox test are listed in Appendix B, Table 2.

Pearson correlation coefficients were used in the correlation analyses.

Block data are presented in Appendix B. Block differences were significant ($p < 0.05$) for all categories except smooth brome tiller density, litter depth, soil particle size analysis, EC and pH.

RESULTS

Soil, Litter and Ground Cover

Soil properties, summarized in Table 2.1, were similar within and among blocks.

Average total litter mass was 7127 kg ha^{-1} and average litter depth was 6.2 cm (Table 2.2). Fallen and decomposed or decomposing components made up the majority of the litter. Standing litter comprised 5% of the total litter mass and was present in less than half of the quadrats.

Average ground cover was 90% litter and 10% live vegetation. Bare ground, moss and manure comprised less than 1% of the ground cover.

Vegetation

Smooth brome comprised 2900 kg ha^{-1} of the total 3766 kg ha^{-1} of plant biomass (Table 2.2). Smooth brome and Kentucky bluegrass were present in almost every quadrat with smooth brome making up the bulk of the species composition (57%) and Kentucky bluegrass being the subdominant species (16%). Kentucky bluegrass was included as an introduced species because it is impossible to visually distinguish between native plants and those which have been introduced and since naturalized (Moss 1983). Timothy was observed in all blocks during the initial vegetation survey but was detected in quadrats in only four plots. Native grasses and sedges were present in very small amounts in three blocks.

Other than forage legumes, introduced forbs were agronomic weeds (Appendix B, Table 6). Canada thistle was the most widespread, present in 12% of the quadrats, and the most likely to pose a weed problem in the future (Appendix B, Table 7). Stinkweed

(*Thlaspi arvense* L.) quickly established on pocket gopher mounds and disappeared as the disturbance was colonized by other species. Native forbs were the most species diverse group. Native forbs which grew in all blocks at a relatively high frequency included: northern bedstraw, golden bean (*Thermopsis rhombifolia* (Nutt.) Richards.), common yarrow (*Achillea millefolium* L.), prairie sagewort (*Artemisia ludoviciana* Nutt.) and wild vetch (*Vicia americana* Muhl.). Rose and buckbrush were present in all blocks, however, shrub biomass and relative composition was greatest in mid slope blocks.

Average tiller density of smooth brome and Kentucky bluegrass was similar, however, a negative linear relationship was detected for smooth brome and Kentucky bluegrass density ($r = -0.61$; $p < 0.01$) and species composition ($r = -0.53$; $p < 0.01$). Where smooth brome comprised a larger proportion of species composition, total species richness was lower ($r = -0.81$; $p < 0.01$) but was positively correlated with total biomass ($r = 0.37$; $p = 0.01$).

Although the vegetation data for smooth brome and native stands cannot be statistically compared, it appears that smooth brome establishment dramatically reduced native graminoid composition and richness as well as total richness (Appendix A, Table 2; Appendix B, Table 8). Native forb richness was also reduced, however, there was no apparent impact on overall composition by native forbs and shrubs.

Seedling Emergence from Soil and Litter

Total Emergence

Total seedling emergence from soil samples was almost three times the emergence from litter samples (Table 2.3) and dicot emergence from soil was 7.8 to 11.5 times greater than emergence from litter. Seven times more native monocots and dicots emerged from the soil than from the litter.

Kentucky bluegrass was the dominant species, comprising approximately 80% of the emerged seedlings from the litter and 37% and 61% from native and smooth brome soils, respectively (Table 2.4). Smooth brome, which emerged at much lower rates, was present in soil and litter from all smooth brome blocks but emerged from only one native litter sample (Appendix B, Table 8). Timothy, the only other introduced grass to emerge, was present in only a few litter and soil samples from two smooth brome blocks.

The only statistically significant difference in emergence between the two plant communities was the higher rate of smooth brome emergence from smooth brome soils. Although not statistically significant, emergence by dicots, native grasses and native forbs was greater from native soils than smooth brome soils. The number of native forbs and grasses which emerged from smooth brome samples was less than half of the number which emerged from native stands.

Species Composition

The total number of emerging species was similar for each community type, however, there were more native graminoids from native grass stands and more introduced grasses from smooth brome stands (Table 2.5). Native forbs were the most diverse group. The majority of emerging species occurred in the site vegetation, however, only a few of the species present in the site vegetation emerged from the soil and litter samples.

Some species emerged in very different proportions than they grew on the site (Table 2.6). Kentucky bluegrass, the predominant emerging species, comprised only 16% and 25% of plant biomass in smooth brome and native grass communities, respectively. Although smooth brome and native grasses were dominant in their respective communities, they made up only a small percentage of the emerged seedlings. Native forb composition of the seedlings from the soil was similar or greater than native forb composition of the vegetation. Native forb contribution to emergence from the litter was considerably lower. Although present in the vegetation, native shrubs did not germinate from the samples.

All grasses growing on and germinating from the study blocks were perennial. Wheatgrasses (*Agropyron* Gaertn. spp.) and sedges were the only identifiable native graminoids occurring in smooth brome samples (Appendix B, Table 8). Sedges and

Parry oat grass were the most abundant native graminoids from the native seed bank. Parry oat grass produced an abundant seed crop in 1994 (personal observation). Other native grasses germinating from native samples were wheatgrasses, rough fescue, Hooker's oat grass (*Helictotrichon hookeri* (Scribn.) Henr.), June grass (*Koeleria macrantha* (Ledeb.) J.A. Schultes f.) and Columbia needle grass (*Stipa columbiana* Macoun). It is likely that the unidentified grasses were native since the native species seemed to have less distinct vegetative characteristics as seedlings and develop at a much slower rate than introduced species; the majority of unidentified grasses germinated from native blocks.

The most abundant introduced dicot, particularly on smooth brome sites, was the annual *Thlaspi arvense*. Absinthe (*Artemisia absinthium* L.), a perennial, was the most abundant introduced forb to emerge from native soil. Canada thistle, the introduced forb of greatest concern, was present in both smooth brome and native soils. Other introduced forbs included burdock (*Arctium* L. spp.), lamb's-quarters (*Chenopodium album* L.), common plantain (*Plantago major* L.) and dandelion (*Taraxacum officinale* Weber).

Twenty-one native forbs germinated: one annual (fairy candelabra (*Androsace septentrionalis* L.)), one annual/biennial (rough cinquefoil (*Potentilla norvegica* L.)), two biennial/perennials (rock cress (*Arabis hirsuta* (L.) Scop. and *Arabis divaricarpa* A. Nels.)) and the remainder were perennials. Puccoon (*Lithospermum ruderale* Lehm.) was the only native forb which was strictly specified as a late successional species by Gerling et al. (1996). Fairy candelabra was the most abundant native forb in soils of both communities. Other common forbs were relatively short-lived, early successional species: rock cress (*Arabis hirsuta*), harebell (*Campanula rotundifolia* L.), rough cinquefoil and an unidentified cruciferae. *Androsace septentrionalis*, *Arabis hirsuta* and *Campanula rotundifolia* were observed in trace amounts in vegetation assessment quadrats.

Pattern of Seedling Emergence

Cumulative seedling emergence from the soil steadily increased throughout the study while cumulative emergence from litter increased at a much slower rate during the last half of the study (Figure 2.1a). Patterns of emergence were similar for seedlings from both communities (Figure 2.1b). Kentucky bluegrass was the only species to continue to emerge throughout the study period at a relatively high rate (Figure 2.1c). Introduced forbs germinated very quickly: 61% introduced forb seedlings germinated by day 6 and 76% by day 10, compared to 27% and 47% of native forbs on the same dates.

DISCUSSION

Vegetation

Smooth brome has been recommended for seeding in the parklands and foothills of Alberta because of its greater forage yield and longer growing season than native range (Looman 1969, 1976). Forage productivity of smooth brome stands in this study was similar to 15 to 35 year old smooth brome fields in the prairie parklands (Looman 1976) and at least 1.4 times greater than foothills rough fescue grassland in excellent condition (Willms et al. 1992). In contrast, Wilson (1989) found that the productivity of disturbed mixed-grass prairie was not improved by seeding smooth brome and other introduced species.

Smooth brome tiller density was only one third of the density in newly established smooth brome fields in the parklands (Pearon et al. 1995) but was similar to six and seven year old ungrazed smooth brome fields in North Dakota (Frank and Hoffman 1994) and slightly higher than 15 to 35 year old pastures (Looman 1976). Smooth brome tiller density in the current study was six times greater than in smooth brome stands in fescue grassland in the Saskatchewan aspen parkland (Grilz 1992) possibly due to a drier climate, greater density of native graminoids and younger, less established stands.

Kentucky bluegrass is native to Alberta (Moss 1983) and was also introduced to eastern North America by the early colonists (Carrier and Bort 1916, cited by Balasko et al. 1995). Kentucky bluegrass propagates readily from seed and dormant rhizomes and usually volunteers in pastures, increasing as taller forage species decline due to overgrazing or lack of winter hardiness (Balasko et al. 1995). Although Kentucky bluegrass provides forage, it is considered less desirable because it competes with more productive grasses for moisture in the cooler parts of the growing season and contributes little productivity in summer (Balasko et al. 1995). Kentucky bluegrass was the subdominant species of old smooth brome fields assessed by Looman (1976), however, the tiller density was less than half the density observed in this study.

Timothy invasion of fescue grassland in Montana reduced canopy cover by native graminoids about 50%, however, forb cover was not significantly different suggesting that native graminoids were more affected than native forbs (Tyser 1992). Grilz (1992) concluded that smooth brome and plains rough fescue appeared to occupy the same ecological niche which was why smooth brome was so effective in displacing fescue. Invasion of fescue grassland by smooth brome and timothy have been reported to reduce species richness (Tyser 1992) and not affect species richness and diversity indices (Grilz 1992). Seeding of smooth brome and other introduced species into disturbed mixed-grass prairie suppressed establishment of native species (Wilson 1989). Richness is influenced by size and frequency of sampling units (Tyser 1992). In this study, plot richness was considerably less than the number of species (22) recorded in old smooth brome pastures by Looman (1976). However, when the overall blocks were considered, the results were similar likely due to the larger sampling area and sample size (i.e. number of quadrats).

Litter

Litter accumulation in ungrazed smooth brome stands in this study was slightly less than the range reported for foothills fescue grassland (0.8 kg m^{-2} to 2 kg m^{-2} (Willms et al. 1986; Naeth et al. 1991)). Litter accumulations of 1.24 kg m^{-2} were thought to be partly responsible for the simplification of plant composition in ungrazed fescue grassland (Johnston 1961). Willms (1988) found that litter levels were greatest on south facing slopes in foothills fescue grassland.

Frank and Hofman (1994) detected an inverse relationship between tiller density and standing and surface litter, however, in this study, no significant relationship was detected between litter mass and tiller density or biomass of smooth brome and Kentucky bluegrass. This was likely because the areas were so similar.

Seedling Emergence and Seed Bank Potential

Seed bank and vegetation species composition are dissimilar (Johnston et al. 1969; Grilz 1992; Rosburg et al. 1992) unless the site is frequently disturbed (Rosburg et al. 1992). Soil disturbances may be expected to result in increased annual seral species and introduced invaders (Willms and Quinton 1995) rather than late successional species. Perennial species allocate more of their resources to vegetative growth and less to seed production and thus do not rely on the production of persistent seed to maintain their presence in the community (Grime 1979). Perennial grasses have a great capacity for immediate germination and thus tend to be short-lived and under-represented in the seed bank (Grime et al. 1981). The palea and lemma of large-seeded species may be less effective in covering the embryo and endosperm resulting in greater susceptibility to predation and disease. Small seeds more quickly enter the soil and escape detection, have less food value and are therefore less predated (Harper 1977).

Rough fescue, Parry oat grass and smooth brome are large seeded perennial grasses. Rough fescue may be a minor or a dominant component of the seed bank of foothills fescue grassland (Johnston et al. 1969; Willms and Quinton 1995) due to sporadic seed production (Johnston and Macdonald 1967), variable precipitation, exacting moisture requirements for germination, based upon a closely related species, *Festuca altaica* ssp. *hallii* (Romo et al. 1991) and time of sampling. Although seed production of Parry oat grass flourished in 1994, relatively few seeds were detected, possibly because the plants retained most of their seeds at time of sampling.

Relatively few smooth brome seeds were detected, possibly because smooth brome stands were decadent (long-established and not grazed for several years) and few stems flowered and produced seed (personal observation). Grilz (1992) found very few smooth brome seeds in smooth brome stands recently established in fescue grassland in Saskatchewan. The presence of a few smooth brome seeds in native litter indicates that some dispersal is occurring. Archibold and Hume (1986) observed smooth brome seeds in the soil (32 seeds m^{-2}) and seed rain (107 seeds m^{-2}) 1 m from the edge of a field but not at distances greater than 7 m. The much higher numbers of seed in the seed rain were taken to indicate that smooth brome seed persistence was low or that the seeds were moved after their initial dispersal. Native grasses growing in the smooth brome stands were few and likely sufficiently competitively stressed to produce little or no seed.

Kentucky bluegrass was the dominant species in the seed bank of lightly to heavily grazed fescue grassland (Willms and Quinton 1995) as well as in this study. It is uncertain whether the 50% decline in Kentucky bluegrass emergence from autumn to the following spring reported by Willms and Quinton (1995) was due to induced dormancy or death. Small percentages of Kentucky bluegrass have been reported to remain viable for as long as 39 years (Toole and Brown 1946). *Poa annua* and *Poa trivialis* have relatively small seeds, variable dormancy (Chippindale and Milton 1934) and persistently large seed banks (Roberts 1981). The same factors likely contribute to the success of Kentucky bluegrass which now threatens to replace the foothills rough fescue community on more mesic sites (Willms and Quinton 1995).

In this study, dicots composed half of the native soil bank, one third of the smooth brome soil bank and only one tenth of the seeds in the litter whereas Willms and Quinton (1995) found that the majority of seeds in the soil were annual and perennial non-rhizomatous native forbs. The dicot seed bank is often dominated by annual ruderal native forbs such as fairy candelabra and willow-herb (*Draba nemorosa* and *Draba reptans*) which are absent or only marginally present in the vegetation (Lagroix-McLean 1990; Grilz 1992; Willms and Quinton 1995).

It was not surprising that seedling emergence from the litter was much lower than from the soil. Shading by litter may enhance seed preservation in the soil by inducing seed dormancy (Williams 1983). Litter is constantly being incorporated into the soil and therefore contains seed produced over a shorter period of time. Environmental conditions in the litter may be less conducive to seed preservation than the soil. Germination may also have been reduced by allelochemicals from Kentucky bluegrass and smooth brome litter (Chung and Miller 1995; Bosy and Reader 1995) and reduced seed to soil contact caused by large pieces of litter. Kentucky bluegrass comprised at least three quarters of the emerged seedlings from the litter, perhaps a result of one or more recent seasons of prolific seed production.

The number of emerging native graminoids and native forbs was considerably lower in this study than observed in the soil and soil surface by Grilz (1992) and Willms and Quinton (1995). Total dicot density was lower than observed by Johnston et al. (1969), Lagroix-McLean (1990), Grilz (1992) and Willms and Quinton (1995). The relatively small native seed bank from smooth brome stands (and even native stands) will have less influence on successional change to native vegetation than anticipated by Grilz (1992).

Viable seed production and availability in the soil vary with the season and over time, based on plant phenology and environmental conditions (Johnston et al. 1969; Lagroix-McLean 1990; Willms and Quinton 1995). Although most grassland species are not innately dormant (Roberts 1986), dormancy may be imposed when conditions for germination are not met. Species vary in their requirements to break dormancy which influences seed bank emergence rates in a study such as this.

A more detailed assessment of the potential of the seed bank to contribute to secondary succession could be obtained by sampling in additional year(s), using a more precise sampling instrument, taking more samples, immediately refrigerating the samples, and documenting emergence for a longer period of time. Willms and Quinton (1995) and Lagroix-McLean (1990) followed seedling emergence for 90 and 175 days, respectively, compared to the 57 days in this study. However, Lagroix-McLean (1990) found that at least half of the seedlings emerged by day 25 in one year, whereas in another year, even though there was a flush of germination in the first 30 days, it took 100 days before at least one half of the seedlings had emerged.

MANAGEMENT IMPLICATIONS

When smooth brome stands are not grazed for several years, substantial amounts of litter may accumulate which has the potential to reduce germination, seedling establishment and plant species diversity. Grazing or controlled burning may be used to reduce litter mass and potential fire hazard. Timing and intensity of these management tools will determine impact on vegetation and seed bank germination.

The potential of Kentucky bluegrass to increase, as indicated by its dominance in the seed bank and the vegetation and its inverse relationship with smooth brome, must be considered when managing smooth brome stands. Invasion of Kentucky bluegrass is considered a serious threat to biodiversity of native prairies in the northern Great Plains (Blankespoor and Bich 1991) and foothills fescue grassland (Willms and Quinton 1995). Grazing increases Kentucky bluegrass seed density in the surface soil (Willms and Quinton 1995) and the composition of the vegetation (Looman 1969; Sundquist et al. 1997; Willoughby 1997); under heavy grazing, it has the potential to become the dominant species (Willoughby 1997). Even when the fescue grasslands are protected from grazing, Kentucky bluegrass may become the subdominant species (Willoughby 1997).

The seed bank of established smooth brome stands contained few native grasses and is probably insufficient for secondary succession to result in a fescue grassland even if the smooth brome plants were successfully eliminated. Other propagules in the soil and seed rain brought in by wind and animals were not measured in this study. However, it is expected that additional seed would be required to reestablish native grass stands. Although there were not large numbers of smooth brome seeds in the seed bank, five years of frequent, close mowing or grazing would be recommended prior to reseeding to eliminate smooth brome from the seed bank (Romo, quoted in Gayton 1996) and local seed rain and to prevent production of Kentucky bluegrass seed.

CONCLUSIONS

1. Species diversity, particularly native grasses, was reduced in smooth brome stands.
2. Few smooth brome seedlings emerged from soil and litter, possibly due to low seed production and low seed persistence in the seed bank.
3. Kentucky bluegrass was the subdominant species in the living vegetation and the dominant species in the soil and litter seed bank of smooth brome and native stands. The potential for Kentucky bluegrass to increase must be considered when managing rangeland.
4. Similar numbers of seedlings emerged from smooth brome and native stands, however, in smooth brome stands, there were few native grasses and native forbs were somewhat reduced.
5. Seedling emergence from the soil was almost three times greater than from the litter.

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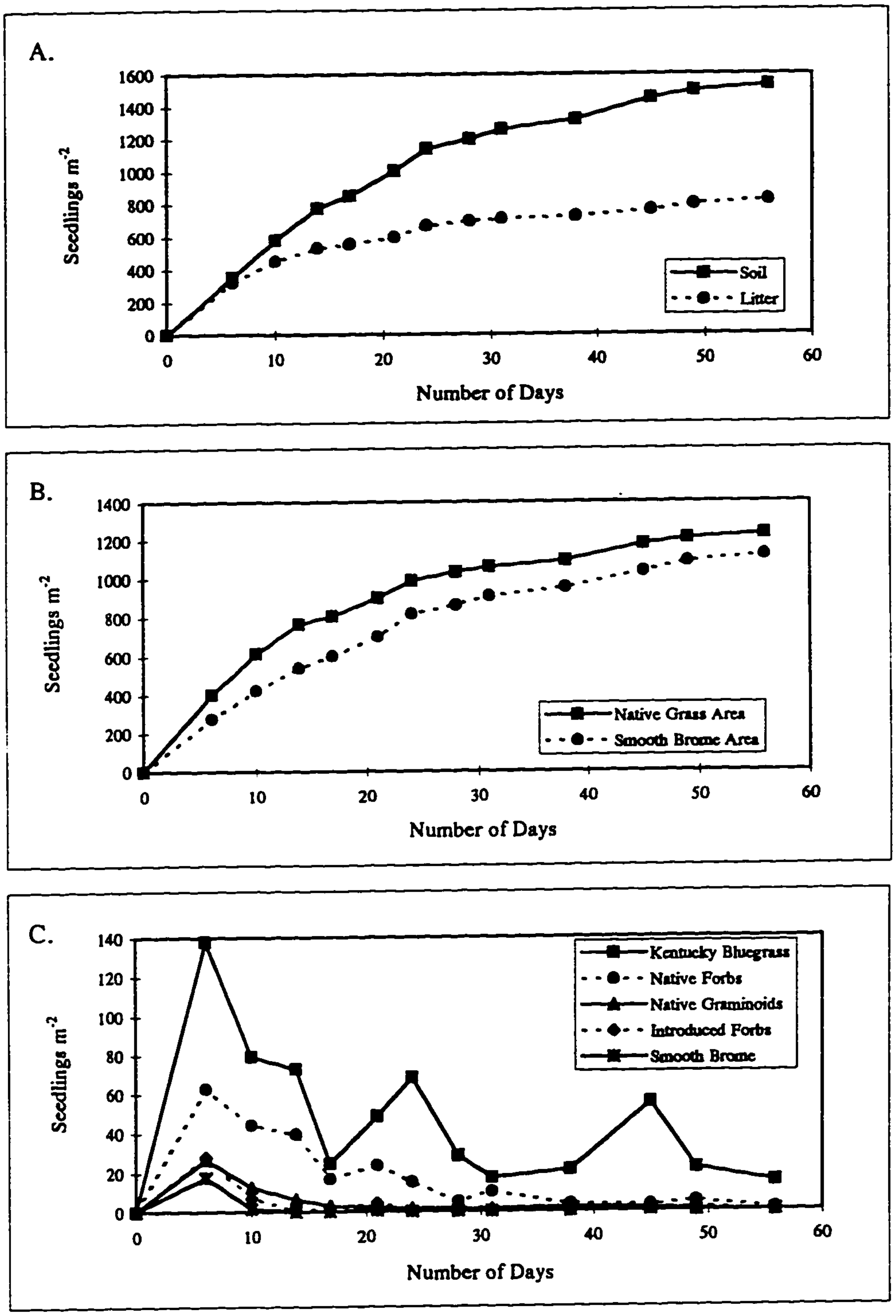

Figure 2.1. Patterns in seedling emergence (seedlings m^{-2}) from soil and litter samples collected from smooth brome and native stands in Autumn 1994.

