FLOWERING AND SEED PRODUCTION IN MEADOW BROMEGRASS

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SUMMARY OF DISSERTATION

Submitted in partial fulfillment of the requirements for the

DEGREE OF DOCTOR OF PHILOSOPHY

by

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ABSTRACT

Meadow bromegrass (*Bromus riparius* Rehm.) is an important forage grass in western Canada. Economical seed production is critical to its use. Seed yield usually declines rapidly after two to three seed crops. Field and growth chamber experiments were conducted to determine the influence of: a) residue removal and N fertilization on tiller density and size, panicle density, silvertop incidence, seed yield and stand longevity, b) tiller size and stand age on panicle production, and c) daylength and temperature during primary and secondary induction on panicle production.

Removing residue after harvest and applying N (100 kg ha^{-1}) increased yield from 200 to 450 kg ha^{-1} compared to not removing residue or adding N in the second seed crop. The difference in seed yield between treated and untreated plots was only 30 to 90 kg ha^{-1} in the third seed crop. The increase was related to an increase in panicle production, however, the correlation between panicle number and seed yield was low. Silvertop incidence (% of panicles affected) increased as the stand aged, but removing residue after harvest reduced silvertop.

In pot studies, the percentage of plants that produced panicles increased as tiller basal diameter increased from one mm to three mm, regardless of the age of the stand. However, fewer large tillers were observed in older stands. Large tillers from a four-yr-old stand produced fewer panicles than large tillers from a two-yr-old stand indicating that tiller size alone is not responsible for the decline in panicle production.

Panicle production increased as the temperature during primary floral induction decreased. However, daylength during primary induction had no effect on panicle production. Varying temperature or daylength during secondary induction had no effect on panicle production; panicles were produced in 85% of plants regardless of temperature, and 67 to 77% of the plants regardless of daylength.

In conclusion, residue removal after harvest and N fertilization improved seed yield in young meadow bromegrass stands. However, these practices were not effective in prolonging seed yield beyond two to three seed crops. Drought, winter injury, competition among tillers and silvertop incidence all play a role in reducing seed production.

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1. INTRODUCTION

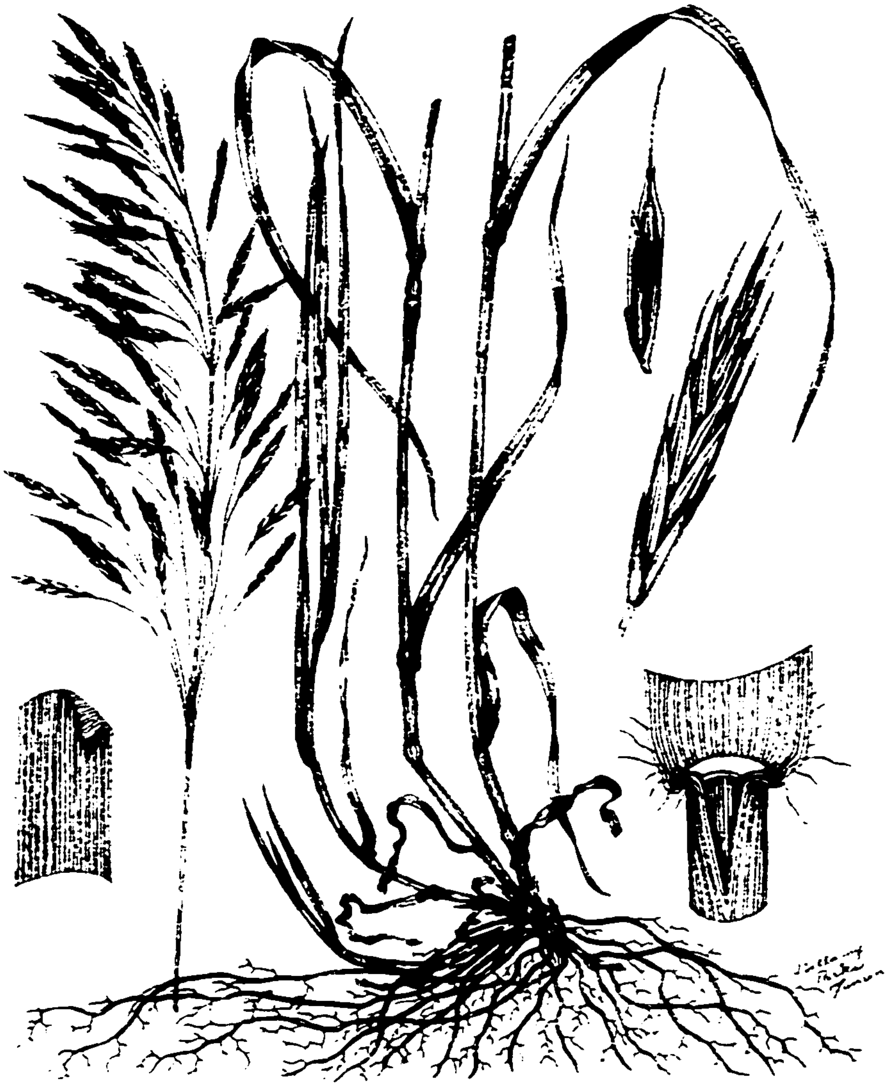
Meadow bromegrass (*Bromus riparius* Rehm.) is a cool-season perennial bunchgrass. It is highly valued in western Canada for its rapid regrowth and good quality forage throughout the season; especially in autumn. As a result of its popularity, seed demand for meadow bromegrass is high; however, seed production is not as consistent as in smooth bromegrass (*B. inermis* Leyss) and seed yields of meadow bromegrass usually decline rapidly as the stand ages (Knowles *et al.* 1993). In other cool-season perennial grasses, nitrogen fertilization and post-harvest residue removal generally improve seed production. (Meijer and Vreeke 1988a and b, Thompson and Clarke 1993) The optimum timing of these management practices depends on when flowering is induced or initiated. Daylength (photoperiod) and/or temperature (vernalization) control flowering in these grasses and many, including smooth bromegrass, have a dual induction system (Heide 1994). This means that they require exposure to either short days or low temperatures, followed by long days, before floral differentiation (initiation) will take place. While the floral induction requirements and management practices have been studied for many cool-season perennial grasses, including smooth bromegrass, relatively little work has been done with meadow bromegrass and no information is available on its floral induction requirements. Likewise, little information is available on the impact of management on silvertop, one of the most important disorders in grass seed production fields. The objectives of this series of studies were to investigate the development and maintenance of seed yield potential in meadow bromegrass. To accomplish this, a series of field, greenhouse and growth cabinet experiments were conducted on meadow bromegrass to determine: a) the effect of residue removal and N fertilization on tiller development, inflorescence development, silvertop incidence and seed yield, b) whether tillers have to reach a certain size before they are capable of flowering, and whether this changes as the stand ages, and c) the daylength and temperature required to induce flowering.

2. LITERATURE REVIEW

Meadow bromegrass is a cool-season perennial grass. It is one of approximately 100 species in the genus *Bromus*, named for the characteristic panicle inflorescence that resembles the oat panicle. Only two of these grasses are cultivated for forage in North America; smooth bromegrass and meadow bromegrass (Vogel *et al.* 1996). Both of these species are Eurasian in origin; meadow bromegrass originated in southeastern Europe, the Caucasus, Turkey and Central Asia (Knowles *et al.* 1993). The cultivar Paddock was selected from introductions from Krasnodar, USSR; Fleet was selected from eight strains from Europe and Asia, including Regar, an America cultivar, and Paddock. Both Paddock and Fleet were registered and released in 1987. Meadow bromegrass is grown for hay and pasture in western Canada and the northwestern US.

2.1 Plant description

Meadow bromegrass can grow to a height of 150 cm (Fig. 2.1). Its rhizomes are shorter than smooth bromegrass and consequently the plant spreads more slowly. One-yr-old spaced plants of meadow bromegrass had an average width of 42 cm compared to 77 cm for smooth bromegrass (Knowles *et al.* 1993). Meadow bromegrass also has narrower, longer leaves with a more basal growth habit than smooth bromegrass. The plant is characterized by pubescence on the leaves, stem and even on the seeds. The leaves usually droop, and the inflorescences rise above the basal clump in erect open



Drawing of meadow bromegrass (*Bromus riparius* Rehm.). (From Vogel *et al.*, 1996. Used with permission.)

panicles, 60 to 120 cm long, with whorled branches. The spikelets are cylindrical and slender, pointed, with 5-13 flowers and 1.5-3.0 cm long awned lemmas. Cultivars of meadow bromegrass have 2n=70 chromosomes (compared to smooth bromegrass with 2n=56). Both meadow bromegrass and smooth bromegrass are cross-pollinated, but meadow bromegrass has a higher degree of self-compatibility than smooth bromegrass.

2.1.1 Adaptation

Meadow bromegrass is adapted to somewhat cooler and moister areas than smooth bromegrass; Black and Gray-wooded soils, Dark Brown soils with good moisture, and Brown soils under irrigation. Leaves of meadow bromegrass will turn brown in response to drought, but this does not impede survival. Meadow bromegrass will not withstand prolonged (10 days) flooding, and is less tolerant of salinity than smooth bromegrass (Knowles *et al.* 1993). Meadow bromegrass is also less winter hardy than smooth bromegrass or crested wheatgrass (*Agropyron cristatum* (L.) Gaertn.), with LT_{50} values of -22 °C, -28 °C and -29 to -35 °C for meadow bromegrass, smooth bromegrass and crested wheatgrass, respectively (Limin and Fowler 1987).

2.1.2 Forage production

One of the most important characteristics of meadow bromegrass is its ability to regrow from existing tillers after cutting rather than from the crown or rhizomes as in smooth bromegrass. This results in much more rapid regrowth, particularly in the first 21 days after cutting (Van Esbroeck *et al.* 1995). The seasonal distribution of forage production in meadow bromegrass is more uniform than for smooth bromegrass and in particular, forage production is superior in July and September. Meadow bromegrass leaves are more frost tolerant than smooth bromegrass leaves; as a result, both color and quality are better in autumn. Meadow bromegrass generally provides valuable grazing until mid-October (Knowles 1987).

2.1.3 Seed production

Seed production in meadow bromegrass ranged from 50- 818 kg ha^{-1} at Saskatoon, SK, depending on cultivar, row spacing and age of stand (Knowles *et al.* 1993). Meadow bromegrass seed yields usually are lower, less reliable and decline more rapidly with stand age than for smooth bromegrass; however, agronomic practices such as row spacing can influence seed production. Paddock and Fleet meadow bromegrass produced over 400 kg ha^{-1} in the fourth seed production year when seeded in rows spaced 90 cm apart. Annual precipitation of 350 to 500 mm, or irrigation, is required for good, consistent seed production (Kruger 1997). Seed shattering is more of a problem in meadow bromegrass than in smooth bromegrass.

Even though forage grass species such as meadow bromegrass are valued primarily for their vegetative characteristics, a reliable seed supply at reasonable cost is essential for rapid adoption of new cultivars by livestock producers. Paddock and Fleet meadow bromegrass were selected for improved seed production characteristics (higher yield, less shattering, reduced awn development) and seed yields are 65% higher than Regar, the only other available cultivar (Knowles 1990a, Knowles 1990b).

Silvertop is one of the most significant disorders of grass seed production. Meadow bromegrass is more susceptible to silvertop than smooth bromegrass (Soroka 1992, Soroka and Gossen 1996). Silvertop prematurely halts the development of the panicle after elongation. It is often associated with a insect feeding injury just above the last node. The nutrient and water supply to the panicle is interrupted and, as a result, no seed develops. Insecticides reduce silvertop incidence in Kentucky bluegrass (*Poa pratensis* L.) and creeping red fescue (*Festuca rubra* L.), suggesting that insects that pierce the stem are the primary causal agent (Peterson and Via 1971, Okuda 1988). The result of silvertop is sterility; therefore, it has the potential to exert a serious negative impact on seed production.

Other insect and disease problems of meadow bromegrass include head smut (*Ustilago bullata* Berk.) (Turnbull and Gossen 1996, Kruger 1997), and seed midge. Smut can cause serious seed losses, but can be avoided by using clean seed,

2.2 Inflorescence and seed production in cool-season perennial grasses

Seed production in many cool-season perennial grasses involves a genotypic response to environmental conditions. This process begins long before the inflorescence emerges. The grass plant must pass through a series of 'gateways' before flowering and seed production will occur (Chastain and Young 1998). The first step is the transition from a juvenile, non-responsive stage to a mature, responsive stage. This is followed by response to a combination of thermal and photoperiodic stimuli that precede and prompt the differentiation of the shoot apex from vegetative to floral development (Heide 1994). Many perennial cool-season grasses require a dual or two-step process for floral induction that involves exposure to short days and/or cold temperature followed by exposure to long days (Heide 1994). These two steps are often referred to as primary induction and secondary induction. Floral initiation and development, internode elongation and seed filling follow.

2.2.1 Juvenility

Juvenility is a phase in the development of the plant during which it will not respond to environmental conditions that would stimulate flowering in more mature plants. To complete this stage, the plant must attain a certain size, accumulate certain metabolites or produce the appropriate type of phytochrome before it is receptive to environmental stimuli that promote flowering (Langer 1972). Phytochrome is the photo reversible plant pigment thought to act as a physiological clock in regulating flowering (Street and Opik 1970). The physiological basis for competence to flower is not well understood; hence, morphological or chronological indicators of the ability to respond to flowering stimuli, such as leaf number, leaf area or plant age, are often used (Lang 1965, Heide 1994).

The length of the juvenile period varies, primarily with genotype. In some grasses, such as ryegrass *(Lolium perenne* L.*)*, vernalization can be achieved in imbibed seeds in complete darkness through exposure to low temperature (2°C). The rate of vernalization, however, is faster in seedlings than in imbibed seeds, and the inflorescences produced by tillers that are present in autumn are larger (Hill and Watkin 1975). Most grasses require several weeks of development after germination before they are capable of responding to floral stimuli (Ikegaya *et al.* 1981, Meijer 1984).

