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ABSTRACT—Smooth brome (*Bromus inermis* Leyss.) is an aggressive invader of fescue prairie; however, little information is available on the germination ecology of this exotic perennial relative to native flora. This information is needed to understand the processes of invasion and to develop strategies to curb the spread of smooth brome. Germination of smooth brome and plains rough fescue (*Festuca altaica* subsp. *hallii* (Vasey) Harms) seeds was compared under various temperature regimes, levels of water stress, and light. Germination of both species was severely restricted by water stress, but not by temperatures between 5 and 25°C. Smooth brome had higher germination over a broader range of temperatures and water stress than plains rough fescue. When incubation temperatures were decreased from 25 to 5°C, total germination was reduced for plains rough fescue relative to temperatures that were increased from 5 to 25°C; germination of smooth brome was similar under increasing or decreasing temperatures. At a given level of water stress at 10 and 20°C, plains rough fescue germination was unaffected by light and darkness. Germination was higher for smooth brome in dark than in light at 10°C, but at 20°C it was generally similar in light and darkness. Germination of smooth brome over a wide range of temperatures, light, and moisture conditions increases the probability that requirements will be met in heterogeneous seedbed conditions. Smooth brome is well adapted to germinate and establish in prairie dominated by plains rough fescue.

Key words: germination ecology, seedbed ecology, water stress, fescue prairie, *Bromus inermis*, *Festuca altaica*

The fescue prairie in western North America originally occupied the aspen parkland, north of the mixed prairie from central Saskatchewan westward to the foothills of the Rocky Mountains (Coupland 1961). It extends south along the foothills of Alberta into west central Montana, contacting the western edge of the drier northern mixed prairie. Fescue prairie is also found in the Cypress Hills of southeastern Alberta and southwestern Saskatchewan, southwestern Manitoba, northwestern North Dakota, western Montana, and British Columbia (Moss and Campbell 1947, Coupland and Brayshaw 1953, Blood 1966, Looman 1969, Barker and Whitman 1988).

Two subspecies of fescue dominate fescue prairie. Plains rough fescue [*Festuca altaica* Trin. subsp. *hallii* (Vasey) Harms] (Harms 1985) dominates the plains region, whereas rough fescue [*Festuca altaica* Trin. subsp. *scabrella* (Vasey) Harms] is found in the foothills and mountain grasslands to the west. Less than 5% of the prairie dominated by plains rough fescue remains; only small and isolated parcels persist because of cultivation and the conversion of this grassland for producing cereals and forage crops. Overgrazing is also a major cause of the deterioration of this grassland. Much of the remnant, plains rough fescue grassland is being invaded by smooth brome (*Bromus inermis* Leyss.)(Romo et al. 1990).

Smooth brome, an exotic, rhizomatous, long-lived perennial, is one of the most widely planted forage grasses in western Canada (Bittman 1985) and it is often used for stabilizing disturbed sites (Newell 1973). It is a prolific seed producer compared to plains rough fescue, which rarely produces seed (Toynbee 1987). Smooth brome also grows faster than many native grasses, including rough fescue (Smoliak and Johnston 1968). These characteristics, together with its wide range of adaptability, widespread seeding, and fragmentation of fescue prairie (Romo et al. 1990), enable smooth brome to invade grasslands dominated by plains rough fescue. Once established in this grassland, smooth brome spreads by rhizomes and seeds and suppresses the growth and abundance of native flora (Looman 1969, Romo et al. 1990).

Smooth brome and its aggressive spread into fescue prairie are viewed as undesirable by those responsible for managing this native grassland for its natural heritage value, biodiversity, research, wildlife habitat, ecological reserves, aesthetics, and recreation. Managers and naturalists need information on the ecological relationships, including the germination ecology of these species, that may assist in understanding the processes of the invasion of fescue prairie by smooth brome. The objective of this research was to compare the germination requirements of smooth brome and plains rough fescue under various temperatures, levels of water stress, and light regimes.

STUDY SITE, MATERIALS AND METHODS

Seeds of plains rough fescue and smooth brome were collected at the University of Saskatchewan's Kernen Prairie (52°10'N, 106°33'W, elev. 510 m), located approximately 1 km east of Saskatoon, Saskatchewan. Kernen Prairie, a 130-ha grassland, is in the transitional zone between the mixed prairie to the south and the fescue prairie of the parkland region to the north (Coupland and Brayshaw 1953, Coupland 1961, Rowe and Coupland 1984). Descriptions of the vegetation of Kernen Prairie are provided by Baines (1973) and Pylypec (1986). Soils are predominantly Bradwell sandy loam on higher areas and Sutherland clay on lower positions (Souster 1979).