A. Cumulative total emergence from soil and litter samples.

B. Cumulative total emergence from native grass and smooth brome dominated areas.

C. Emergence of monocots and dicots over time.

Table 2.1. Physical and chemical properties of soil from smooth brome stands in June 1994.

Soil	Soil Depth (cm)				
Property	0-15	15-30	30-45	45-60	60-75
Particle Size and Texture					
% sand	25.6	24.0	25.2	25.9	27.9
	(1.7)	(1.4)	(2.7)	(5.1)	(4.2)
% silt	36.5	38.5	38.4	40.9	39.8
	(2.2)	(2.3)	(1.9)	(2.9)	(1.1)
% clay	37.9	37.4	36.5	33.2	32.4
	(1.4)	(2.0)	(2.6)	(4.7)	(3.7)
Texture	clay loam	clay loam	clay loam	clay loam	clay loam
Carbon Content					
% carbon	7.9	4.7	2.5		
	(0.6)	(0.2)	(0.3)		
Water Holding Capacity					
1/3 Bar (%)	41.3	36.9	32.2	29.8	27.7
	(0.9)	(0.8)	(0.7)	(0.9)	(0.7)
15 Bar (%)	26.6	21.1	17.2	15.7	13.8
	(0.8)	(0.6)	(0.7)	(0.7)	(0.3)
AWHC	14.7	15.8	15.0	14.1	13.9
	(0.9)	(0.6)	(0.5)	(0.5)	(0.5)
Chemical Properties					
EC (dS/m)	3.0	2.0	1.0	1.0	1.0
	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)
pH	6.5	6.8	7.1	7.5	7.7
	(0.1)	(0.1)	(0.1)	(0.1)	(0.1)

Standard error of the mean is shown in brackets.

At 0-45 cm depth, N=48 except N=12 for particle size at 0-45 cm and carbon content at 30-45 cm.

At 45-60 cm depth, N=36 except N=9 for particle size.

At 60-75 cm depth, N=6 for particle size, N=24 for water holding capacity, N=22 for EC and N=23 for pH.

Table 2.2. Litter, ground cover and vegetation of smooth brome stands in June-July 1994.

Parameter	Mean	SEM[†]
Litter		
Mass (kg ha^{-1})		
Standing	323	138
Fallen	3780	459
Decomposed or Decomposing	3024	322
Total	7127	641
Depth (cm)	6.2	0.5
Ground Cover (%)		
Litter	90	1
Live Vegetation	10	1
Biomass (kg ha^{-1})		
Smooth Brome	2900	409
Other Grasses/Sedges	369	104
Forbs	319	124
Shrubs	179	117
Total	3766	380
Species Composition (%)		
Smooth Brome	57	6
Kentucky Bluegrass	16	3
Other Introduced Grasses	1	2
Native Grasses/Sedges	1	1
Introduced Forbs	3	1
Native Forbs	15	3
Native Shrubs	7	2
Plot Richness		
Introduced Grasses[‡]	2.1	0.1
Native Grasses/Sedges	1.0	0.4
Introduced Forbs	1.0	0.3
Native Forbs	7.1	1.2
Native Shrubs	1.2	0.3
Total	12.5	1.5
Tiller Density (tillers m^{-2})		
Smooth Brome	591	51
Kentucky Bluegrass	513	99

[†] Standard error of the mean.

[‡] Introduced grasses include Kentucky bluegrass.

N=240 for litter, biomass and tiller density; N=480 for ground cover and species composition; N=48 for plot richness.

Table 2.3. Emergence (seedlings m^{-2}) from soil and litter collected in Autumn 1994.

Plant Group	Litter	Soil	SEM[†]	P[‡]
Monocots	505	893	185	0.23
Kentucky Bluegrass	447	732	185	0.36
Smooth Brome	12	29	6	0.16
Other Introduced Grasses	2	3	0	
Native Grasses/Sedges	25	92	22	0.12
Unidentified Graminoids	19	37	13	0.40
Dicots	65 b	637 a	31	<0.01
Introduced Forbs	10	82	26	0.14
Native Forbs	47 b	414 a	9	<0.01
Unidentified Forbs	8 b	141 a	29	0.05
Native Monocots/Dicots	72 b	506 a	15	<0.01
Total	570 b	1530 a	204	0.04

[†] Standard error of the mean.

[‡] Probability of significant difference between sample types from analysis of variance.

Means within a row followed by the same letter are not significantly different ($P \leq 0.05$).

N=80.

Table 2.4. Emergence (seedlings m^{-2}) from soil and litter collected from smooth brome and native stands in Autumn 1994.

Plant Group	Soil				Litter			
	Brome	Native	SEM[†]	P[‡]	Brome	Native	SEM[†]	P[‡]
Monocots	946	840	113	0.55	512	498	124	0.94
Kentucky Bluegrass	857	607	135	0.28	472	422	130	0.80
Smooth Brome	58 a	0 b	12	0.04	20	4	4	0.07
Other Introduced Grasses	6	0	2		4	0	2	
Native Grasses/Sedges	6	178	48	0.08	4	46	13	0.11
Unidentified Graminoids	20	55	9	0.07	12	26	8	0.31
Dicots	469	805	125	0.15	60	70	37	0.86
Introduced Forbs	101	63	27	0.40	8	12	33	0.79
Native Forbs	290	538	133	0.28	40	54	6	0.42
Unidentified Forbs	78	204	39	0.11	12	4	5	0.64
Native Monocots/Dicots	296	716	145	0.13	44	100	33	0.32
Total	1415	1645	138	0.32	572	568	132	0.98

[†] Standard error of the mean.

[‡] Probability of significant difference between stand types from analysis of variance.

Means within a row followed by the same letter are not significantly different ($P \leq 0.05$).

N=40.

Table 2.5. Average number of species growing in the vegetation and emerging from soil and litter of smooth brome and native stands and the number of species common to vegetation and soil (veg-soil) and vegetation and litter (veg-litter).

	Total # Species			# Common Species	
Stand/Plant Group	Vegetation	Soil	Litter	Veg-Soil	Veg-Litter
Smooth Brome					
Monocots					
Introduced[†]	2.3	2.5	2.5	2.3	2.3
Native Grasses/Sedges	2.8	0.5	0.3	0.5	0.3
Dicots					
Introduced Forbs	3.3	2.5	1.0	1.8	0.5
Native Forbs	18.5	7.0	3.0	3.5	1.3
Native Shrubs	2.3	0.0	0.0	0.0	0.0
Native Monocots/Dicots	23.5	7.5	3.3	4.0	1.5
Total	29.0	12.5	6.8	8.0	4.3
Native					
Monocots					
Introduced[†]	1.0	1.0	1.3	1.0	1.0
Native Grasses/Sedges	7.3	3.3	2.0	2.8	1.5
Dicots					
Introduced Forbs	1.0	1.8	0.8	0.5	0.0
Native Forbs	13.8	7.3	2.5	3.3	0.8
Native Shrubs	2.3	0.0	0.0	0.0	0.0
Native Monocots/Dicots	23.3	10.5	4.5	5.8	2.3
Total	25.3	13.3	6.5	7.3	3.3

[†] Introduced monocots include Kentucky bluegrass.

For total species, N=40 for soil and litter (Autumn 1994), N=480 for smooth brome vegetation (July 1994) and N=60 for native vegetation (September 1996). For common species, N=4.

Table 2.6. Vegetation composition and seedling emergence from soil and litter expressed as percent for smooth brome and native stands.

Stand/Plant Group	Vegetation	Seedling Emergence	
		Soil	Litter
Smooth Brome			
Monocots	74	61	86
Kentucky Bluegrass	16	55	74
Smooth Brome	57	4	8
Native Grasses/Sedges	1	1	1
Dicots	24	39	14
Introduced Forbs	3	7	1
Native Forbs	15	26	10
Native Shrubs	7	0	0
Native			
Monocots	77	48	87
Kentucky Bluegrass	25	32	74
Smooth Brome	0	0	1
Native Grasses/Sedges	53	13	9
Dicots	23	52	13
Introduced Forbs	1	5	3
Native Forbs	15	35	9
Native Shrubs	8	0	0

N=40 for soil and litter (Autumn 1994), N=480 for smooth brome vegetation (July 1994) and N=60 for native vegetation (September 1996).

3. THE EFFECT OF CATTLE, SHEEP, MOWING, GLYPHOSATE AND BURNING ON SMOOTH BROME (*BROMUS INERMIS* LEYSS.) AND KENTUCKY BLUEGRASS (*POA PRATENSIS* L.) IN FOOTHILLS FESCUE GRASSLAND

> *'In one sense, the loss of diversity is the most important process of environmental change. I say this because it is the only process that is wholly irreversible.'*
>
> *--E. O. Wilson (1989)*

INTRODUCTION

Smooth brome (*Bromus inermis* Leyss.) invades native grassland and replaces key indigenous species, reducing plant species diversity. The competitiveness of this species is suggested by its early spring growth, productivity, aggressive rhizome and root system and prolific seed production (Walton 1980; Casler and Carlson 1995). Wilson (1989) reported smooth brome to be the most competitive of several introduced species in a mixed prairie in Manitoba and that seeding smooth brome in disturbed areas suppressed native species. Smooth brome, when grown with intermediate wheatgrass (*Thinopyrum intermedium* (Host) Barkworth & D.R. Dewey), largely replaced the wheatgrass after ten years and provided excellent weed control (Knowles 1987). Lindquist et al. (1996) concluded that the greater competitiveness of smooth brome prevented spotted knapweed (*Centaurea maculosa* Lam.) from becoming established on roadsides dominated by smooth brome whereas native grasslands dominated by bluebunch wheatgrass (*Agropyron spicatum* (Pursh) Scribn. & Smith) or Idaho fescue (*Festuca idahoensis* Elmer.) were often invaded.

Kentucky bluegrass (*Poa pratentsis* L.) is native to North America, including the study area (Moss 1983) and was also introduced to eastern North America by the early colonists soon after 1600 (Carrier and Bort 1916, cited by Balasko et al. 1995). Kentucky bluegrass propagates readily from seed and dormant rhizomes and usually volunteers in pastures, increasing as taller forage species decline due to overgrazing or lack of winter hardiness (Balasko et al. 1995). Invasion and spread of this vigorous, highly competitive species is a serious threat to biological diversity of native prairies in the northern Great Plains (Blankespoor and Bich 1991). Willoughby (1997) predicts that rough fescue-Idaho fescue-Parry oatgrass communities, even when protected from grazing, will be replaced by a rough fescue-Kentucky bluegrass community; when overgrazed, Kentucky bluegrass may become dominant.

Smooth brome typically declines in permanent pastures in the prairie parklands (McCartney and Bittman 1994) indicating that smooth brome may be reduced by frequent severe defoliation. In Saskatchewan, smooth brome ground cover decreased as grazing intensity increased. Smooth brome had relatively poor persistence under three and four cuts in Minnesota and Wisconsin (Smith et al. 1973; Sheaffer et al. 1990). Damage was greatest when plants were cut at boot or early boot (Marten and Hovin 1980) or pre-anthesis (Smith et al. 1973). Defoliation of smooth brome at elongation or early boot when carbohydrate reserves are lowest removes shoot apices; regrowth is delayed because it must be initiated from below ground buds (Sheard and Winch 1966).

Glyphosate wicking of smooth brome at elongation, when height difference with native species was maximized, reduced brome tiller density 45% in the first year in plains rough fescue grassland in Saskatchewan and minimized impact on native species (Grilz 1992). Spring burning prior to growth increased glyphosate effectiveness by removing litter, stimulating early growth, thereby increasing the height differential, the area of herbicide application and possibly the rate of translocation; smooth brome tillers were almost entirely eliminated (Grilz 1992). Fall burning was less effective than spring burning because reduced snow trapping resulted in drier moisture conditions which limited growth the following year. Spraying an old smooth brome - crested wheatgrass field with glyphosate dramatically increased germination of seeded mixed grass prairie species (Wilson and Gerry 1995). Neither mode of glyphosate application eliminated smooth brome.

The objective of this study was to determine the effect of combinations of grazing, mowing, glyphosate wicking and prescribed spring burning on smooth brome in fescue grassland as assessed by tiller density, plant species composition, carbohydrate reserves and etiolated regrowth.

MATERIALS AND METHODS

Site Description and History

Research was conducted at the Ann and Sandy Cross Conservation Area, approximately 3 km southwest of Calgary, Alberta (Section 7E, 8W, 8NE, 8SE, 17 and 18E Township 22 Range 2 W5). The conservation area is located in the Rocky Mountain Foothill Ecodistrict of the Aspen Parkland Ecoregion (Strong and Leggat 1992). Aspen (*Populus tremuloides* Michx.) covers north facing slopes. Native grasses, chiefly foothills rough fescue (*Festuca campestris* Rydb.) and Parry oat grass (*Danthonia parryi* Scribn.), grow on steep south facing slopes. Gentle slopes and plateaus have been seeded to pasture and hayland dominated by smooth brome, timothy (*Phleum pratense* L.) and alfalfa (*Medicago sativa* L.) (Steeves 1993). A more detailed description of the study area and study blocks is presented in Chapter 2.

Study blocks were situated in smooth brome stands on mid (Blocks 1 and 3) to upper (Blocks 2 and 4) portions of south facing hillsides in proximity to areas of native vegetation. Radiation, soil temperature, temperature fluctuation, evapotranspiration and potential drought stress are greater on south facing slopes than other aspects (Bennett et al. 1972). Consequently, south facing slopes were thought to be the most likely location to stress smooth brome which grows best in deep fertile soils (Casler and Carlson 1995). However, smooth brome is able to withstand drought by becoming dormant (Casler and Carlson 1995) and by resuming compensatory growth following drought (Sheaffer et al. 1992). Slopes ranged from 10 to 19%. Soils were clay loam Orthic Black Chernozems. Kentucky bluegrass was the subdominant species in the smooth brome dominated study area.

The history of the areas encompassing the study blocks was interpolated from aerial photographs. The blocks were in their natural state in 1920, but by 1944, fields were established in the vicinity of Block 1, immediately adjacent Block 2 and on Blocks 3 and 4. Blocks 3 and 4 were seeded to smooth brome, frequently mowed (and/or grazed in the case of Block 3) and likely reseeded, with the most recent reseeding occurring prior to 1985 (Rempel 1995). Smooth brome in Blocks 1 and 2 may have established by natural invasion as well as cultivation and seeding, however, it is likely that these areas were cultivated and seeded much less frequently than Blocks 3 and 4 (for more details, refer to Appendix A). The grazing regime in the 1980s was fall grazing in Block 1, mid-summer grazing in Blocks 2 and 3 and haying in Block 4 (Rempel 1995). Cattle grazing was not conducted for seven years prior to this study.

Weather Conditions

The humid microthermal climate is characterized by warm summers and relatively cool winters which are moderated by chinook winds (MacMillan 1987). Compared to the thirty year normals for the area, 1994 was warmer and drier than average and 1995 and 1996 were cool (Appendix B, Table 1). The growing season (April to September) was warmer and drier than average in 1994 and cooler and wetter than average in 1995. Although summer 1996 was drier than average, heavy winter snowfall preceded the growing season and large amounts of rain and snow were received in May; summer temperatures were average but the winter was cooler than average.

Experimental Design and Treatments

Twelve treatments were replicated across four blocks in a randomized complete block design. Plots were 10 by 30 m, oriented parallel to the slope. In summer 1994, four treatments were imposed: cattle grazing (4 plots), sheep grazing (2 plots), glyphosate wicking (5 plots) and reference (1 plot). Combinations of grazing, mowing, glyphosate and burning differentiated treatments in 1995 (Table 3.1). The treatments were designed to reduce competitiveness and vigour of smooth brome, however, as the research proceeded, it became clear that the response of Kentucky bluegrass, the subdominant species in the stands, would be a key element in evaluating treatment impacts.

In 1995, grazing, mowing and glyphosate treatments were initiated during smooth brome elongation and, as much as possible, sheep and cattle grazing and mowing were carried out concurrently. Wet weather delayed glyphosate application by almost one week in June 1995.

Grazing intensity for all cattle treatments was heavy, defoliating elongated stems to 5 to 10 cm height; vegetative tillers were grazed to a lower height of approximately 3 to 4 cm. Water was located outside all plots and salt was placed in the opposite end of each plot. In 1994, cattle grazing commenced in late August with six cow-calf pairs (6 AU). In 1995, two cows (2 AU) were used for each grazing session.

All sheep grazings were of heavy intensity (to a height of 5 cm or lower), except the midsummer 1995 grazing in S-S3L which was moderate (to a height of approximately 7 cm). The latter treatment was designed to provide rough fescue a longer recovery period after the first grazing by removing sheep as soon as they began to graze plants other than smooth brome. Sheep grazing was with 25 ewes and 8 lambs (5 AU) in 1994; 1995 grazings were with 20 ewes (4 AU) for the first grazing and 15 ewes (3 AU) for the latter two grazings.

A hand lawn mower was used for the first mowing of all mowing treatments in 1995 and for the second mowing of C-M4. Subsequent mowings were with a tractor-drawn rotary lawnmower. Vegetation was mowed to a height of 6 cm and left on the plots in all mowings.

A 2:1 solution of water:glyphosate (Round-Up) was selectively applied to smooth brome using a hand-held hockey stick wick applicator. Selective application was possible because smooth brome was taller than most other plants present.

A moderate intensity burn was carried out on March 29, 1995 using a backfire on Block 1 and a strip headfire on the other blocks under southeast winds of 0 to 14.4 km hr^{-1}, temperatures of 5 to 11 °C and relative humidities of 20 to 38%. Weather data were collected using a belt weather kit. Fuel loads were calculated from litter (standing, fallen and partially or totally decomposed dead plant material) collected in 3 randomly located 0.1 m^2 quadrats per plot. Average fuel load over all the plots was 8155 kg ha^{-1}.

Vegetation and Litter

Individual species composition of total live plant biomass was assessed in 10 randomly located permanent 0.1 m^2 quadrats per plot in July 1994, September 1995 and September 1996. Ground cover by live vegetation, litter, bare ground, manure and rocks was also assessed in each quadrat.

Grass tillers and other plants were counted in five permanent stratified random quadrats (0.1 m^2) in each plot in areas of predominantly smooth brome. Counts were conducted prior to the commencement of defoliation and glyphosate treatments and at the end of the growing season in 1994, 1995 and 1996. During the May 1995 count, the extent of blackened or burned ground cover was visually assessed.

Live plant material was clipped to 6 cm above the litter layer from 5 stratified random 0.1 m^2 quadrats per plot in July 1994 and September 1994. Samples were oven dried at 65 °C and weighed. The July samples were separated into smooth brome, other grasses, forbs and shrubs.

Litter, defined as dead plant material not incorporated with mineral soil and occurring above the soil mineral horizon (Naeth et al. 1991), was separated into three categories: standing, fallen and partially or totally decomposed. Five 0.05 m^2 samples were collected from each plot in a pattern to prevent resampling. Samples were oven dried at 65 °C and weighed. Litter depth to mineral soil was measured at each litter sampling location. Litter was sampled in June 1994, September 1994 and September 1995.

In all cases, sampling location was at least 1 m from plot boundary.

Total Nonstructural Carbohydrates

Three soil-plant cores, 10 cm diameter by 7 cm deep, were collected in a stratified random manner from each plot in late September 1995. Care was taken to ensure samples contained brome and were representative of the plot. Samples were kept in cool, dark conditions until they were transported to a freezer (-16 °C). Samples were thawed a few hours prior to washing. Smooth brome rhizomes, crowns and shoots to 3 cm above soil level were washed, dried at 55 °C, and stored in glass jars until ground in a Retsch high speed mill to pass through a 0.5 mm screen. Ground samples were stored in glass jars until total nonstructural carbohydrate (TNC) analysis was completed.

TNC were analyzed using the hot 0.2 N H_2SO_4 extraction method (Smith et al. 1964; Suzuki 1971). For each sample, approximately 55 mg ground tissue and 50 ml 0.2 N H_2SO_4 were placed in test tubes and refluxed for one hour in a 90 °C bath. The hot solution was filtered through #40 filter paper and the residue was washed with 40 ml hot distilled water. Once cooled, the solution was made up to 100 ml with distilled water. Sugar concentration of duplicate solutions were determined by the phenol sulfuric acid colorimetric method using fructose as a standard (Dubois et al. 1956). Five ml concentrated sulfuric acid were added to a mixture of 0.5 ml of the sugar solution and 1 ml 5% phenol and immediately mixed on a vortex mixer to ensure complete and uniform mixing. After standing 10 minutes, the solution was mixed with a vortex mixer and placed in a 25 to 30 °C water bath for 15 minutes. Absorbance at 490 nm was read and % fructose was determined from the standard curve prepared from solutions of known fructose concentrations. The result was expressed as % fructose on a dry weight basis.

