The biology of Canadian weeds. 134. *Bromus inermis* Leyss

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Otfinowski, R., Kenkel, N. C. and Catling, P. M. 2007. **The biology of Canadian weeds. 134. *Bromus inermis* Leyss.** Can. J. Plant Sci. **87**: 183–198. Smooth brome (*Bromus inermis* Leyss.), a native of central Eurasia, was introduced to Canada as a forage and hay crop around 1888. Early reports of plants escaped from cultivation appear in 1903, and based on the number of collections prior to 1920, smooth brome spread most rapidly in western Canada. It is common along roadsides, forest margins, clearings, shorelines and disturbed areas, but its most detrimental impact is on the diversity of prairies and native grasslands. For example, in Riding Mountain National Park, MB, plant diversity of fescue prairies recently invaded by smooth brome decreased by 70%. Vegetative proliferation through underground rhizomes is key to the invasiveness of smooth brome, but long-range dispersal of seeds is facilitated by animals, wind and the transport of hay. Smooth brome is effectively controlled using selective applications of glyphosate and well-timed clipping. However, restoration of infested areas depends on the composition of native seed banks. Smooth brome remains valuable as a forage and cover crop in every province and territory in Canada.

Key words: *Bromus inermis*, weed biology, prairie, Canada distribution, alien, smooth brome, biological invasion

Otfinowski, R., Kenkel, N. C. et Catling, P. M. 2007. **La biologie des mauvaises herbes au Canada. 134. *Bromus inermis* Leyss**. Can. J. Plant Sci. **87**: 183–198. Le brome inerme (*Bromus inermis* Leyss.), plante indigène du centre de l'Eurasie, a été introduit au Canada pour la production fourragère vers 1888. Les premiers rapports mentionnant des plants retournés à l'état sauvage datent de 1903. D'après le nombre de prélèvements effectués avant 1920, on constate cependant que l'espèce s'est répandue plus rapidement dans l'ouest du pays. Le brome inerme colonise souvent le bas-côté des routes, la lisière des bois, les clairières, les rivages et les terres perturbées, mais l'espèce nuit le plus à la diversité de la flore des prairies et des pâturages naturels. Dans le parc national Riding Mountain, au Manitoba, on a noté une diminution de la diversité des plantes de 70 % dans les prairies à fétuques récemment envahies par le brome inerme. L'efficacité du brome inerme vient essentiellement de sa reproduction végétative par rhizomes, mais les animaux, le vent et le transport du foin favorisent la dispersion des graines sur de grandes distances. L'application sélective de glyphosate et une coupe opportune permettent une lutte efficace contre cette adventice. Toutefois, la restauration des lieux infestés dépend de la composition des réserves de semences indigènes. Le brome inerme garde son utilité comme culture fourragère et culture abri dans toutes les provinces et tous les territoires du Canada.

Mots clés: *Bromus inermis*, biologie des mauvaises herbes, prairie, répartition au Canada, exotique, brome inerme, invasion biologique

1. Name

Bromus inermis Leyss. – **smooth brome**, awnless brome, Austrian brome, Austrian brome grass, Austrian brome hay, brome grass, Hungarian brome, Hungarian brome grass, Hungarian fodder grass, Russian brome, smooth brome, smooth brome grass (Clark and Malte 1913; Newell and Keim 1943; Heinriches 1969; Scoggan 1978; Darbyshire et al. 2000); **brome inerme**, brome sans arêtes, brome de Hongrie (Häfliger and Scholz 1981; Darbyshire et al. 2000). Poaceae, grass family, Poacées. The name *Bromus* is derived from the Greek *broma*, meaning food, and *bromos*, meaning oat (Zimdahl 1989).

2. Description and Account of Variation

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

No reports of chromosome numbers specific to Canada have been found, but those cited in the literature range between $2n$ = 28, 42, 49, 54–56–58, 70 (Wagnon 1952; Mitchell 1967; Gleason and Cronquist 1991; Moss 1992;

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

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

Smooth brome (*Bromus inermis* Leyss.) can be distinguished from the native Pumpelly's brome (*B. pumpellianus* Scribn.), which is similar in its rhizomatous habit, by the glabrous or scabrous culms, lemmas and leaf blades, and rudimentary or absent auricles (Mitchell 1967; Voss 1972; Table 1). When present, the lemma awns of *B. inermis* do not exceed 3 mm (Scoggan 1978). The nodes, lemmas and blades of *B. pumpellianus* are pubescent with long, soft hairs (0.5 mm or longer), especially near the margins (Wagnon 1952; Voss 1972). Also characteristic of the native species are its longer lemma awns (1.5–4 mm), a lower glume broadened above the base and better developed auricles at the summit of each leaf sheath. Both taxa occur primarily as octoploids ($2n = 8x = 56$) (Armstrong 1982).