In Kentucky bluegrass, tillers must produce eight to nine leaves and attain a certain minimum width and number of vascular bundles before they will respond to flowering stimuli (Parker-Clarke *et al.* 1996). Schoberlein (1987) found a strong positive correlation between leaf number at the time of induction and receptiveness to flowering stimuli in orchardgrass (*Dactylis glomerata* L.), meadow fescue (*Festuca pratensis* Huds.) and timothy (*Phleum pratensis* L.). In meadow fescue, as much as 92% of the variation in panicle production could be explained by the leaf area of tillers before exposure to inductive conditions (Havstad 1996a). Chastain *et al.* (1997), on the other hand found no relationship between leaf number in autumn, when floral induction presumably occurs, and flowering in Kentucky bluegrass. Although plant size is apparently a factor in floral induction in Kentucky bluegrass, biomass production was not related to seed yield (Chastain *et al.* 1997). Carbohydrate reserves in tiller bases of creeping red fescue were also unrelated to flowering (Meints *et al.* 1996). Height, however, was consistently less in plants that flowered and produced seed in that study, which may be related to the importance of mowing rather than juvenility.

2.2.2 Floral induction

Once the grass plant achieves a stage in which it is receptive to flowering stimuli, it must still go through a complex series of steps referred to as 'induction' before the apex changes from vegetative to reproductive. Induction involves "the perception, transduction and transmission of environmental signals resulting in a change in plant development patterns from vegetative to reproductive" (Heide 1994). The environmental signal that Heide refers to are generally a combination of daylength and temperature that signals the changing of the seasons from autumn to winter and winter to spring. This system of environmental cues results in the plant flowering at a time during which viable seed can be formed. Thus, induction requirements generally identify the origin or the agronomic environment under which the species, cultivar or ecotype evolved or was bred. As a result, ecotypes of different geographic origin within the same species can differ in their flowering requirements.

2.2.2.1 Induction systems

In general, temperate grasses fit into two categories in terms of photoperiodic and/or temperature or vernalization requirements for flowering: 1) those that require only exposure to long days to flower and 2) those that must be exposed to both short days (SD) and/or low temperatures followed by long days before they will flower (dual induction). The first group, which includes timothy, will flower in the year of seeding (Heide 1982).

More common among temperate grasses is the dual induction system. The first stage, exposure to short days and/or low temperatures, is referred to as primary induction, whereas the second stage, exposure to long days, is referred to as secondary induction. Within this group, certain species (*Poa pratensis*, *Hordeum bulbosum* and *Alopecurus pratensis* and certain cultivars of winter wheat) will go through induction and initiate flowers through exposure to SD conditions (Heide 1994). As a result, floral primordia are present in the fall and long days are required simply for elongation of the flowering culm, development of the inflorescence and anthesis. This is particularly important for alpine and northern species that must survive and produce seed in a very short growing season, because this system allows for rapid flowering and seed set once the growing season begins (Hodgson 1966).

The other species in the dual induction group are induced to flower by short days and/or low temperatures, but do not differentiate floral initials until after they have been exposed to long days. This group includes many of the important forage and turf species such as perennial ryegrass, meadow fescue, orchardgrass, creeping red fescue and smooth bromegrass. Within this group, some species respond to either short days or low temperature, for example, exposure to cold temperature (vernalization) eliminates the need for short days in meadow fescue (Heide 1988). However, the site of response apparently differs, depending on whether photoperiodism or vernalization is involved. In the case of photoperiodic induction, the signal is received by the leaves and transmitted to the apex; success or failure depends on the sensitivity of the leaves, not the apex. Vernalization, however, occurs at the shoot apex and the carbohydrate supply to that apex is critical (Lang 1965). Evidence suggests that different pathways are used by these two different inductive processes (Evans 1987).

Smooth bromegrass and orchardgrass differ from other dual induction grasses in that the requirement for short days cannot be replaced by exposure to cold temperatures (Heide 1984, Heide 1987). In fact, the flowering response in smooth bromegrass was not as great at lower temperatures (3, 6 or 9 °C), as it was at temperatures ranging from 12 to 24°C.

The critical photoperiod for secondary induction in orchardgrass was between 12-13 hours; the longer days are required for cultivars of more northerly origin (Heide 1987). In smooth bromegrass, the critical daylength for secondary induction was 14 hours for the

American cv. "Manchar" and 16 hours for the Norwegian cv. 'Lofar'. In Carlton smooth bromegrass, initiation occurred in early May in northern Alberta under field conditions (Elliott 1966). At this time, daylength was between 15 and 17 hours, whereas the mean temperature was between 2 and 7 °C, with minimum temperatures often below freezing. This indicates that the physiological processes involved in floral initiation can proceed at relatively low temperatures. The photoperiodic component of primary induction, on the other hand, is hampered by low temperature (Heide 1994). This raises questions as to the nature of the photoperiodic response.

2.2.2.2 Induction requirement: Whole plant or individual tiller?

It is generally thought that each individual tiller must go through the primary induction process. In fact, Heide (1994) states "Basic to the understanding of flowering control in dual induction grasses, is the fact that the primary induction effect is local, i.e. induced tillers cannot induce later-formed adjacent tillers." However, flowering occurred in unexposed tillers of both tall fescue (*F. arundinacea* Schreb.) (Hare 1993) and meadow fescue (Havstad 1996a, Havstad 1996b). This indicates that: the concept of juvenility does not apply at all; it does not apply to individual tillers; or, that the floral stimuli are transmissible from uninduced to induced tillers. Small tillers of meadow fescue, which were not visible at the time of exposure to inductive conditions, would probably have still been dependent on the mother plant. This would provide a strong sink for carbohydrate from the mother plant. Since florigen is thought to follow carbohydrate movement from source to sink, this would provide a conduit for transmission to the newly formed tillers.

2.2.2.3 Induction requirement: Quantitative vs qualitative?

Another concept that may apply to responses where the flowering response is not as clear cut as it is in some of Heide's work is that of 'qualititative' versus 'quantitative' response (Lang 1965). Is the response 'all or none' (obligate) or does exposure to a particular daylength or temperature merely hasten the development of the floral meristem (facultative)? It may be that the majority of tillers have a qualititative requirement for certain conditions for flowering, while others are governed by less strict requirements. The fact that tillers that are not visible at the time of induction, whether they are present in the leaf sheath or not, does not support the hypothesis that a tiller must reach a certain leaf stage in order to be receptive.

2.2.3 Floral initiation

The next phase, which is referred to as either secondary induction or floral initiation, is characterized by well-recognized morphological changes. Floral initiation in long day plants may occur in autumn or in spring. However, in many dual induction grasses, no morphological changes take place until after exposure to long days. The critical number of long day cycles varies with the species or ecotype and is also influenced by the degree of induction during primary induction. The more effective the primary induction, the shorter the requirement for secondary induction.

As mentioned earlier, some grasses go through both induction and initiation under short day conditions, but require long days for elongation of the flowering culm. This is characteristic of high latitude and high altitude ecotypes (Haborg 1978). In these grasses, the floral initials are able to withstand cold temperatures, whereas in other grasses floral initials that arise in the fall are killed by frost. While Heide (1984) found that smooth bromegrass did not flower until it had been exposed to long days, Carlton smooth bromegrass produced floral initials in autumn under field conditions in northern Alberta (Elliott 1966). This indicates that either the long day requirement is facultative in smooth bromegrass or that bromegrasses that originate from different latitudes differ in their flowering requirements. The cultivars that Heide used in his test were Manchar, an American cultivar intermediate between the southern and northern types, and a Norwegian cultivar of unknown origin, whereas Carlton is a northern cultivar (Vogel *et al.* 1996).

Although the impact of environmental conditions on floral induction has received more research attention, temperature and daylength also have an impact on floral differentiation (initiation) and development. Differentiation and development of the inflorescence is a typical growth process that is positively correlated with temperature. Exposure to short days during inflorescence development not only inhibits floral development, but will result in developmental delays that cannot be overcome by re-exposure to long days (Heide 1994). Very few researchers have studied culm elongation; however, it was determined that the critical daylength for culm elongation in orchardgrass was longer than the daylength required for floral initiation (Niemelainen 1990).

2.2.4 Seed production

Seed filling in perennial grasses is similar, in some ways, to annual grasses. Seed yield is a function of tiller density, inflorescence density, the number of spikelets per inflorescence, the number of florets per spikelet, the seeds per floret, and the weight of each seed. Yield loss occurs when a) tillers do not become reproductive, b) florets are not pollinated, not fertilized or are aborted, c) seeds shatter or d) seed size is so small that it is not recovered in the combining operation (Warringa 1997).

2.3 The effect of management practices on inflorescence and seed production

Environmental factors play a major role in the control of flowering (Heide 1994). For this reason, the response to management practices often reflects the interaction between plant growth and environmental signaling. For example, applying nitrogen in the spring to a species that undergoes floral induction in autumn will have quite a different effect than if nitrogen is applied to a long day species or a species with a very short vernalization requirement. In the former case, the result will be the proliferation of vegetative tillers, in the latter, the chance that reproductive tiller numbers will increase is much greater. Understanding the floral induction and initiation processes allows for the development of management practices that capitalize on these powerful forces and use them to improve seed production (Chastain and Young 1998). Working with the juvenility concept is relatively straight forward, in that one assumes an optimal size or nutritional status can be achieved with timely applications of nitrogen. "Timely" management requires an understanding of when induction events occur.

2.3.1 Nitrogen fertilization and residue removal: Effect on flowering

Two of the most important management practices for grass seed production include nitrogen fertilization and residue removal. Both fertilization and residue removal affect tiller density and size (Thompson and Clark 1993); residue removal improves light penetration through the canopy (Meijer and Vreeke 1988b) and presumably changes light quality (Silvertown 1980). The differences in floral induction conditions, time of initiation and management requirements are summarized in Table 2.1. In general, the timing of N application and residue removal is more related to floral induction and initiation than to the development of a greater supply of inducible tillers. In Holland, delaying spring N application from the end of February (before growth is initiated) until the end of March or April resulted in fewer fertile tillers in red fescue, orchardgrass, meadow fescue and perennial ryegrass. In all but orchardgrass, however, seed number tiller^{-1} and seed weight compensated so that seed yield was not significantly reduced as a result of the delay. Floral initiation in orchardgrass occurs very early (January or February), and late application of N stimulated vegetative growth at the expense of reproductive growth. Since the importance of tiller development at the time of floral induction has been demonstrated (Havstad 1996a Parker-Clarke *et al.* 1996), we must assume that in these field studies adequate resources (seed, N, light, water) were provided to ensure an adequate number of appropriately sized tillers for induction. Wright (1978) found that 30% of the fertile tillers of perennial ryegrass died before elongation. Increasing light penetration during elongation improved seed yield of creeping red fescue and Kentucky bluegrass (Meijer and Vreeke 1988b). This suggests that lack of resources at post-induction stages of flowering may be the primary limiting factor in seed production. Schoberlein *et al.* (1995) used labelled N to demonstrate that nitrogen applied in late summer, autumn or spring was used mainly for

Table 2.1. **Floral induction requirements and management recommendations for cool-season perennial grasses.**

Species	Induction requirements	Authority	Management recommendations (timing)	Authority
1. Timothy (*Phleum pratense*)	Long day	Heide 1982	N spring,	Neimelainen and Jarvi 1995
			N split 30% autumn : 70% spring(10 cm of growth)	Nordestgaard 1983
			Res. removal - no effect	Entz *et al.* 1994, Fulkerson 1980
2. Perennial ryegrass (*Lolium perenne*)	Cold temp. (12-16 wks*) + long day	Heide 1994	N - as soon growth starts in spring	Nordestgaard, 1983
3. Kentucky bluegrass (*Poa pratensis*)	Short day (6-10 wks) or cold temp. (8-12 wks) + long days**	Heide 1994	N split - 1/3 autumn , 2/3 early spr.	Meijer and Vreeke 1988a
			N split - 50:50	Nordestgaard 1983
			Res. removal - after seed harvest	Meijer and Vreeke 1988b Thompson and Clarke 1989

Species	Induction requirements	Authority	Management recommendations (timing)	Authority
4. Creeping red fescue (*Festuca rubra*)	Short days (12-20 wks) or cold temp (20 wks) + long days	Heide 1994	N split - 1/3 autumn , 2/3 early spring	Meijer and Vreeke 1988,
			N split - 50:50	Nordestgaard 1983
			Res removal - immed. after harvest	Meijer and Vreeke 1988, Nordestgaard 1980
5. Orchardgrass (*Dactylis glomerata*)	Short days (8-10 wks) or cold temp. (>20 wk) + long days	Heide 1994	N -split 30% autumn:70% spring, spring application asap.	Nordestgaard 1983
6. Smooth bromegrass (*Bromus inermis*)	Short days (4-6 wks) + long days	Heide 1994	Res. removal - fall, Aug 15th optim.	Fulkerson 1980
			N - Sept.	Knowles and Cooke 1952
			Res. removal - fall, Oct 15th	Fulkerson 1980
			October or April	Knowles 1966

* Length varies with genotype

** Initiation begins in fall for northern latitude and higher altitude genotypes.

inflorescence emergence in ryegrass, timothy, orchardgrass, Kentucky bluegrass and meadow fescue.

2.3.2 Nitrogen effect on seed production

Much of the research on the effects of nitrogen and residue management has focused on seed production rather than tiller development and flowering. The effect of nitrogen on grass seed production depends on many factors including species (Nordestgaard 1983, Meijer and Vreeke 1988a), time of application (Harrison and Crawford 1941, Knowles and Cooke 1952, Nordestgaard 1983), growth stage at time of application (Meijer and Vreeke 1988a), soil moisture (Harrison and Crawford 1941) and soil mineral N (Meijer and Vreeke 1988a). The seed yield response of smooth bromegrass and crested wheatgrass to N increased as the stand aged (Canode and Law 1978). Meadow bromegrass fertilized after seedling emergence and again the following spring (2 x 84 kg ha $^{-1}$ N) produced significantly less seed than when it was fertilized in the fall of the establishment year in one of two locations (Upton 1983). At the other location, no difference occurred in response to N rate or time of application. Seed yield of smooth bromegrass generally increases more in response to fall-applied than to spring-applied N (Knowles and Cooke 1952, Buller *et al.* 1955). However, in certain cases (Horton 1991), spring N application resulted in higher seed yield of smooth bromegrass than fall N application. These inconsistencies in response to time of application may be related to time of precipitation. Higher seed yield of smooth bromegrass following N application in mid-May versus mid April was related to rainfall timing (Harrison and Crawford 1941). In Holland and Denmark, where precipitation is generally abundant, grass seed crops benefit from both fall and spring applications of N (Nordestgaard 1980, Nordestgaard 1983, Meijer and Vreeke 1988a). N rate responses, based on soil mineral N, have been calculated for perennial ryegrass, Kentucky bluegrass and red fescue, under Dutch conditions (Meijer and Vreeke 1988a). Similar response curves have been developed for smooth bromegrass, crested wheatgrass, intermediate wheatgrass (*Agropyron intermedium*) and timothy in Saskatchewan (Loeppky *et al.* 1999). In soils with intermediate levels of available N and P (2 mg kg^{-1} N and 8 mg kg^{-1} P, 0-60 cm and 0-15 cm depths respectively), the estimated smooth bromegrass response to 50 kg ha^{-1} N plus 9 kg ha^{-1} P_2O_5 was 540 kg ha^{-1}.