Etiolated Regrowth

Three soil-plant cores were collected from each plot in the manner described for carbohydrate analysis in late September 1995. Six additional cores were collected from H-H2 (the most severe herbicide treatment) at Blocks 1, 2 and 3 to determine whether smooth brome tillers which appeared dead after glyphosate application would produce new tillers. Three cores were selected to contain actively growing smooth brome while the other three contained dead smooth brome (as determined by tiller appearance and stem colour beneath the sheath).

Samples were kept in cool, dark conditions (10 to 15 °C) until potted into 13 cm clay pots with clay-loam topsoil. Pots were placed in a growth chamber at 15 °C under a regime of 12 hours high intensity light and 12 hours dark for 25 days to ensure root re-establishment. Etiolated regrowth under dark conditions was monitored for 100 days at 12 °C, to minimize stress to cool season smooth brome (Horton 1991), then for 25 days at 22 °C, to stimulate growth and stress the plants. Relative humidity varied from 45 to 75%, as temperature regimes changed and to accommodate watering two to three times per week. Live tillers and plant stems were counted, clipped to 2 cm and the clippings dried at 55 °C at potting, prior to being placed in the dark and approximately every 18 days thereafter. Clippings from each temperature regime (five at 12 °C and two at 22 °C) were combined, redried and weighed. All weighing was done on a Mettler HK160 balance to 0.0001 g and rounded to 0.001 g.

Statistical Analyses

Treatment means were analyzed with a SAS analysis of variance program and Fisher's protected LSD was used to separate means. Split block analysis of variance was used to determine treatment*time interactions. Statistical assumptions were tested using SAS Proc Univariate, Wilcox test for normality of experimental error and Bartlett's tests for homogeneity of variances.

Results based on untransformed data are reported. The majority of categories and times of any dataset met the statistical assumptions using the untransformed data. Preliminary transformation of percentage and count data detected similar levels of statistical significance and suitability in terms of meeting statistical assumptions. Harris (1975, cited in Green 1979) noted that most univariate normal distribution-based statistical tests are "extremely robust" under violations of the assumptions of normality and homogeneity of within-group variation. Bartlett's and Hartley's tests are more sensitive to departures from normality than the Anova F-test and may detect nonnormality rather than heterogeneity of variance (Steel and Torrie 1980). When samples sizes are nearly equal, as they were in the current study, the variances can be markedly different and the p-values for analysis of variance will only be mildly distorted (Steel and Torrie 1980).

The only datasets for which statistics are not reported are species composition of other introduced grasses and richness of introduced grasses because timothy, the key species in both groups, was present in only a few quadrats and did not occur in all blocks. Datasets for which statistics are reported but which did not pass the Wilcox test are listed in Appendix B, Table 2.

RESULTS AND DISCUSSION

Tiller Density

Few summer initiated smooth brome tillers survived a late summer grazing by cattle or sheep in 1994, however, grazing stimulated fall tiller initiation (Table 3.2), resulting in significantly increased tiller density the following spring (Table 3.3.). This higher level of tiller density was maintained into September 1995 for all graze-mow treatments except the lightest defoliation treatment (C-M2) and persisted into September 1996 in only the heaviest defoliation treatment (S-S3). All other treatments returned to baseline levels by fall 1996. Teel (1956, cited in Sheard and Winch 1966) also observed that a large number of tillers died when shoot apices were removed by grazing.

Glyphosate wicking in 1994 moderately reduced summer and autumn tillers (Table 3.2) resulting in a significant decrease in smooth brome density in September 1994 (Table 3.3). Although May 1995 tiller density in herbicide treatments remained significantly lower than pretreatment levels in all but one treatment (H-M3), density was higher than the previous autumn. The only herbicide treatment to significantly reduce tiller densities in 1995 from pretreatment levels was H-H2 whereas in 1996 treatments which included two glyphosate wickings or burning (H-H2, H-BH2 and H-BM3) reduced densities to 0.5, 0.6 and 0.7 or pretreatment levels, respectively. Perhaps the burning which was conducted after smooth brome had broken dormancy and was beginning to grow stressed smooth brome more than was initially apparent in

1995. Several small, reddish, twisted and obviously stressed, smooth brome tillers were observed in May 1995.

Smooth brome tiller density tended to be significantly lower in herbicide treated plots (especially H-H2, H-BH2 and H-H) than other treatments when individual sampling periods were analyzed. Densities tended to be highest under cattle and sheep grazing, however, high baseline densities in the C-C3 plots may have influenced this trend. Densities in the reference and treatments including mowing were intermediate. Within a given sampling period, herbicide effectiveness did not increase with burning or application frequency, however, when analyzed over time, only treatments with two wickings or burning significantly reduced smooth brome tiller density.

Early spring burning in 1995 dramatically increased Kentucky bluegrass tiller density in May 1995. By September 1995, Kentucky bluegrass tiller densities were greater than pretreatment levels in all treatments except the reference and continued to increase in 1996 in those treatments. However, this increase was significant only under sheep (S-S3 and S-S3L), herbicide-mow (H-BM3 and H-M3) and herbicide (H-H) treatments. Treatment effects within an individual sampling period were significant for Kentucky bluegrass only in September 1996 when density was least in the reference and greatest in H-BM3 which was 4.6 times baseline levels.

Plant Species Composition and Richness

Plant species composition was similar among plots prior to treatment implementation. Treatment effects were significant over time and within post-treatment samplings for smooth brome, Kentucky bluegrass and native forbs, the only species groups to occur in all plots (Table 3.4).

In 1996, smooth brome composition was significantly reduced from baseline levels in all treatments except the reference and the lightest graze-mow treatments (C-M2, C-M3 and S-S3L); on average, smooth brome was 0.6 and 0.9 of pretreatment levels in herbicide and graze/mow treatments, respectively. Within sampling periods, smooth brome composition was higher in treatments which included grazing or mowing than in herbicide treatments which did not include mowing, but not significantly so. This was presumably due to increased tiller density. There was no significant difference among the five herbicide treatments. In 1996, smooth brome was significantly higher in the reference than in other treatments; this trend was present but less pronounced in 1995.

Kentucky bluegrass composition was significantly greater than baseline composition in all treatments except the reference in 1995 and in all treatments except the reference and the lightest graze-mow treatment (C-M2) in 1996. In September 1996, Kentucky bluegrass composition was significantly higher in herbicide and heavy sheep grazing (S-S3) treatments than the reference, and generally greater than the other graze-mow treatments. Treatment trends were similar but less distinct in 1995.

Native forb composition, when compared over time, significantly increased in herbicide treatments lacking burning or mowing (H-H and H-H2) in September 1995 and significantly decreased in several treatments which included grazing or mowing (C-M3, C-C3, S-S3, S-S3L and H-M3). The net effect over the duration of the study was a decrease in native forbs from pretreatment levels in the reference and two grazing treatments (C-C3 and S-S3L). Within individual sampling periods, post-treatment native forb composition tended to be lowest in the reference and grazing treatments (C-C3, S-S3 and S-S3L) and highest in the herbicide treatments without defoliation (H-H2, H-H and H-BH2).

Canada thistle (*Cirsium arvense* (L.) Scop.) appeared to increase in H-H, C-C3 and S-S3 in 1995 and 1996 (Appendix B, Tables 10 to 12). Perennial lupine (*Lupinus sericeus* Pursh) and golden bean (*Thermopsis rhombifolia* (Nutt.) Richards.) appeared to decline in 1995 and 1996; little biomass of these early season forbs remained by mid-September when sampling was conducted.

Total species richness was reduced significantly from 1994 to 1995 by heavy grazing (C-C3 and S-S3) and increased to baseline levels in S-S3 after grazing was discontinued in 1996 (Table 3.5). Treatments did not have an ecologically significant effect on richness within individual sampling periods.

Biomass

From July to September 1994, live vegetation biomass significantly decreased in two of six grazed treatments (C-C3 and S-S3L) and significantly increased in three of five herbicide treatments (H-BH2, H-BM3 and H-H) (Table 3.6). There were similar but not significant trends in the other herbicide treatments and most of the grazing treatments. When individual sampling periods were analyzed, there was no significant difference among plots in July 1994 but in September 1994, biomass tended to be greater in herbicide treated plots than where plant material was removed by grazing.

Litter Mass and Depth

Burning (H-BH2 and H-BM3) significantly reduced total litter mass to 0.3 and 0.4 pretreatment levels, respectively (Table 3.6). Total litter was also significantly impacted during the study by H-H2 and two of six graze/mow treatments (C-M4 and S-S3L). Standing litter significantly increased in four of five herbicide treatments in September 1994 (H-BM3, H-BH2, H-H and H-H2) and decreased to pretreatment levels in September 1995, resulting in no significant net change in standing litter over time. Decomposing litter significantly increased under sheep grazing and in two of five herbicide treatments in September 1994 and significantly decreased under burning (H-BM3 and H-BH2) and sheep grazing (S-S3L) in September 1995. The only treatment with a significant net increase in decomposing litter by September 1995 was H-H2. Fallen litter mass did not change over time. Litter depth significantly decreased in one of four cattle treatments and significantly increased in two of five herbicide treatments in September 1994 but declined in all treatments in 1995, resulting in a significant net overall decrease in all treatments.

Although burning did not remove all surface litter, litter depth and mass tended to be least in burn treatments in 1995. Litter was greatest in the reference and unburned herbicide treatments and intermediate under grazing and mowing. Fallen litter and litter depth were generally less under sheep grazing than other graze-mow treatments, but not significantly so.

Willms et al. (1986) also found grazing and clipping reduced litter in plains rough fescue grassland. Litter was least when mowed and the clippings removed for three years; mowing without removing the clippings resulted in significantly less litter than where no clipping was implemented. Similarly, grazing reduced litter mass in foothills rough fescue grassland (Johnston 1961; Willms 1988; Naeth et al. 1991).

Ground Cover

Live ground cover in H-BM3 significantly increased from 9 to 14% in 1994 to 1995 (Table 3.7). This was likely due to Kentucky bluegrass tiller density and composition which at least tripled over the time period. Live cover decreased the following year, as did Kentucky bluegrass composition; however, tiller density which was measured in different quadrats was even higher. Live cover in C-M3 also temporarily increased in 1995, perhaps due to increased growth on urine spots.

Burning significantly reduced litter cover from July 1994 to September 1995: from 91% to 82% in H-BM3 and from 89% to 68% in H-BH2. The extent of burned or blackened ground cover was similar in May 1995 (42% and 40% in H-BM3 and H-BH2, respectively). Subsequent differences may be attributed to the greater growth and ground cover of Kentucky bluegrass in H-BM3 and to pocket gopher activity in H-BH2 (Table 3.8).

The majority of bare ground in other treatments where litter cover declined significantly over time (C-M4 and C-C3 in 1995; C-C3, H-H and H-H2 in 1996) was attributed to pocket gopher (*Geomys bursarius*) disturbance. In 1994, only 3 of 480 quadrats contained evidence of previous pocket gopher activity. By 1996, pocket gopher activity was noted in 54 of 480 quadrats and averaged 4% of the 48 m^2. It is unlikely that these decreases in litter cover between 1995 and 1996 were due to treatment, since no treatment action was taken in that time period.

Reichman and Smith (1985) noted that pocket gopher activity creates a mosaic of successional microsites, often in select patches of the most productive vegetation and nitrogen rich soil which in turn decreases nitrogen concentration (Inouye et al. 1987).

In contrast, other studies cited by Inouye et al. (1987) reported that pocket gopher activity enhanced productivity by increasing surface soil nutrients and moisture retention.

The gaps created by pocket gopher mounds in the canopy and ground cover are ideal sites for seedling establishment. In the current study, mounds were most frequently colonized by introduced forbs with the most predominant being stinkweed (*Thlaspi arvense* L.); smooth brome and Kentucky bluegrass rhizomes also readily recolonized mounds. Total species richness and cover by annuals and introduced species increased in an old field with pocket gopher activity whereas cover by native perennials declined, thus slowing the rate of succession (Inouye et al. 1987). Plant productivity may also be reduced by the tunneling of pocket gophers. Smooth brome biomass directly over burrows was reduced by less than 40% whereas major forb species were reduced by almost 90% (Reichman and Smith 1985). Impacts are moderated by the relatively small size of the burrows, new burrow construction and revegetation of abandoned or refilled burrows (Reichman and Smith 1985). In the current study, there were no pronounced pocket gopher impacts on tiller density or individual species composition.

Total Nonstructural Carbohydrates

Total nonstructural carbohydrate (TNC) content of smooth brome crown and rhizomes tended to be highest in C-M3 and the reference, however, treatment differences were not significant (Table 3.9). Although smooth brome total available carbohydrate (TAC) reserves decrease dramatically after removal of shoot apices, TAC may rebound by the end of autumn if not prior to the next cut, providing sufficient regrowth time is allowed (Reynolds and Smith 1962; Smith 1967; Paulsen and Smith 1968). Thus more frequent or severe defoliation for a greater number of years may be required to stress smooth brome. Including an autumn defoliation may help prevent restoration of reserves resulting in a lower capacity to regrow after early spring defoliation.

Photosynthesis is the major source of carbon for regrowth after defoliation and stored carbohydrates are but a small buffer (Richards 1984); however, in early spring when the availability of active intercalary and apical meristems are not limited, a reduced carbohydrate pool may limit regrowth. Reductions in carbohydrate concentrations during rapid growth (Reynolds and Smith 1962; Smith 1967; Paulsen and Smith 1969) do not indicate that reserves are being depleted, instead, the increase in biomass results in an increase in the total carbohydrate pool (Richards 1984).

Etiolated Regrowth

There were no significant treatment differences in smooth brome tiller density at the time soil-plant cores were potted (Table 3.9). Significant differences were detected for Kentucky bluegrass, with densities being highest in H-BH2. However, these samples were too small and too few to adequately document tiller density.

Smooth brome tiller density generally peaked 25 days after potting, prior to being placed in the dark (data not shown). Kentucky bluegrass tiller density peaked 18 to 36 days after being placed in the dark (43 to 61 days after potting). By the end of the experiment, smooth brome tiller densities were 25% or less of the original densities; Kentucky bluegrass tiller densities were 18 to 89% of the densities potted.

Cores collected as dead developed an average of 0.9 smooth brome tillers (7 tillers developed in 3 of 9 samples) and 1.9 Kentucky bluegrass tillers/core (17 tillers developed in 3 of 9 quadrats) by the time cores were potted; each species produced approximately 0.2 mg regrowth. In contrast, regrowth from live cores averaged 23 mg from 15 smooth brome tillers and 23 mg from 12 Kentucky bluegrass tillers.

Regrowth per 100 tillers was not significantly different among treatments for smooth brome or Kentucky bluegrass. The 22 °C regime stimulated growth, however, total regrowth under these conditions was less than under the 10 °C due to a reduced exposure period and plants nearing the end of their reserves.

Smooth Brome Response

Grazing and mowing over two years did not stress smooth brome as evidenced by tiller density, TNC and etiolated regrowth. However, a decrease in smooth brome composition was detected for the three heaviest defoliation treatments (C-M4, C-C3 and S-S3). Perhaps treatments were implemented for too short a time period, especially considering that the stands had not been grazed for several years. In contrast, smooth brome decreased in ground cover under four years of grazing (two, three and five times to 2-5 cm) in Saskatchewan parkland (McCartney and Bittman 1994) and had relatively poor persistence under three and four cut schedules conducted for two or three years in Minnesota and Wisconsin (Smith et al. 1973; Marten and Hovin 1980; Sheaffer et al. 1990).

Although increased frequency of grazing and mowing decreased smooth brome ground cover (McCartney and Bittman 1994; Marten and Hovin 1980), no significant differences in smooth brome growth were detected in treatments varying in mowing frequency in the current study. Smooth brome productivity was also much lower under continuous grazing than under rotational grazing in aspen parkland (Walton et al. 1981). Insufficient severity or longevity of treatments may have been a factor in this lack of treatment response.

Cattle and sheep grazing tended to result in more smooth brome tillers than mowing, but not significantly so. Mowing does not include the grazing effects of trampling, pulling, selectivity, manure deposition, compaction or potential growth stimulation by saliva (Quesenberry and Ocumpaugh 1979, cited by McCartney and Bittman 1994; Dyer 1980, cited by Vinton and Hartnett 1992; Vinton and Hartnett 1992). Although Casler and Carlson (1995) report that grazing is usually less severe than mowing for removing shoot apices, almost all smooth brome leaves are within the bite level of livestock (Alberta Agriculture, Food and Rural Development 1981).

Sheep (Jung et al. 1989), cattle and ungulates select forage to optimize nutrients and maximize energy (Willms et al. 1980). Although the abundance and frequency of the native grasses was too low to document the effect on the species, it was observed that smooth brome was the forage of choice for both sheep and cattle. Sheep grazed more selectively than cattle, however, this difference was lost due to the heavy grazing intensity imposed (McCartney and Bittman 1994). Sheep grazed plants to a lower height than cattle and more readily switched to forbs and shrubs and then native grasses after the most palatable young smooth brome growth was consumed. The closer grazing heights could result in reduced energy reserves, snow trapping and smooth brome ground cover and persistence (Raese and Decker 1966; Lawrence and Ashford 1969; Knutti and Hidiroglou 1967).

Glyphosate reduced smooth brome tiller density for at least one season and species composition for two years. Two herbicide wickings (H-H2) effected the greatest decrease in smooth brome tiller density (1996 densities were 0.5 baseline levels). Glyphosate reduction of smooth brome is expected to be relatively short lived; tiller density increased (but not significantly) in 1995 and 1996 even with additional glyphosate applications in 1995. Grilz (1992) noted a similar decrease and rebound in smooth brome resulting in tiller densities 0.7 pretreatment levels one year after application. In the current study, the effectiveness of each subsequent glyphosate wicking was diminished as the number of smooth brome tillers which extend above the canopy of the desirable species decreased. Mowing stimulated a short term increase in tillering compensating for the tillers previously killed by glyphosate but resulting in no net change in tiller density.

The only herbicide treatments to significantly reduce smooth brome in 1996 were those which included burning (H-BH2 and H-BM3). Grilz (1992) found that dormant spring burning increased glyphosate wicking effectiveness, resulting in smooth brome densities that were 0.03 of baseline densities one year after application. In the current study, burning did not increase herbicide effectiveness relative to the treatment that did not include burning (H-M3 and H-H2). Although burning reduced litter mass by two-thirds, smooth brome growth was delayed rather than accelerated because the plants had just broken dormancy and were beginning to green at the time of the burn. Any decrease in smooth brome was likely due to burn stress rather than increased herbicide effectiveness. When May 1995 tiller counts were conducted approximately six weeks after the burn, several small, reddish, twisted smooth brome tillers were noted.

Late spring burning of growing smooth brome has been used to reduce smooth brome in tall and mixed grass prairie (Blankespoor and Larson 1994). Burning is most effective in reducing smooth brome when a substantial warm-grass component is present and there is adequate soil moisture throughout the growing season to enable warm grasses to gain a competitive advantage over fire-injured smooth brome (Blankespoor and Larson 1994). However, in foothills fescue grassland, there are few warm season grasses. Growth of rough fescue, the dominant species, begins very early in spring and is reduced by growing season burns (Sinton and Bailey 1980). Careful consideration must be given when planning burns since dormant season burns alone do not reduce smooth brome and a single burn may even encourage its growth and dominance (Grilz 1992; Grilz and Romo 1994).

Treatments appeared to revitalize smooth brome. In September 1996, reference plots were readily distinguished by their lack of flowering, shorter stature and more advanced senescence. This supports other research results. Smooth brome will become 'sod-bound' when allowed to grow undisturbed for at least two to three years, resulting in fewer fertile shoots (Watkins 1940) whereas stubble removal increases smooth brome seed production (Fulkerson 1980). Ungrazed stands will also have lower tiller densities (Frank and Hofmann 1994).

Kentucky Bluegrass Response

Unlike smooth brome, Kentucky bluegrass tiller densities continued to increase in 1996 in all defoliation treatments and species composition increased in all defoliation treatments except C-M2 possibly indicating greater tolerance and a longer period of responsiveness to defoliation. Also, Kentucky bluegrass continued to produce tillers after being placed in the dark and a greater percentage of tillers remained alive at the end of the etiolated regrowth experiment, whereas smooth brome only developed new tillers during the light establishment phase.

These observations support other research on the grazing tolerance of Kentucky bluegrass. Kentucky bluegrass has a higher percentage of leaf area close to the soil surface so it is better able to withstand close frequent grazing and is often found under continuous grazing by horses or sheep (Balasko et al. 1995). Kentucky bluegrass is reported to volunteer in pastures, increasing as taller forage species decline due to overgrazing or lack of winter hardiness (Balsako et al. 1995). It often becomes dominant in pastures in northeastern Saskatchewan where red fescue (*Festuca rubra* L.) has not been introduced (McCartney and Bittman 1994). Over four years of close grazing, Kentucky bluegrass ground cover increased at least 20% in smooth brome fields in Saskatchewan parkland (McCartney and Bittman 1994). Kentucky bluegrass increased from a minor species to a major component of fescue grassland under heavy (22.3% basal area (Willms and Quinton 1995)) and severe grazing (74% cover (Trottier 1986)).