Some authors have considered *B. pumpellianus* a subspecies of the introduced *B. inermis* (Scoggan 1978; Great Plains Flora Association 1986). The reduction of *B. pumpellianus* to subspecific rank is based primarily upon evidence of introgressive hybridization with *B. inermis* (Wagnon 1952). However, the high fertility of hybrids likely results from the preferential pairing of chromosomes rather than their homology (Armstrong 1982). Although the distinction between these taxa requires further work, the vast majority of specimens are easily distinguished at the species level and most treatments recognize their specific rank (Mitchell 1967; Voss 1972; Dore and McNeill 1980; Looman and Best 1987; Gleason and Cronquist 1991; Soreng et al. 2003).

(c) *Intra-specific variation. Bromus inermis* (*sensu stricto*) is a highly variable taxon. Even in its native range in Europe, many forms have been recognized based on minor variation in pubescence and awn development (Tutin et al. 1980). In Canada, two varieties have been distinguished based on the aspect of their panicle branches. In contrast with the widely spreading to reflexed panicle branches of var. *divaricatus* Rohlena, those of var. *inermis* are spreading-ascending to erect (Fernald 1950; Scoggan 1978). Within var. *inermis*, three forms have been recognized. Awnless or blunt lemmas characterize f. *inermis* and f. *proliferus* Louis-Marie (Scoggan 1978), while short awns (< 3 mm) are typical of f. *aristatus* (Schur) Fern. (Scoggan 1978). Where present, pubescent types are not geographically delimited (Mitchell 1967). In f. *proliferus*, the florets have the form of leafy propagules, the glumes normal but the lemma and palea leaf-like and 3–6 mm long (Louis-Marie 1940). Other variable traits include: stature, the extent of clonal growth and the fullness and colour of panicles (Dore and McNeill 1980). Recent treatments of the genus do not recognize the above infraspecific taxa and place all names in synonymy with *B. inermis* (Soreng et al. 2003).

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

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

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

(d) *Illustrations*. A single plant, its panicle and an individual spikelet are illustrated in Fig. 1. Colour photographs and additional illustrations can be found on the United States Department of Agriculture's PLANTS database (http://plants.usda.gov/index.html) and other internet resources.

Table 1. Features distinguishing introduced *Bromus inermis* Leyss. and native *B. pumpellianus* Scribn. The summarized characters were compiled from the following sources: Elliott (1949a), Wagnon (1952), Mitchell (1967), Voss (1972), Scoggan (1978), Looman and Best (1987), Dore and McNeill (1980), Gleason and Cronquist (1991), Pavlick (1995)

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

3. Economic Importance

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

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

Several reports illustrate the impacts of smooth brome invasions on communities of birds. At the Last Mountain Lake Refuge, an area of mixed-grass prairie in Saskatchewan, bird richness in infested areas declined from eight to two species (Romo and Grilz 1990). In Manitoba, upland sandpipers (*Bartramia longicauda* Bechstein) and Sprague's pipits (*Anthus spragueii* Audubon) were significantly more abundant in native mixed-grass prairies than in areas dominated by smooth brome (Wilson and Belcher 1989). Decreased forb cover and increased visual obscurity in areas dominated by smooth brome lead to declined use of uplands by sage grouse (*Centrocercus urophasianus* Bonaparate), eastern meadowlarks (*Sturnella magna* Linnaeus) and grasshopper sparrows (*Ammodramus savannarum* Gmelin; Scott et al. 2002; Bunnell et al. 2004). Invasions of smooth brome may have other indirect effects. For example, low preference of native ungulates and cattle for smooth brome leads to overgrazing of uninfested areas and creates additional invasion foci (Frank and McNaughton 1992; Austin et al. 1994; Trammell and Butler 1995; Moisey et al. 2005).