2.3.3 Residue removal effect on seed production

Residue removal increases seed yield in many grass species, including crested wheatgrass, red fescue, smooth bromegrass (Knowles 1966, Canode and Law 1978, Nordestgaard 1980, Meijer and Vreeke 1988b), Kentucky bluegrass (Meijer and Vreeke 1988b, Thompson and Clarke, 1989) and meadow bromegrass (Upton 1983), but not timothy (Entz *et al.* 1994). In addition to the benefit of increasing seed yield, grazing results in animal weight gain (Lawrence and Lodge 1975). Method (burning, mowing or grazing), timing and height or severity of the removal treatment all have an impact. Pest control accounts for some of the impact of residue removal. Silvertop incidence can be significantly reduced by burning or very close mowing in Kentucky bluegrass and creeping red fescue (Kamm 1979, Soroka and Gossen 1996).

Yield improvements are also related to direct stimulation of reproductive development (Chilcote *et al.* 1980). In Kentucky bluegrass and red fescue, inflorescence production and seed yield increased proportionately with residue removal (Meijer and Vreeke 1988b). Addition of N and residue removal are often studied together even though interactions between these two factors are relatively rare. In meadow bromegrass, however, a second-year stand responded well to residue removal after harvest only if N was applied in the fall (Upton 1983).

3. CROP RESIDUE REMOVAL AND NITROGEN FERTILIZATION AFFECTS TILLER DENSITY AND DEVELOPMENT AND SEED PRODUCTION IN MEADOW BROMEGRASS

3.1 Introduction

Meadow bromegrass is a temperate zone bunchgrass. Its rapid regrowth potential makes it especially suitable for grazing and, as a result, it has become widely accepted as a pasture species, particularly in the moister areas across the Canadian Prairies. Due to its popularity as a forage species, demand for meadow bromegrass seed is generally high. Seed production of meadow bromegrass, however, is less reliable than smooth bromegrass and a significant decline in seed yield is often observed after the first two seed crops (Upton 1983, Knowles *et al.* 1993). Since the cost of establishment, estimated at \$356.80 CAN ha^{-1} (Kruger 1997), must be amortized over the life of the stand, prolonging the productive life of a stand could significantly improve the economics of meadow bromegrass seed production.

Seed production in many temperate perennial grasses is closely related to fall tiller development (Schoberlein 1987, Boelt 1999). This is particularly important in grasses with a dual floral induction system, including smooth bromegrass (Heide 1994). In such species, tillers must not only be present when conditions which favor primary induction occur, but they must be inducible. Whether the tillers are inducible or not often depends on whether they have gone through the transition from juvenile, non-responsive growth to mature, responsive growth. The physiological basis for maturity is not well understood, but one of the most accurate morphological indicators of maturity is leaf stage. A significant correlation has been reported between the number of leaves in the fall and the percentage of fertile tillers the following year in orchardgrass, meadow fescue, timothy, Kentucky bluegrass, red fescue and, to a lesser extent, perennial ryegrass (Nordestgaard 1980, Schoberlein 1987, Boelt 1999). Canode and Law (1978) found that large spring (Mar 31st) tillers produced more heads than small spring tillers of smooth bromegrass and crested wheatgrass. Recently, Chastain and coworkers (1998) found that fall tiller size did not account for the variability in seed yield related to various residue management techniques in Kentucky bluegrass. This effect was particularly noticeable as stands aged. Tiller height was more closely (negatively) correlated to flowering and seed production than leaf stage, basal diameter or biomass production. This may be related to the importance of residue removal in Kentucky bluegrass rather than stage of maturity.

Two of the most important management practices for grass seed production include nitrogen fertilization and crop residue removal. Both practices affect tiller density and size, flowering and seed production (Canode and Law 1978, Nordestgaard 1980, Thompson and Clark 1989, Thompson and Clarke 1993). Residue removal improves light penetration through the canopy (Meijer and Vreeke 1988b) and presumably changes light quality (Silvertown 1980). They are often studied together even though interactions are rare.

Two critical stages of nitrogen application have been identified: a) pre-induction, to ensure that an adequate number of well developed tillers are present for induction, and

b) inflorescence elongation, to ensure that adequate N is available to support elongation and floret filling. Nitrogen fertilizer increased tiller density and basal diameter in Kentucky bluegrass (Thompson and Clarke 1993). It also increased panicle production and seed yield (Thompson and Clarke 1989). Meadow bromegrass fertilized with 84 kg ha^{-1} N two weeks after emergence in the spring, and again in the spring of the first seed production year produced significantly less seed than a single application of 84 kg ha^{-1} N in the fall prior to the first seed crop (Upton 1983). In Holland, delaying spring N application from the end of February (before growth is initiated) until the end of March or April resulted in fewer fertile tillers in red fescue, orchardgrass, meadow fescue and perennial ryegrass (Meijer and Vreeke 1988a). In all but orchardgrass, however, seed number tiller^{-1} and seed weight compensated so that seed yield was not affected by the delay in N application. Floral initiation in orchardgrass occurs very early (January or February); late application of N stimulated vegetative growth at the expense of reproductive growth.

Under dry conditions, increasing N rate decreased seed yield of smooth bromegrass and crested wheatgrass. However, nitrogen fertilization increased seed yield in both crops when precipitation was adequate (Canode and Law 1978).

Soil mineral N influences N fertilizer response. Based on soil mineral N, N fertilizer rate response has been calculated for perennial ryegrass, Kentucky bluegrass and red fescue under Dutch conditions and for smooth bromegrass, crested wheatgrass, intermediate wheatgrass and timothy in Saskatchewan (Meijer and Vreeke 1988a, Loeppky *et al.* 1999). In soils with intermediate levels of available N and P (2 mg kg^{-1} N and 8 mg kg^{-1} P, at 0-60 cm and 0-15 cm, respectively), the estimated seed yield response of smooth bromegrass to 50 kg ha^{-1} N plus 9 kg ha^{-1} P is 540 kg ha^{-1}.

Removing crop residue after seed harvest often increases seed production in perennial grass crops (Canode 1965, Canode and Law 1978, Nordestgaard 1980, Upton 1983, Thompson and Clarke 1989). Residue management is frequently studied in conjunction with N fertilization, although interactions between these two factors are reported infrequently (Nordestgaard 1980, Upton 1983). In smooth bromegrass and crested wheatgrass, tiller density and size, and seed yield were greater following burning than following mechanical removal (Canode and Law 1978). Removing residue increased panicle production and seed yield in smooth bromegrass in southern Ontario (Fulkerson 1980). Time of residue removal was important; late fall (October 15th) removal produced the highest panicle density and yield compared to non-removal or early removal (Aug 15th, Sept 15th or both Aug 15th and Sept 15th). On the other hand, Knowles (1966) found that, while residue removal by burning or mowing increased smooth bromegrass seed yield, time of removal was not important. Burning red fescue delayed regrowth and, as a result, additional defoliation by mowing did not increase seed yield (Nordestgaard 1980). However, it did increase panicle production compared to mechanical residue removal. In the same experiment, when mechanical residue removal was practised, delaying N application was important to maximize panicle production. Delaying N was not necessary when residue was removed by burning. In Montana, under irrigation, seed yield in a second yr stand of meadow bromegrass was significantly higher when residue was removed either in the fall or after harvest plus fall only if N (84 kg ha^{-1}) was applied in the fall as well (Upton 1983). This combination of residue removal and N fertilization increased seed yield more than either residue removal or N fertilization alone, however, seed yield was still much lower in the second seed yr than in the first. The Montana study was discontinued after the second seed crop was harvested. No information is available on the effect of nitrogen fertilzation and crop residue removal on meadow bromegrass seed production under dryland conditions. In addition, no information has been reported on the influence of these practices on tiller growth and development or how fall tiller development is related to flowering and seed production in the following year.

The objectives of this study were to determine whether a) crop residue removal and N fertilization increased meadow bromegrass seed production and prolonged the productive life of the stand, b) crop residue removal and N fertilization influenced meadow bromegrass tiller growth, development and fertility and c) flowering and seed production in meadow bromegrass were related to fall tiller density and development.

3.2 Materials and methods

Field trials were conducted under rainfed conditions at Saskatoon, SK (52° 07' 106° 38') and under irrigation at Outlook SK (51°30" 107° 03'). Both sites are located on Typic Haploboroll soils. At Saskatoon growing season precipitation (April to October) was 307, 282, 366 and 247 mm in 1994-1997, respectively. At Outlook growing season precipitation amounted to 216 mm with an additional 150 mm of irrigation applied in 1994, 272 mm rainfall + 225 mm irrigation in 1995, 298 mm rainfall + 106 mm irrigation in 1996 and 197 mm rainfall + 319 mm of irrigation in 1997. See Appendix Table A1 for precipitation and irrigation details.

Paddock meadow bromegrass was seeded on 10 June 1994 at 12 kg ha $^{-1}$ in rows spaced 30 cm apart. Fifty kg ha $^{-1}$ of P_2O_5 and 11 kg ha $^{-1}$ of N (11-51-0) were incorporated during seedbed preparation. Each fall, all plots received an additional 50 kg ha $^{-1}$ of P_2O_5 and 11 kg ha $^{-1}$ of N (11-51-0). Treatments consisted of three rates of N (0, 50, 100 kg ha $^{-1}$) and four residue removal treatments (none, after harvest, October, or after harvest + October). Seed was harvested in the last week of July, and after harvest treatments were applied within a week of harvest each year. The October time of removal represents the end of the growing season on the Canadian Prairies. Treatments were replicated four times. The design was a split plot with N rate as the main plot and residue removal as the sub-plot. Sub-plots were 1.5 X 6.0 m. Ammonium nitrate (34-0-0) was broadcast at the prescribed N rates in early to mid September each year starting in 1994. Residue treatments consisted of removal with a forage harvester, then scalping with a flail mower to a height of 2.5 cm each year starting in 1995. Two 0.25 m^2 quadrats were marked in each plot. Starting in the fall of 1995, tiller density and leaf stage were determined each fall and spring. Panicles were counted in the same quadrats after anthesis each year. Seed and biomass were harvested from 0.25 m^2 quadrats at seed maturity each year to determine harvest index (seed weight/biomass). Seed was harvested from the whole plot annually, dried to eight to ten percent moisture and weighed.

All variables were subjected to an analysis of variance using the general linear model (GLM) of SAS (SAS Institute Inc. 1985) (Appendix Tables A2-A8b). Sites were considered fixed effects because only two were used and certain responses varied by site. The data for the two sites were analyzed separately when the site*N*residue removal interaction was significant. The effects of N rates were partitioned into linear and quadratic components, and the residue removal treatment means were evaluated through a series of *a priori* contrasts. Orthogonal contrasts were also used to determine the nature of interactions between N rate and residue removal treatments. Differences were considered statistically significant at $P \leq 0.05$. Standard errors were calculated for all means.

3.3 Results and discussion

3.3.1 Seed yield

In general, removing crop residue and applying N increased seed production of the second seed crop (Appendix Tables A2 and A2a). However, seed yield response to these treatments differed at the two locations in 1996. At Saskatoon, seed yield increased linearly with increasing rates of N fertilizer (Table 3.1). Crop residue removal also increased seed yield, especially if it was removed after harvest or both after harvest and in October. The interaction of the linear effect of N fertilization and no removal vs removal of residue resulted from the highest seed production when residue was removed twice and the highest rate of N (100 kg ha^{-1}) was applied as contrasted to the relative lack of response to N fertilization for the no removal of residue treatment. At Outlook in 1996, however, the residue removal treatments resulted in higher seed yield than if residue was left. None of the other treatments or interactions was significant. Increased winter injury, based on the change in tiller density, from fall to spring, was observed at Outlook, particularly with the late October residue removal treatments (both single and double) (Table 3.2, Appendix Table A3). This would explain the negative impact of the combination of N fertilization

Table 3.1 The effect of residue removal and N fertilization on second year seed yield in Paddock meadow bromegrass at Saskatoon and Outlook in 1996.

Residue management	N rate (kg ha^{-1})	Seed yield (kg ha^{-1}) Saskatoon	Seed yield (kg ha^{-1}) Outlook
None	0	153	150
	50	193	151
	100	209	261
After harvest (AH)	0	382	248
	50	556	377
	100	617	358
October (Oct)	0	184	134
	50	354	185
	100	521	218
AH + Oct	0	332	308
	50	599	292
	100	725	113
S.E.(Site*N*res)		42	
Contrasts:		P>F	P>F
N-linear (NL)		0.00	0.39
N-quadratic (NQ)		0.23	0.32
No removal vs removal (Res 1)		0.00	0.00
Single (AH, Oct) vs double vs AH+ Oct) (Res 2)		0.00	0.08
Early (AH) vs late (Oct) (Res3)		0.00	0.18
NL x Res 1		0.00	0.32
NQ x Res 1		0.49	0.79
NL x Res 2		0.06	0.58
NQ x Res 2		0.38	0.26
NL x Res 3		0.11	0.32
NQ x Res 3		0.30	0.17

Table 3.2. The effect of residue removal on the change in tiller density (fall/spring) of Paddock meadow bromegrass at Saskatoon and Outlook, 1996-1997.