Kentucky bluegrass tiller density and species composition increased in all herbicide treatments, presumably due to decreased competition by smooth brome and tiller stimulation by mowing and litter removal. The dramatic increase in Kentucky bluegrass tillers in H-BM3 was attributed to Kentucky bluegrass being dormant at the time of the burn. Litter removal by burning enhanced growth and tillering was further stimulated by mowing.

As with smooth brome, defoliation also stimulated seed production in Kentucky bluegrass in 1996. Burning has been commonly used to reduce litter and increase seed production of Kentucky bluegrass; mowing removes less litter than burning and is less effective in increasing seed production (Hickey and Ensign 1983). Burning in August in Idaho released tiller apical dominance over rhizomes (Hickey and Ensign 1983) resulting in greater numbers of tillers, panicles and seed (Canode and Law 1979) whereas burning after initiation of fall regrowth reduced tiller density and seed yield (Ensign et al. 1983). As with smooth brome (Fulkerson 1972), stand thinning stimulated seed production in Kentucky bluegrass (Evans 1980) but production decreased as gaps were allowed to fill in. Openings created in the canopy, by the death of smooth brome tillers by herbicide, would provide additional space for Kentucky bluegrass which is tolerant of light shade but which grows best in full sunlight (Alberta Agriculture Food and Rural Development 1981). Any gaps in the soil could soon be reinvaded by rhizomes of Kentucky bluegrass or smooth brome.

Other Species Response

Forb composition was generally less than 20% and shrubs and native grasses were present in small amounts in only two of four blocks, therefore, only general statements can be made about anticipated and observed treatment impacts.

It was anticipated that treatments including defoliation might reduce native grasses, forbs and shrubs and that cattle would have the least negative impact because grazing height was the greatest and forbs and shrubs were generally avoided. The least frequent and lightest defoliation treatments (C-M2 and S-S3L) were expected to have the least impact on rough fescue. The last defoliation in all treatments was conducted in mid-September and likely had minimal impact on rough fescue (McLean and Wikeem 1985; Willms 1991; Willms and Fraser 1992). Perhaps surprisingly, native forb composition declined in only C-C3, S-S3L and the reference over time and in 1996, C-C3 and S-S3 had significantly less forb composition than C-M2. Herbicide treatments which included mowing (H-BM3 and H-M3) had less native forbs than some of the other herbicide treatments, when individual sampling times were analyzed.

By nature of the wicking application, it was expected that herbicide treatments would have minimal negative impact on established native plants. Native forb composition and richness did not significantly change from 1994 to 1996 in herbicide treatments in the current study. Germination of seeded mixed grass prairie species increased 20 times in an old field when competition by smooth brome and crested wheat was reduced by glyphosate (Wilson and Gerry 1995). In the current study, the thick litter layer in unburned treatments would have prevented seedling emergence. Seedling establishment, primarily of introduced species such as stinkweed, was only noted on pocket gopher disturbances.

The early spring burn was expected to have minimal impact on rough fescue which had not begun to grow (Bailey and Anderson 1978; Sinton and Bailey 1980), however, the crowns of a few rough fescue and Parry oat grass plants were burned out. Heavy litter accumulation may prolong burning in rough fescue crowns (Jourdonnais and Bedunah 1990), particularly in those greater than 20 cm diameter (Antos et al. 1983). It is likely that the tufted plant material protects perennating buds from fire (Johnston and Macdonald 1967) only when the clump is damp in the spring (Antos et al. 1983). A single spring fire in fescue grassland may result in a short term increase in forb cover and a decrease in graminoid cover (Bailey and Anderson 1978) or have no impact on forb and shrub biomass (Redmann et al. 1993). Although fire kills seed in the litter and upper soil, it may also stimulate seedling germination and emergence by scarifying seed and removing litter which acts as a barrier to emergence (Bosy and Reader 1995). No significant burn impact on native graminoids, forbs and shrubs was detected in the current study.

Although glyphosate was applied to Canada thistle in all herbicide plots, a large increase in Canada thistle was detected in H-H which had the greatest area of bare ground due to pocket gopher activity. Canada thistle also appeared to increase under C-C3 and S-S3. Cattle avoided grazing the thistle, whereas sheep would consume some of the younger plants and flowers, particularly under heavy grazing.

MANAGEMENT IMPLICATIONS

Smooth brome stands should be grazed or mowed at least once per summer to prevent seed formation and to minimize contribution to the seed bank. Infrequent grazing, mowing or burning may revitalize grassland by removing litter and increasing plant tillering, germination and richness. To stress smooth brome, graze-mow treatments need to be conducted for more than two years and possibly be more frequent and severe than those implemented in this study. Autumn defoliation, while smooth brome is still growing, should be included.

An alternative approach would be to use grazing or mowing to release apical dominance and to stimulate tillering prior to herbicide application. Where smooth brome and fescue stands are intermixed, a regime which allows summer grazing of smooth brome but removes animals before native grasses are consumed may be more appropriate for maintaining vitality of fescue which is not tolerant of growing season grazing (Willms 1991). Advantages of selective grazing behaviour are lost when heavy grazing is imposed.

Glyphosate wicking is not a permanent solution and will not eliminate smooth brome. As the number of smooth brome tillers which extend above the canopy of the desirable species decreases, the effectiveness of an additional herbicide application is diminished. In old smooth brome fields with few desirable species, it would likely be more effective to directly eliminate all smooth brome with herbicide and reseed with desirable species.

Plant physiological stage at time of treatment implementation is a vital factor in determining effectiveness as evidenced by smooth brome response to burning. Smooth brome may be decreased by a dormant season burn followed by glyphosate wicking (Grilz 1992) or by a growing season burn, however, impact on desirable species must also be considered.

The potential of Kentucky bluegrass to increase and become dominant, especially under heavy grazing must be considered when managing smooth brome stands. Kentucky bluegrass is considered a less desirable range species because it competes with more productive grasses for moisture in the cooler parts of the growing season and contributes little productivity in summer when it is dry (Balasko et al. 1995). Nor is Kentucky bluegrass desirable for hay because most of its growth is basal (Alberta Agriculture Food and Rural Development 1981).

Disturbed areas (oil and gas wells, pipelines, road allowances) in native rangeland should not be seeded to smooth brome to avoid new centres of invasion.

CONCLUSIONS

1. Two years of heavy grazing and mowing did not stress smooth brome as evidenced by tiller density, etiolated regrowth and total nonstructural carbohydrates; however, the three heaviest defoliation treatments (C-M4, C-C3 and S-S3) effected a decrease in species composition.
2. Defoliation stimulated a short term increase in smooth brome tiller density; the more intense the grazing treatment, the longer the effect endured.
3. Glyphosate wicking reduced, but did not eliminate, smooth brome. This reduction is expected to be relatively short lived. Repeated application (H-H2) was most effective, reducing tiller density to 0.5 pretreatment levels one year after application.
4. Although burning reduced litter mass by two thirds, smooth brome growth was stressed because the plants were beginning to green; as a result, glyphosate effectiveness was not enhanced by burning. Growth of Kentucky bluegrass, which had not yet broken dormancy, was stimulated.
5. Mowing stimulated a short term increase in smooth brome tillering which compensated for the tillers previously killed by glyphosate, resulting in no net change in tiller density.
6. Kentucky bluegrass increased in all treatments except the reference. Tillering was likely stimulated by defoliation, litter removal, increased light and reduced competition from smooth brome. Kentucky bluegrass appears to be more tolerant to defoliation than smooth brome as indicated by its longer period of increased tiller densities, ability to produce tillers in the dark and more basal growth form.
7. Flowering of smooth brome and Kentucky bluegrass increased in all treatments except the reference one year after the two years of treatments.

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Table 3.1. Treatments implemented in smooth brome stands in 1994 and 1995.

Treatment	1994	1995
C-M2	Cattle (Aug 28 - Sept 11)	Mowing 2x, starting at elongation (June 9-14; Sept 14-15)
C-M3	Cattle (Aug 28 - Sept 11)	Mowing 3x, starting at elongation (June 9-15; Aug 5-9; Sept 14-15)
C-M4	Cattle (Aug 28 - Sept 11)	Mowing 4x, starting at elongation (June 9-14; June 25-29; Aug 5-9; Sept 14-15)
C-C3	Cattle (Aug 28 - Sept 11)	Heavy cattle grazing 3x, starting at elongation (June 2-18; July 21-Aug 4; Aug 29 - Sept 12)
S-S3	Sheep (Aug 7-17)	Heavy sheep grazing 3x, starting at elongation (May 31- June 16; July 9-22; Aug 30 - Sept 14)
S-S3L	Sheep (Aug 7-17)	Heavy sheep grazing at elongation, light - moderate grazing in summer and heavy fall grazing (total 3x) (May 31- June 16; July 9-22; Aug 30 - Sept 14)
H-BM3	Herbicide (July 27 - Aug 3)	Spring burn (March 29), mowing 3x starting at elongation (June 9-14; Aug 5-9; Sept 14-15)
H-M3	Herbicide (July 28 - Aug 3)	Mowing 3x, starting at elongation (June 9-15; Aug 5-9; Sept 14-15)
H-BH2	Herbicide (Aug 22-23)	Spring burn (March 29), herbicide at elongation (June 15-24; Aug 3-6)
H-H	Herbicide (Aug 22-23)	Herbicide at elongation (June 15-24)
H-H2	Herbicide (July 27 - Aug 3)	Herbicide 2x at elongation (June 23-24; Aug 3-6)
REF	Reference	Reference

Table 3.2. Treatment response of smooth brome tiller density by tiller age (summer initiated and fall initiated tillers m^{-2}) in September 1994.

	Treatment													
Tiller Age	C-M2	C-M3	C-M4	C-C3	S-S3	S-S3(L)	H-BM3	H-M3	H-BH2	H-H	H-H2	REF	SEM[†]	P[‡]
Summer Initiated	44 bcd	26 cd	21 cd	20 cd	2 d	5 d	91 b	101 b	47 bcd	82 bc	99 b	259 a	23	<0.01
Autumn Initiated	350 c	429 bc	452 abc	486 abc	586 a	564 abc	97 d	130 d	81 d	111 d	101 d	173 d	52	<0.01

Treatment abbreviations are listed in Table 3.1.

[†] Standard error of the mean.

[‡] Probability of significant difference among treatments based on analysis of variance. N=240 for analysis of individual sampling periods.

Means within a row followed by the same letter are not statistically different.

Table 3.3. Treatment response of smooth brome and Kentucky bluegrass tiller density m^{-2} over time and within a given sampling period.

Species	Treatment C-M2	C-M3	C-M4	C-C3	S-S3	S-S3(L)	H-BM3	H-M3	H-BH2	H-H	H-H2	REF	SEM[†]	P[‡]
Smooth Brome (SEM = 54; P<0.01)[§]														
July 1994	561 B	572 CD	564 B	690 C	560 C	616 CD	711 A	557 AB	514 A	532 A	612 A	605 AB	51	0.24
September 1994	394 C bc	455 D ab	472 B ab	506 D ab	587 C a	568 D a	188 D d	231 C cd	128 C d	192 C d	199 C d	432 C ab	59	<0.01
May 1995	904 A bc	944 A abc	940 A abc	1166 A a	963 A abc	1062 A ab	402 C d	435 B d	290 B d	287 BC d	355 B d	749 A c	90	<0.01
September 1995	599 B bcd	788 B bcd	816 A ab	945 B a	946 A a	801 B ab	642 AB bc	627 A bc	365 AB d	387 AB cd	356 B d	659 AB b	89	<0.01
September 1996	589 B bcde	620 C abc	540 B cde	780 C a	761 B ab	738 BC ab	499 BC cde	431 B def	321 B f	424 AB ef	299 BC f	598 B bcd	60	<0.01
Kentucky Bluegrass (SEM=137; P<0.01)														
July 1994	639 B	578 B	479 C	276 B	573 C	444 C	539 CD	439 C	656 BC	525 C	483 B	525 A	99	0.42
September 1994	450 B	416 B	439 C	171 B	516 C	267 C	310 D	277 C	484 C	426 C	395 B	536 A	95	0.24
May 1995	750 B	751 B	729 BC	444 B	721 C	551 BC	904 C	487 BC	1014 B	527 C	631 B	649 A	169	0.47
September 1995	1182 A	1178 A	1073 AB	524 B	1231 B	904 B	1924 B	843 B	1412 A	1077 B	1177 A	843 A	285	0.19
September 1996	1485 A bc	1249 A bcd	1410 A bcd	934 A cd	1795 A ab	1511 A bc	2489 A a	1354 A bcd	1565 A bc	1693 A abc	1462 A bcd	645 A d	288	0.02

Treatment abbreviations are listed in Table 3.1.

[†] Standard error of the mean.

[‡] Probability of significant difference among treatments within individual sampling periods based on analysis of variance. N=240.

[§] Standard error of the mean and treatment*time P for split block analysis. N=1200.

Means within a column followed by the same upper case letter are not statistically different.

Means within a row followed by the same lower case letter are not statistically different.

Table 3.4. Treatment effect on species composition (%) over time and within a given sampling period.

Species	Treatment C-M2	C-M3	C-M4	C-C3	S-S3	S-S3(L)	H-BM3	H-M3	H-BH2	H-H	H-H2	REF	SEM[†]	P[‡]
Smooth Brome (SEM=3; P<0.01)[§]														
July 1994	49	48	65	65	55	56	66	54	48	51	63	71	6	0.10
	A	A	A	A	A	A	A	A	A	A	A	A		
September 1995	34	41	55	54	46	48	38	39	30	25	33	69	6	<0.01
	B cde	A bcde	B ab	B ab	AB bcd	A bc	B bcde	B bcde	B de	B e	B cde	A a		
September 1996	42	43	55	55	42	55	43	37	31	33	35	76	5	<0.01
	AB bc	A bc	B b	B b	B bc	A b	B bc	B c	B c	B c	B c	A a		
Kentucky Bluegrass (SEM=3; P=0.13)														
July 1994	19	19	14	9	20	15	14	17	17	18	17	16	2	0.28
	B	B	B	B	C	B	C	B	B	B	C	A		
September 1995	39	33	26	19	30	29	42	40	26	26	32	20	5	0.05
	A ab	A abc	A bc	A c	B abc	A abc	A a	A ab	A bc	A bc	B abc	A c		
September 1996	24	27	23	23	37	23	34	35	29	29	40	15	5	0.03
	B bcd	A abcd	A cd	A cd	A ab	A cd	B abc	A abc	A abc	A abc	A a	A d		
Other Introduced Grasses[1] (SEM=1)														
July 1994	0	5	0	0	0	0	0	3	0	2	0	0	2	
September 1995	2	2	0	0	0	0	0	3	0	3	0	0	1	
September 1996	1	2	0	0	0	0	0	1	0	1	0	0	1	
Native Grasses (SEM=1; P=0.52)														
July 1994	4	1	0	1	2	1	1	1	2	1	1	1	1	0.69
September 1995	5	2	2	0	3	2	4	1	5	1	1	0	2	0.59
September 1996	6	1	1	0	3	2	1	1	4	1	0	0	2	0.29

Table 3.4 (continued)

Species	Treatment C-M2	C-M3	C-M4	C-C3	S-S3	S-S3(L)	H-BM3	H-M3	H-BH2	H-H	H-H2	REF	SEM	P
Introduced Forbs (SEM=2; P=0.52)														
July 1994	5	2	3	4	2	3	2	2	5	2	3	1	1	0.64
September 1995	5	4	5	9	7	4	1	1	11	13	7	0	4	0.42
September 1996	5	3	4	7	4	3	4	4	7	14	4	1	4	0.66
Native Forbs (SEM=2; P=0.02)														
July 1994	16	16	12	14	11	17	11	17	22	17	11	11	3	0.43
	AB	A	A	A	A	A	A	A	A	B	B	A		
September 1995	12	11	10	8	5	8	11	11	22	23	19	8	3	<0.01
	B bc	B bc	A c	B c	B c	B c	A bc	B bc	A a	A a	A ab	AB c		
September 1996	17	15	13	7	7	10	12	12	22	16	15	5	3	0.01
	A ab	AB abcd	A bcde	B cde	AB de	B bcde	A bcde	AB bcde	A a	B ab	AB abc	B e		
Native Shrubs (SEM=2; P=0.18)														
July 1994	7	9	5	7	10	7	6	7	6	7	5	1	2	0.36
September 1995	2	8	2	10	10	9	4	5	5	8	8	2	3	0.32
September 1996	5	9	4	8	7	7	6	9	7	7	4	2	2	0.17

Treatment abbreviations are listed in Table 3.2.

[†] Standard error of the mean.

[‡] Probability of significant difference among treatments within individual sampling periods based on analysis of variance. N=480.

[§] Standard error of the mean and treatment*time P for split block analysis. N=1440.

[¶] The only species included in Other Introduced Grasses is timothy.

Means within a column followed by the same upper case letter are not statistically different.

Means within a row followed by the same lower case letter are not statistically different.

Table 3.5. Treatment effect on plot species richness over time and within a given sampling period.

	Treatment													
Plant Group	C-M2	C-M3	C-M4	C-C3	S-S3	S-S3(L)	H-BM3	H-M3	H-BH2	H-H	H-H2	REF	SEM[†]	P[‡]
<u>Introduced Grasses</u>[1] (SEM=0.1)[§]														
July 1994	2.3	2.3	2.0	2.0	2.0	2.0	2.0	2.3	2.0	2.3	2.0	2.0	0.1	
September 1995	2.3	2.3	2.3	2.0	2.0	2.0	2.3	2.3	2.0	2.3	2.0	2.0	0.1	
September 1996	2.3	2.3	2.3	2.0	2.0	2.3	2.0	2.3	2.0	2.3	2.0	2.0	0.1	
<u>Native Grasses</u> (SEM=0.3; P=0.24)														
July 1994	1.3	0.8	1.0	1.5	1.3	1.5	0.5	0.8	1.0	1.0	1.3	0.5	0.4	0.75
September 1995	1.0	1.0	0.5	0.8	0.5	1.0	0.3	1.3	1.8	1.0	0.8	0.8	0.5	0.71
September 1996	0.8	1.3	0.8	0.8	1.3	1.0	0.5	1.3	2.0	1.3	0.3	0.5	0.4	0.21
<u>Introduced Forbs</u> (SEM=0.4; P=0.60)														
July 1994	2.3 a	1.3 bc	0.8 cd	0.8 cd	1.0 cd	0.8 cd	0.8 cd	1.3 bc	1.5 abc	0.8 cd	2.0 ab	0.3 d	0.3	0.01
September 1995	1.5	1.5	0.8	0.5	1.3	1.5	1.5	0.8	2.3	2.3	2.3	0.3	0.5	0.07
September 1996	1.5	1.3	1.0	0.8	0.8	1.5	2.0	1.5	1.8	1.8	2.3	1.0	0.4	0.36
<u>Native Forbs</u> (SEM=0.8; P=0.30)														
July 1994	8.8	7.5	7.8	7.3	6.5	7.0	5.3	9.3	7.8	6.3	6.3	5.3	1.2	0.40
September 1995	7.8	8.5	6.5	4.5	4.3	6.3	6.3	8.3	9.0	6.8	6.8	4.3	1.6	0.42
September 1996	8.5	8.5	7.3	5.5	8.0	6.8	6.0	9.3	9.3	7.0	5.8	4.3	1.3	0.14
<u>Native Shrubs</u> (SEM=0.2; P=0.65)														
July 1994	1.8	1.3	1.3	1.3	0.8	0.8	1.0	1.3	1.0	1.3	1.3	1.3	0.3	0.36
September 1995	1.3	1.3	1.0	0.8	0.8	1.0	1.3	1.0	0.8	1.0	1.0	1.3	0.2	0.69
September 1996	1.3	1.5	1.0	1.0	0.8	1.0	1.0	1.5	1.0	1.3	1.0	1.3	0.3	0.78

Table 3.5 (continued)

Plant Group	C-M2	C-M3	C-M4	C-C3	S-S3	S-S3(L)	H-BM3	H-M3	H-BH2	H-H	H-H2	REF	SEM	P
						Treatment								
Total (SEM=0.9; P=0.02)														
July 1994	16.3 A	13.0 A	12.8 A	12.8 A	11.5 A	12.0 A	9.5 A	14.8 A	13.3 A	11.5 A	12.8 A	9.3 A	1.5	0.13
September 1995	13.8 A	14.5 A	11.0 A	8.5 B	8.8 B	11.8 A	11.5 A	13.5 A	15.8 A	13.3 A	12.8 A	8.5 A	2.0	0.17
September 1996	14.3 A	14.8 A	12.3 A	10.0 B	12.8 A	12.5 A	11.5 A	15.8 A	16.0 A	13.5 A	11.3 A	9.0 A	1.6	0.10

Treatment abbreviations are listed in Table 3.1.

[†] Standard error of the mean.

[‡] Probability of significant difference among treatments within individual sampling periods based on analysis of variance. N=48.

[§] Standard error of the mean and treatment*time P for split block analysis. N=144.

[¶] Kentucky bluegrass was included in Introduced Grasses because native and introduced elements are indistinguishable (Moss 1983).

Means within a column followed by the same upper case letter are not statistically different.

Means within a row followed by the same lower case letter are not statistically different.

Table 3.6. Treatment response of live vegetation and litter mass (kg/ha) and litter depth (cm) over time and within a given sampling period.