Plants of smooth brome proliferating along ditches and field margins serve as pest and disease reservoirs. In

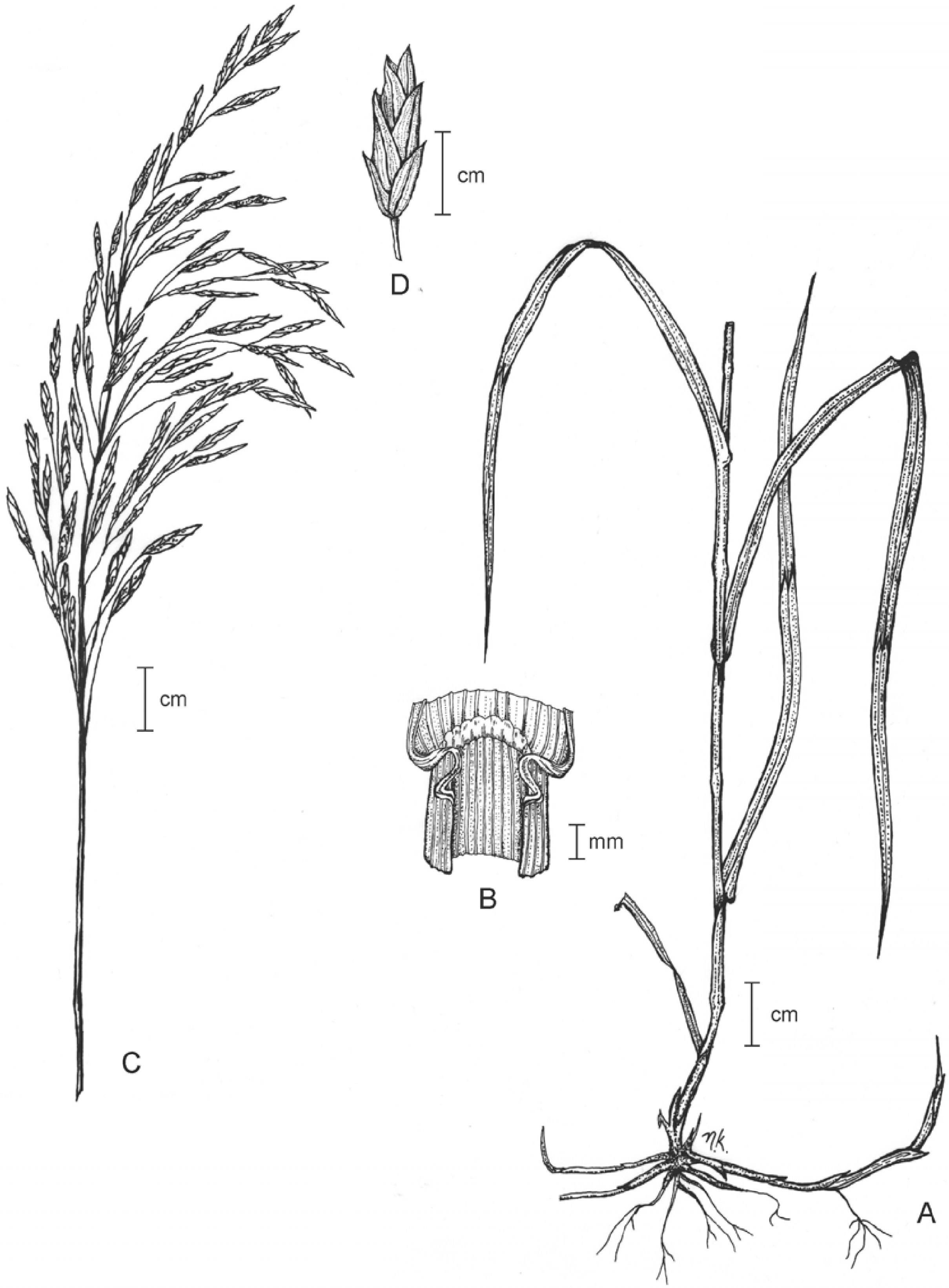

Fig. 1. *Bromus inermis* Leyss. a, habit sketch of a culm illustrating the proliferating rhizome; b, detail of leaf illustrating the rudimentary auricles; c, inflorescence of a mature plant; d, detail of a single spikelet illustrating the glabrous glumes and the glabrous, awnless lemmas.

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

Recently, smooth brome was ranked as the 8th most serious invasive alien plant threatening natural habitats in Canada (Catling and Mitrow 2005). In a national survey, smooth brome was considered a species of "national concern" and regarded as a "serious invader of grasslands" by over half the respondents from the prairie region (Haber 1996). Romo and Grilz (1990) reported that western Canadian grasslands are seriously threatened by smooth brome and suggested that "a passive or hand-off approach to managing natural areas will eventually result in invasion."