Residue removal	1996		1997
	Saskatoon	Outlook	Sites combined
	Fall/spring tillers (%)		
None	96	146	111
After harvest (AH)	86	131	163
October (Oct)	98	87	141
AH + Oct	106	88	161
S.E. (Site*Res)	17		18
Contrasts:	P>F	P>F	P>F
No removal vs removal	0.93	0.05	0.05
Single (Ah, Oct) vs double (AH + Oct)	0.10	0.35	0.05
Early (AH) vs late (Oct)	0.21	0.12	0.02

and late crop residue removal on yield. Adequate nutrients are important to ensure winter survival, but high rates of N, especially if applied late in the season, generally increase incidence of winter injury in perennial grasses (Smith 1987). Late clipping reduced total soluble carbohydrates in meadow fescue and significantly reduced winter survival (Huokona 1974). The combination of N, and late clipping may have been exacerbated by the availability of water (irrigation) late in the season at Outlook. Under Canadian Prairie conditions, uncut residue has the potential to trap snow which would provide insulation and reduce winter injury. However, in this study, residue removal alone did not reduce seed yield.

Third year seed production in 1997 was low at both sites (Tables 3.3 and 3.4, Appendix Tables A2 and A2a). However, it was particularly poor in Saskatoon; 90% of the total seed production in the two years of the study occurred in 1996 (Table 3.5). N fertilization did not affect third year seed production at Saskatoon, but the 100 kg ha^{-1} rate increased seed yield at Outlook (Table 3.3). Crop residue removal improved third year seed yield at both sites, regardless of timing and frequency (Table 3.4). In a study conducted in Saskatoon from 1984-1989, seeding in 90 cm wide rows rather than 30-cm rows resulted in lower seed production in the first year, however, overall yields were higher with the wider rows. In the fourth year, the wide rows produced 427 kg ha^{-1} compared to 98 kg ha^{-1} for the 30-cm rows (Knowles *et al.* 1993). In the present study, 30-cm row spacing was chosen to determine whether residue removal and N fertilization could improve and prolong seed production in this more intensive system. While these treatments did improve seed production, they did not stop the decline in yield over time. Competition between vegetative

Table 3.3. The effect of N fertilization on third year seed yield in Paddock meadow bromegrass at Saskatoon and Outlook, 1997.

N rate	Seed yield (kg ha^{-1})		
(kg ha^{-1})	Saskatoon		Outlook
0	28		93
50	35		87
100	18		183
S.E. (Site*N)		13	
Contrasts:	P>F		P>F
N linear	0.52		0.01
N quadratic	0.33		0.04

Table 3.4. The effect of residue removal on third year seed yield in Paddock meadow bromegrass at Saskatoon and Outlook, 1997.

	Seed yield (kg ha^{-1})		
Residue removal	Saskatoon		Outlook
None	5		53
After harvest (AH)	40		147
October (Oct)	18		119
AH + Oct	46		165
S.E. (Site*Res)		13	
Contrasts:	P>F		P>F
No removal vs removal	0.03		0.00
Single (AH, Oct) vs double (AH + Oct)	0.24		0.08
Early (AH) vs late (Oct)	0.18		0.18

Table 3.5. The effect of residue removal and N fertilization on total (second and third year combined) seed yield of Paddock meadow bromegrass at Saskatoon and Outlook 1996 and 1997.

Residue management	N rate (kg ha^{-1})	Seed yield (kg ha^{-1}) Saskatoon	Seed yield (kg ha^{-1}) Outlook
None	0	161	187
	50	196	175
	100	211	357
After harvest (AH)	0	434	330
	50	591	519
	100	650	575
October (Oct)	0	198	234
	50	370	258
	100	544	401
AH + Oct	0	367	459
	50	685	403
	100	739	348
S.E. (Site*N*Res)		46	
Contrast:		P>F	P>F
N-linear (NL)		0.00	0.01
N-quadratic (NQ)		0.10	0.44
No removal vs removal (Res 1)		0.00	0.00
Single (Ah, Oct) vs double (AH+ Oct)(Res 2)		0.00	0.67
Early (AH) vs late (Oct) (Res 3)		0.00	0.00
NL x Res 1		0.00	0.45
NQ x Res 1		0.31	0.22
NL x Res 2		0.14	0.00
NQ x Res 2		0.05	0.96
NL x Res 3		0.08	0.49
NQ x Res 3		0.42	0.20

and reproductive tillers is often cited as a reason for poor seed production, especially in perennial grasses such as meadow bromegrass, and this occurred in this study.

At Saskatoon, very dry conditions in the fall of 1996 suppressed fall tiller growth (Table 3.2 and Appendix Tables A3 and A3a). Good tiller survival and subsequent early tiller growth at both sites in the spring of 1997 resulted in increased tiller density of 11and 63 % (residue not removed and residue removed after harvest, respectively). Since tillers arising in the spring are not induced, they generally remain vegetative, competing with reproductive tillers for resources and reducing seed production. Harvest index was greater when residue was removed at Saskatoon in 1996 and at both sites in 1997 (Table 3.6).

Second year seed yield was lower at Outlook than at Saskatoon (Table 3.1 and Appendix Tables A3 and A3a), even though that site was irrigated, whereas precipitation at Saskatoon (250 to 350 mm during the growing season) is considered barely adequate for seed production (Coulman *et al.* 1997). In 1996, biomass production was approximately 18% higher at Outlook than at Saskatoon (data not shown). Biomass accounted for a greater proportion of the total production at harvest at Outlook, compared to Saskatoon, resulting in a lower harvest index at Outlook (Table 3.6 and Appendix Tables A4 and A4a). In cereals, Simons (1982) reported a net flow of assimilates from the reproductive stem to the other tillers, even during grain filling. In perennial ryegrass, vegetative tillers may also receive a large proportion of assimilate from the stem and leaves of reproductive tillers (Clemence 1982). Recent evidence, however, indicates that competition from new tillers that develop after the onset of anthesis does not account for low or variable seed yield in perennial ryegrass (Warringa 1997). In Warringa's studies, low ovule dry weight was

Table 3.6. The effect of residue removal on harvest index in Paddock meadow bromegrass at Saskatoon and Outlook, 1996 and 1997.

Residue removal	1996		1997
	Saskatoon	Outlook	Sites combined
	----Harvest index ----		
None	0.02	0.01	0.01
After harvest (AH)	0.06	0.03	0.04
October (Oct)	0.05	0.01	0.02
AH + Oct	0.06	0.03	0.04
S.E. (Site*res, Res, respectively)	0.01		0.01
Contrasts:		P> F	
No removal vs removal	0.00	0.23	0.05
Single (AH, Oct) vs double (AH+ Oct)	0.80	0.29	0.06
Early (AH) vs late (Oct)	0.20	0.24	0.02

linked to differences in seed dry weight and seed yield, and it was suggested that factors that control panicle development and the sequence of floret differentiation could be responsible. In this study, biomass was only determined after anthesis, however, tiller density was higher at Outlook than at Saskatoon. In 1996, when second year seed yield was lower at Outlook than at Saskatoon, tiller fertility (percentage of tillers with panicles)was lower at Outlook than at Saskatoon. This is further evidence that more resources were dedicated to vegetative growth than to reproductive development at Outlook than at Saskatoon.

At current meadow bromegrass seed prices of approximately CAN \$2.50 kg^{-1}, assuming the cost of N fertilizer is \$0.66 kg^{-1} and the cost of removing residue is approximately \$25.00 ha^{-1} (Kruger 1997) , removing residue after harvest and adding 100 kg ha^{-1} N would have been profitable only at Outlook. Seed yield declined steadily at both sites, and it is unlikely that economic seed production could be sustained beyond three years, even with these treatments. Break-even yields to cover total costs in the third seed crop have been estimated at 137 kg ha^{-1} when the seed value is \$2.50CAN kg^{-1} (Kruger 1997). Based on this model, total yield in three seed crops should exceed 632 kg ha^{-1} to cover the total cost of production. Total seed yields in this study exceeded that level in all cases except at Outlook when residue was not removed and less than 100 kg ha^{-1} N were added each year (data not shown).

3.3.2 Tiller density, development and fertility

Tiller density was lower when residue was removed late (October) compared to early (after harvest) at both sites in the fall of 1995 (Table 3.7 and Appendix Tables A5 and A5a). In the spring of 1996, tiller density decreased due to winter injury in treatments where the residue was removed in October. Reduced tillering was also attributed to late residue removal (burning) in timothy (Entz *et al.* 1994). Kentucky bluegrass and creeping red fescue also require a regrowth period after residue removal (Meier and Vreeke 1988b). However, in the present study, late removal reduced tiller density only in one of the two years.

By the fall of 1996, tiller densities had increased to over 3000 m^{-2} at Outlook in treatments where residue was removed after harvest (Tables 3.7 and Appendix Tables A5 and A5a). In Saskatoon, tiller numbers were much lower, and residue removal had no effect. Higher moisture levels at Outlook, combined with mowing stimulated tillering, whereas in Saskatoon the dry fall conditions and lack of rainfall after N fertilization suppressed tiller development in the fall. In the spring of 1997, tiller numbers were much higher in treatments where residue was removed regardless of timing or frequency. Tiller density in the fall of 1995 and spring of 1997 increased linearly with increasing N rate at both sites, regardless of residue removal treatment (data not shown).

When residue was removed, stage of development (leaf number tiller $^{-1}$) was equal to or greater than when residue was not removed (Table 3.8 and Appendix Tables A6, A6a and A6b). At Saskatoon in the spring of 1996, all residue removal treatments resulted in higher leaf number tiller $^{-1}$ than no removal; double removal resulted in more advanced tillers than single removal. At Outlook, in 1996, the interaction between N and single vs double residue removal resulted from leaf number tiller $^{-1}$ increasing with increasing N rate in the single residue removal treatments, but decreasing with increasing N rate when the residue was removed twice (Table 3.9 and Appendix Tables A6 and A6b). In the fall of 1996, residue removal increased leaf number tiller $^{-1}$ at both sites (Table 3.9 and Appendix Tables A6, A6a, A6b and A6c). Residue

Table 3.7. The effect of residue removal on tiller density in Paddock meadow bromegrass at Saskatoon and Outlook, 1995-1997.

Residue removal	Fall 1995	Spring 1996	Fall 1996		Spring 1997	
	Sites combined	Sites combined	Saskatoon	Outlook	Saskatoon	Outlook
	--Tiller density (no. m^{-2})--					
None	2485	2840	2250	2270	2580	2080
After harvest (AH)	2680	2880	1990	3110	3530	4110
October (Oct)	2185	1950	2170	2670	3020	3450
AH + Oct	2220	2105	1960	3250	3330	4400
S.E.	135	254	147		244	
Contrasts:	P>F	P>F	P>F		P>F	
No removal vs removal	0.42	0.08	0.17	0.00	0.01	0.00
Single (AH) vs double AH+Oct)	0.20	0.33	0.47	0.08	0.83	0.06
Early (AH) vs late (Oct)	0.01	0.01	0.36	0.06	0.12	0.09

removal also had a positive effect on leaf development at Saskatoon in the spring of 1997. Residue removal had no effect at Outlook in 1997.

In 1996, the interaction between N (quadratic) and single vs double residue removal was significant for fertile tiller density due to the low fertile tiller density for the double residue removal treatment at 100 kg ha^{-1} N, whereas early residue removal resulted in a linear response to N rates (Table 3.10 and Appendix Table A7).

In 1997, fertile tiller density increased with increasing N rate (256, 363, 375 panicles m^{-2} with 0, 50, 100 kg ha^{-1} N, respectively) and residue removal (Appendix Table A7). More panicles were produced when residue was removed early than late (350 vs 76). A second removal increased panicle density compared to the mean of the two early removals (322 vs 229). Residue removal was associated with increased panicle production in Kentucky bluegrass and creeping red fescue (Meier and Vreeke 1988b, Thompson and Clarke 1989).

The effect of residue removal on percentage fertile tillers varied between sites in both years (Table 3.11and Appendix Tables A8, A8a and A8b). At Saskatoon in 1996, a significant increase in tiller fertility occurred when residue was removed compared to the no removal treatment, and within the removal treatments, double removal resulted in a greater proportion of fertile tillers than single removal. At Outlook in 1996, a higher percentage of fertile tillers occurred in early removal compared to late removal treatments. In 1997, the percentage of fertile tillers had decreased, but it was higher when residue was removed compared to not removed, at both sites. At Saskatoon, double removal resulted in higher percentage fertile tillers than single removal, and early residue removal was higher

Table 3.8. The effect of residue removal on stage of development in Paddock meadow bromegrass at Saskatoon and Outlook, 1995-1997.

Residue removal	Fall 1995		Fall 1996	Spring 1997	
	Saskatoon	Outlook	Sites combined	Saskatoon	Outlook
	--	-----Leaf number $tiller^{-1}$-----	--		

None	2.30	2.39	2.31	2.23	2.71
After harvest (AH)	2.38	2.99	2.68	2.65	2.68
October (Oct)	-----[1]	-----	-----	2.43	2.77
AH + Oct	-----	-----	-----	2.62	2.63
S.E.	0.04		0.06	0.07	
Contrasts:	P>F		P>F	P>F	
No removal vs removal	0.29	0.00	0.00	0.00	0.84
Single (AH, Oct) vs double (AH+ Oct)	-----	-----	-----	0.35	0.29
Early (AH) vs late (Oct)	-----	-----	-----	0.03	0.43

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[1] Tiller development in Oct treatments was the same as None and both AH + Oct were the same as AH due to time of removal.

Table 3.9 The effect of residue removal and N fertilization on stage of development in Paddock meadow bromegrass at Outlook, May 1996.

Residue management	N rate (kg ha^{-1})	Leaf number tiller $^{-1}$	
		Saskatoon	Outlook
None	0	2.5	2.4
	50	2..5	2.5
	100	2.2	2.4
After harvest (AH)	0	2.8	2.6
	50	2.7	2.7
	100	2.8	2.6
October (Oct)	0	2.9	2.2
	50	2.5	2.1
	100	2.6	2.5
AH + Oct	0	2.8	2.6
	50	3.0	2.7
	100	3.0	2.2
S.E.(Site*N*Res)		0.07	
Contrasts:		P>F	P>F
N-linear (NL)		0.37	0.60
N-quadratic (NQ)		0.95	0.72
No removal vs removal (Res 1)		0.00	0.53
Single (AH, Oct) vs double (AH+ Oct) (Res 2)		0.02	0.63
Early (AH) vs late (Oct) (Res 3)		0.09	0.00
NL x Res 1		0.13	0.99
NQ x Res 1		0.10	0.88
NL x Res 2		0.08	0.03
NQ x Res 2		0.06	0.19
NL x Res 3		0.14	0.17
NQ x Res 3		0.29	0.14

Table 3.10. The effect of residue removal and N fertilization on fertile tiller density and percentage (based on previous fall tiller density) in Paddock meadow bromegrass. Sites combined, 1996.