Kernen Prairie is very important ecologically because it is one of the larger tracts of plains rough fescue prairie that remains. It is representative of most remnant prairie dominated by plains rough fescue because it is surrounded by a grid of roads and cultivated land that is used for annual crop and forage production. A common practice for revegetating road allowances in this region is the seeding of smooth brome. These seedings have probably been the main source of genetic material for the invasion of smooth brome into Kernen Prairie and other remnant patches of fescue prairie. Patches of varying size of smooth brome occur throughout Kernen Prairie, while a nearly continuous and pure strip occupies the interface between roads or cultivated land and the native grassland. The spread along the margins of the prairie is likely from rhizomes and seeds, while the dispersed and widespread patches of smooth brome that are several hundred meters from the edges the prairie suggests that it has established from seeds. Romo et al. (1990) proposed that seeds may be transported into the prairie by wind blowing them over snow or by rodents collecting and caching them.

Seeds of plains rough fescue and smooth brome were collected by hand-stripping from several thousand plants in July 1987 and 1988. Each species and year of harvest was considered a collection. After seeds were collected they were hand threshed, screened, and stored in the laboratory at room temperature in paper envelopes. Germination tests were conducted on each collection 4-6 months following harvest.

Osmotic Potentials and Constant Temperatures

Solutions were prepared to depress osmotic potentials by adding polyethylene glycol (PEG) (M.W. 20,000) to distilled water. Distilled water was used as the control (0.0 MPa). Osmotic potentials of these PEG solutions were determined using a Wescor vapor pressure osmometer. Mean osmotic potentials and standard errors (n=4) for the PEG solutions used for the 1987 collections were -0.20±0.02, -0.50±0.01, -0.81±0.02, -0.90±0.03, and -1.17±0.02 MPa. They were -0.29±0.01, -0.68±0.02, -0.99±0.02, -1.27±0.03, and -1.64±0.05 MPa for the 1988 collections. Variation in osmotic potentials between years is attributed to differences in molecular weights of different lots of PEG used.

We used a randomized complete block design with replicates being started at two-day intervals, and in each run, treatments were randomly placed in the incubator. The main effects of temperature, osmotic potentials, and species were factorially applied within years to each of four replicates. Fifty seeds were placed in closed petri dishes on 1-mm thick germination paper that was moistened by adding 7 ml of distilled water or PEG solution. These petri dishes were enclosed and sealed in polyethylene bags to prevent desiccation.

Seeds were incubated at 5, 10, 15, 20, and 25°C in darkness for 400 degree days (DD) (Base temperature=0°C). Germination is a temperature-sensitive process, and erroneous conclusions can be drawn by comparing data in experiments with multiple temperatures and chronological time limits because equal thermal units do not accumulate at all temperatures. Therefore, because DD integrate time and temperature (Johnson and Thornley 1985), the length of the incubation period was based on a set number of DD so the influences of arbitrarily set time limits could be eliminated and the effects of temperature isolated (Romo et al. 1991).

Germination counts were made at two-day intervals; a seed was considered germinated when the plumule and radicle were at least 5 mm long. Germinated seeds were removed from petri dishes, and after completing the test, those that had not germinated were dissected to determine seed fill. Germination data are expressed as a percentage of florets that had fully developed caryopses. Total germination percentages were transformed with arcsin square-root and subjected to factorial analysis of variance (Snedecor and Cochran 1980). Comparisons were not made between years. The best-fit polynomial regression equations were then developed for total germination P≤0.05 (Steele and Torrie 1980).

Ascending and Descending Temperatures

The effects of osmotic potential and temperatures decreasing from 25 to 10°C or increasing from 10 to 25°C were used to simulate cooling temperatures of summer-early autumn and warming temperatures of spring-early summer. Temperatures were increased or decreased at 0.5°C/day. The main effects of temperature regimes, osmotic potentials and species were factorially applied within years in a randomized complete block design with four replicates.