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

Mixed pastures of smooth brome and alfalfa provide shelter for deer mice (*Peromyscus maniculatus* Wagner), montane voles (*Microtus montanus* Peale) and northern pocket gophers (*Thomomys talpoides* Richardson; Bechard 1982), as well as American bitterns (*Botaurus lentiginosus* Rackett), northern harriers (*Circus cyaneus* Linnaeus) and short-eared owls (*Asio flammeus* Pontoppidan; Duebbert and Lokemoen 1977). In Indiana, areas reclaimed with smooth brome were used by Henslow's and grasshopper sparrows (*Ammodramus henslowii* Audubon, *A. savannarum* Gmelin), eastern meadowlarks, common yellowthroats (*Geothlypis trichas* Linnaeus), dickcissels (*Spiza americana* Gmelin) and red-winged blackbirds (*Agelaius tricolor* Audubon; Scott et al. 2002). Escaped and planted populations of smooth brome provide nesting cover for ducks and attract gray partridges (*Perdix perdix* Linnaeus), as well as vesper (*Pooecetes gramineus* Gmelin), clay-coloured (*Spizella pallida* Swainson) and grasshopper sparrows (Wilson and Belcher 1989; Lokemoen et al. 1990; Carroll and Crawford 1991). Although invasions by smooth brome reduce the biomass of native forages (Trammell and Butler 1995), brome can provide winter forage for elk (*Cervus elaphus* Linnaeus), mule deer (*Odocoileus hemionus* Rafinesque) and white-tailed deer (*O. virginianus* Zimmermann; Hobbs et al. 1981; Austin et al. 1994; Stubbendieck et al. 1997).

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

4. Geographical Distribution

Smooth brome is found growing without cultivation in every Canadian province and territory (Fig. 2). It appears to be best established in the eastern prairie and parkland region of Manitoba and Saskatchewan, in southern Ontario and southern Quebec and in the Okanagan and Thompson valleys of southern British Columbia.

Smooth brome is native across central Eurasia (Elliott 1949b). In continental Europe, its range extends westward to the Netherlands, Belgium, Luxemburg, France, Spain and NW Italy, and southward to the Balkans, Bulgaria, and Turkey. Introduced populations are also found in Switzerland, Britain, Denmark, Sweden, Norway, Finland, and Iceland (Tutin et al. 1980). In the New World, smooth brome has been introduced to South America, including Argentina, Bolivia, Chile and Uruguay, as well as the Caribbean, Australia, New Zealand, areas of northern, tropical and southern Africa, temperate and tropical Asia, and islands in the Atlantic, Indian and Pacific Oceans; it is also found throughout the United States and Mexico (Häfliger and Scholz 1981; Soreng et al. 2003; Weber 2003).

5. Habitat

(a) *Climatic requirements* – Smooth brome is a cool season grass. Its ability to tolerate dry conditions has made it a valuable forage and pasture crop in western Canada (Malte 1915). In greenhouse experiments, plants were more tolerant of moisture stress than the native green needle grass (*Stipa viridula* Trin.) and northern wheat grass (*Agropyron dasystacyum* (Hook.) Scribn.; Reekie and Redmann 1990). However, prolonged drought decreased shoot dry weight, induced dormancy (Dibbern 1947; Donkor and Bork 2002) and limited the establishment of smooth brome in southern Alberta (Thomson 1937; Palmer 1949) and central British Columbia (Willis 1965). The annual precipitation required for the establishment and proliferation of smooth brome is between 280 and 450 mm (Hardy BBT Limited 1989).

In Canada, smooth brome may be found in subalpine regions (Moss 1992), but does not reseed above 3000 m (Dibbern 1947). The species tolerates severe winter conditions (Gilbey 1954), including long periods of freezing (Rogler 1943), but does not survive flooding or waterlogging (Abbott 1954; Burns 1964).