Biomass/Litter Category	Treatment													
	C-M2	C-M3	C-M4	C-C3	S-S3	S-S3(L)	H-BM3	H-M3	H-BH2	H-H	H-H2	REF	SEM[†]	P[‡]
Live Vegetation (SEM=373; P=<0.01)[§]														
July 1994	3682	3935	3845	4650	2911	4248	3502	3340	3503	3934	4139	3502	380	0.19
	A	A	A	A	A	A	B	A	B	B	A	A		
September 1994	3387	3243	3635	3299	3146	2456	5343	4258	5305	5343	4520	4443	448	<0.01
	A bcd	A bcd	A bcd	B bcd	A cd	B d	A a	A abc	A a	A a	A ab	A ab		
Standing Litter (SEM=164; P<0.01)														
June 1994	294	281	255	279	480	352	397	301	503	255	316	165	138	0.90
	A	A	A	A	A	A	B	A	B	B	B	A		
September 1994	209	222	93	306	75	253	1406	670	1185	1306	1312	458	238	<0.01
	A c	A c	A c	A c	A c	A c	A a	A bc	A ab	A ab	A ab	A c		
September 1995	336	203	212	285	179	225	262	210	376	333	629	436	64	<0.01
	A bcd	A cd	A cd	A bcd	A d	A cd	B bcd	A cd	B bc	B bcd	B a	A b		
Fallen Litter (SEM=391; P=0.11)														
June 1994	3466	3698	4343	3713	3361	3560	4423	3922	3934	4036	3166	3735	459	0.75
September 1994	3707	3270	3965	4323	3491	3226	3457	3941	3524	3292	3872	3817	451	0.85
September 1995	1713	1747	2033	2296	1395	1535	700	2400	721	2619	2654	2354	222	<0.01
	cde	bcde	adbd	abc	e	e	f	a	f	a	a	ab		
Decomposing Litter (SEM=453; P<0.01)														
June 1994	2931	2889	3621	3171	2687	3064	3151	3528	2638	3428	2183	2994	322	0.15
	A	A	A	A	B	B	B	A	AB	A	B	A		
September 1994	3145	3302	3680	4298	4493	4992	4787	3830	2893	3627	4670	3213	568	0.15
	A	A	A	A	A	A	A	A	A	A	A	A		
September 1995	4055	3627	3754	3458	3647	2967	2104	4504	1236	3636	3987	3695	585	0.03
	A a	A ab	A ab	A ab	AB ab	B ab	B bc	A a	B c	A ab	A a	A ab		

Table 3.6 (continued)

Biomass/Litter Category	Treatment C-M2	C-M3	C-M4	C-C3	S-S3	S-S3(L)	H-BM3	H-M3	H-BH2	H-H	H-H2	REF	SEM	P
<u>Total Litter</u> (SEM=562; P<0.01)														
June 1994	6691	6868	8219	7163	6529	6977	7971	7751	7075	7719	5664	6894	641	0.32
	A	A	A	B	AB	A	B	A	A	AB	C	A		
September 1994	7060	6794	7737	8927	8058	8471	9651	8441	7602	8225	9854	7488	663	0.06
	A	A	A	A	A	A	A	A	A	A	A	A		
September 1995	6105	5577	5999	6039	5221	4728	3065	7113	2333	6588	7269	6485	702	<0.01
	A abc	A abc	B abc	B abc	B bc	B cd	C de	A ab	B e	B abc	B a	A abc		
<u>Litter Depth</u> (SEM=0.5; P<0.01)														
June 1994	6.1	6.1	7.0	5.4	5.2	6.5	5.8	6.9	6.6	6.2	5.2	7.1	0.5	0.10
	A	A	A	A	A	A	A	A	B	A	B	A		
September 1994	5.7	5.0	4.9	6.3	4.4	5.2	7.0	7.6	8.2	6.5	7.3	6.7	0.6	<0.01
	A cdef	A def	B ef	A bcde	A f	A def	A abc	A ab	A a	A abcde	A abc	A abcd		
September 1995	1.7	1.6	1.7	1.5	1.3	1.2	0.8	1.7	0.8	2.2	2.7	3.1	0.3	<0.01
	B cd	B cd	C cd	B cde	B de	B de	B e	B cd	C e	B bc	C ab	B a		

Treatment abbreviations are listed in Table 3.1.

[†]Standard error of the mean.

[‡]Probability of significant difference among treatments within individual sampling periods based on analysis of variance. N=240.

[§]Standard error of the mean and treatment*time P for split block analysis. N=480 for live vegetation and N=720 for litter.

Means within a column followed by the same upper case letter are not statistically different.

Means within a row followed by the same lower case letter are not statistically different.

Table 3.7. Treatment response of ground cover (%) by live vegetation and litter over time and within a given sampling period.

	Treatment													
Ground Cover	C-M2	C-M3	C-M4	C-C3	S-S3	S-S3(L)	H-BM3	H-M3	H-BH2	H-H	H-H2	REF	SEM[†]	P[‡]
Live Vegetation (SEM=0.5; P<0.01)[§]														
July 1994	10	9	10	9	10	10	9	10	11	10	9	9	1	0.05
	A ab	B c	A abc	A c	A bc	A abc	C c	A abc	A a	A abc	A c	A bc		
September 1995	10	14	11	10	11	9	14	10	11	10	9	8	1	<0.01
	A cd	A ab	A bc	A cd	A c	A cd	A a	A cd	A abc	A cd	A cd	A d		
September 1996	10	10	10	10	10	10	11	10	11	8	9	8	1	0.48
	A	B	A	A	A	A	B	A	A	A	A	A		
Litter (SEM=2.1; P<0.01)														
July 1994	90	90	90	91	90	89	91	90	89	90	89	91	1	0.63
	A	A	A	A	A	A	A	A	A	A	A	A		
September 1995	88	85	83	83	86	86	82	87	68	85	84	91	3	<0.01
	A ab	A ab	B ab	B ab	A ab	A ab	B b	A ab	B c	A ab	AB ab	A a		
September 1996	86	89	87	84	88	87	85	87	73	76	81	89	3	0.01
	A a	A a	AB a	B a	A a	A a	AB a	A a	B c	B bc	B ab	A a		

Treatment abbreviations are listed in Table 3.1.

[†] Standard error of the mean.

[‡] Probability of significant difference among treatments within individual sampling periods based on analysis of variance. N=480.

[§] Standard error of the mean and treatment*time P for split block analysis. N=1440.

Means within a column followed by the same upper case letter are not statistically different.

Means within a row followed by the same lower case letter are not statistically different.

Table 3.8. Ground cover disturbance (%) in permanent species composition and ground cover quadrats over time.

	Treatments											
Disturbance Type	C-M2	C-M3	C-M4	C-C3	S-S3	S-S3(L)	H-BM3	H-M3	H-BH2	H-H	H-H2	REF
Total Bare Ground												
July 1994	0.1	0.7	0.1	0.0	0.1	0.6	0.0	0.1	0.3	0.2	2.0	0.2
September 1995	1.8	5.8	2.7 *	1.6 *	0.5	1.7	4.8 *	2.5	20.5 *	5.5	7.5	0.9
September 1996	3.7	1.5	1.8	3.6 *	1.7	2.7	4.7	2.8	16.2 *	16.4 *	10.7 *	3.1
Pocket Gopher Disturbance												
July 1994	0.0	0.6	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	1.8	0.0
September 1995	0.0	0.5	2.6 *	1.0 *	0.0	0.0	0.0 *	1.4	7.5 *	5.3	3.9	0.9
September 1996	2.9	0.4	0.7	1.9 *	0.7	1.3	0.6	2.7	9.9 *	14.0 *	9.6 *	3.0
Number of Quadrats with Pocket Gopher Disturbance												
July 1994	0	1	0	0	0	0	0	0	1	0	1	0
September 1995	0	1	2 *	1 *	0	0	0 *	1	4 *	5	2	1
September 1996	4	2	1	3 *	1	3	1	5	9 *	12 *	9 *	4

Treatment abbreviations are listed in Table 3.1.

N=480.

'*' indicates treatments for which litter cover decreased significantly over time (Table 3.7).

Table 3.9. Treatment effect on smooth brome total nonstructural carbohydrates (%fructose) and etiolated regrowth (mg 100 tillers-1) of smooth brome and Kentucky bluegrass samples collected in September 1995.

	Treatment													
Species/ Temperature Regime	C-M2	C-M3	C-M4	C-C3	S-S3	S-S3(L)	H-BM3	H-M3	H-BH2	H-H	H-H2	REF	SEM[†]	P[‡]
Total Nonstructural Carbohydrates														
Smooth Brome	18.9	24.0	20.4	18.1	18.7	18.5	20.2	17.8	17.4	19.2	18.2	23.5	1.7	0.14
Etiolated Regrowth														
Smooth Brome														
10°C	0.41	0.32	0.29	0.27	0.17	0.31	0.36	0.28	0.54	0.30	0.29	0.47	0.05	0.57
22°C	0.15	0.19	0.13	0.16	0.13	0.20	0.14	0.13	0.26	0.04	0.04	0.16	0.04	0.63
Total	0.55	0.50	0.42	0.42	0.31	0.51	0.50	0.41	0.80	0.34	0.33	0.62	0.06	0.70
Kentucky Bluegrass														
10°C	0.23	0.24	0.15	0.27	0.59	0.29	0.17	0.18	0.16	0.19	0.16	0.34	0.06	0.48
22°C	0.08	0.10	0.04	0.07	0.20	0.11	0.05	0.08	0.04	0.04	0.04	0.20	0.03	0.18
Total	0.31	0.34	0.19	0.34	0.78	0.39	0.22	0.26	0.20	0.23	0.19	0.55	0.06	0.38
Tiller Density per Core at time of Potting Etiolated Regrowth Experiment														
Smooth Brome	10	11	9	13	14	11	10	11	10	11	10	10	2	0.89
Kentucky Bluegrass	12 bc	13 bc	13 bc	5 c	16 ab	10 bc	11 bc	10 bc	24 a	12 bc	15 b	9 bc	3	0.02

Treatment abbreviations are listed in Table 3.1.

[†] Standard error of the mean.

[‡] Probability of significant difference among treatments based on analysis of variance. N=144.

Means within a row followed by the same letter are not statistically different.

4. SYNTHESIS

'A plant's tolerances and capabilities in the biophysical environment will give it either a wide or narrow address in the infinite neighborhood of niche.'
– Don Gayton (1990)

INTRODUCTION

Grassland recovering from cultivation eventually reverts to native species (Dormaar and Smoliak 1985) unless competitive alien plants have been introduced (Wilson 1989), in which case, species composition stabilizes with the invaded species rather than succeeding back to the original vegetation (Westoby et al. 1989). Smooth brome (*Bromus inermis* Leyss.) and Kentucky bluegrass (*Poa pratensis* L.) are both very competitive species which invade native grassland throughout the Northern Great Plains (Grilz 1992; Nagel et al. 1994; Willms and Quinton 1995; Willoughby 1997). In this synthesis, results from the current study and the literature are explored to provide an understanding of the characteristics and processes by which smooth brome and Kentucky bluegrass may become dominant. Possible management options for reducing their competitiveness relative to native species are also suggested. The chapter concludes with a summary of the contributions of the current study.

COMPETITIVE CHARACTERISTICS

Smooth brome and Kentucky bluegrass are well suited to grow in the prairie parklands since they evolved in similar climates (Looman 1969); Kentucky bluegrass is also native to the area (Moss 1983). They have a longer growing season than native grasses, beginning growth earlier in the spring and growing later in autumn (Looman 1969; Trottier 1986). They withstand midsummer drought by becoming temporarily dormant (Balasko et al. 1995; Casler and Carlson 1995). Prolific seed production and vigorous vegetative reproduction by rhizomes allow them to readily occupy spaces in the community. Smooth brome germinates under a wide variety of soil moisture, temperature and light conditions (Grilz et al. 1994) and Kentucky bluegrass is reported to have a broad range of safe sites for germination (Bookman 1983). Litter produced by these species is allelopathic to at least a few species of forbs (Bosy and Reader 1995; Chung and Miller 1995). Both species are tolerant of defoliation (Balasko et al. 1995; Casler and Carlson 1995).

POTENTIAL INVASION PROCESS

Smooth Brome

Smooth brome invades as an advancing front (Grilz 1992) likely due to aggressive rhizome development and relatively heavy seed which does not disperse far (Hume and Archibold 1986). Seed is relatively large and is not expected to persist in the seedbank (Harper 1977; Grime et al. 1981). Smooth brome germinates, emerges and grows more rapidly, producing larger seedlings than several native species, including foothills rough fescue (*Festuca campestris* Rydb.) and Parry oat grass (*Danthonia parryi* Scribn.) (Smoliak and Johnston 1968). Nevertheless, smooth brome seedlings establish best when competition is reduced (Bowes and Zentner 1992). Soil disturbance, such as pocket gopher mounds, stimulate seed bank germination and provide establishment sites for seeds subsequently dispersed. These areas serve as foci for further expansion.

Smooth brome begins growth early in the spring and likely suppresses growth of other species by reducing available light, moisture and nutrients. Foothills rough fescue and Parry oat grass are grassland climax species and may not be tolerant of shading by the taller smooth brome and as a result, may decline in productivity. Tillering and inflorescence development of Kentucky bluegrass is known to decrease in response to increased shade and litter accumulation (Canode and Law 1979; Ensign et al. 1983).

The nature of root systems is an important factor affecting competing plants. Smooth brome is sod-forming and relatively deep rooted, with roots extending to at least 46 cm and at least 56% of roots and rhizomes are located in the top 8 cm of the soil (Gist and Smith 1948). Foothills rough fescue roots are tufted and extend to 1.4 m but almost 90% are located in the top 46 cm (Johnston 1961). Although no references on rooting depth of Parry oat grass were located, it is expected that its rooting depth is less than rough fescue because it grows in thinner soils on drier sites (Coupland and Johnston 1965; Johnston and Dormaar 1970). As a result, Parry oat grass may be in more direct competition with smooth brome than is rough fescue. This may be a factor contributing to the greater number of rough fescue clumps in smooth brome stands when Parry oat grass was the predominant species on the adjacent native grassland (personal observation). Also, it is possible that smooth brome which grows best in deep, moist fertile soils (Casler and Carlson 1995) invaded rough fescue stands and that further invasion was halted by the drier thinner soils and steeper slopes dominated by Parry oat grass. Mesic ecoregions (i.e., the boreal forest, aspen parkland, fescue grassland and areas of the mixed grass prairie which support woody vegetation) are the most susceptible to smooth brome invasion (Romo et al. 1990).

As smooth brome becomes more dominant, litter accumulates and shade increases, particularly if the area is not grazed or mowed. In response, growth of other species may decline and bunch grasses (e.g. rough fescue and Parry oat grass) may become smaller and fewer. It becomes increasingly difficult for germinating seeds to emerge above the litter layer (Bosy and Reader 1995) and species which reproduce vegetatively, such as smooth brome and Kentucky bluegrass, are favoured because there is more energy available to establish a new tiller or plant. The litter may also reduce seed germination by allelopathy (Bosy and Reader 1995; Chung and Miller 1995) and microclimatic changes. However, litter may enhance seed preservation by maintaining seed dormancy (Williams 1983, cited in Willms and Quinton 1995) or reducing exposure of seed to predation and environmental hazards. Over time, as litter accumulates, species richness of the vegetation declines (Johnston 1961) and eventually so does the species richness of the seed bank. Small soil disturbances within smooth brome stands will be rapidly colonized by short-lived ruderals such as stinkweed (*Thlaspi arvense* L.) and re-invaded by rhizomatous smooth brome and Kentucky bluegrass; few other species are likely to become established from the depleted seed bank.

Over time, old smooth brome stands become sod-bound and forage and seed production decline. This condition may be caused by an accumulation of toxic substances released by the roots or produced during root tissue decomposition or be due to immobilization of nitrogen in the roots (Benedict 1941; Meyer and Anderson 1942).

Eventually, smooth brome may naturalize. There is some debate that it is breeding with northern awnless brome (*Bromus inermis* ssp. *pumpellianus* (Scribn.) Wagnon) (Harms, cited in Romo et al. 1990). Kentucky bluegrass is already considered to be naturalized.

Kentucky Bluegrass

Kentucky bluegrass is present in minor amounts in foothills fescue grassland which is lightly or not grazed and increases with grazing (Willms and Quinton 1995) and may remain subdominant after grazing pressure is removed (Willoughby 1997). Once Kentucky bluegrass reaches a critical threshold in the landscape, it may invade areas protected from grazing and become subdominant (Willoughby 1997), however, it poses the greatest threat to rough fescue grassland in more mesic sites (Willms and Quinton 1995). Invasion would be expected to be greatest in wet years. Kentucky bluegrass also readily volunteers in seeded pastures (Balasko et al. 1995), becoming subdominant in smooth brome pastures (Looman 1976) and dominant in fields where creeping red fescue (*Festuca rubra* L.) has not been introduced (McCartney and Bittman 1994). Kentucky bluegrass is very tolerant to close, frequent defoliation because it has the majority of its leaf area close to the soil surface (Balasko et al. 1995), growing points located below the ground surface throughout the growing season, rhizomes and a long growth period (Trottier 1986).

Bookman and Mack (1982) suggest that Kentucky bluegrass is less affected by root interference because it has a sod-forming root system. It is shallower rooted than most species, with the majority (88%) of its roots and rhizomes located within the top 8 cm of the soil (Gist and Smith 1948). Consequently, Kentucky bluegrass may be less drought tolerant (Gist and Smith 1948). However, it is able to become temporarily dormant (Casler and Carlson 1995) and its root system would enable it to intercept summer showers better than other species.

Kentucky bluegrass produces large amounts of small seeds which disperse more widely than smooth brome. Seeds may stay viable in the seed bank for as long as 39 years (Toole and Brown 1946). In the current study, Kentucky bluegrass comprised the majority of the seed bank in smooth brome and native stands. Kentucky bluegrass seed densities in foothills fescue grassland were ten times greater in grazed than ungrazed areas (Willms and Quinton 1995). Only under light grazing, did Kentucky bluegrass comprise the majority of the seed bank (Willms and Quinton 1995), likely because heavier grazing prevented seed production. Kentucky bluegrass is able to establish in small-scale disturbances such as pocket gopher mounds which have relatively small light gaps; this ability is attributed to a relatively low light compensation point and increased light utilization efficiency (Bookman and Mack 1983). When larger overstory species are reduced by grazing, Kentucky bluegrass is able to increase in biomass and composition.

Where Kentucky bluegrass litter accumulation is 10 cm or greater, density of Kentucky bluegrass is very sparse and few other species grow (personal observation); Kentucky bluegrass leaves are narrow, elongated and lighter green in colour and roots are shallower, developing in the heavy thatch (Canode and Law 1979).

POTENTIAL IMPACTS

Defoliation

When grazing or mowing are not implemented, litter accumulates and tiller densities decline. Litter accumulation also reduces seed production of smooth brome (Fulkerson 1980) and Kentucky bluegrass (Ensign et al. 1983) making spread responsible primarily by vegetative means. Over time, species diversity also declines.

Occasional grazing (i.e. not every year) is likely to result in a short term increase in seed production and tiller densities of smooth brome and Kentucky bluegrass.

Annual grazing to remove smooth brome stem apices before flowering will likely reduce seed production of smooth brome and Kentucky bluegrass. Although grazing may initially stimulate tiller development, tiller densities will eventually decline if grazing is sufficiently severe. Repeated grazing of smooth brome at elongation, boot or pre-anthesis would be the most likely stage to stress smooth brome by reducing carbohydrate reserves (Sheard and Winch 1966; Smith et al. 1973; Marten and Hovin 1980). Obviously it will take more than two years of intense grazing and possibly at more frequent intervals than used in the current study to weaken smooth brome. As smooth brome declines, Kentucky bluegrass, which is more tolerant to grazing, would increase and grassland productivity would decrease (Balasko et al. 1995). Reduction of grazing pressure or discontinuation of grazing would allow smooth brome stands to recover (Marten and Hovin 1980). Tiller densities may eventually return to pre-grazing levels. The heavier and more frequent the grazing, the longer the effects are likely to last.

Heavy grazing results in all species, at least all grasses, being grazed (McCartney and Bittman 1994) and hence is not suitable for areas with smooth brome and native stands. Smooth brome might eventually be greatly reduced but because it is more tolerant to grazing, most other native grasses would be eliminated. Looman (1969) reports that overgrazed permanent smooth brome pastures resemble overgrazed native range except that smooth brome replaces the dominant native grasses and is accompanied by a few common weedy forbs and shrubs. Overgrazing, especially in the spring, greatly increases weediness (Looman 1976). Trampling during heavy grazing likely hastens decomposition by reducing litter particle size and increasing litter-soil contact (Naeth et al. 1991a). Snow trapping is reduced, resulting in reduced soil moisture and a drier, warmer microclimate. Soil compaction and pocket gopher activity are likely to increase under heavy grazing (Dormaar and Willms 1990).