Fifty seeds were incubated for 600 DD in closed petri dishes prepared as above. Mean osmotic potentials and standard errors (n=4) were -0.22±0.02, -0.71±0.02, -1.10±0.05, -1.64±0.06, and -1.84±0.07 MPa for the 1987 collections and -0.34±0.01, -0.58±0.01, -0.78±0.03, -0.95±0.02, and -1.08±0.04 MPa for the 1988 collections. Distilled water was used as the control (0.0 MPa). Data were analyzed with analysis of variance within years using the procedures previously described. Data of the four replicates were averaged and the best-fit polynomial regression equations were developed.

Light, Temperature, and Osmotic Potentials

The effects of light, osmotic potential, and temperature on germination were evaluated within species and years of collection by incubating seeds at 10 or 20°C for 400 DD in light or darkness. A 24-hr photoperiod for the light treatment was maintained with Philips Cool White florescent tubes with a photon flux of 56-64 $\mu mol\ m^{-2}\ s^{-1}$. Seeds were enclosed in light-proof boxes for the dark treatment. Mean osmotic potentials and standard errors (n=4) were -0.58±0.01, and -0.95±0.02 MPa and distilled water was used as the control (0.0 MPa). Petri dishes were prepared as above and arranged in randomized complete block design with 50 seeds in each of four replicates. Replicates were started at two-day intervals. Germination of seeds was recorded as above and total germination percentages were transformed with arcsin square-root and subjected to factorial analysis of variance using light, temperature, and osmotic potentials as main effects (Snedecor and Cochran 1980). Tukey's honestly significant difference (Tukey's HSD) was calculated for mean comparisons at P≤0.05 (Petersen 1985).

Constant and Alternating Temperatures

Seeds of all collections were sent to the U.S.D.A. Agriculture Research Service Laboratory in Reno, NV, where germination in constant and alternating temperatures was investigated (Evans et al. 1982). A randomized complete block design with 25 seeds in each of four replicates was used in germination tests. Seeds were incubated for four weeks in dark germinators in closed petri dishes on 1 mm thick germination paper that was kept moist with water. Constant temperature regimes were 0, 2, 5, and 5°C increments through 40°C. Alternating temperature regimes consisted of a 16-hr cold period and an 8-hr warm period, at all possible higher temperatures each 24-hr interval. For example, a 2°C cold period was alternated with 5, 10, 15, 20, 25, 30, 35, or 40°C warm period, whereas a 30°C cold period was alternated with a warm period of 35 or 40°C. Germination of seeds was recorded after 1, 2, and 4 weeks of incubation. Seeds were considered germinated when the radicle was at least 5 mm long; thus germination results may be higher than in the temperature-osmotic potential, ascending and descending temperatures, and light-temperature-osmotic potential experiments because of the less restricted criterion for germination. Quadratic response surfaces were developed for germination using multiple regression analysis, and estimated germination and confidence limits were derived for each species and year of collection (Evans et al. 1982).

RESULTS

Temperature and Water Stress

Within years, germination was significantly different for species x osmotic potentials, but not among temperatures between 5 and 25°C. Germination of smooth brome was significantly higher than plains rough fescue in both years (Figs. 1 and 2). Total germination of the 1988 collection of plains rough fescue was significantly lower than that of 1987, but smooth brome germination was relatively high in both years.

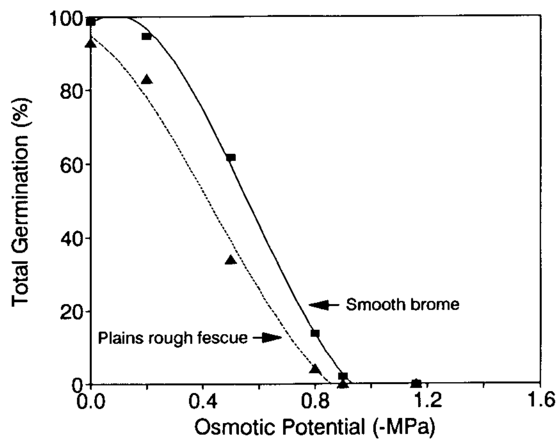

Figure 1. Regression lines for germination of plains rough fescue and smooth brome seeds incubated in darkness at constant temperatures between 5 and 25°C in 1987. Each symbol is the mean of four replicates.