Residue removal	Nitrogen	Fertile tillers	
		------no.m^{-2}------	------%------
None	0	140	8.3
	50	174	6.9
	100	256	8.4
After harvest (AH)	0	315	12.2
	50	466	18.0
	100	640	20.3
October (Oct)	0	238	13.9
	50	188	9.5
	100	260	12.0
AH + Oct	0	332	16.5
	50	624	32.3
	100	342	14.4
S.E.		52	2.3

Contrasts:	P>F	P>F
NL* No removal vs removal	0.98	0.82
NQ*No removal vs removal	0.37	0.17
NL*Single (AH, Oct) vs double (AH + Oct)	0.21	0.37
NQ*Single vs double	0.01	0.00
NL*Early (AH) vs late (Oct)	0.05	0.15
NQ*Early vs late	0.70	0.37

Table 3.11. The effect of residue removal on the percentage of tillers with panicles (based on fall tiller density) in Paddock meadow bromegrass at Saskatoon and Outlook, 1996 and 1997.

Residue removal	1996		1997	
	Saskatoon	Outlook	Saskatoon	Outlook
	--Panicles (%of fall tillers)--			
None	9	7	0.6	4
After harvest (AH)	20	14	13	12
October (Oct)	19	4	5	8
AH + Oct	30	12	17	11
S.E. (Site *Res)	2		2	
Contrasts:	P>F	P>F	P>F	P>F
No removal vs removal	0.00	0.40	0.00	0.00
Single (AH, Oct) vs double (AH+Oct)	0.00	0.44	0.00	0.58
Early (AH) vs late (Oct)	0.78	0.05	0.00	0.21

than late residue removal.

3.3.3 Relationship between tiller growth and development and seed yield

Fall tiller growth and development are of particular interest to those involved in seed production of temperate perennial grasses, due to the fact that flowering and seed yield are correlated to fall tiller growth in many species (McDonald and Copeland 1996, Schoberlein 1987, Boelt 1999). In the present study, correlations between fall or spring tiller density and panicle density or seed production were low and not always significant (Tables 3.12 and 3.13). Fall or spring leaf stage (tiller development) was generally more closely correlated to panicle density and seed production the following season than fall or spring tiller density. However, even significant correlations were low, explaining less than 50% or the variation in flowering, and seed production.

While Schoberlein (1987) found a significant correlation between fall leaf stage and flowering tillers the following year in orchardgrass, timothy and meadow fescue, he also found that once a certain stage had been reached, flowering occurred. Schoberlein's findings support the theory that a juvenile period exists in many perennial plants during which flowering will not occur even if the plant is exposed to conditions which will stimulate flowering at a later growth stage (Heide 1994). However, Havstad (1996a), has presented evidence that tillers, which emerge during induction conditions are capable of becoming reproductive in Scandinavian cultivars of smooth bromegrass, Kentucky bluegrass, meadow fescue, orchardgrass and ryegrass. Growth chamber studies indicate that this is also the case with meadow bromegrass (Chapter 6).

Table 3.12. Correlation coefficents (r) between panicle density and tiller density and stage of tiller development (leaf number tiller^{-1}) in Paddock meadow bromegrass at Saskatoon and Outlook, 1996 and 1997.

	1996		1997	
Panicle density (no. m^{-2}) and:	Saskatoon	Outlook	Saskatoon	Outlook
Fall tiller density	0.07	0.32*	-0.10	0.42**
Fall tiller development	0.29*	0.34*	0.67**	0.44**
Spring tiller density	0.05	0.44**	0.50**	0.38**
Spring tiller development	0.50**	0.45**	0.54**	0.28*

*, ** Significant at 0.05 and 0.01 levels, respectively

Table 3.13. Correlation coefficents (r) between second year (1996) and third year (1997) seed yield and tiller density, stage of tiller development (leaf number tiller^{-1}) and panicle density in Paddock meadow bromegrass at Saskatoon and Outlook, 1996 and 1997.

	1996		1997	
Seed yield (kg ha^{-1}) and:	Saskatoon	Outlook	Saskatoon	Outlook
Fall tiller density	0.17	0.20	0.41**	0.00
Fall tiller development	0.13	0.39**	0.29*	0.30*
Tiller survival	-0.12	0.39**	0.07	0.02
Spring tiller density	0.11	0.44**	0.34*	0.04
Spring tiller development	0.35*	0.57**	0.18	0.37**
Panicle density	0.68**	0.65**	0.77**	0.37**

*, ** Significant at 0.05 and 0.01 levels, respectively.

The variable most closely correlated to seed yield at both sites in both years was fertile tiller density. This is also the case with Kentucky bluegrass and creeping red fescue (Meier and Vreeke 1988b), and it has been suggested that more tillers are induced to flower than actually flower. Meier and Vreeke (1988a) speculate that competition for light and nutrients during elongation, rather than the number of inducible tillers, limits heading. In this study, weather conditions between fall and flowering the following year (drought and winter injury), apparently had a major impact on tiller growth and development. This, coupled with the ability of the plant to compensate, may explain the low correlation between fall tiller development and seed yield.

3.4 Summary and conclusions

Residue removal and N fertilization generally improved seed yield. However, when winter survival was an issue, N fertilization had a negative impact on seed production when combined with double residue removal. In addition, under dry conditions, response to N may be delayed and result in the proliferation of vegetative tillers which can have a negative impact on seed production.

In spite of the positive effects of residue removal and N fertilization on seed production, yield declined in the third production year, particularly under rainfed conditions. The reason for this is not well understood, however, it appears that competition between vegetative and reproductive tillers may contribute to this decline.

The relationship between fall tiller density and development and seed production, while statistically significant, was low, and, as such, cannot be used as a tool to predict whether or not seed production will be economically viable the following year.

4. CROP RESIDUE REMOVAL AND N FERTILIZATION AFFECTS SILVERTOP INCIDENCE IN MEADOW BROMEGRASS.

4.1 Introduction

Silvertop is a condition which affects many temperate grasses, including crested wheatgrass, intermediate wheatgrass, smooth bromegrass, meadow bromegrass, creeping red fescue, sheep's fescue (*F. ovina* L.), Kentucky bluegrass, and others (Coulman and Jefferson 1997, Soroka 1998). Differences in susceptibility to silvertop occur both among and within species (Berkenkamp and Meeres 1975, Howard *et al.* 1996). Affected inflorescences are silvery-white, dead, and the flowering stalk can easily be pulled from the sheath. The stems are also white above the top node, they appear restricted and piercing marks typical of insect damage are generally visible just above the top node. Silvertop does not generally affect all of the heads on a plant (Soroka 1992).

Plant pathogens have been associated with silvertop (Soroka and Gossen 1996), but evidence suggests that they are not the primary causal agents (Hardison 1959, Gagne and Gagnon 1985). Over 30 species of arthropods have been associated with silvertop (Peterson and Via 1971, Gagne and Gagnon 1984). Piercing insects, particularly plant bugs (families Miridae and Capsidae), are the prime suspects in North America (Hardison 1959, Arnott and Bergis 1967, Kamm 1979), whereas stink bugs (family Pentatomidae) are the predominant insects associated with silvertop in eastern Europe (Burges *et al.* 1995).

Capsus bugs (*Capsus einctus* Kol.), caged on Kentucky bluegrass stems in the greenhouse, produced symptoms of silvertop and field studies confirmed a high correlation between Capsus bug populations and silvertop in Kentucky bluegrass fields in Minnesota (Peterson and Via 1971). The eggs of Capsus bugs overwinter in residue, and post-harvest burning destroys eggs laid in grass stems (Hardison, 1959). As a result, burning often reduces silvertop incidence (Kiel 1942, Kamm 1979). In some cases mechanical residue removal is not as effective as burning, presumably because eggs may remain in the field after the residue is removed (Kamm 1979). Soroka and Gossen (1996) found, however, that very low mowing and removal of residue after harvest was as effective as burning for reducing silvertop infection in Kentucky bluegrass and red fescue. Insecticides reduced or eliminated silvertop in the field (Okuda 1988).

Environment plays an important role in silvertop expression. Cool wet conditions early in the season favor the development of fungal pathogens which may invade insect wounds in grass stems and kill otherwise mildly injured stems (Soroka, unpublished data). When hot dry weather occurs at flowering, insect feeding is more injurious (Soroka 1992).

Insect populations build up over time, resulting in more injury in older stands (Okuda 1988). Once silvertop is visible in a grass seed field, little can be done to reduce the damage that season. Current recommendations suggest that if the silvertop infestation in a field is over 10%, residue removal should be implemented to reduce incidence the following year (Soroka 1992). In addition, the field should be sprayed with an insecticide before heading the following year. These recommendations are based on research conducted primarily on Kentucky bluegrass and fine fescues. It has been observed that meadow bromegrass generally suffers higher silvertop levels than does smooth bromegrass (Soroka, unpublished data), but no research reports are available on silvertop in meadow bromegrass.

The objectives of this study were to determine the effect of residue removal and nitrogen fertilization on silvertop incidence in Paddock meadow bromegrass.

4.2 Materials and methods

Field trials were conducted under rainfed conditions at Saskatoon, SK (52° 07' 106° 38') and under irrigation at Outlook SK (51°30" 107 ° 03'); both located on Typic Haploboroll soils. At Saskatoon, growing season precipitation (Apr.-Oct.) was 307, 282, 366 and 247 mm in 1994-1997, respectively. At Outlook, growing season precipitation was 216 mm with an additional 150 mm of irrigation applied in 1994, 272 mm rainfall + 225 mm irrigation in 1995, 298 mm rainfall + 106 mm irrigation in 1996 and 197 mm rainfall + 319 mm of irrigation in 1997. See Appendix Table A1 for precipitation and irrigation details.

Paddock meadow bromegrass was seeded on 10 June 1994 at 12 kg ha $^{-1}$ in 30 cm rows. Fifty kg ha $^{-1}$ of P_2O_5 and 11 kg ha $^{-1}$ of N (11-51-0) were incorporated during seed bed preparation. Each fall all plots received an additional 50 kg ha $^{-1}$ of P_2O_5 and 11 kg ha $^{-1}$ of N (11-51-0). Treatments consisted of three rates of N (0, 50,or 100 kg ha^{-1}) and four residue removal treatments (none, after harvest, October, or after harvest + October). Seed was harvested in the last week of July, and after harvest treatments were applied within a week of harvest each year. The October time of removal represents the end of the growing season on the Canadian Prairies. Treatments were replicated four times. The design was a split plot with N rate as the main plot and residue removal as the sub-plot. Sub-plots were 1.5 m by 6.0 m. Ammonium nitrate (34-0-0) was broadcast at the prescribed N rates in early to mid September each year starting in 1994. Residue treatments consisted of removal with a forage harvester, then scalping with a flail mower to a height of 2.5 cm each year starting in 1995. Two 0.25 m^2 quadrats were marked in each plot. The number of healthy panicles and the number of panicles with silvertop were determined after anthesis each year. Seed yield, as well as tiller density and stage of development were recorded and are reported in Chapter 3. In addition, stand survival ratings and heading dates were recorded at Outlook each year.

All variables were subjected to an analysis of variance using the general linear model (GLM) of SAS (SAS Institute Inc. 1985) (Appendix Tables A9 and A10). Data on the percentage of panicles with silvertop were not transformed because the range of percentages was not greater than 40 (Little and Hills 1978). Plots with no panicles were excluded from the analysis based on the fact that silvertop infection cannot occur in the absence of panicles. Certain responses varied by site and since only two sites were used, they were considered fixed effects. The effect of N rates was partitioned into linear and quadratic components; the residue removal treatment means were evaluated through a series of *a priori* contrasts. Differences were considered statistically significant at the $P \leq 0.05$ level. Standard errors were calculated for all means.

4.3 Results and discussion

In 1996, silvertop density was higher in Paddock meadow bromegrass at Saskatoon (100 affected panicles m^{-2}) than Outlook (40 affected panicles m^{-2}), but neither nitrogen nor residue management had an effect on silvertop density (Appendix Table A9). As well, the percentage of affected panicles did not vary between sites or amongst treatments.

In 1997, both N fertilization and residue removal had an impact on the number and percentage of panicles affected (Tables 4.1 and 4.2; Appendix Table A10). Silvertop (density and percentage) generally increased with increasing N rates (Table 4.1). This response was consistent over residue removal treatments, but differed between the two sites. At Saskatoon, a linear increase in both density and percentage occurred with increasing N rates. At Outlook, silvertop density was not affected by N, and percentage of affected panicles peaked at 50 kg ha^{-1} N.

The response of silvertop density to residue removal was the same at both sites (Table 4.2 and Appendix Table A10). Silvertop density was lower with no residue removal than when residue was removed. It was also lower when residue was removed once vs twice or late vs early removal. The percentage of affected panicles was less when residue was removed but there was no difference between single and double or early and late removal. In Kentucky bluegrass, both burning and mechanical removal reduced silvertop percentage (Peterson and Via 1971, Howard *et al.* 1996, Soroka and Gossen 1996). Burning was often more effective. This is thought to be due to the fact that burning destroys the grass stem where Capsus bugs lay their eggs (Peterson and Via 1971). In the present study, however, time of removal had a significant impact, indicating that the impact of

Table 4.1. The effects of N fertilization on silvertop density and percentage of panicles with silvertop in Paddock meadow bromegrass at Saskatoon and Outlook, 1997.

	Silvertop affected panicles			
	Density (no. m^{-2})		Percentage affected (%)	
N rate (kg ha $^{-1}$)	Saskatoon	Outlook	Saskatoon	Outlook
0	61	41	49	24
50	65	109	63	44
100	158	85	79	29
S.E.	16		5	
Contrasts:	P>F			
N linear	0.00	0.10	0.03	0.43
N quadratic	0.15	0.08	0.88	0.01

Table 4.2. The effect of residue management on silvertop density and percentage of panicles with silvertop in Paddock meadow bromegrass, 1997 (Sites combined).