Moderate levels of summer grazing may be the most appropriate approach for controlling the spread of smooth brome patches in fescue grassland. By allowing cattle to graze smooth brome which is most palatable and removing them before fescue is grazed, smooth brome would be prevented from setting seed. Vigour of rough fescue which is not tolerant to growing season grazing would not be reduced, however, the competitiveness of smooth brome may be sufficiently affected to prevent or minimize further expansion. Moderate summer grazing is compatible with late fall and winter grazing of fescue grassland which maximizes fescue yields (Willms and Beauchemin 1991), does not harm rough fescue (McLean and Wikeem 1985; Willms et al. 1986) and may stimulate tillering by reducing litter (Willms et al 1986). Where the dominant native grass is Parry oat grass, a slightly higher summer grazing pressure may be allowed since it is tolerant of summer grazing (Willms et al. 1992), however, it may be less able to compete with smooth brome as noted above and this more intense grazing pressure is less likely to allow the rough fescue to recover.

Although Kentucky bluegrass is native to the study area, dominance by this species would not be desired. Heavy stocking early in the season when Kentucky bluegrass is most productive, and continuing into summer when Kentucky bluegrass is least able to recover, may be the best way to reduce Kentucky bluegrass patches should they develop. Defoliation height less than 5 to 10 cm will likely result in shallow rooting, open sod, weed invasion and insect damage (Balasko et al. 1995). This regime would need to be maintained for several years to reduce Kentucky bluegrass persistence since short periods of under or over utilization are not harmful to this species (Alberta Agriculture, Food and Rural Development 1981). Such heavy grazing prevents the development of mature, low quality forage and subsequent litter accumulation (Balasko et al. 1995), however, it is unlikely that many other species would be able to withstand this grazing pressure. Lighter grazing intensities may allow weeds and brush to invade (Alberta Agriculture, Food and Rural Development 1981).

Although mowing does not include the grazing effects of trampling, pulling, selectivity, manure deposition, compaction or potential growth stimulation by saliva (Vinton and Hartnett 1992), the impact of mowing on smooth brome and Kentucky bluegrass would be expected to be similar to that of grazing. Because mowing is nonselective and defoliates all plants, it would not be recommended for areas where smooth brome is interspersed with fescue.

Burning

Burning has minimal impact on plants which are dormant. Their growth may increase due to removal of litter or due to reduced competition from other plants which were growing at the time of the burn.

A single dormant season burn will have minimal impact on rough fescue growth (Bailey and Anderson 1978; Gerling et al. 1995) and may favour smooth brome because its growth is reduced for a shorter period of time than native graminoids (Grilz 1992). Autumn burning may cause a greater reduction in smooth brome and native graminoid tiller density the following spring than dormant spring burning because of reduced snow trapping resulting in lower soil moisture availability. These differences diminish later in the growing season as soil moisture is depleted by accelerated growth on the spring burn sites (Grilz 1992).

Burns are expected to be most damaging to smooth brome during elongation and boot stages, however fire may not burn well when there is a substantial amount of green plant material (Nagel et al. 1994). Unfortunately, rough fescue would also be growing at this time of year. A single spring burn when rough fescue was actively growing reduced its cover for at least three years (Bailey and Anderson 1978); the more advanced the growth, the greater the negative impact (Gerling et al. 1995). A single spring fire in fescue grassland may result in a short term increase in forb cover and a decrease in graminoid cover (Bailey and Anderson 1978) or have no impact on forb and shrub biomass (Redmann et al. 1993; Chapter 3). Theoretically it is possible to time a burn when growth of smooth brome is just beginning and native grasses have not yet begun growing, however, this window is very narrow, possibly less than a week and would require careful monitoring of the vegetation as well as the weather.

Midsummer burns when *Poa* is dormant due to drought but other plants are actively growing, often result in increased *Poa* (Antos et al. 1983). A hot summer wildfire in the foothills when *Poa sandbergii* was dormant but fescue was growing, increased forbs and *Poa* but reduced fescue for at least three years, (Antos et al. 1983).

Repeated spring burning may reduce smooth brome and the dominant fescue grassland species and increase species which thrive in the warmer, drier mixed grass prairie (Anderson and Bailey 1980). To maintain a healthy fescue grassland, Antos et al. (1983) recommended a burning frequency of five to ten years. Longer intervals allow heavy litter accumulation which may prolong burning in rough fescue crowns (Jourdonnais and Bedunah 1990), particularly in those greater than 20 cm diameter (Antos et al. 1983). Fire suppression does not prevent smooth brome from invading fescue grassland (Romo et al. 1990).

Herbicide

Herbicide may be selectively applied to smooth brome by wicking. Kentucky bluegrass, if present, would be expected to increase because of its shorter stature. Where there are few desirable species present in the smooth brome stand, spraying may be more effective in reducing smooth brome. Smooth brome tillers may also be sprayed before native seedlings emerge on a seeded site. A single application is not likely to eliminate smooth brome.

Although herbicide application would be expected to increase bare ground, root competition would not necessarily decrease (Wilson and Gerry 1995). Soil nitrogen levels may increase as plant uptake decreases and dead plants decompose (Wilson and Gerry 1995). Application of organic material to tie up soil nitrogen may be useful in reducing smooth brome (Wilson and Gerry 1995) which is more competitive at higher levels of nitrogen (Lindquist et al. 1996).

Treatment Combinations

It is unlikely that defoliation, herbicide or fire will eliminate smooth brome nor will seeding alone create fescue grassland. Management tools may be more effective when combined based on the characteristics of each site. Areas where smooth brome stands or patches are interspersed with native grassland will require approaches which reduce smooth brome and favour native species. In old fields or other sites where there are few desirable species, elimination of smooth brome and reseeding with native species may be the most practical approach.

Smooth Brome Stands

Based on the current study and other research, the following is a possible series of events leading to elimination of smooth brome and establishment of native species in smooth brome stands with few desirable species (e.g., old smooth brome fields). A likely first step is frequent heavy grazing (or mowing) throughout the summer or autumn for at least five years to reduce viable smooth brome in the seed bank (Romo quoted in Gayton 1996) and to weaken and reduce smooth brome and Kentucky bluegrass. The longer the period of defoliation and the more intense the defoliation, the greater the expected reduction in smooth brome and Kentucky bluegrass. Defoliation effectiveness could be greatly enhanced by preceding it with growing season burning, especially at elongation or boot. Grazing height will be lower due to the removal of the litter barrier and the production of more palatable forage (Willms et al. 1980). Opportunities for seedling establishment would also be enhanced by removal of the litter barrier. Heavy grazing for several years will also reduce litter and eventually create bare patches for seed to establish and possibly result in increased pocket gopher activity (Dormaar and Willms 1990). However, smooth brome would still be more competitive than native seedlings.

Herbicide could then be applied to the remaining smooth brome and Kentucky bluegrass during active growth. It is likely that more than one herbicide application will be required. Cultivation to prepare a seedbed for drill seeding of native species may stimulate seed bank germination and growth from remaining rhizomes. It is important to eliminate or reduce smooth brome and Kentucky bluegrass as much as possible because they are much more competitive than seedlings of native species which establish slowly. For this reason, herbicide may be applied more than once prior to seeding or seedling emergence. Establishment of noxious or perennial weeds must be prevented, however, short-lived weedy species may be allowed to remain to provide cover, reduce erosion and moderate the microclimate. Incorporation of sawdust prior to seeding to reduce available soil nitrogen may reduce smooth brome growth and increase bare ground for native species to establish (Wilson and Gerry 1995). Mowing may also be used to reduce competition of any remaining smooth brome and Kentucky bluegrass.

In smooth brome stands which have not been grazed for several years, herbicide effectiveness may be increased by defoliation prior to herbicide application which releases apical buds and stimulates growth. Established tillering rhizomes are essentially independent of the parent plant, and although they remain physically attached, there is little exchange of carbohydrates (Nyahoza et al. 1973). However, when defoliated, tillers become a sink for assimilate from nondefoliated tillers, whether from parent or rhizome tillers (Nyahoza et al. 1973). In the current study, herbicide was applied to actively growing but relatively mature tillers and it is likely that the herbicide only affected the tiller immediately contacted and was not translocated to other tillers. Had the stand been actively regrowing from defoliation prior to herbicide application, it is possible that greater herbicide translocation may have taken place. However, by the time the tillers were tall enough to be wicked, they may have become independent.

Kentucky Bluegrass Stands

In Kentucky bluegrass stands with large accumulations of litter where roots tend to be shallow, a hot burn during active spring growth may be used to set back development and weaken Kentucky bluegrass. Subsequent grazing may pull many of the remaining shallow rooted tillers from the sod. Negative impact on native species is not a concern because few grow in such stands. Spring burning prior to growth and burning late in the growing season would not be recommended since they promote tiller and seed production (Chapter 3; Hickey and Ensign 1983).

Mixed Stands

Multi-season grazing may be used to reduce smooth brome and to accomodate rough fescue intolerance of summer grazing. Smooth brome may be repeatedly grazed in the summer with minimal impact on rough fescue by removing the animals just as or before they begin to graze rough fescue which is less palatable. Weekly summer clipping to 20 cm did not reduce rough fescue vigour in interior British Columbia (McLean and Wikeem 1985). In autumn and winter, rough fescue becomes the forage of choice because it maintains its forage quality. Dormant season grazing increases fescue tiller density and reduces litter and its water holding capacity (Willms et al. 1986; Naeth et al. 1991a, 1991b). The resulting drier microclimate may deter invasion by smooth brome and Kentucky bluegrass.

Where stands are large enough, dormant spring burning of smooth brome stands could be used to focus grazing on smooth brome. Litter removal by burning increases productivity and quality of forage and preference and utilization by deer and cattle (Willms et al. 1980). The resulting high degree of forage utilization may lead to plant death (Willms et al. 1980).

A dormant spring burn may be used to stimulate smooth brome growth, increase height differential with native species and enhance herbicide application (Grilz 1992). Herbicide effectiveness in smooth brome stands which have not been grazed for several years may also be increased by moderate grazing to release apical buds and increase tillering prior to application. Herbicide application will be most effective if the site and the surrounding area are grazed or mowed to prevent smooth brome and Kentucky bluegrass seed set for several years prior to application. Herbicide wicking will not eliminate smooth brome and follow-up applications will be required. It is possible that the composition of the seed bank will not be sufficient to restore native grassland in the smooth brome stands. Native seed could also be broadcast after the burn if sufficient soil is exposed. However, the burned areas will have a hotter, drier microclimate and seedling establishment will be more difficult. Soil disturbance from drill seeding could stimulate germination and favour the establishment of Kentucky bluegrass which may be the dominant species of the seed bank. Mowing may be used to reduce competition and shading by persisting smooth brome and Kentucky bluegrass.

SUMMARY

In chapter two, the vegetation, litter and seed bank of smooth brome stands in foothills fescue grasslands were documented. Smooth brome is a strongly competitive species; its greater height, biomass and litter production likely all contributed to the reduced species diversity in the study blocks relative to native grassland. Chapter two provides the context or baseline in which chapter three research was conducted and is thus useful in interpreting chapter three results and potential future impacts.

Grazing history (i.e., not being grazed for several years prior to the study) likely influenced smooth brome and Kentucky bluegrass response to treatment. Defoliation and glyphosate wicking reduced the plant canopy, increased light to the remaining plants and removed apical dominance, thereby stimulating tillering. The more intense the defoliation, the more plant material removed and litter trampled and the greater the increase in tillering which persisted for a longer period of time. Burning reduced litter and stimulated Kentucky bluegrass tillering; mowing further increased tillering by removing apical dominance. Flowering of smooth brome and Kentucky bluegrass, also influenced by light, was stimulated in all treatments except the reference.

Two years of heavy defoliation in the current study did not stress smooth brome sufficiently to reduce tiller density, etiolated regrowth or TNC. Only one grazing event was conducted in each of the grazing treatments in 1994 because of the time taken to establish the study site and collect baseline data. Obviously, the treatments would have been more intense had more defoliations been conducted in the first year.

Repeated glyphosate wicking caused the greatest reduction in smooth brome tiller density. Smooth brome tiller density increased in 1995 even though additional glyphosate wickings were applied. This may have been due to stimulation of tillering by the decrease in canopy due to tiller death the previous year. Also, September data would have included the autumn flush of tillering which occurs in cool season grasses. Glyphosate may be more effective when applied later in the season as it was in 1994. Wicking, when applied to avoid desirable species, will never eliminate smooth brome; as the number of smooth brome tillers extending above the desirable species decreases, herbicide application and effectiveness will decrease.

Stage of plant development may be critical in determining treatment effectiveness. Spring burning reduced smooth brome which was beginning to grow at the time of the burn but stimulated tillering by Kentucky bluegrass which was dormant. Fire may be used to reduce smooth brome by burning actively growing smooth brome or by burning dormant smooth brome to enhance growth and herbicide application.

The order in which treatment elements are combined is important. Glyphosate wicking followed by mowing was not an effective treatment. The short term stimulation in tillering caused by mowing compensated for the tillers previously killed by glyphosate, resulting in no net change in smooth brome. A more effective combination would have been to first mow the area to stimulate tillering and then apply herbicide.

Kentucky bluegrass, the subdominant species of smooth brome stands, increased in tiller density, composition and seed production in all treatments except the reference. Growth of Kentucky bluegrass was likely favoured by reduced competition from smooth brome due to glyphosate wicking and somewhat selective grazing. Kentucky bluegrass appeared to have a greater tolerance to defoliation than smooth brome and remained above baseline levels for a longer period of time.

Although the impact of the 1994 and 1995 treatments may have been most dramatically expressed in spring 1996, data collected during the autumn flush of tillering may provide an indication of treatment longevity. The increase in smooth brome tillering had subsided one year after treatments in all but the heaviest defoliation treatment, however, a decrease in composition persisted for at least one year for three of the heaviest defoliation treatments. In the herbicide treatments, tillering had also subsided in 1996, possibly because of increased canopy and shading or a later flush of autumn tillering than the previous year due to a dry summer. Kentucky bluegrass tiller density and composition remained greater than baseline levels in 1996 in all treatments except the least intense defoliation and the reference. Smooth brome tiller and Kentucky bluegrass density and composition did not change over time in the reference.

Although Kentucky bluegrass was the dominant species of the seed bank in smooth brome stands, seedling establishment was not the reason for its increase in response to treatment. In all treatments except those which were burned, litter provided an effective barrier to seedling emergence. Even in the burned plots where two thirds of the litter was removed, the spring and autumn increase in Kentucky bluegrass tillers appeared to be due to tillering and not seedling establishment. Kentucky bluegrass and smooth brome readily established on pocket gopher mounds by rhizomes not seedling establishment. A few of the annual weedy forbs documented in the seed bank also readily established on the pocket gopher mounds. Larger, more dramatic soil disturbances would likely be required for the seed bank to play a larger role.

The composition of the seed bank differed from the vegetation of the existing smooth brome stands and the native fescue grassland. No rough fescue and relatively few other native grasses were present in the seed bank. Based on the species composition of the seed bank, foothills rough fescue grassland would not be regenerated from the seed bank if smooth brome were successfully eliminated. Although there were relatively few seeds of smooth brome in the seed bank, it is likely that there are sufficient to maintain this species even if the topgrowth and rhizomes were to be killed. For the purposes of reducing smooth brome and Kentucky bluegrass in the seed bank, smooth brome stands should be defoliated every year, at least once a year during elongation or later, to prevent these grasses from setting seed.

An understanding of the issues and questions arising from this study may be contributed by research in the following areas. To fully evaluate treatment impact, the grazing and mowing treatments need to be implemented for a few more years and an extended period of post-treatment monitoring is required to determine the longevity of treatment impact. Treatments worthy of future research include: increased frequency and intensity of defoliation; defoliation prior to glyphosate application to stimulate growth and enhance application; potential use of growing season fires in cool season grassland to reduce smooth brome and Kentucky bluegrass; burning (growing or dormant season) to increase intensity of subsequent grazing. The influence of grazing history (e.g. heavily grazed versus ungrazed) on treatment impacts is also worthy of investigation. Although it is assumed that the expansion of smooth brome and Kentucky bluegrass is greatest under moist conditions, the influence of weather cycles (e.g. drought) on the rate of smooth brome expansion in various ecoregions is not known. Much may be gained from monitoring community boundaries over time and under various management techniques.

CONCLUSION

Restoration of native grassland is most likely to succeed when seeds and plants of desired species are present. Old smooth brome fields, where the seed bank and vegetation are depleted of native species, challenge our limited knowledge of grassland restoration. Management of mixed areas containing stands of smooth brome and native grassland requires the ability to understand and balance treatment impacts on native and introduced species.

It may not be possible to eliminate smooth brome from an area. Combinations of management techniques may only reduce smooth brome in the short term or minimize its further expansion. Treatment impact on other species must always be considered, especially when Kentucky bluegrass, an equally competitive species, is often present in the seed bank and is able replace smooth brome or native grasses when given the opportunity.

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APPENDIX A.

HISTORY AND IMPACT OF LAND MANAGEMENT IN THE RESEARCH AREA

HISTORY AND IMPACT OF LAND MANAGEMENT IN THE RESEARCH AREA

Land Management History

The history of the areas encompassing the study blocks was interpolated from aerial photographs taken in 1920, 1944, 1950, 1962, 1966, 1974, 1976, 1979, 1980, 1982 and 1987. It appears that both natural invasion and cultivation played a role in the establishment of smooth brome in Blocks 1 and 2. Cultivation and seeding were the key factors in establishment of smooth brome in Blocks 3 and 4 which are located in old agricultural fields.

In 1920, an agricultural field was in the process of being established in vicinity of Block 1. In 1944, smooth brome appeared to cover Block 1, due to either cultivation and seeding or natural expansion; small fields were evident lower in the valley and immediately to the east of Block 1. There was no evidence of subsequent field work in the area.

Other blocks remained in their natural state in 1920 but by 1944, the field adjacent Block 2 was established. In May 1976, it appears that this adjacent hayfield had been enlarged to extend into the area of Block 2. By 1980 and 1982, the area to the west of block 2 and also adjacent to the hay field is also clearly covered by a different grass than the hillside, presumably smooth brome, whether due to natural invasion or another seeding event is unknown. Again in September 1987, this area was darker in the photographs, possibly due to reseeding or grazing differences (a fence divided the zone prior to decommissioning of fences under management of the conservation area). It is unknown whether the extent of smooth brome expansion from the hayfield has been most influenced by cultivation, time or the dramatic topographic change from gently rolling till plain plateau to steep south facing hillside.

Blocks 3 and 4 were grazed in 1920, established as fields by 1944 and have been more frequently hayed (especially Block 4) or grazed. It is also expected that these fields have been cultivated and reseeded more frequently than Blocks 1 and 2. The most recent reseeding was prior to 1985 (Rempel 1995).

The land use regime in the 1980s was fall grazing in Block 1, mid-summer grazing in Blocks 2 and 3 and haying in Block 4 (Rempel 1995). Cattle grazing was not conducted for seven years prior to this study.

Impact of Land Management on Vegetation and Soils

Although the site history is not completely known, it is possible that some impacts of land management may be inferred from the differences between invaded/seeded blocks (1 and 2) and the seeded and more frequently disturbed blocks (3 and 4) (Appendix B, Table 4).

Smooth brome establishment reduced species richness from 25 species on native stands to 17 species on invaded/seeded sites and 8 on frequently disturbed sites (Table 2). Native graminoids comprised over half of the biomass from native stands but were almost eliminated by the invasion and seeding of smooth brome. *Danthonia parryi* Scribn. (Parry oat grass), *Festuca campestris* Rydb (foothills rough fescue) and *Agropyron* Gaertn. spp. (wheat grass) were the dominant native grass species of the native stands. Smooth brome, native forb and shrub composition and Kentucky bluegrass tiller density were greater in more frequently disturbed sites (blocks 3 and 4). Seedling emergence was similar from both site types (Table 3).

There were no obvious differences in soil properties, however, earthworm activity was only observed in the seeded/frequently disturbed blocks. Reduced litter mass and the absence of an organic mat in the seeded blocks was attributed to incorporation of organic material and enhancement of decomposition by earthworms, originally introduced by farm implements. Even so, the litter layer was as thick as naturally invaded blocks and would be an impediment to germination. Although the soil may eventually change in response to earthworm activity and vegetation, there were no obvious differences between site types in 1994.

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Table 1. Vegetation cover (km^2 and %) of the Ann and Sandy Cross Conservation Area over time (Steeves 1993).

Year	Native Grassland	Cultivated Meadows	Trees and Shrubs
1926	3.07 40%	0.48 6%	4.13 54%
1944	0.94 14%	1.70 22%	4.79 62%
1962	0.84 11%	1.93 25%	4.89 63%
1993	0.65 8%	1.96 25%	5.09 66%

Table 2. Influence of site history on vegetation, ground cover and litter of smooth brome and native stands in July 1994.