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

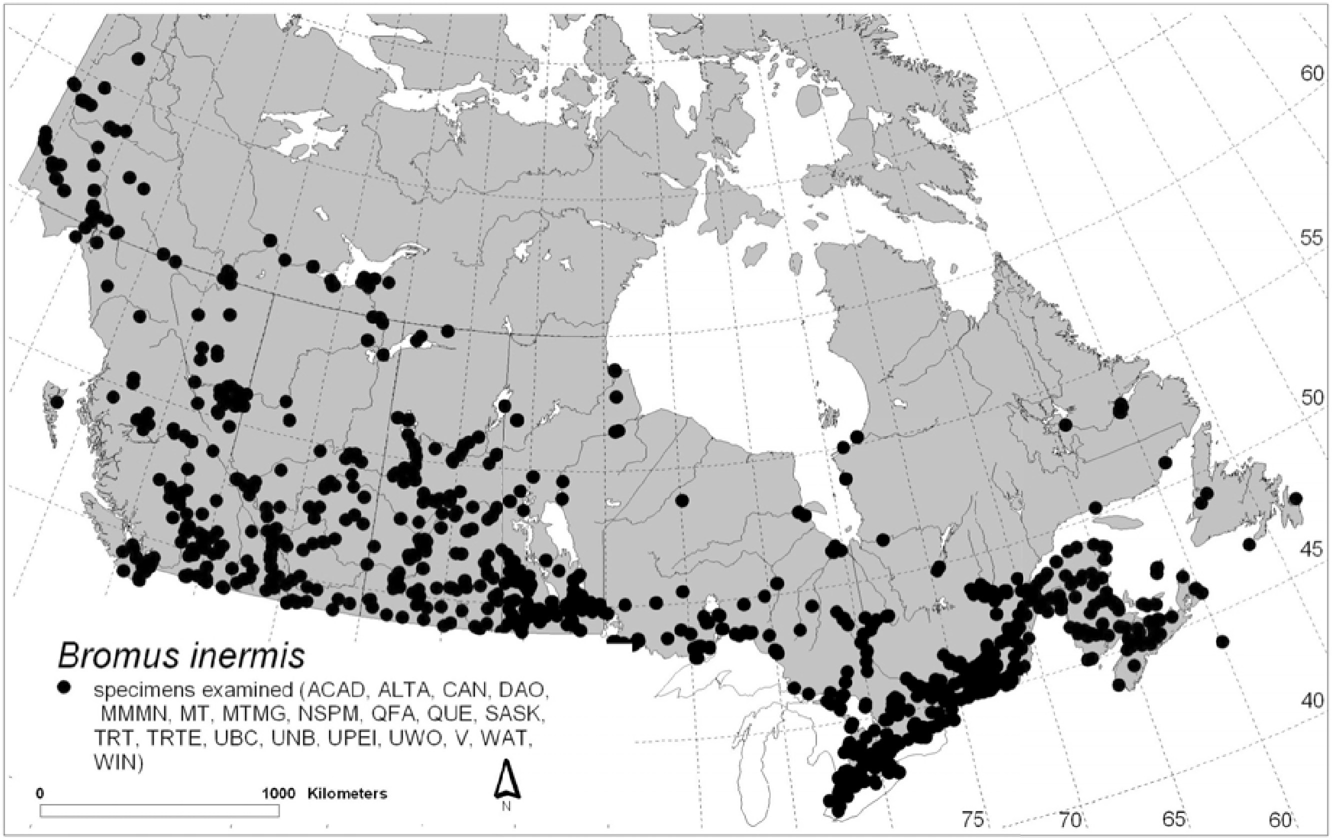

Fig. 2. Distribution of smooth brome (*Bromus inermis* Leyss.) growing without cultivation in Canada. Map is based on 2344 specimens examined and verified in 20 herbaria across Canada, including ACAD, ALTA, CAN, DAO, MMMN, MT, NSPM, OAC, QFA, QUE, SASK, TRT, TRTE, UAC, UBC, UNB, UWO, V, WAT, and WIN (acronyms according to Holmgren et al. 1990).

Southern strains are more tolerant of midsummer heat and drought (Newell and Keim 1943).

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

The productivity of smooth brome, and its ability to displace native plants, increases with the availability of soil nitrogen (Harrison and Crawford 1941, Leyshon and Campbell 1995, Wilson and Gerry 1995). Even small patches of nutrients may increase its vigour. In central Minnesota, smooth brome plants growing on thatching ant mounds (*Formica obscuripes* Forel) were larger and produced more pollen compared to those in undisturbed prairie (McKone 1989). However, additions of nitrogen may also reduce the vegetative encroachment. In fertilization experiments, nitrogen reduced the growth of roots and rhizomes of smooth brome and increased its above-ground biomass (Watkins 1940, Wilson and Gerry 1995).