	Silvertop	
Residue removal	Density (no m^{-2})	Panicles affected (%)
None	22	60
After harvest (AH)	121	42
October (Oct)	66	51
After harvest + October	134	39
S.E.	11	4
Contrasts:	P>F	
No removal vs removal	0.00	0.01
Single (AH, Oct) vs double (AH+ Oct)	0.01	0.13
Early (AH) vs late (Oct)	0.00	0.11

removal is not merely the result of insect egg removal. If that were the case, removal in October should have reduced silvertop as effectively as removal after harvest.

Silvertop density was highest when residue was removed after harvest (single or double) (Table 4.2 and Appendix Table A9). At the same time, a trend towards lower percentage affected panicles occurred in the same treatments. Hence, the residue removal treatments with the greatest number number of silvertop affected panicles were the ones with the lowest percentage of silvertop infection. This reflects the fact that the magnitude of increase in panicle density was generally greater than the magnitude of the increase in silvertop density. For example, at Saskatoon in 1997, removing residue after harvest resulted in an increase in panicle density of approximately 20-fold, compared to not removing residue, whereas this treatment resulted in a 15-fold increase in silvertop density compared to no removal. Removing residue again in October resulted in an additional, but small, increase in both panicle and silvertop density at Saskatoon, but a decrease in both at Outlook. Hence, silvertop density was positively correlated to panicle density. The positive correlation between panicle density and silvertop density has been observed in other grass seed crops (Soroka, unpublished data). Evidence suggests that piercing the stem by an insect occludes the xylem, blocking the movement of nutrients to the panicle (Soroka, unpublished data). However, silvertop has been observed in stems with no evidence of piercing. This indicates that other stressors may be involved. Soroka (1992) observed that insect feeding is more injurious when hot weather occurs at flowering. Anthesis is a stage at which winter wheat is particularly sensitive to drought (Entz and Fowler 1988). The occurrence of hot dry weather, exacerbated by the proliferation of vegetative tillers, may have resulted in moisture stress at Saskatoon at flowering and contributed to the subsequent increase in the percentage of silvertop affected panicles. This is supported by the fact that N fertilization increased panicle production, increased vegetative tillers, and also resulted in a significant increase in the percentage of silvertop affected panicles. However, since stems were not examined for piercing marks, the evidence is merely circumstantial.

It was expected that seed yield panicle^{-1} would be higher in treatments where silvertop incidence was lower, due to the fact that fewer dead panicles were present; however, the opposite was true. Seed yield per panicle (Table 4.3 and Appendix Table A10) was lower in the treatments which reduced the percentage of panicles affected by silvertop (after harvest, single or double) in both years. In addition, seed yield panicle^{-1} was higher in 1996 than in 1997. This indicates that competition for resources occurred between fertile tillers. Other researchers have found evidence of competition amongst tillers for resources at various stages in the developmental process in perennial grasses (Wright 1978, Schoberlein 1987, Meijer and Vreeke 1988a, Warringa 1997). It is possible that in the present study there was sufficient nitrogen or water, for example, to stimulate panicle production (differentiation and elongation) but not enough to support complete seed filling on all panicles.

In conclusion, while removing residue significantly reduced silvertop incidence compared to no removal, residue removal alone did not provide a sufficient reduction to be recommended as a control measure on its own. It was also unclear as to whether or not insects were involved, and to what extent. Further research is required to a) identify the causal agent (s), b) to identify threshold levels of the causal agent(s), and c) to identify other

Table 4.3. The effect of residue removal on seed yield per panicle in Paddock meadow bromegrass, 1996 and 1997 (Sites combined).

Residue removal	Seed yield (g panicle^{-1})	
	1996	1997
None	1.91	0.69
After harvest (AH)	1.41	0.44
October (Oct)	2.36	0.85
AH + Oct	1.30	0.41
S.E.	0.25	0.21
Contrasts :	P>F	
No removal vs removal	0.47	0.63
Single (AH, Oct) vs double (AH+ Oct)	0.10	0.48
Early (AH) vs late (Oct)	0.00	0.10

control strategies that could be used in conjunction with residue removal.

In addition, although increasing the number of fertile tillers and reducing the loss of fertility due to silvertop incidence improved seed yield, other factors such as competition between tillers limit seed yield in meadow bromegrass. This area requires further research to determine what resources are the most limiting, and if and when critical times and threshold levels occur for these resources.

5. STAND AGE AND TILLER SIZE AFFECTS FLOWERING IN MEADOW BROMEGRASS

5.1 Introduction

Meadow bromegrass has become very popular for both pasture and hay in western Canada (Knowles *et al.* 1993). As a result, demand for seed has been high, however, seed producers have found that seed production in meadow bromegrass is different from the traditional smooth bromegrass. Smooth bromegrass produces as many as ten seed crops, whereas meadow bromegrass seed yield declines dramatically after two to three seed crops (Kruger 1997). This is due to a low percentage of reproductive tillers in older stands. A greater understanding of why seed yield declines so rapidly in meadow bromegrass could lead to the development of systems that prolong seed production, thereby improving its economics.

Seed production in many cool-season perennial grasses is dependent on events that occur long before the inflorescence is visible. In fact, it is estimated that as much as 92% of the seed yield potential is determined before the flowering process begins (Havstad 1996a, Chastain and Young 1998). A number of stages, or 'gateways' have been identified, through which the plant or tiller must pass in order to flower and produce seed (Heide 1994, Chastain and Young 1998). The first step generally involves attaining sufficient size or 'maturity' to respond to the environmental stimuli that trigger flowering (Heide 1994). In seedlings of Kentucky bluegrass, tillers had to produce 8-9 leaves before they would respond to inductive stimuli (Parker-Clarke *et al.* 1996). The length of the juvenile or non-responsive stage varies among species (Heide 1994). Perennial ryegrass has a very short juvenile period and can be vernalized as an imbibed caryopsis, whereas other grasses require weeks or even months from germination before they will respond to environmental conditions that stimulate flowering.

Some disagreement exists as to whether the plant can become 'mature' as a whole or whether individual tillers each attain this status separately. Meijer (1984) provided evidence that tillers of Kentucky bluegrass and creeping red fescue that arose shortly after exposure to inductive conditions did not flower. Havstad (1996a), on the other hand, found that in meadow fescue (*F. pratensis* L.), tillers that emerged after exposure to primary induction could become reproductive. This indicates that either the tillers were induced before they emerged from the leaf sheath (i.e. no juvenility on an individual tiller basis), or, that the flowering stimulus was transmitted from mother to daughter tiller. Small tillers, not yet independent from the mother plant, provide a strong sink for carbohydrates. If the flowering hormone, florigen, follows the path of carbohydrates from source to sink, then this provides a conduit for florigen to move from mother plant to newly emerging tillers (Havstad 1996a).

Although questions still arise regarding the concept of juvenility, evidence indicates that the stage of development in autumn is positively correlated to flowering and seed yield in some grass species. A significant positive correlation has been reported between the number of leaves in autumn and the proportion of fertile tillers the following year in cocksfoot, meadow fescue, and Kentucky bluegrass (Nordestgaard 1980, Schoberlein 1987). The response in timothy and perennial ryegrass has been less consistent, which is understandable because these grasses have little or no cold requirement so that tillers initiated in the spring can, and will, flower. In tall fescue (*Festuca arundinacea* Schreb.) the correlation between autumn tiller density and seed yield decreases over the life of the stand (Chastain and Young 1998).

The relative importance of the various tillers may change over time. For example, in meadow fescue, first generation tillers (T_1) played a more important role in seed production than either the mainstem or secondary tillers (T_2). As the stand aged, third and fourth generation tillers became more important for seed production than any of the earlier generations (Lambert and Jewiss 1970).

While some evidence indicates that stand age and tiller size influence flowering and seed production in other grass crops, no information is available on how these factors affect meadow bromegrass or whether they are linked to the seed yield decline in meadow brmegrass observed in the field. The objectives of this study were to determine the influence of stand age and tiller size on the production of inflorescences in meadow bromegrass.

5.2 Materials and methods

5.2.1 General methodology

Plant material for the following three sets of experiments (two on each of individual tillers, potted plants and intact segments of field rows) was dug from Paddock meadow bromegrass field plots at the end of October in 1995 and 1997. The field plots were located on a Typic Haploboroll soil at Saskatoon (52°07' 106°38'). Depending on the experiment, residue was either removed after harvest or left intact, and the plots either received no N or 100 kg ha^{-1} N each year in September. Selection and preparation varied for each experiment. However, all were transplanted in a soil-less mix of vermiculite, peat moss and sand (10:5:1) with a pH between 5 and 6. The mix contained a controlled release fertilizer with N, P, K plus superphosphate fines, trace elements and chelated iron.

After transplanting, all plants were stored in an unheated greenhouse with no supplemental lighting until November 15th. At this time it was assumed that they had sufficient exposure to conditions (short days and/or cold temperature) known to induce flowering in other cool season grasses, including smooth bromegrass (Bob Knowles, pers. com.).

Plants were then placed in a greenhouse where natural light was supplemented with 350 μmols m^{-2} s^{-1} from high pressure sodium lamps to provide 16 hr light day $^{-1}$. Temperature was maintained at 20 °C during the day and 12 °C at night to promote floral initiation and elongation (Knowles 1982, Heide 1994).

Once flowering commenced, panicles were tagged as they emerged from the boot so that the rate of floral development could be calculated. Ninety days after planting, the percentage of plants with inflorescences, tiller number plant $^{-1}$, inflorescence number plant $^{-1}$, rate of inflorescence development (days from Nov 15th to emergence of the flag leaf) and panicle length were recorded. In intact segments, the distance from the center of the row to each tiller producing an inflorescence was determined; however, too many tillers were produced in these segments to record the number of tillers.

5.2.2 Experiments 1 and 2: Individual tillers

In 1995, treatments consisted of comparisons of tillers from stands of two different ages: two-yr-old compared to ten-yr-old. In both cases, residue had been removed after harvest (August); however, the plots had not been fertilized. Plants were washed and divided into individual tillers. These were sorted according to basal diameter of the stem 1 cm above the roots. In 1995, sufficient large-sized tillers were not available in the ten-yr-old stand, as a result, only medium-sized tillers (2mm basal diameter) were potted in 2.5 x 20 cm containers. Pots with individual tillers were placed in flats in a randomized complete block design (RCBD) with three replications of eight plants per treatment. Lodging was prevented with a frame of 5 cm square wire mesh (stucco wire) that rested on a stack of containers that could be extended as the plants grew in height.

In 1997, plants were taken from two- and four-yr-old field plots of Paddock meadow bromegrass that had been fertilized with 100 kg ha^{-1} N in September each year. Residue had been removed after harvest in both cases. Plants were separated into individual tillers as stated above, and sorted into three size categories according to basal diameter (1, 2 or 3 mm). Tillers were potted in 2.5 x 20 cm containers and placed in flats in a RBCD with nine replication of five plants per treatment. The treatment design was a two by three factorial (age by size). Wire mesh was used to prevent lodging.

5.2.3 Experiments 3 and 4: Potted plants

In 1995, potted plants from two-yr-old plots, where residue was either removed after harvest or left intact, were compared to plants from a ten-yr-old stand where the residue had been removed. None of the plots had been fertilized. Once potted in 20 cm pots using soil-less mix, plants were arranged in a RCBD with ten plants per treatment and three replications, and treated as per the general methods.

In 1997, changes were made so that the effects of residue removal and N fertilization on older stands could be determined, as well as the effect of stand age. All plants were taken from Paddock meadow bromegrass plots that were either two or four yrs old. In the two-yr-old plots, residue had been removed after harvest and they had been fertilized (100 kg ha^{-1} N) in September. Four-yr-old plants were taken from stands where residue had been removed after harvest, with or without an annual application of N (0 vs 100 kg ha^{-1}N), or from plots without either residue removal or N fertilization. In this way the effect of age of stand was studied on well managed plots, plus the effect of residue removal and N fertilization wasdetermined on plants from an older stand. Treatment design, and the number of samples and replications were the same as in 1995.

5.2.4 Experiments 5 and 6: Intact row segments

In addition to individual tillers and 20 cm plants, 25 cm lengths of row were transplanted into large flats. These row segments varied in width according to the natural row width in the field. Since meadow bromegrass spreads a bit each year, in general, the older the stand the wider the row. The treatments (three in 1995, four in 1997) were the same as in the potted plant experiments (Exp. 4 and 5). In the greenhouse they were arranged in a RCBD with five replications.

All variables were subjected to an analysis of variance using the general linear model (GLM) of SAS (SAS Institute Inc. 1985) (Appendix Tables A11, A12 and A13). *A priori* contrasts were used to determine if: a) differences occurred in response of tillers from different age classes, b) differences occurre in response to differing tiller size that could be described by a linear or quadratic equation and c) an interaction existed between stand age and tiller size (Exp.1 and 2). Contrasts were also used to compare plants or clumps from different age, residue removal or N fertilization treatments (Exp. 3-6). Arcsin transformations were considered for all proportion data, but the range of proportions was not great enough to warrant transformation (Little and Hills 1978); thus, untransformed data were used. Differences were considered statistically significant at the $P \leq 0.05$ level. Standard errors were calculated for all means.

5.3 Results and discussion

Stand age influenced flowering in meadow bromegrass, regardless of whether it was individual tillers, potted plants or segments of row being tested. This effect was observed in percentage of plants with flowers, number of inflorescence per flowering plant and percentage of flowering tillers in flowering plants.

When plants were split into individual tillers and potted, more plants from younger stands produced panicles compared to older stands (Table 5.1 and Appendix Table A11). In field studies (Chapter 3), inflorescence production also declined as the stand aged. In tillers from both two- and four-yr-old stands, the percentage of plants that produced inflorescences increased linearly as the size of the original tiller increased. In studies involving other grass species, researchers have found that reproductive development was highly positively correlated to tiller size, however, competition during subsequent stages

Table 5.1. The effect of stand age and tiller size on flowering in plants from individual tillers of Paddock meadow bromegrass.