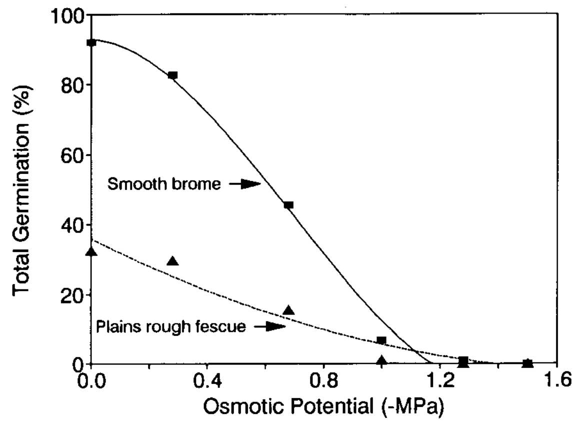

Figure 2. Regression lines for germination of plains rough fescue and smooth brome seeds incubated in darkness at constant temperatures between 5 and 25°C in 1988. Each symbol is the mean of four replicates.

In 1987, 89 and 94% of the variation in total germination for plains rough fescue and smooth brome, respectively, was accounted for by osmotic potential. Osmotic potential accounted for 71 and 90% of the variation in total germination in 1988. Thus, when seeds were germinated for an equal number of DD at different temperatures, water stress was the most important factor controlling germination.

Ascending and Descending Temperatures

The temperature regime x osmotic potential x species interaction was significant for germination in 1987 and 1988. When incubated with temperatures ascending from 10 to 25°C or descending from 25 to 10°C, smooth brome had significantly greater germination over a wider range of osmotic potentials than plains rough fescue (Figs. 3 and 4). Plains rough fescue had significantly higher germination at all osmotic potentials when incubated under ascending than under descending temperatures; total germination and the range of osmotic potentials where seeds germinated in the 1988 collection was significantly lower than that of the 1987. In 1987, smooth brome seeds germinated over a broader range of osmotic potentials under ascending temperatures than under descending temperatures. Smooth brome germination was statistically similar under the two regimes in 1988.

Water stress was the major factor contributing to variation in total germination. Ninety-seven to 99% of the variation in germination of plains rough fescue, and 95-97% in smooth brome, was attributed to osmotic potential.

Light, Temperature, and Osmotic Potentials

Total germination was significantly influenced by the interacting effects of light, temperature, and osmotic potential for both species in 1987 (Table 1). Plains

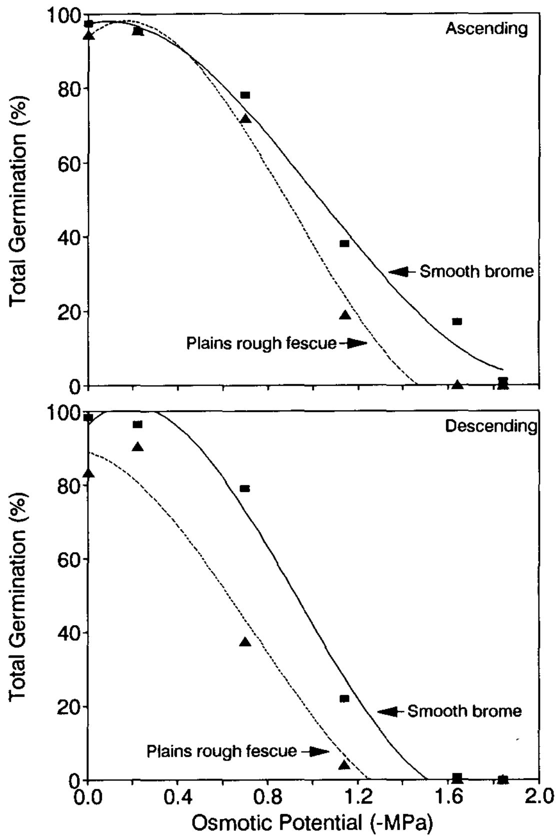

Figure 3. Regression lines for germination of plains rough fescue and smooth brome seeds incubated in darkness at temperatures ascending from 5 to 25°C or descending from 25 to 5°C in 1987. Each symbol is the mean of four replicates.

rough fescue germination was greatest at 10°C in light or darkness with no water stress; a few seeds germinated at -0.95 MPa at 10°C in darkness but not in light. Germination of smooth brome was highest at 0.0 MPa at 10°C and 20°C in light or darkness, and lowest at -0.95 MPa at 10°C in light and at 20°C.