	Smooth Brome Stands				Native Stands	
Parameter	Invaded/ Seeded (Blocks 1 & 2)	Seeded (more frequently) (Blocks 3 & 4)	SEM†	P‡	Mean	SEM†
Richness						
Introduced Grasses§	2.0	2.2	0.1	0.02	1.0	0.0
Native Grasses/Sedges	2.0	0.1	0.2	<.01	7.3	0.2
Introduced Forbs	1.0	1.3	0.2	0.23	1.0	0.2
Native Forbs	10.2 a	3.9 b	0.5	<.01	13.5	0.9
Native Shrubs	1.7	0.6	0.1	<.01	2.3	0.1
Total	16.8 a	8 b	0.7	<.01	25.0	0.9
Species Composition (%)						
Smooth Brome	47 b	68 a	3	<.01	0	0
Kentucky Bluegrass	18	15	1	0.06	25	3
Other Introduced Grasses	0	2	1	0.08	0	0
Native Grasses/Sedges	3	0	1	<.01	53	3
Introduced Forbs	1	4	1	<.01	1	0
Native Forbs	22a	8 b	1	<.01	15	1
Native Shrubs	9a	4 b	1	<.01	8	0
Ground Cover (%)						
Live Vegetation	11a	8 b	0	<.01	10	0
Litter	89 b	92 a	0	<.01	84	1
Tiller Density (tillers m^{-2})						
Smooth Brome	561	621	22	0.06		
Kentucky Bluegrass	601 a	425 b	41	<.01		
Biomass (kg ha^{1})						
Smooth Brome	3020	2780	182	0.36		
Other Graminoids	462	275	44	<.01		
Forbs	439	198	52	<.01		
Shrubs	249	109	47	0.04		
Total	4169 a	3363 b	164	<.01		
Litter						
Mass (kg ha-1)						
Standing	381	265	53	0.13		
Fallen	3165 b	4394 a	179	<.01		
Partially Decomposed	4393 a	1654 b	141	<.01		
Total	7940 a	6314 b	267	<.01		
Depth (cm)	6.3	6.1	0.2	0.42		

[†] Standard error of the mean.

[‡] Probability of significant difference.

[§] Introduced grasses include Kentucky bluegrass.

t' indicates less than 1% species composition.

For smooth brome stands, N=480 for species richness, species composition and groundcover; N=240 for tiller density, biomass and litter. For native stands, N=60.

Table 3. Influence of site history on emergence (seedlings m^{-2}) from soil and litter of smooth brome stands in Autumn 1995.

Plant Group	Invaded/ Seeded (Blocks 1 & 2)	Seeded (more frequently) (Blocks 3 & 4)	SEM[†]	P[‡]
<u>Litter</u>				
Monocots	724	300	225	0.31
Kentucky Bluegrass	672	272	224	0.33
Smooth Brome	16	24	8	0.55
Other Introduced Grasses	4	4	4	
Native Grasses/Sedges	8	0	6	0.42
Unidentified Graminoids	24	0	6	0.10
Dicots	100	20	60	0.45
Introduced Forbs	12	4	4	0.29
Native Forbs	68	12	43	0.46
Unidentified Forbs	20	4	14	0.51
Native Monocots/Dicots	76	12	49	0.45
Total	824	320	177	0.18
<u>Soil</u>				
Monocots	719	1173	496	0.58
Kentucky Bluegrass	633	1081	470	0.57
Smooth Brome	40	75	24	0.41
Other Introduced Grasses	6	6	6	
Native Grasses/Sedges	6	6	6	1.00
Unidentified Graminoids	35	6	25	0.50
Dicots	546	391	80	0.30
Introduced Forbs	138	63	81	0.58
Native Forbs	368	213	156	0.55
Unidentified Forbs	40	115	17	0.09
Native Monocots/Dicots	374	219	161	0.57
Total	1265	1564	426	0.67

[†] Standard error of the mean.

[‡] Probability of significant difference.

N=80.

APPENDIX B.
SUPPLEMENTARY DATA

Table 1. Mean temperature (°C) and total precipitation (mm) for High River[†] for the years 1994 to 1996.

Climate Parameter	Jan	Feb	Mar	April	May	June	July	Aug	Sept	Oct	Nov	Dec	Annual
Mean Temperature (°C)													
1994	-7.3	-13.5	2.5	4.9	9.5	12.3	16.8	15.4	12.9	5.3	-2.9	-4.9	4.3
1995	-6.0	-6.2	-2.5	2.2	7.7	12.2	14.3	12.9	10.9	3.9	-3.7	-9.7	3.4
1996	-14.4	-4.7	-5.7	5.0	5.6	12.7	15.5	16.3	8.5	4.4	-9.6	-13.3	1.6
30 year mean (1961-1990)	-9.1	-6.1	-2.6	3.5	8.7	12.9	15.2	14.7	9.8	5.5	-2.4	-7.7	3.5
Total Precipitation (mm)													
1994	20.0	28.4	14.8	19.0	90.2	87.0	34.2	80.0	3.0	35.8	30.8	15.4	458.6
1995	1.2	25.0	13.2	55.6	149.2	112.2	105.0	52.4	61.0	47.4	47.0	32.8	702.0
1996	39.6	18.0	61.2	8.1	159.6	58.2	32.6	9.6	82.2	17.4	68.8	51.2	606.5
30 year mean (1961-1990)	23.0	22.6	26.5	40.9	60.3	86.8	58.7	55.5	47.1	19.9	18.8	25.2	485.3

[†] The elevation of High River is 1200 m and the elevation of the study site is 1200-1300 m.

Source: Environment Canada.

Table 2. Untransformed datasets which did not pass Wilcox test for normality of experimental error.

Dataset	Type of Statistical Analyses
Soil	
Water Holding Capacity	15 bar at 75-90 cm
EC	0-15 cm; 75-90 cm
Species Composition	
Introduced Graminoids	July 1994; September 1995; September 1996; split block
Native Graminoids	July 1994; September 1995; September 1996; split block
Introduced Forbs	September 1996; split block
Native Shrubs	September 1995; split block
Plot Richness	
Introduced Graminoids	July 1994; September 1995; September 1996; split block
Ground Cover[†]	
Litter	July 1994; September 1996; split block
Live	September 1996
Litter Mass	
Standing	June 1994; September 1994; split block
Fallen	September 1994
Biomass	
Shrubs	July 1994
Seedling Emergence	
Soil	Total
Litter	Other Introduced Grasses
Litter-Soil	Native Grasses; Other Introduced Grasses
Total Nonstructural Carbohydrates	September 1995
Etiolated Regrowth	
Smooth Brome	10°C; 22°C
Kentucky bluegrass	10°C; 22°C

[†] Outlier values were quadrats which contained pocket gopher mounds.

Table 3. Soil particle size and texture in smooth brome stands in June 1994.

Textural Properties	Block 1	Block 2	Block 3	Block 4	Mean	SEM[†]	P[‡]
0-15 cm							
% sand	26.0	29.9	25.7	20.9	25.6	1.7	0.06
% silt	37.8	33.9	37.1	37.1	36.5	2.2	0.63
% clay	36.2	36.2	37.2	42.0	37.9	1.4	0.07
Texture	clay loam	clay loam	clay loam	clay	clay loam		
15-30 cm							
% sand	25.2	24.7	26.7	19.6	24.0	1.4	0.04
% silt	42.3	38.2	35.7	37.9	38.5	2.3	0.30
% clay	32.5	37.1	37.6	42.6	37.4	2.0	0.06
Texture	clay loam	clay loam	clay loam	clay	clay loam		
30-45 cm							
% sand	29.7	23.7	27.5	19.9	25.2	2.7	0.16
% silt	40.8	35.4	39.6	37.7	38.4	1.9	0.32
% clay	29.6	40.9	32.9	42.5	36.5	2.6	0.04
Texture	clay loam	clay	clay loam	clay	clay loam		
45-60 cm							
% sand	32.2		25.1	20.3	25.9	5.1	0.34
% silt	39.6		39.5	43.7	40.9	2.9	0.56
% clay	28.2		35.4	36.0	33.2	4.7	0.49
Texture	clay loam		clay loam	clay loam	clay loam		
60-75 cm							
% sand	32.9		22.8		27.9	4.2	0.23
% silt	39.1		40.4		39.8	1.1	0.48
% clay	28.0		36.7		32.4	3.7	0.24
Texture	clay loam		clay loam		clay loam		

[†] Standard error of the mean.

[‡] Probability of significant difference among blocks based on analysis of variance.

N=12 for 0-45 cm depths, N=9 for 45-60 cm and N=6 for 60-75 cm.

Table 4. Soil carbon content, water retention capacity, electrical conductivity and pH in smooth brome blocks in June 1994.

Parameter/ Depth (cm)	Block 1	Block 2	Block 3	Block 4	Mean	SEM[†]	P[‡]
Carbon Content (%)							
0-15	7.0	9.8	8.0	6.6	7.9	0.6	<0.01
15-30	5.2	3.7	5.6	4.4	4.7	0.2	<0.01
30-45	3.5	2.0	2.4	2.3	2.5	0.3	0.04
Water Holding Capacity (%)							
1/3 Bar							
0-15	38.8	42.2	41.8	42.4	41.3	0.9	0.03
15-30	35.0	34.4	39.2	39.0	36.9	0.8	<.01
30-45	29.7	30.6	33.7	34.8	32.2	0.7	<.01
45-60	26.6		31.1	31.7	29.8	0.9	<.01
60-75	25.6		29.8		27.7	0.7	<0.01
15 Bar							
0-15	24.6	29.2	25.8	26.9	26.6	0.8	<.01
15-30	20.5	19.0	20.7	24.0	21.1	0.6	<.01
30-45	16.0	15.7	16.8	20.3	17.2	0.7	<.01
45-60	13.6		15.3	18.2	15.7	0.7	<.01
60-75	12.7		14.8		13.8	0.3	<.01
Available Water Holding Capacity							
0-15	14.1	12.9	16.0	15.5	14.7	0.9	0.10
15-30	14.5	15.4	18.5	15.0	15.8	0.6	<.01
30-45	13.6	14.9	16.9	14.5	15.0	0.5	<.01
45-60	13.0		15.9	13.5	14.1	0.5	<.01
60-75	12.8		15.0		13.9	0.5	0.02
Electrical Conductivity (dS m^{-1})							
0-15	0.3	0.3	0.4	0.3	0.3	0.0	0.35
15-30	0.2	0.1	0.2	0.2	0.2	0.0	<0.01
30-45	0.1	0.1	0.1	0.1	0.1	0.0	0.41
45-60	0.1		0.1	0.1	0.1	0.0	0.38
60-75	0.1		0.1		0.1	0.0	0.28
pH							
0-15	6.5	6.5	6.5	6.6	6.5	0.1	0.88
15-30	7.0	6.8	6.8	6.8	6.8	0.1	0.31
30-45	7.4	6.7	7.1	7.1	7.1	0.1	<0.01
45-60	7.6		7.6	7.3	7.5	0.1	0.25
60-75	7.7		7.7		7.7	0.1	1.00

[†] Standard error of the mean.

[‡] Probability of significant differences among blocks based on analysis of variance.

N=48 except N=12 for 35-45 cm carbon content, N=36 for 45-60 cm EC and pH, N=24 for 60-75 cm water holding capacity, N= 23 for 60-75 cm pH and N=22 for 60-75 cm EC.

Table 5. Ground cover, litter and vegetation characteristics of smooth brome stands in June-July 1994.

	Block 1	Block 2	Block 3	Block 4	Mean	SEM[†]	P[‡]
Ground Cover (%)							
Litter	89	88	91	92	90	1	<0.01
Live Vegetation	10	12	9	7	10	0	<0.01
Litter							
Mass (kg ha^{-1})							
Standing	390	372	128	402	323	80	
Fallen	2830	3500	4360	4428	3780	265	<0.01
Partly/Fully Decomposed	4314	4474	1998	1310	3024	186	<0.01
Total	7534	8346	6486	6142	7127	370	<0.01
Depth (cm)	6.1	6.6	6.5	5.6	6.2	0.3	0.11
Biomass (kg ha^{-1})							
Smooth Brome	3472	2567	2930	2630	2900	236	0.04
Other Grasses/Sedges	265	659	294	256	369	60	
Forbs	277	601	133	264	319	71	<0.01
Shrubs	469	28	214	5	179	67	
Total	4482	3856	3571	3154	3766	220	<0.01
Plot Richness							
Introduced Grasses[§]	2.0	2.0	2.3	2.0	2.1	0.1	
Native Grasses/Sedges	2.0	1.9	0.2	0.0	1.0	0.2	<0.01
Introduced Forbs	0.4	1.5	0.6	1.9	1.1	0.2	<0.01
Native Forbs	10.3	10.1	5.0	2.8	7.1	0.7	<0.01
Native Shrubs	1.7	1.8	1.1	0.2	1.2	0.1	<0.01
Total	16.4	17.3	9.2	6.9	12.5	0.9	<0.01
Species Composition (%)							
Smooth Brome	50	44	67	70	57	3	<0.01
Kentucky Bluegrass	13	22	14	15	16	1	<0.01
Other Introduced Grasses	0	0	3	0	1	1	
Native Grasses/Sedges	2	3	t	0	1	1	
Introduced Forbs	t	2	1	7	3	1	<0.01
Native Forbs	19	25	7	8	15	2	<0.01
Native Shrubs	16	3	7	t	7	1	<0.01
Tiller Density (tillers m^{-2})							
Smooth Brome	574	548	654	589	591	30	0.09
Kentucky Bluegrass	515	686	354	497	513	57	<0.01

[†] Standard error of the mean.

[‡] Probability of significant differences among blocks based on analysis of variance.

[§] Introduced grasses include Kentucky bluegrass.

't' indicates species composition was less than 1%.

N=480 for ground cover and species composition; N=240 for litter, biomass and tillers;
N=48 for plot richness.

Table 6. Plant species composition (%) of smooth brome stands in July 1994.

Species	Block 1	Block 2	Block 3	Block 4	Mean
Introduced Grasses					
Bromus inermis	50	44	67	70	58
Phleum pratense	*	*	3	*	1
Poa pratensis	13	22	14	15	16
Native Grasses					
Agropyron sp.	t	t	t		t
Calamagrostis montanensis		t			t
Carex sp.	2	t	t		t
Danthonia parryi	t	t			t
Festuca campestris	t	2			1
Koeleria macrantha	*				*
Introduced Forbs					
Arctium sp.		*		*	*
Chenopodium album		*			*
Cirsium arvense	t	2	1	5	2
Medicago sativa				2	t
Melilotus officinalis	t				t
Polygonum convolvulus				*	*
Sonchus asper	*				*
Sonchus sp.			*		*
Taraxacum officinale		t	t	t	t
Thlaspi arvense		t		t	t
Tragopogon dubius	*	1	*	1	t
Trifolium hybridum				*	*
Trifolium pratense			*		*
Native Forbs					
Achillea millefolium	1	1	1	t	1
Agoseris glauca		1	t	*	t
Allium sp.		*			*
Anemone cylindrica	t		t		t
Anemone multifida	t	*			t
Anemone patens	t	*			t
Arabis hirsuta	*				*
Artemisia dracunculus		*			*
Artemisia ludoviciana	4	2	1	*	2
Aster ericoides	t	t	t	*	t
Aster laevis	t	t	t	*	t
Astragalus dasyglottis	t	t	1		1
Astragalus sp.			*		*
Campanula rotundifolia		t	*	*	t
Cerastium arvense	t	t		t	t
Comandra umbellata	t	t			t
Erigeron speciosus		1	t	2	1
Fragaria virginiana	t	*			t

Table 6 (continued)

Species	Block 1	Block 2	Block 3	Block 4	Mean
Gaillardia aristata	*	*	*	*	*
Galium boreale	1	3	2	t	2
Gentianella amarella	t				t
Geranium viscosissimum	t	t	t	1	t
Geum triflorum	t	t	t		t
Glycyrrhiza lepidota		*			*
Hedysarum alpinum		*			*
Helianthus subrhomboideus	1	1			0
Heterotheca villosa	*	*			*
Heuchera richardsonii		t			t
Lactuca pulchella		*	1		t
Lathyrus ochroleucus	t	t		*	t
Linum lewisii	t	*			t
Lithospermum ruderale	1	*	*	*	t
Lupinus sericeus	1	6	t	*	2
Monarda fistulosa	4	t	t	*	1
Oxytropis splendens		*			*
Oxytropis sp.	*				*
Potentilla arguta		t			t
Potentilla gracilis		*	*		*
Potentilla pensylvanica		*		t	t
Potentilla sp.		t			t
Silene drummondii	*				*
Sisyrinchium montanum	*	*			*
Smilacina stellata	t		*		t
Solidago canadensis	1				t
Solidago missouriensis	t	1	t	3	1
Thermopsis rhombifolia	3	6	t	1	3
Urtica dioica			*		*
Vicia americana	1	1	t	t	1
Viola sp.			*		
<u>Native Shrubs</u>					
Amelanchier alnifolia	t		*		t
Prunus virginiana	*				*
Rosa sp.	1	3	t	t	1
Salix bebbiana	*				*
Symphoricarpos occidentalis	15	t	7	t	5
Pleurozium sp.	t		t		t
Unknown	t	t	t		t

't' indicates species composition was < 1%.

'*' indicates species found in plots but not in quadrats.

N=480.

Table 7. Species frequency† in smooth brome stands in July 1994.

Species	Block 1	Block 2	Block 3	Block 4	Mean	SEM‡
Introduced Grasses						
Bromus inermis	100	99	100	100	100	0
Phleum pratense	96	99	83	97	94	4
Poa pratensis			21		5	5
Native Grasses						
Agropyron sp.	6	7	1		3	2
Calamagrostis montanensis		10			3	3
Carex sp.	29	4	2		9	8
Danthonia parryi	2	2			1	0
Festuca campestris	6	6			3	0
Introduced Forbs						
Cirsium arvense	5	15	9	18	12	3
Medicago sativa	1			12	3	3
Taraxacum officinale		1	2	1	1	0
Thlaspi arvense		1		1	t	0
Tragopogon dubius		4		6	2	1
Native Forbs						
Achillea millefolium	33	32	15	3	20	7
Agoseris glauca		16	1		4	4
Anemone cylindrica	1		1		t	0
Anemone multifida	6				1	1
Anemone patens	1				t	0
Artemisia ludoviciana	48	17	14		20	10
Astragalus dasyglottis	3	7	15		6	3
Aster ericoides	5	5	1		3	1
Aster laevis	4	3	2		2	1
Campanula rotundifolia		2			t	0
Cerastium arvense	1	1		1	1	0
Comandra umbellata	7	4			3	2
Erigeron speciosus		3	1	5	2	1
Fragaria virginiana	2				t	0
Galium boreale	18	70	21	5	28	14
Gentianella amarella	5				1	1
Geranium viscosissimum	2	1	3	3	2	1
Geum triflorum	2	4	1		2	1
Helianthus subrhomboideus	3	5			2	1
Heuchera richardsonii		1			t	0
Lactuca pulchella			9		2	2
Lathyrus ochroleucus	6	3			2	1
Linum lewisii	1				t	0
Lithospermum ruderale	8				2	2
Lupinus sericeus	5	34	1		10	8
Monarda fistulosa	33	2	3		9	8

Table 7 (continued)

Species	Block 1	Block 2	Block 3	Block 4	Mean	SEM
Potentilla arguta		1			t	0
Potentilla pensylvanica				1	t	0
Potentilla sp.		1			t	0
Smilacina stellata	1				t	0
Solidago canadensis	3				1	1
Solidago missouriensis	3	13	2	8	7	3
Thermopsis rhombifolia	35	58	2	7	25	13
Vicia americana	23	22	8	10	16	4
Native Shrubs						
Amelanchier alnifolia	1				t	0
Rosa sp.	10	35	3	1	12	8
Symphoricarpos occidentalis Hook.	79	9	29	1	30	18

[†] Calculated as the percentage of quadrats in a plot in which a species occurred.

[‡] Standard error of the mean.

't' indicates frequency was less than 1%.

N=48.

Table 8. Emergence (seedlings m^{-2}) from soil and litter collected from smooth brome and native grass stands in Autumn 1994 and vegetative composition of these areas.