Treatment:	Flowering plants	Inflorescence number	Tiller number	Flowering tillers
Exp. 1: (1995/96)	-----%-----	# plant $^{-1}$	# plant $^{-1}$	----%----
2 yr	75	1.9	15	14
10 yr	58	1.3	14	8
S.E.	12	0.26	1.4	1.8
Age	0.08	0.05	0.53	0.01
Exp. 2: (1997/98)				
2 yr:				
Small (1-2mm dia)	32	0.99	5.4	18
Medium (2-3mm dia)	59	1.00	5.8	19
Large (3-4mm dia)	80	1.00	4.9	26
4 yr:				
Small (1-2mm dia)	2	1.01	6.2	16
Medium (2-3mm dia)	36	1.06	5.7	25
Large (3-4mm dia)	36	1.02	4.8	24
S.E.	6	0.02	0.3	3.5
Contrasts:		P>F		
Age - 2 yr vs 4 yr	0.00	0.41	0.31	0.87
Size - linear (L)	0.00	0.94	0.00	0.20
Size - quadratic (Q)	0.06	0.47	0.12	0.76
Age*size L	0.30	0.98	0.21	0.95
Age*size Q	0.20	0.53	0.28	0.29

of floral development can have a significant, negative impact on flowering (Wright 1978, Schoberlein 1987). In this case, competition was virtually eliminated during floral initiation and elongation, as the tillers were provided with abundant space and were well-watered and fertilized. Nonetheless, tillers from a four-yr-old stand performed differently than tillers from a two- yr-old stand. This indicates that tiller size or competition alone do not explain the decline in flowering in meadow bromegrass that occurs as stands age. An increase in apical soluble carbohydrates following inductive conditions has led Bodson (1977) to believe that an increase in carbohydrate is directly related to flowering. However, Jones (1990) demonstrated that the increase in carbohydrate occurs following inductive conditions, even in mutant plants not capable of flowering. Havstad (1996a and b) found that the percentage of water soluble carbohydrates was independent of tiller size, but it was also not related to flowering.

The difference between two- and ten-yr-old stands that is not evident from the data (Table 5.1) is the scarcity of large-sized tillers (based on basal diameter) in older stands. The difference in flowering response amongst different sized tillers was not studied in the first experiment because of the fact that no large-sized tillers were available in the ten-yr-old stand. Relatively few large-sized tillers were present in the four-yr-old stand compared to the two-yr-old stand, as well. Field studies (Chapter 3) did not reveal a decrease in the leaf stage over time. In Kentucky bluegrass, basal diameter and leaf stage are closely linked (Chastain and Young 1998). However, in field trials in this study, (Chapter 3) only leaf stage was recorded.

The number of tillers produced after potting was the same regardless of the age of the stand from which the tiller originated(Tables 5.1 and Appendix Table A11). The number of inflorescences (per flowering plant) was significantly higher in tillers from a two-yr-old stand than from a ten-yr-old but not different from a four-yr-old stand.

In Exp. 1, the average number of inflorescences plant^{-1} was greater than one regardless of stand age (Table 5.1 and Appendix Table A11). Since only one tiller had been exposed to induction conditions, this is an indication that the requirement for exposure to short days and/or cold temperatures is either facultative, or that the floral stimulus can be transferred from mother to daughter tiller. Meadow fescue produces flowers from tillers that have not been fully exposed to induction conditions (Havstad 1996a).

The percentage of tillers that formed flowers in flowering plants was greater in plants from two-yr-old than ten-yr-old stands, but not four-yr-old stands (Exp 1 and 2, Table 5.1). This may reflect differences in the two experiments rather than differences in reproductive capability between four- and ten-yr-old stands.

The decline in flowering with stand age was similar in potted plants compared to individual tillers (Table 5.2and Appendix Table A12). In addition, plants from a four-yr-old stand that had not been fertilized annually with N produced more inflorescences than those from a four-yr-old stand that had received 100 kg ha^{-1}N annually. The reason for this is unclear.

In potted plants taken from four-yr-old stands, a higher percentage of flowering was observed in plants from stands where residue was removed than in plants from stands where residue was left intact. This was also the case in field studies (Chapter 3). More inflorescences, more tillers, and a higher percentage of flowering tillers were produced in

Table 5.2. The effect of stand age, residue removal and N fertilization on flowering in potted plants of Paddock meadow bromegrass.

Treatment:	Flowering plants	Inflorescence number	Tiller number	Flowering tillers
Exp. 3 (1995/96)	-----%-----	---# plant $^{-1}$---	# plant $^{-1}$	----%-----
1. 2 yr/RR[2]/ no N	97	8.0	93	8
2. 2 yr/RI[3]/no N	83	5.3	64	7
3. 10 yr/RR/no N	63	2.0	52	7
S.E.	6	1.4	3	2
Contrast:		P>F		
1. 2yr/ RR vs 10 yr/RR	0.01	0.01	0.00	0.57
2. 2 yr/ RR vs 2 yr /RI	0.11	0.13	0.00	0.54
Exp 4: (1997/98)				
1. 2 yr / RR /100 kg ha $^{-1}$N	97	13	49	29
2. 4 yr/ RR / no N	80	2	36	7
3. 4 yr/ RR /100 kg ha $^{-1}$N	43	1	33	7
4. 4 yr/ RI /no N	53	1	34	6
S.E.	9	1.2	3	3
Contrasts:		P>F		
1. 2 yr vs 4 yr (1 vs 3)	0.00	0.00	0.00	0.00
2. 4 yr no N vs 100 kg N ha $^{-1}$	0.01	0.43	0.47	0.81
3. 4 yr RR vs 4 yr RI	0.02	0.43	0.53	0.59

---

[2] RR= residue removed after harvest

[3] RI= residue intact

flowering plants from two-yr-old stands than plants from four- or ten-yr-old stands. In field studies, the percentage of fertile tillers was 20% in the 2nd year and 14% in the 3rd year in plots where residue was removed and 100 kg ha $^{-1}$ N was added.

Inflorescence production also decreased with stand age in intact row segments (Table 5.3 and Appendix Table A13). Row width increased as the stand aged (data not shown), and distance from mid-row to the tillers from which inflorescence originated was less in two yr old than in ten yr old stands. No difference in inflorescence production occurred between two-yr-old and four-yr-old stands. This concurs with Lambert and Jewiss (1970) who found that flowering occurred further
from the mainstem over time.

Stand age had a significant effect on the rate of panicle development and panicle length only in experiments with individual tillers (Exp. 1 and 2) (data not shown). In Exp. 1, where "old" tillers were taken from a ten-yr-old stand, panicle development was slower than in those from the new stand (94 vs 61 days from digging to panicle emergence). In Exp. 2, where the old stand was only four-yr-old, an interaction occurred between tiller size and stand age. Medium-sized tillers from the new stand flowered in approximately the same time as tillers from the old stand regardless of size (73 vs 75, 80 or 74 days for new, medium vs old small, medium and large, respectively). Large and small tillers from the new stand took much longer to flower; 130 and 103 days for small and large tillers, respectively. This delay in flowering may have been due to the fact that more transplanting shock occurred with both small and large tillers from the new stand.

Panicle length was consistently greater when the rate of development was slower

Table 5.3. The effect of stand age, residue removal and N fertilization on flowering in 25 cm lengths of row of Paddock meadow bromegrass.

	Panicle			
Treatment:	Number	Distance fr mid-row	Rate of development	Length
Exp 5: (1995/96)	# plant $^{-1}$	----cm----	----days-----	---cm----
1. 2 yr/RR[4]/ no N	36	11	48	13
2. 2 yr/RI[5]/no N	17	11	45	15
3. 10 yr/RR/no N	13	20	47	16
S.E.	8	1	1	1
Contrast:				
1. 2yr/RR vs 10 yr/RR	0.09	0.00	0.41	0.09
2. 2 yr RR vs 2 yr RI	0.14	0.68	0.03	0.26
Exp 6: (1997/98)				
1. 2 yr/RR/100 kg N ha $^{-1}$	49	8.2	37	11
2. 4 yr/RR/no N	12	8.7	40	15
3. 4 yr/RR/100 kg N ha $^{-1}$	19	9.7	36	13
4. 4 yr/RI/no N	3	6.2	33	12
S.E.	6	1	5	2
Contrasts:				
1. 2 yr vs 4 yr (1 vs 3)	0.01	0.32	0.86	0.42
2. 4 yr no N vs 100 kg N ha $^{-1}$	0.42	0.52	0.56	0.58
3. 4 yr RR vs RI	0.23	0.13	0.36	0.45

---

[4] RR= residue removed after harvest

[5] RI= residue intact

(Table 5.3 and Appendix Table A13). Panicles on tillers from the ten-yr-old stand were longer than two-yr-old stands (26 vs 21 cm), whereas in Exp 2, panicles from the two-yr-old stand were longer than from the four-yr-stand (20 vs 13cm). The same trend was observed in Exp. 4 and 5. In perennial ryegrass, spike length was greater when they developed more slowly (Warringa 1997). This was not always the case in this set of experiments; however, it has been observed that seed production usually is greater in meadow bromegrass fields in cool springs which would delay development, providing adequate moisture is available.

In conclusion, this set of experiments indicates that tiller size and stand age influence flowering in meadow bromegrass. However, the differences associated with stand age are independent of tiller size, which indicates that factors other than competition are responsible for the decline in flowering over time in meadow bromegrass.

6. FLORAL INDUCTION AND INITIATION IN MEADOW BROMEGRASS.

6.1 Introduction

The flowering process in many cool-season perennial grasses is a step wise process in which the plants must pass through a series of consecutive 'gateways' before flowering takes place (Chastain and Young 1998). The first of these gateways involves attaining sufficient size or maturity so that the plant or tiller can respond to the environmental conditions that stimulate flowering. Once tillers have gone through the transition from juvenile, vegetative growth to mature tissue, capable of producing an inflorescence, they often require exposure to short days and/or cool temperatures, followed by long days, before floral initials are formed. These two stages (short days/cool temperatures and long days) are termed primary and secondary induction (Heide 1994). Generally no morphological changes are associated with the completion of primary induction in dual induction grasses, whereas floral initials form following secondary induction. Floral initiation is often the end product of secondary induction, and is sometimes referred to as initiation, or evocation (Evans 1969, Bernier 1988). Grasses that requirement both primary and secondary induction are referred to as dual induction grasses. The final stages are elongation, anthesis and seed filling.

The environmental signals that stimulate flowering vary among and even within species (Cooper and Calder 1964, Hodgson 1966, Heide 1980, Heide 1982, Heide 1992).

Differences in flowering requirements have evolved over time in response to local climatic conditions. For example, floral initiation occurs in the fall in many native Alaskan grass species, whereas related species from more southern locations undergo induction in the fall, but do not initiate floral primordia until they have been exposed to long days the following spring (Hodgson 1966). In fall-initiating species, morphological changes precede secondary induction. Most forage and turf species, on the other hand, undergo both primary and secondary induction before floral initiation. While floral primordia in fall-initiating Arctic grasses will survive low temperatures, floral primordia of many grasses cannot survive freezing temperatures; and the long day requirement is a way of ensuring survival. In grasses in which initiation occurs in spring, latitude of origin is often positively correlated to flowering requirements; the higher the latitude, the longer the daylength required to stimulate secondary induction (Hodgson 1966). Timothy is somewhat unique among the forage species in that it has no requirement for short days or cool temperatures for flowering (Heide 1982). As a result, timothy often flowers in the year of seeding.

The flowering requirements of smooth bromegrass have been studied quite extensively (Allard and Evans 1941, Evans and Wilsie 1946, Gall 1947, Newell 1951, Klebesadel 1970, Clarke and Elliott 1974, Knowles 1982, Heide 1994). Early authors described smooth bromegrass as a long-day plant, indicating that floral initiation did not occur without exposure to long days. More recently, researchers have found that long days are a secondary requirement and that smooth bromegrass requires exposure to short days or low temperatures during primary induction (Heide 1984). No research has been reported on the flowering requirements of meadow bromegrass.

The objectives of this series of experiments were to determine the flowering response of meadow bromegrass to temperature and daylength during primary and secondary induction, and to determine if and when primary induction occurs in meadow bromegrass tillers in the field.

6.2 Materials and methods

Two sets of experiments on meadow bromegrass were carried out in the greenhouse and growth cabinets between October 1995 and March 1998; one set to determine primary induction requirements (Exp. 1, 2 & 3) and the other to determine secondary induction requirements (Exp. 4 & 5). Since these experiments were run simultaneously, induction treatments were followed by conditions that were known to promote floral initiation in smooth bromegrass and were thought to stimulate flowering in meadow bromegrass (Knowles 1982, Knowles, pers comm, Heide 1994). Material for the secondary induction studies was left outdoors under natural conditions until mid- November, when it was assumed that primary induction requirements had been met. All field-grown plant material was taken from meadow bromegrass stands that were two or three yrs old at the time of digging. These plots received 50 kg ha $^{-1}$ P_2O_5 and 11 kg ha $^{-1}$ N (11-51-0) each year, the first application was incorporated during seedbed preparation and subsequent applications were broadcast in fall. Plots were cut and residue was removed in the fall of the seedling year and in late July and early September of the second year.

6.2.1 Experiment 1

Plants were dug at weekly intervals from 1 September to mid-November 1997, separated into individual tillers, and 30 medium-sized (2-3 mm basal diameter) tillers were potted in 2.5 x 20 cm containers and placed in flats (15 plants/flat). A blend of vermiculite, peat moss and sand (10:5:1) with a pH of between 5 and 6 was used for potting. The mix contained a controlled release fertilizer with N, P, K plus superphosphate fines, trace elements and chelated iron. Plants were placed in a greenhouse where natural light was supplemented with 350 μmols m^{-2} s^{-1} from high pressure sodium lamps to provide a 16-hr day. Temperature was maintained at 20 °C during the day and 12 °C at night to promote floral initiation and elongation (Knowles 1982, Heide, 1994). Flats were arranged in a randomized complete block design (RCBD) with two replications. Lodging was prevented with a frame of 5 cm square wire mesh (stucco wire) mounted so that the height could be increased as the plants grew. Ninety days after planting, the proportion of plants with inflorescences, tiller number $plant^{-1}$, inflorescence number $plant^{-1}$, rate of inflorescence development (days to emergence from the flag leaf) and panicle length were recorded.