(c) *Communities in which the species occurs* – Smooth brome is common along roadsides, forest margins, clearings, shorelines and disturbed areas throughout Canada (Sather 1987, Dunster 1990, Pavlick 1995, Leeson et al. 2005; Table 2). In Manitoba, smooth brome invades mixed-grass prairies composed of *Bouteloua gracilis*, *Carex obtusata*, *Juniperus horizontalis*, *Schizachyrium scoparium* and *Stipa spartea* (Wilson and Belcher 1989). Also vulnerable are areas of fescue prairie, composed of slender wheat grass [*Elymus trachycaulus* (Link) Gould], rough fescue [*Festuca hallii* (Vasey) Piper], needle grasses (*Stipa* spp)., yarrow (*Achillea millefolium* L.), smooth aster (*Aster laevis* L.), northern bedstraw (*Galium boreale* L.) and other native grasses and forbs (Otfinowski and Kenkel 2005). Smooth brome is also common along shorelines and in the understory of open forests throughout western and eastern Canada

(Moss 1992; Moreland and Promaine 2000; Lesica 2002; Table 2).

Impacts of smooth brome appear greatest in open prairie communities where invasions often produce large, monospecific stands (Sather 1987; Romo and Grilz 1990; White et al. 1993; Haber 1996). The size of invading patches ranges between 50 and 900 m^2 (Caners 1999) and large infestations in North Dakota can occupy as much as 20 000 m^2 of mixed-grass prairie (Trammell and Butler 1995).

6. History

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

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

In western Canada, agricultural immigration contributed to the introduction of exotic forages. In northern areas of the Prairie provinces, exotic forages were cultivated in forest clearings (Stacey 1949; McCartney 1993), and native meadows were supplemented with smooth brome to increase productivity (Lesica 2002). In southern Alberta and Saskatchewan, farm settlement restricted the open wintering range of cattle ranches. By 1913, most ranchers resorted to exotic hay to compensate for the lost winter range of their animals (Potyondi 1995). Such purposeful introductions for hay likely contributed to the early establishment of smooth brome across Canada. For example, smooth brome was cultivated for hay on Sable Island, Nova Scotia, in 1899 (Macoun 22680, CAN). Subsequently, it established but remained rare in this extreme environment (Catling et al. 1984). There are several collections from apparently natural habitats in the Yukon between 1887 and 1902 (before and during the goldrush), where smooth brome is now well established (Cody 2000). Additional introductions resulted from the construction of railroads. For example, disturbance of natural habitats along the mouth of the Moose River in Ontario likely led to the introduction of smooth brome into this area after 1935 (Riley 2003).

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

Despite reference to apparently natural habitats on early collection labels, it is difficult to determine whether or not the collected plants established on their own. However, if present behaviour in newly colonized sites can be accepted as an indication of the past, then smooth brome in many areas likely spread rapidly from plantings by seeds and rhizome fragments. Consequently many collections that are not clearly of cultivated plants are likely to have established naturally. The earliest dates of collection of non-cultivated plants for each Canadian province and territory are: Alberta in 1890 and 1898, British Columbia in 1887 and 1902, Manitoba in 1901 and 1906, New Brunswick in 1910 and 1927, Newfoundland in 1911 and 1927 (several collections from Goose Bay, Labrador in 1950), Northwest Territories in 1950 (several collections), Nova Scotia in 1939 and 1940, Ontario in 1890 and 1903, Prince Edward Island in 1945 and 1952, Quebec in 1914 and 1915, Saskatchewan in 1896 and 1903 and Yukon in 1899 and 1902.

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

7. Growth and Development

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

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

Table 2. Examples of plant species associated with *Bromus inermis* Leyss. growing without cultivation in Canada. Summary is based on a review of 448 specimens from the Agriculture and Agri-Food Canada herbarium in Ottawa, ON (DAO). Nomenclature according to Gleason and Cronquist (1991)

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

[z]Reports based on reviewed DAO specimens and the following sources: Anderson and Bailey (1980), Pylypec (1986), Wilson and Belcher (1989), Otfinowski and Kendel (2005).

(c) *Physiological data* – The productivity of smooth brome declines by late summer (Tinline 1937). In Melfort, Saskatchewan, the leaf conductance of plants inside rain shelters decreased between Jul. 04 and Aug. 22 (Bittman and Simpson 1989). In contrast, shading resulted in a decrease in the number of shoots, rhizomes and inflorescences, and shorter daylengths produced denser stands of shorter, decumbent shoots (Watkins 1940).

(d) *Phenology* – Smooth brome grows most rapidly in the spring, remaining green through the summer months, during which time it makes little additional growth (Dibbern 1947). On the Canadian prairies, growth commences in early May (Looman 1983), and in Saskatoon, irrigated plants produced only 8% of their total annual yield after Aug. 08 (Knowles and Sonmore 1985). Similar results were reported from Nebraska, where maximum yields were harvested as early as May 25 (Engel et al. 1987). In Wisconsin, cultivated plants began growth ahead of alfalfa (*Medicago sativa* L.) and timothy (*Phleum pratense* L.), with tillering starting in late March and anthesis and seed maturing by the middle of June and July, respectively (Reynolds and Smith 1962).