For the 1988 collection of plains rough fescue, light, temperature, and osmotic potential interacted to influence total germination, whereas germination of smooth brome was significantly affected by temperature x osmotic potential, light x osmotic potential, and light x temperature interactions (Table 1). Germination of plains rough fescue was greatest in light at 10 and 20°C under no water stress. Smooth brome germination at -0.58 and -0.95 MPa was greater in light than

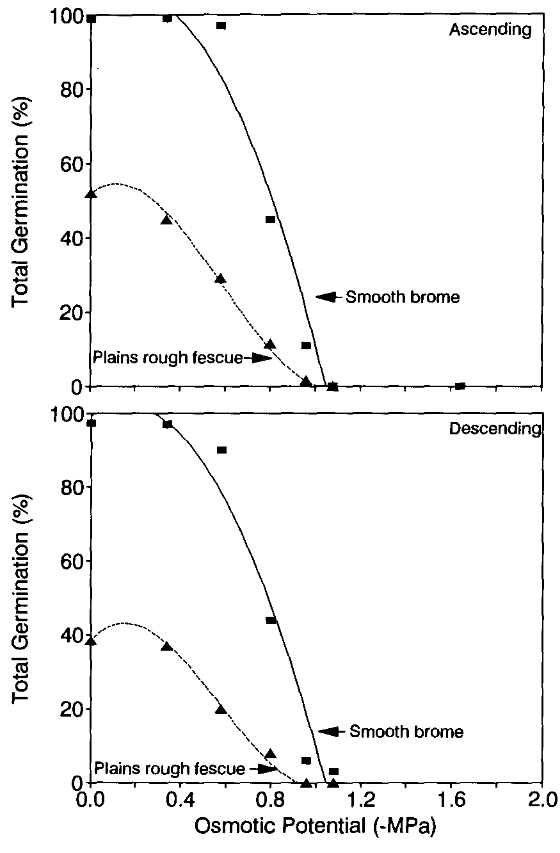

Figure 4. Regression lines for germination of plains rough fescue and smooth brome seeds incubated in darkness at temperatures ascending from 5 to 25°C or descending from 25 to 5°C in 1988. Each symbol is the mean of four replicates.

darkness at 10°C in both years. With the exception of -0.58 MPa at 20°C, germination of smooth brome was statistically similar in light and darkness.

Constant and Alternating Temperatures

Year-to-year variability occurred in total germination for both species; however, the range of optimal temperatures varied little within species (Tables 2 and 3). Smooth brome germinated over a wider range of temperatures and had a higher total germination than did plains rough fescue. Seeds of plains rough fescue germinated in 82% of the temperature regimes in both years, while smooth brome germinated at all temperatures except 0°C.

Table 1. Mean total germination (%) for the light, temperature and osmotic potential interaction for the 1987 and 1988 seed collections of plains rough fescue and smooth brome incubated for 400 degree days (base temperature equals 0°C) under light and dark photoperiods at 10 or 20°C in a gradient of osmotic potentials.

		Plains rough fescue		Smooth brome	
		Light Treatment			
Temperature (°C)	Osmotic Potential (MPa)	Light	Darkness	Light	Darkness
		1987			
10	0.00	97.5a[1]	96.0a	94.5ab	98.5a
	-0.58	52.0c	53.5c	79.0c	87.5b
	-0.95	0.0e	0.5e	0.0e	15.0d
20	0.00	71.5b	80.0ab	98.5a	99.0a
	-0.58	43.5cd	30.0d	88.0b	92.5ab
	-0.95	0.0e	0.0e	7.0de	6.5e
		1988			
10	0.00	69.0ab	77.5a	94.0a	97.0a
	-0.58	56.5bc	59.4bc	45.5d	67.0c
	-0.95	0.0e	0.5e	0.0e	3.5e
20	0.00	81.0a	59.5bc	98.0a	98.0a
	-0.58	43.5cd	36.0d	66.5c	83.5b
	-0.95	0.0e	0.0e	3.0e	2.5e

[1] A different letter within a species and year indicates significant ($P \leq 0.05$) differences among means using Tukey's HSD. A similar letter indicates means are not significanly ($P \geq 0.05$) different.

The maximum germination of plains rough fescue was nearly four-fold higher in 1987 than in 1988; 100% germination was observed for smooth brome both years. Dormancy cannot be ruled out as contributors to this yearly variation in total germination in plains rough fescue. In 1987 and 1988, seed fill averaged 95±2 and 78±1% in plains rough fescue and 99±1 and 98±1% for smooth brome, respectively.