Species	Smooth Brome			Native Grass		
	Soil	Litter	Vegetation (%)	Soil	Litter	Vegetation (%)
<u>MONOCOTS</u>	946 (129)	512 (98)		840 (177)	498 (91)	
<u>Introduced</u>						
Bromus inermis	58 (18)	20 (7)	58 (1)		4 (4)	
Phleum pratense	6 (4)	4 (3)	1 (0)			
Poa pratensis	857 (126)	472 (98)	16 (1)	607 (176)	422 (93)	25 (3)
<u>Native</u>						
Agropyron sp.		4 (4)	t	6 (4)		10 (2)
Bouteloua gracilis						1 (1)
Calamagrostis montanensis			t			1 (1)
Calamovilfa longifolia						1 (1)
Carex sp.	6 (4)		t	86 (25)	20 (10)	4 (1)
Danthonia parryi			t	58 (44)	16 (6)	18 (3)
Festuca campestris			1 (0)	6 (4)	8 (6)	10 (3)
Helictotrichon hookeri					2 (2)	*
Koeleria macrantha			*	20 (10)		4 (1)
Muhlenbergia richardsonis						2 (1)
Stipa columbiana				3 (3)		
Stipa curtiseta						2 (1)
Stipa viridula						t
Unidentified Grasses	20 (17)	12 (6)		55(14)	26 (9)	
<u>DICOTS</u>	469 (75)	60 (18)		805 (127)	70 (29)	
<u>Introduced</u>						
Arctium sp.			*		2 (2)	
Artemisia absinthium				43 (19)	10 (7)	
Chenopodium album		2 (2)	*	6 (6)		
Cirsium arvense	26 (9)		2 (0)	9 (5)		t
Medicago sativa			t			
Melilotus officinalis			t			
Plantago major	3 (3)					
Polygonum convolvulus			*			
Sonchus asper			*			
Sonchus sp.			*			
Taraxacum officinale	6 (4)	2 (2)	t			t
Thlaspi arvense	66 (33)	4 (3)	t	6 (6)		t
Tragopogon dubius			t			
Trifolium hybridum			*			
Trifolium pratense			*			
<u>Native</u>						
Achillea millefolium	3 (3)	2 (2)	1 (0)	14 (7)		t
Agoseris glauca			t			t
Allium sp.			*	3 (3)		*
Androsace septentrionalis	164 (49)	2 (2)		290 (52)		t
Anemone cylindrica	6 (6)	4 (4)	t			

Table 8 (continued)

Species	Smooth Brome Soil	Smooth Brome Litter	Smooth Brome Vegetation (%)	Native Grass Soil	Native Grass Litter	Native Grass Vegetation (%)
Anemone multifida			t			*
Anemone patens			t			t
Antennaria sp.						*
Apocynum androsaemifolium						t
Arabis divaricarpa	3 (3)				2 (2)	
Arabis hirsuta	3 (3)		*	72 (58)	26 (26)	
Artemisia campestris						t
Artemisia dracunculus			*			
Artemisia frigida						*
Artemisia ludoviciana	9 (5)		2 (0)	3 (3)	2 (2)	2 (1)
Aster ericoides			t			1 (1)
Aster laevis			t			t
Astragalus dasyglottis			1 (0)			t
Astragalus gilviflorus						t
Astragalus sp.			*	3 (3)		
Campanula rotundifolia	9 (5)	2 (2)	t	52 (32)	8 (5)	t
Cerastium arvense	9 (5)		t	9 (5)		t
Comandra umbellata			t			1 (1)
Epilobium angustifolium				6 (4)	4 (3)	
Epilobium ciliatum	3 (3)	2 (2)			2 (2)	
Epilobium sp.	3 (3)					
Erigeron caespitosus					4 (4)	t
Erigeron speciosus			1 (0)			*
Fragaria virginiana			t			
Gaillardia aristata			*			*
Galium boreale	9 (6)		2 (0)	20 (9)		2 (0)
Gentianella amarella			t			
Geranium viscosissimum			t			*
Geum triflorum			t			t
Glycyrrhiza lepidota			*			
Hedysarum alpinum			*			
Helianthus subrhomboideus			t			
Heterotheca villosa			*			*
Heuchera richardsonii	3 (3)		t			
Lactuca pulchella			t			t
Lathyrus ochroleucus			t			
Liatris punctata						t
Linum lewisii			t			t
Lithospermum ruderale		2 (2)	t	17 (17)	4 (4)	*
Lupinus sericeus			2 (0)	3 (3)		1 (1)
Monarda fistulosa	12 (12)	2 (2)	1 (0)	3 (3)		t
Oxtropis sericea						t
Oxytropis splendens			*			*
Oxytropis sp.			*			t
Petalostemon purpureum						*
Phlox hoodii						t
Potentilla arguta			t			t

Table 8 (continued)

Species	Smooth Brome			Native Grass		
	Soil	Litter	Vegetation (%)	Soil	Litter	Vegetation (%)
Potentilla fruticosa						*
Potentilla gracilis.			*			
Potentilla norvegica	32 (15)	2 (2)				
Potentilla pensylvanica			t			*
Potentilla sp.			t			
Silene drummondii			*			
Sisyrinchium montanum			*			
Smilacina stellata			t			*
Solidago canadensis	9 (5)	2 (2)	0 (0)			
Solidago missouriensis	12 (7)	2 (2)	1 (0)	12 (6)	2 (2)	2 (1)
Solidago sp.	3 (3)	8 (8)				
Thermopsis rhombifolia			3 (0)			4 (1)
Urtica dioica	3 (3)	10 (10)	*	29 (29)		
Vicia americana			1 (0)			t
Viola sp.			*			
Cruciferae	32 (16)	4 (3)		112 (34)		*
Fabaceae	3 (3)			6 (4)		
Native Shrubs						
Amelanchier alnifolia			t			2 (1)
Prunus virginiana			*			
Rosa sp.			1 (0)			2 (1)
Salix bebbiana			*			
Symphoricarpos occidentalis			5 (1)			4 (1)
Unidentified Dicots	43 (16)	8 (8)	0 (0)	92 (34)	4 (3)	0 (0)
Total	1415 (135)	572 (100)		1647 (223)	568 (102)	

Standard error of the mean is shown in brackets.

't' indicates species contributing less than 1% to species composition of the plot.

'*' indicates species found in plots but not in quadrats.

N=40 for soil and litter (Autumn 1994); N=480 for smooth brome vegetation (July 1994); N=60 for native vegetation (September 1996).

Table 9. Emergence (seedlings m^{-2}) from soil and litter collected from smooth brome and native grass stands in Autumn 1994.

Sample Type/ Plant Group	Smooth Brome						Native Grass					
	Block 1	Block 2	Block 3	Block 4	Mean	SEM[†]	Block 1	Block 2	Block 3	Block 4	Mean	SEM[†]
Soil												
Monocots	334	1104	587	1760	946	113	345	587	828	1599	840	113
Kentucky Bluegrass	299	966	506	1656	857	135	219	150	529	1530	607	135
Smooth Brome	23	58	46	104	58	12	0	0	0	0	0	12
Other Introduced Grasses	0	12	12	0	6	2	0	0	0	0	0	2
Native Graminoids	12	0	12	0	6	48	115	345	219	35	178	48
Unidentified Grasses	0	69	12	0	20	9	12	92	81	35	55	9
Dicots	644	449	449	334	469	125	483	909	828	1001	805	125
Introduced Forbs	23	253	69	58	101	27	69	115	35	35	63	27
Native Forbs	575	161	288	138	290	133	345	621	426	759	538	133
Unidentified Forbs[‡]	46	35	92	138	78	39	69	173	368	207	204	39
Total	978	1553	1035	2093	1415	138	828	1495	1656	2599	1645	138
Litter												
Monocots	480	968	96	504	512	124	544	448	208	792	498	124
Kentucky Bluegrass	440	904	56	488	472	130	424	328	192	744	422	130
Smooth Brome	8	24	32	16	20	4	0	16	0	0	4	4
Other Introduced Grasses	0	8	8	0	4	2	0	0	0	0	0	2
Native Graminoids	16	0	0	0	4	13	72	88	8	16	46	13
Unidentified Grasses	16	32	0	0	12	8	48	16	8	32	26	8
Dicots	184	16	32	8	60	37	56	56	40	128	70	37
Introduced Forbs	16	8	0	8	8	33	24	0	24	0	12	33
Native Forbs	128	8	24	0	40	6	24	56	16	120	54	6
Unidentified Forbs[‡]	40	0	8	0	12	5	8	0	0	8	4	5
Total	664	984	128	512	572	132	600	504	248	920	568	132

[†] Standard error of the mean.

[‡] Unidentified forbs were largely comprised by one Cruciferae species.

N=40.

Table 10. Species composition (%) of smooth brome stands by treatment in July 1994.

Plant Species	Treatment											
	C-M2	C-M3	C-M4	C-C3	S-S3	S-S3L	H-BM	H-M3	H-BH2	H-H	H-H2	REF
Introduced Grasses												
Bromus inermis	49	48	65	65	55	56	60	60	48	52	63	71
Phleum pratense	t	5	*	*	*	*	*	3	*	2	*	*
Poa pratensis	19	19	14	9	20	17	15	14	17	17	17	16
Native Grasses												
Agropyron sp.	t	t	t	t		t	t	t	t	t	t	
Calamagrostis montanensis			t	t			t		t	t	t	
Carex sp.	t	1	t	t	t	t	1	1	t	1	1	t
Danthonia parryi	t			t	1				*		*	
Festuca campestris	4	*	t	1	2	t	t		1	t	*	t
Koeleria macrantha		*										
Introduced Forbs												
Arctium minus				*			*					
Chenopodium album				*			*					
Cirsium arvense	4	2	1	3	1	t	2	3	4	2	1	*
Medicago sativa	t		1	*	*	1	t		1	*	1	1
Melilotus officinalis											t	
Polygonum convolvulus	*											
Sonchus asper						*						
Sonchus sp.		*										
Taraxacum officinale	t	*	*	*	*	*		t	t	*	*	
Thlaspi arvense	*		*	*	*	*	*		*	*	t	*
Tragopogon dubius	t	1	1	1	1	1	*		t	t	t	*
Trifolium pratense										*		
Trifolium hybridum	*		*			*			*			
Native Forbs												
Achillea millefolium	1	1	1	1	1	1	1	t	1	1	1	1
Agoseris glauca	t	1	t	*	1	*	t	t	t	t	*	t
Allium sp.					*						*	*
Anemone cylindrica	*	t	*						t	*	*	*
Anemone multifida		*	*			t		t	1		t	
Anemone patens	*		*		*	*			t		*	
Arabis hirsuta	*											
Artemisia dracunculus	*			*			*			*		
Artemisia ludoviciana	2	3	2	3	1	1	3	2	1	2	t	1
Aster ericoides	t	t	t	t	*	t	*	t	t	t	*	t
Aster laevis	t	t	t	*	*	*	*	t	t	*	*	t
Astragalus dasyglottis	1	t	1	t	t	t	*	t	1	2	t	t
Astragalus sp.										*		
Campanula rotundifolia	*	t		*	*	*	*		*	*	*	*
Cerastium arvense	*		*	t			t					
Comandra umbellata	*	*	t	t	t	t			t		t	*
Erigeron speciosus	1	t	*	4	1	*	3		*	1	*	*
Fragaria virginiana	t	*	*						*		*	
Gaillardia aristata	*	*	*	*	*	*	*		*	*	*	t

Table 10 (continued)

	Treatment											
Plant Species	C-M2	C-M3	C-M4	C-C3	S-S3	S-S3L	H-BM	H-M3	H-BH2	H-H	H-H2	REF
Galium boreale	2	2	1	1	1	1	2	2	1	2	1	1
Gentianella amarella	*		t			*			t		t	
Geranium viscosissimum	t	t	t	1	1	*	*	t	*	1	*	*
Geum triflorum	t	*	*	*	1	t	t	t	*	*	*	1
Glycyrrhiza lepidota	*											
Hedysarum alpinum									*		*	
Helianthus subrhomboideus	1	1			t	*		1	1			
Heterotheca villosa						*				*		*
Heuchera richardsonii			*			t	*				*	*
Lactuca pulchella		*	t	*	1	t	t		1	t	t	*
Lathyrus ochroleucus	1	t	t	*	*	t	*	t	*	*	t	t
Linum lewisii						t						
Lithospermum ruderale	t	*	t	*	*	t	*	t	*	*	1	*
Lupinus sericeus	3	2	2	1	2	4	2	t	3	2	2	t
Monarda fistulosa	1	2	t	1	1	1	1	2	2	t	1	2
Oxytropis splendens		*										
Oxtropis sp.											*	
Potentilla arguta	*		*		*	t			*		*	
Potentilla gracilis	*	*	*	*	*	*	*		*	*	*	
Potentilla pensylvanica			*	*		*				*	2	*
Potentilla sp.										t		
Silene drummondii						*						
Sisyrinchium montanum	*	*	*								*	*
Smilacina stellata		*							t			
Solidago canadensis	1				1				t	*	t	*
Solidago missouriensis	1	2	t	t	1	1	1	1	3	t	t	t
Thermopsis rhombifolia	2	1	3	2	2	4	3	2	5	4	2	4
Urtica dioica			*									*
Vicia americana	t	1	1	1	1	1	1	1	2	t	t	t
Viola sp.											*	*
Native Shrubs												
Amelanchier alnifolia	*		*	*	*	*			t			
Prunus pensylvanica			*		*							
Rosa arkansana	2	1	1	1	1	1	1	1	2	1	t	1
Salix bebbiana					*							
Symphoricarpos occidentalis	5	8	4	6	10	7	4	6	5	7	5	1
Pleurozium sp.								t	t			
Unidentified	t	t	t		t		t	t	t	t	t	

Treatment abbreviations are listed in Table 3.1.
't' indicates species composition is less than 1%.
'*' indicates species observed in plots but not in quadrats.
N=480.

Table 11. Species composition (%) of smooth brome stands by treatment in September 1995.

Plant Species	C-M2	C-M3	C-M4	C-C3	S-S3	S-S3L	H-BM	H-M3	H-BH2	H-H	H-H2	REF
	Treatment											
Introduced Grasses												
Bromus inermis	34	41	55	54	46	48	38	39	30	25	33	69
Phleum pratense	2	2	t				t	3		3		
Poa pratensis	39	33	26	19	30	29	42	40	26	26	32	20
Native Grasses												
Agropyron sp.		1	t	t		t		t	t	t	t	
Calamagrostis montanensis						t			t	t		
Carex sp.	1	1	2	t	1	2	4	t	3	t	1	t
Danthonia parryi	t							t	t		*	
Festuca campestris	4	*	*	t	2	*	*	t	2	*	*	t
Muhlenbergia richardsonis									t			
Koeleria macrantha	t											
Stipa sp.		t										
Introduced Forbs												
Arctium minus							t	*	*	*		
Chenopodium album									*		*	
Cirsium arvense	3	4	2	9	6	3	t	1	6	8	2	*
Lappula occidentalis									*			
Medicago sativa	2		3			t	t		*	t	2	t
Melilotus officinalis											t	
Polygonum convolvulus							*			*		
Taraxacum officinale	1	t	t		t	t	t	t	5	2	t	
Thlaspi arvense	*					*	*	*	1	2	2	*
Tragopogon dubius		t		*		t	t		t	1	t	*
Trifolium hybridum					1							
Native Forbs												
Achillea millefolium	1	2	3	1	1	2	1	1	1	1	1	t
Agoseris glauca		t	t			t	t	1	t	t	t	
Anemone cylindrica	*	1	t		*		*	t	t	*	t	*
Anemone sp.											1	
Anemone multifida		t	t						t			
Anemone patens									t			
Antennaria sp.		*										
Artemisia dracunculus										*		
Artemisia ludoviciana	2	3	2	1	t	1	3	t	2	6	2	1
Aster ericoides		*	1	*		t	1	t	t	t	*	t
Aster laevis	t	*	t	*	t	*	*	1	1	*	t	
Astragalus dasyglottis	1	t	1	t	t		t	1	1	2	t	1
Astragalus sp.									*			
Campanula rotundifolia	t	t	t		t	t	t	*	t	t	t	
Castilleja sp.								t				
Cerastium arvense		t		1		t	t					
Comandra umbellata							t		t		t	
Erigeron speciosus	t	1	*	2	t	t	1	t	*	3	t	t
Fragaria virginiana	t		*	t					t		*	

Table 11 (continued)

Plant Species	Treatment C-M2	C-M3	C-M4	C-C3	S-S3	S-S3L	H-BM	H-M3	H-BH2	H-H	H-H2	REF
Gaillardia aristata	*								*			
Galium boreale	1	1	1	t	t	1	1	1	3	4	3	1
Gentianella amarella									t		*	
Geranium viscosissimum		*	*	*	*	*	t	*	t	*	*	
Geum triflorum	*	t	*			t	*	t	*		*	
Habenaria viridis									*			
Helianthus subrhomboideus	t	t	t						*	*		
Heterotheca villosa	*								*		*	
Heuchera richardsonii	*		*				*	t			*	
Lactuca pulchella		t						t	1	t	2	
Lathyrus ochroleucus	t	1	*	t			t	*	1	t	t	t
Lithospermum ruderale		*			*		*	*	*		*	
Lupinus sericeus	1	t	t		t	t	*	t	2	t	1	t
Monarda fistulosa	t	t	*	1	1	t	1	1	1	t	t	2
Potentilla arguta	*		*						*	t		
Potentilla gracilis	*	*	*		*		*	*				
Potentilla pensylvanica											1	
Heuchera richardsonii											*	
Sisyrinchium montanum									t			
Solidago canadensis	*	t	t				*		1	*	*	t
Solidago missouriensis	2	1	t	t	t	2	1	t	4	t	3	t
Thermopsis rhombifolia	1	t	1	2	1	1	1	1	3	3	3	1
Urtica dioica									*		*	
Vicia americana	1	1	t	*	t	t	1	1	2	1	t	t
Viola sp.		*			*		*	t	t	t	*	
Native Shrubs												
Rosa arkansana	1	t	1	2	t	1	2	1	1	1	1	1
Salix bebbiana					*							
Symphoricarpos occidentalis	1	8	1	8	10	8	2	4	4	7	6	1
Asteraceae										1		
Unidentified			t		t	t	t	t	t			

Treatment abbreviations are listed in Table 3.1.
't' indicates species composition is less than 1%.
'*' indicates species observed in plots but not in quadrats.
N=480.

Table 12. Species composition (%) of smooth brome stands by treatment in September 1996.

	Treatment											
Plant Species	C-M2	C-M3	C-M4	C-C3	S-S3	S-S3L	H-BM	H-M3	H-BH2	H-H	H-H2	REF
Introduced Grasses												
Bromus inermis	42	42	55	55	42	55	43	37	31	33	35	76
Phleum pratense	1	2	t	*		t	*	1	*	1	*	*
Poa pratensis	24	27	23	23	37	23	34	35	29	29	40	15
Native Grasses												
Agropyron sp.				t	t	t		t	t	t		
Calamagrostis montanensis			t			t			t	t		t
Carex sp.	1	1	1	t	t	1	1	t	1	t	t	t
Danthonia parryi		t			t				t			
Festuca campestris	5	*	*	*	3	*	*	1	2	t	*	*
Koeleria macrantha		*							*	*	*	
Stipa columbiana									t			
Stipa sp.		1					*		*			
Introduced Forbs												
Arctium minus								*	*		*	
Chenopodium album								*	t		t	
Cirsium arvense	4	2	3	7	4	2	2	3	4	12	2	1
Cirsium vulgare								*				
Descurainia sophia									*		*	
Lepidium densiflorum							*					
Medicago sativa	*		1			*	t				t	t
Melilotus officinalis								*			t	
Sonchus uliginosus									*			
Taraxacum officinale	1	1				t	t		t	t		
Thlaspi arvense	*		t	*		*	t	t	3	1	2	t
Tragopogon dubius	t	1	t	*	*	1	1	1	t	1	*	t
Trifolium hybridum	*	*		t	*	*		*	*	1	t	
Native Forbs												
Achillea millefolium	1	2	2	1	1	2	1	1	1	1	2	t
Agoseris glauca	*	t	t	*	t	t	*	t	t	t	t	*
Anemone cylindrica	*	*			t	*		t	t	*	*	
Anemone multifida					t				t			*
Anemone patens		*							*			
Artemisia dracunculus				*						*		
Artemisia ludoviciana	3	4	2	1	1	1	3	1	5	4	4	1
Aster ericoides	t	t	t	t	*	t	*	t	t	t	t	*
Aster laevis	*	t	1	*	*	*	*	1	1	*	*	*
Astragalus dasyglottis	2	t	t		t		*	1	1	t		
Astragalus drummondii				*								
Astragalus sp.				t	t							
Campanula rotundifolia	t	1	*		t	t	*	*	t		t	*
Cerastium arvense	t	t		t	t	t		t				
Collomia linearis											*	
Comandra umbellata	t		t		t	t	t	t	1		t	
Epilobium latifolium									*			

Table 12 (continued)

	Treatment											
Plant Species	C-M2	C-M3	C-M4	C-C3	S-S3	S-S3L	H-BM	H-M3	H-BH2	H-H	H-H2	REF
Erigeron speciosus	2	t	t	2	*	*	3	*	*	1	*	*
Fragaria virginiana	t			t					t		*	
Gaillardia aristata	*	*		*		*	*	*			*	
Galium boreale	2	3	1	1	1	2	1	3	2	5	1	t
Gentianella amarella		*	*						t	*	*	
Geranium viscosissimum	*	t		t	*	*	*	t	*	t	*	*
Geum triflorum	*	t			t	t	t	t	*	*	*	*
Helianthus subrhomboideus	2	t		*	*					*		
Heterotheca villosa	*		*						*		*	
Heuchera richardsonii	*		*		*			t			*	t
Lactuca pulchella	t	t	t		t	*	t		1	t	1	*
Lathyrus ochroleucus	1	1	t		*		t	t	1	t	t	*
Linum lewisii												
Lithospermum ruderale	*	*	*	*	*		*	*		*	t	*
Lupinus sericeus	1	t	2	t	1	1	t	*	2	1	*	t
Monarda fistulosa	1	1	*		1	1	1	1	1	t	1	1
Potentilla arguta	*								*			
Potentilla gracilis						*	*		t			
Potentilla norvegica									t			
Potentilla pensylvanica				*					*	t	1	
Silene drummondii		t			t							
Sisyrinchium montanum									*			
Smilacina stellata												
Solidago canadensis	t		1		1		*	*	1	*	t	*
Solidago missouriensis	1	1	1	t	t	1	t	1	3	t	3	t
Thermopsis rhombifolia	1	t	1	1	2	2	1	2	1	1	2	2
Urtica dioica									*	*	*	
Vicia americana	1	1	t	1	t	1	1	t	1	1	1	t
Viola sp.								t		t		
<u>Native Shrubs</u>												
Amelanchier alnifolia												
Prunus pensylvanica	*							t		*		
Rosa arkansana	1	1	1	1	t	t	2	1	2	1	t	1
Salix bebbiana												
Symphoricarpos occidentalis	4	8	3	7	7	6	5	8	5	6	4	1
Cruciferae			t							*		
Unidentified	t			t	t							

Treatment abbreviations are listed in Table 3.1.
't' indicates species composition is less than 1%.
'*' indicates species observed in plots but not in quadrats.
N=480.