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

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

8. Reproduction

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

(b) *Seed production and dispersal* – Seeds of smooth brome are wind dispersed and dispersal is greatest when seed moisture falls below 25% (Knowles et al. 1969). In Riding

Mountain National Park, seeds did not disperse beyond 3.5 m from invading clones (Otfinowski and Kenkel 2005), but may travel much farther by wind transport over encrusted snow (Hume and Archibold 1986; Morton and Hogg 1989; Romo and Grilz 1990). Seeds may also be dispersed by attachment to animal fur, by ants and small rodents developing food caches, transported with hay and mulch and distributed by seed companies (Sather 1987).

Among 30 self-sterile clones of smooth brome, fertility ranged between 2.6 and 75.8%, and open-pollinated plants produced 156–10 080 viable seeds (Lowe and Murphy 1955). Cormack (1961) found that seed production was higher in northern strains of smooth brome where only 30% of florets were sterile, compared with over 50% for plants of southern origins. On average, commercial crops of smooth brome yield 100 kg seed ha^{-1}, but may exceed 1100 kg (Campbell et al. 1966; Knowles et al. 1969). Applications of nitrogen had no effect on the number of spikelets per panicle, but heavily fertilized plants produced more florets per spikelet (Harrison and Crawford 1941).

(c) *Seed banks, seed viability and seed germination* – In a fescue prairie near Saskatoon, SK, seedlings of smooth brome emerged only from soil cores collected inside patches of smooth brome and not from those collected in the adjacent native prairie (Grilz and Romo 1995). However, in Riding Mountain National Park, seedlings of smooth brome germinated from cores collected as far as 4.0 m away from established clones (Otfinowski and Kenkel 2005). Seeds of Manchar, a commercial variety of smooth brome, retained viability of more than 70% for 6 yr when stored under cool, dry conditions (Hafenrichter et al. 1968).

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

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

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

9. Hybrids

The absence of reproductive barriers between *Bromus inermis* and *B. pumpellianus* has prompted questions regarding species validity (Elliott 1949a; Wagnon 1952). In greenhouse experiments, the average fertility of crosses was approximately half of intraspecific matings of both parents (Elliott 1949a). Although both taxa occur primarily as octoploids, hybrids of naturally occurring tetraploids may also produce seeds (Armstrong 1982).

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

10. Population Dynamics

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

Smooth brome is a strong competitor. In greenhouse experiments, lower establishment and yield of alfalfa grown with smooth brome were attributed to shading (Groya and Sheaffer 1981). However, the establishment of grass and broadleaf seedlings was unaffected by the removal of smooth brome shoots, suggesting strong below-ground competition (Gerry and Wilson 1995). In other experiments, the low emergence of Canada goldenrod (*Solidago canadensis* L.) transplants was attributed to the deep litter deposited by smooth brome (Goldberg 1987).

11. Response to Herbicides and Other Chemicals

Smooth brome is effectively controlled using selective applications of glyphosate (N-(phosphonomethyl) glycine; Grilz and Romo 1995) and Sather (1987) recommended treatment at 0.5 to 1.1 kg glyphosate ha^{-1}, applied before flowering. In overgrazed tall-grass prairie in south-eastern Nebraska, spring application of atrazine (6-Chloro-N^{2}-

ethyl-N4-isopropyl–1,3,5-triazine-2,4-diamine) or glyphosate [*N*-(Phosphonomethyl)glycine] shifted community dominance from smooth brome and Kentucky bluegrass (*Poa pratensis* L.) toward native warm-season grasses (Waller and Schmidt 1983). However, the restoration of native prairie infested with smooth brome depends on the ability of the native seedbank and rhizome bank to compete with the regrowth of brome tillers (Willson and Stubbendieck 1996).