DISCUSSION

Germination of smooth brome and plains rough fescue was primarily controlled by water stress and not by temperature. These responses imply that if seeds are positioned in the seedbed and exposed to equal DD, water stress will place the

Table 2. Estimated total germination (%) and confidence intervals for the 1987 collections of smooth brome and plains rough fescue seeds incubated four weeks in darkness at 55 constant and alternating temperatures.[1]

Cold-period temperature (°C) 16h	Warm-period temperature (°C) 8h: 0	2	5	10	15	20	25	30	35	40
Smooth brome										
0	0 (9)	19 (6)	45 (6)	78 (5)	99 (6)	100 (6)	100 (6)	87 (6)	58 (7)	17(10)
2		20 (7)	46 (6)	79 (4)	100 (5)	100 (5)	100 (5)	90 (5)	61 (5)	20 (8)
5			47 (6)	81 (4)	100 (4)	100 (4)	100 (4)	93 (4)	65 (4)	24 (7)
10				82 (6)	100 (4)	100 (4)	100 (4)	97 (4)	69 (4)	30 (6)
15					100 (7)	100 (5)	100 (4)	99 (4)	72 (5)	33 (7)
20						100 (7)	100 (5)	98 (4)	73 (5)	34 (7)
25							100 (7)	96 (5)	71 (5)	34 (7)
30								92 (7)	68 (5)	31 (7)
35									62 (8)	26 (8)
40										20(12)
Plains rough fescue										
0	0 (7)	0 (6)	0 (5)	0 (4)	1 (5)	2 (5)	0 (5)	0 (5)	0 (5)	0 (8)
2		8 (6)	12 (5)	16 (4)	18 (4)	18 (4)	15 (4)	11 (4)	5 (4)	0 (7)
5			33 (5)	37 (3)	39 (3)	39 (4)	36 (4)	32 (3)	25 (4)	16 (6)
10				64 (5)	65 (4)	65 (3)	62 (3)	57 (3)	50 (4)	41 (5)
15					81 (6)	80 (4)	77 (4)	72 (4)	65 (4)	55 (6)
20						85 (6)	82 (4)	76 (3)	68 (4)	59 (6)
25							75 (6)	69 (4)	61 (4)	51 (6)
30								52 (6)	44 (4)	33 (6)
35									15 (7)	4 (7)
40										0 (6)

[1] Maximum values are underlined and defined as those values not lower than the maximum minus 1/2 its confidence interval ($P<0.05$). The values in parentheses are one-half the confidence interval.

greatest restrictions on germination regardless of temperatures. These restrictions may insure that germination is limited to extended periods with high moisture and prevent seeds from germinating under low or transient soil moisture. On the other hand, by having few limitations imposed by temperatures, seedlings may be exposed to unfavorable growing conditions. Optimal temperatures for seedling growth are 13-18°C for rough fescue and 18-27°C for smooth brome (Smoliak and Johnston 1968).

The relatively insensitive reaction to temperature combined with the requirements of low moisture stress for germination of plains rough fescue presumably represent evolutionary adaptations in fescue prairie where most precipitation is received during the growing season. In smooth brome, adaptations for high germination over a broad range of temperatures are probably the product of selection of best-adapted genotypes by plant breeders and natural selection within

Table 3. Estimated total germination (%) and confidence intervals for the 1988 collections of smooth brome and plains rough fescue seeds incubated four weeks in darkness at 55 constant and alternating temperatures.[1]

Cold-period temperature (°C) 16h	Warm-period temperature (°C) 8h									
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2		20 (7)	46 (6)	79 (4)	100 (5)	100 (5)	100 (5)	90 (5)	61 (5)	20 (8)
5			47 (6)	81 (4)	100 (4)	100 (4)	100 (4)	93 (4)	65 (4)	24 (7)
10				82 (6)	100 (4)	100 (4)	100 (4)	97 (4)	69 (4)	30 (6)
15					100 (7)	100 (5)	100 (4)	99 (4)	72 (5)	33 (7)
20						100 (7)	100 (5)	98 (4)	73 (5)	34 (7)
25							100 (7)	96 (5)	71 (5)	34 (7)
30								92 (7)	68 (5)	31 (7)
35									62 (8)	26 (8)
40										20(12)
					Plains rough fescue					
0	0 (3)	0 (3)	0 (2)	2 (2)	3 (2)	3 (2)	2 (2)	1 (2)	0 (2)	0 (3)
2		2 (3)	3 (2)	5 (2)	6 (2)	6 (2)	5 (2)	3 (2)	0 (2)	0 (3)
5			8 (2)	10 (1)	10 (1)	10 (1)	8 (1)	6 (1)	3 (1)	0 (2)
10				16 (2)	16 (2)	15 (1)	13 (1)	11 (1)	7 (2)	3 (2)
15					20 (2)	19 (2)	17 (1)	14 (1)	10 (2)	5 (2)
20						21 (2)	19 (2)	15 (1)	11 (2)	5 (2)
25							19 (2)	15 (2)	10 (2)	4 (2)
30								13 (2)	8 (2)	1 (2)
35									4 (3)	0 (3)
40										0 (4)