In Minnesota, May applications of glyphosate and dalapon (2,2-dichloropropionic acid) were also effective in suppressing smooth brome prior to seeding alfalfa (Martin et al. 1983). Applications of glyphosate were most effective in May, when the grasses were 15 cm tall and beyond the three leaf stage. In rangelands, applications of imazapic [(±)-2-(4,5-dihydro-4-methyl-4-(1-methylethyl)-5-oxo-1*H*-imidazol-2-yl)-5-methyl-3-pyridinecarboxylic acid] at rates above 70 g ha^{-1} caused visible injury to smooth brome (Shinn and Thill 2004), but the biomass of plants was not affected by applications of picloram (4-amino-3,5,6-trichloro-pyridine-2-carboxylic acid; Shinn and Thill 2002). Within a year of application, smooth brome was also susceptible to diallate (*S*-(2,3-Dichloroallyl) diisopropyl-thiocarbamate) and trillate (*S*-(2,3,3-Trichloroallyl) diisopropyl-thiocarbamate; Knowles et al. 1969) and not affected by paraquat (1,1’-Dimethyl-4,4’-bipyridinium dichloride; Martin et al. 1983).

12. Response to Other Human Manipulations

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

Fire can also be used to suppress smooth brome. However, timing of the burn, community composition and environmental conditions are critical in determining its success (Sather 1987; Blankerspoor and Larson 1994). In eastern Nebraska, Willson (1991) found a 50% reduction in smooth brome tiller density following a prescribed burn during tiller elongation, and Old (1969) reported decreases in July dry matter production following an April fire in Illinois. Community composition is crucial to the success of the burn. In tall-grass prairies, early spring burning suppress smooth brome at a time when the native, warm-season grasses are dormant (Hover and Bragg 1981). However, in fescue prairies in Manitoba and Saskatchewan, spring burning may adversely affect the dominant native cool-season grasses (Anderson and Bailey 1980; Redmann et al. 1993) and increase the abundance of smooth brome (Grilz and Romo 1994). Burning is less effective where the recovering plants are not subject to competition from native species (Willson and Stubbendiek 1996). As a result, Willson and Stubbendiek (2000) recommend avoiding burning areas where native warm-season grasses contribute less than 20% to the community. Regrowth of smooth brome following defoliation is reduced in dry years (Harrison and Romo 1994).

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

In production, yields of smooth brome hay decline after 3 to 4 yr (Lowe 1950), but may recover following applications of fertilizer or by mixed seeding with alfalfa (Alberta Agriculture Food and Rural Development 1981). Stands are also rejuvenated by ploughing (Cormack 1961), burning, or mowing (Knowles et al. 1969).

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

13. Response to Herbivory, Disease and Higher Plant Parasites

Herbivory

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

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

(b) *Birds and/or other vertebrates* – Smooth brome is palatable to Canada and blue geese (*Branta canadensis* Linnaeus, *Chen caerulescens* Linnaeus; Burgess 1969; Gauthier and Bedard 1991).

(c) *Insects* – In Alberta, insects in the genera *Irbisia* and *Capsus* were reported to damage forage grasses (Alberta Agriculture Food and Rural Development 1981). Seed production of smooth brome is reduced by seed midges (*Stenodiplosis bromicola* Marikovsky & Agafonova) and thrips (Neiman and Manglitz 1973; Carlson and Newall 1985). In Wisconsin, an insect infestation which caused a shortage in the supply of smooth brome seed during 1956 may have been caused by midges (Itinididae, *Phytophaga*; Nielson and Burks 1958). Escape holes of chalcid flies (Eulophidae, *Tetrastichus*), a likely parasite of the midge, have been observed on mature caryopses of native fringed brome (*Bromus ciliatus* L.), arctic brome (*B. kalmii* A. Gray) and *B. pumpellianus* (Nielson and Burks 1958).

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

(d) *Nematodes and/or other non-vertebrates* – Smooth brome is susceptible to the root-lesion nematodes *Pratylenchus penetrans* (Cobb) Filipjev & Schur-Stekhoven (Petersen et al. 1991) and *P. neglectus* (Rensch) Filipjev & Schur-Stekhoven (Societé de protection des plantes du Québec 1992). In Québec, the following genera of soil-borne plant-parasitic nematodes were recovered from soil samples collected from cultivated fields of smooth brome: *Pratylenchus* spp., *Meloidogyne* spp., *Helicotylenchus* spp., *Heterodera* spp., *Tylenchorhynchus* spp. (Santerre and Lévesque 1982). In greenhouse trials, seedlings of smooth brome became infected with the ectoparasitic nematodes *Paratylenchus projectus* Jenkins and *Helicotylenchus digonicus* Perry, as well as the migratory endoparasites *Pratylenchus neglectus* Rensch and *P. penetrans* Cobb (Townshend and Potter 1976).

Disease

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

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

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

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

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

Higher plant parasites – There are no reported higher plant parasites of smooth brome.

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