[1] Maximum values are underlined and defined as those values not lower than the maximum minus 1/2 its confidence interval ($P<0.05$). The values in parentheses are one-half the confidence interval.

the environment of the fescue prairie to which it was introduced. How much genetic variation exists in the germination of fugitive populations of smooth brome has yet to be determined.

If protracted periods with high moisture occur in the summer when temperatures are high, smooth brome is likely to germinate earlier and grow faster (Smoliak and Johnston 1968) than plains rough fescue. Likewise under intermittent precipitation, smooth brome seeds may germinate because of more rapid germination than plains rough fescue (Grilz 1992). In contrast, plains rough fescue may not be able to exploit temporarily favorable moisture conditions because of slow germination.

Lower germination of plains rough fescue under descending temperatures relative to those that were ascending is an adaptation for autumn conditions in the plains rough fescue grassland (Romo et al. 1991). Reduced germination under decreasing temperatures in the summer-early autumn may allow some seeds to enter the seedbank and possibly germinate in the future. However, the persistence of viable rough fescue seeds in the soil is low (Johnston 1961) and germination of plains rough fescue is reduced by exposure to moist conditions at low temperatures (Romo et al. 1991).

The lack of response of smooth brome to warming or cooling temperatures potentially allows it to occupy niches and exploit resources as they become available, provided seeds are present and suitable moisture conditions are met. A shortcoming of germination under decreasing temperatures is that seedlings may be predisposed to damage or mortality by low winter temperatures. Winter damage to seedlings of perennial grasses is inversely related to the number of leaves (White and Currie 1980). The LT_{50} for seedlings of smooth brome seeded in late August ranged from -22 to -23°C in late October, indicating that it is well adapted to winter conditions in western Canada (Limin and Fowler 1987).

Seeds of smooth brome that do not germinate in the autumn may pass into the seed bank and be available to germinate the following spring. Smooth brome suffers a slight decrease in germination after exposure to winter temperatures in the soil, but the rate of germination is hastened (Wilson et al. 1974), allowing it to establish early in the spring.

Plains rough fescue prairie protected from grazing or fire characteristically develops large concentrations of dead plant material (Johnston and MacDonald 1967), and the light intensity at the soil surface is reduced. The soil beneath the litter layer has more available moisture and less fluctuation in temperatures than open or bare ground (Evans and Young 1970, Johnston et al. 1971). The requirement for darkness in most seeds at low temperatures, along with high germination of smooth brome under low levels of water stress, improves the chances that adequate moisture is available for germination in fescue prairie. If moisture conditions are within the range for germination, some seeds of smooth brome can germinate in light or in darkness. These same conditions are also conducive to germination of plains rough fescue. Germination and survival of pumpelly brome (*Bromus pumpellianus* Scribn.) and rough fescue seedlings was poorest when seeds were placed in the sod of rough fescue, intermediate under litter, and greatest when seeds were buried about 12 mm deep in the soil (Johnston 1961). Although it has not been demonstrated, establishment of smooth brome and plains rough fescue is likely highest where fescue has died or where competition is reduced at some distance from established plants.

The germination responses under controlled conditions provide clues to the abiotic limitations and ecological relations in germination of plains rough fescue and smooth brome in the field. Smooth brome can germinate in greater numbers over wider ranges of temperature and water stress, thus increasing the probability that requirements for germination can be met for some seeds under varied conditions. Smooth brome's prolific production of seeds further increases the likelihood that many seeds reach the seedbed. After germination, the growth of smooth brome also exceeds rough fescue (Smoliak and Johnston 1968). This superior performance of smooth brome is not surprising because it has been subjected to intense selection pressure for high vigor in all stages of germination, establishment, and growth. Research is needed to determine the specific processes in fescue prairie that makes it vulnerable to invasion by this exotic grass.

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