6.2.2 Experiment 2

One hundred and fifty medium-sized tillers of Paddock meadow bromegrass, dug on 1 August 1997, were potted as described above, and then placed in growth cabinets with 8 or 16 hr daylength and temperatures of 5, 10 or 20 °C. Twenty-five plants in each treatment, arranged in a RCBD in flats, were placed in each growth cabinet. Light levels of 200 to 240 μmolsm^{-2} s^{-1} were provided by fluorescent and incandescent lamps. After eight weeks in the growth cabinets, the plants were moved to a greenhouse with a 16 hr day and temperatures of 20D/12N, as described in the previous experiment. Ninety days after planting, the proportion of plants with inflorescences, tiller number plant^{-1}, inflorescence number plant^{-1}, rate of inflorescence development (days to emergence from the flag leaf) and panicle length were recorded.

6.2.3 Experiment 3

A similar experiment was conducted the following year with seedlings, tillers and plants of Paddock meadow bromegrass and Carlton smooth bromegrass. In this study, seedlings were grown in the soil-less mix described above in a greenhouse with a 16 hr day and temperatures of 20 D/12N for six weeks. Tillers were dug, separated and sorted as described above; plants were dug with a 5 cm soil sampler and transplanted intact. All plant material was clipped to 1 cm above ground and transplanted into trays of 5 x 10 cm pots in a RCBD, with five samples of each species and stage of development (seedling, tiller, plant) per replication and four replications of each species/stage treatment. These trays were then placed in a greenhouse with a 16-hr day and temperatures of 20D/12N for two weeks before they were placed in growth cabinets with the daylength/temperature combinations described in Exp 2. All plants were fertilized with a solution of 10-15-10 after four weeks in the growth cabinets. After eight weeks, plants were transferred to the greenhouse and treated as described in Exp 1. to promote floral initiation and elongation.

6.2.4 Experiments 4 and 5

To study the requirements for secondary induction, tillers were dug from field stands of Paddock meadow bromegrass at the end of October, separated and potted as described for Exp. 1. They were then placed in unheated, unlit cold frames outdoors until Nov 15th, when they were moved into growth cabinets and exposed to 200-240 μmols m^{-2} s^{-1} of light for 10, 13 or 16 hr day^{-1} with temperatures of 20D/12N (Exp. 4); or temperatures of 10D/5N, 15D/10N, or 20D/12N with a 16-hr day (Exp. 5). Plants were exposed to these conditions for four weeks after which they were transferred to a greenhouse with a 16-hr day and temperatures of 20D/12N until flowering was completed (90 days). The percentage of plants with inflorescences, number of tillers $plant^{-1}$, number of inflorescences $plant^{-1}$, rate of inflorescence development and panicle length were recorded.

Data were analyzed using PROC GLM (SAS 1985) (Appendix Tables A14, A15 and A16). However, in Exp. 2 and 3 only tillers from meadow bromegrass were analyzed in this manner, because these were the only studies in which the temperature and daylength treatments were replicated. Orthogonal contrasts were used to examine the relationship between temperature and flowering during primary induction in the remaining treatments of Exp 2 and 3. In addition, orthogonal contrasts were used to determine the relationship between date of sampling in the fall and flowering (Exp. 1) and the effects of daylength or temperature during secondary induction and flowering (Exp. 4 and 5). Differences were considered statistically significant at the $P \leq 0.05$ level.

6.3 Results and discussion

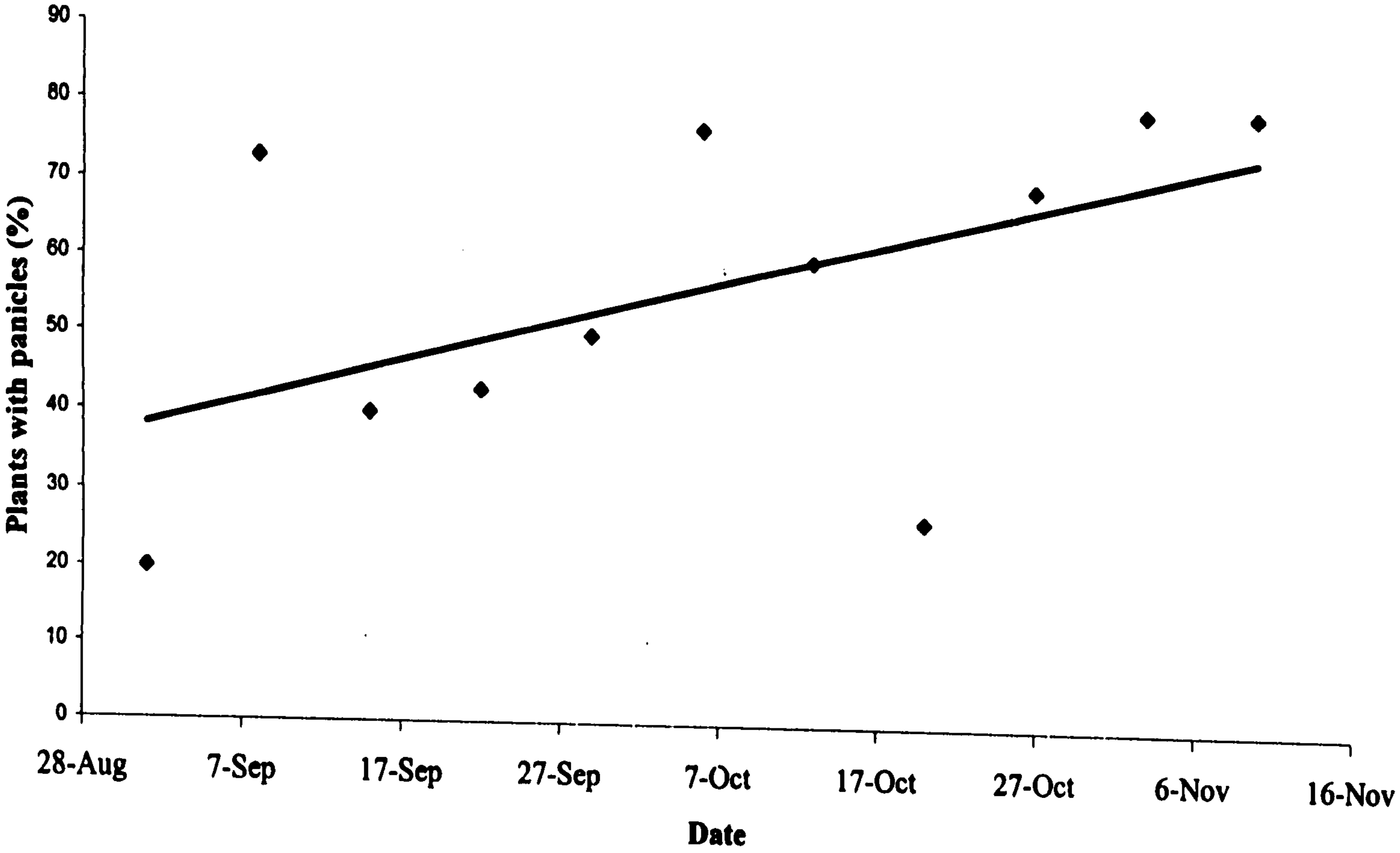
6.3.1 Primary induction (Exp 1, 2 and 3)

In the first experiment, which examined the time of primary induction in the field, a percentage of the plants produced panicles from tillers dug and exposed to long days and warm temperatures regardless of the date when they were subjected to these conditions (Fig. 6.1 and Appendix Table A14). Approximately 35% of plants dug in September formed panicles; this percentage increased linearly to reach more than 70% by mid-November. The fact that flowering increased with time indicates that short days and/or low temperatures promote flowering in meadow bromegrass. Similar response was observed in smooth bromegrass (Heide 1994). The fact that 35% of plants formed panicles in September indicates that the requirement for short days and/or cool temperatures may be facultative rather than obligatory or that shortening daylength rather than short days triggers flowering.

When meadow bromegrass tillers were exposed to different daylengths and temperatures during primary induction (Exp 2), a linear decline occurred in the percentage of plants that flowered as temperature increased (Fig. 6.2 b and Appendix Table A15). The quadratic response was significant as well, in certain cases, but no biological significance for the quadratic response was determined. There was no flowering response to daylength. Heide (1984) found that daylength rather than temperature was important for flowering in smooth bromegrass seedlings. He also found that in smooth bromegrass the percentage of plants that flowered was not as great at temperatures below 12° C as it was at temperatures between 15 and 21° C.

When the experiment was repeated (Exp 3), it was expanded to include seedlings, tillers and plants of both meadow bromegrass and smooth bromegrass. Once again, a significant negative correlation was observed between temperature and the percentage of plants that produced panicles in all plant material regardless of daylength (Figs. 6.2 and 6.3 and Appendix Table A14 and A15). The reason for the difference in smooth bromegrass

Figure 6.1. Percentage of plants with panicles in Paddock meadow bromegrass plants sampled at weekly intervals from 1 September to 10 November, 1998 (Exp 1., Dates linear P>f= 0.01).



response, compared to Heide's findings, is unclear; however, floral induction requirements vary not only with species but also with ecotype within a particular species (Elliott 1966, Heide 1994). Differences among ecotypes are generally related to the climate in the geographical origin of the ecotype. For example, Canadian common smooth bromegrass was not affected by exposure to different temperature regimes during secondary induction while a southern, American strain was affected (Evans and Wilsie 1946). However, Elliott (1966) found that Carlton smooth bromegrass had an obligate rather than a facultative requirement for short days and low temperature during primary induction. This finding is different from that of the present study, and the reason for this is unclear.

Differences in response between the two species of bromegrass were more pronounced following exposure at 10°C than at either 5°C or 20°C (Table 6.1 and Appendix Table A16). At this temperature, flowering was greater in smooth bromegrass than in meadow bromegrass. Transplanted plants were often less responsive to differences in temperature and daylength during primary induction than tillers or seedlings. Following exposure to 5°C and 8 hr light day $^{-1}$, flowering occurred more frequently in seedlings than in tillers and more frequently in tillers than in plants.

Similar differences were observed in other treatments. This may be due to the competition that occurred either in the field or in the greenhouse after transplanting. Tillers of seedlings raised in the greenhouse were generally larger than field-grown tillers, while individual field-grown tillers were sorted and only those with a basal diameter of 2 to 3 mm were used. As a result these were larger, on average, than tillers in field plants that were transplanted directly into pots. In other growth cabinet experiments (Chapter 5), flowering

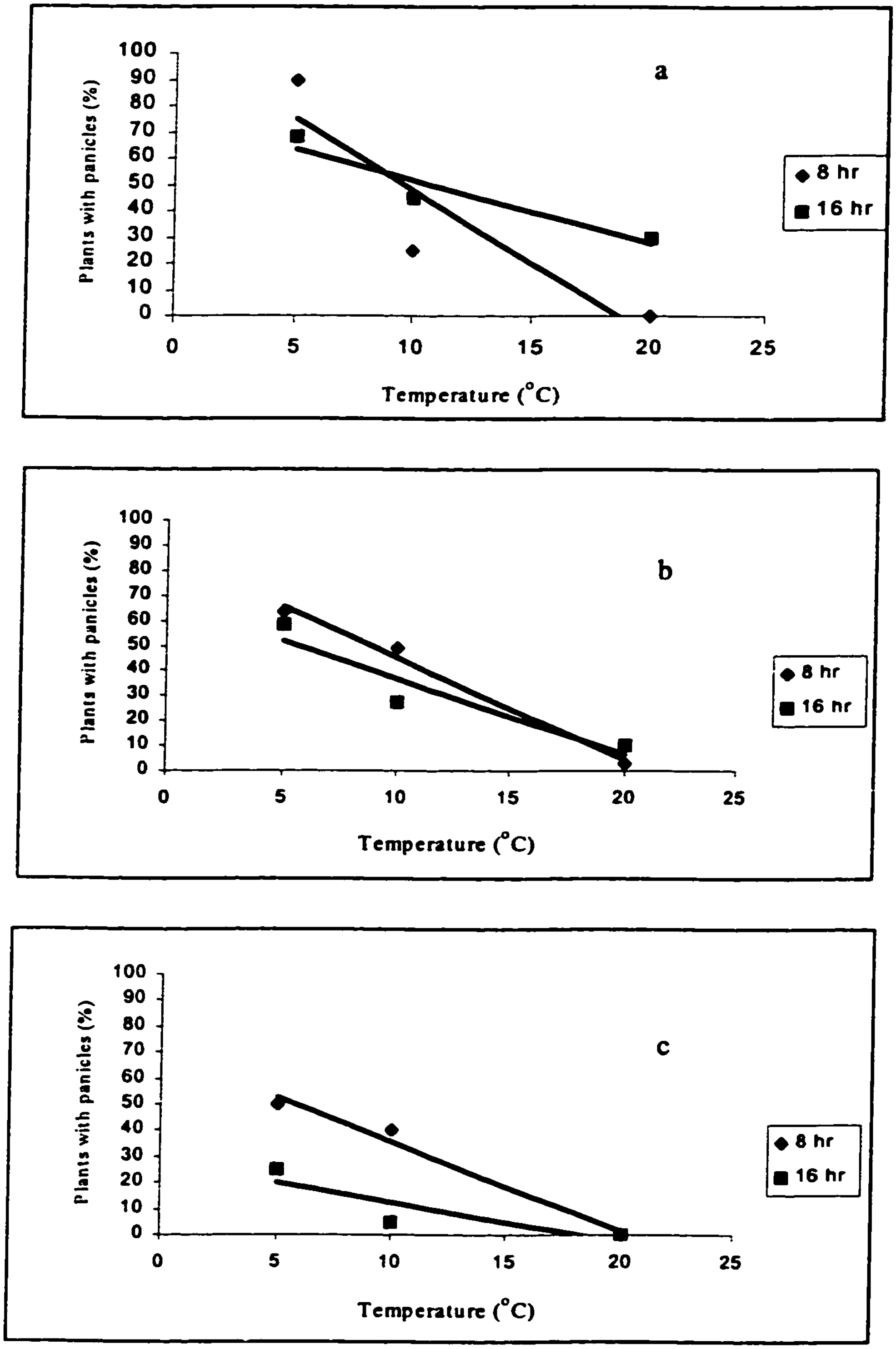


Figure 6.2. The effect of temperature at two daylengths during primary induction on panicle production in Paddock meadow bromegrass a) seedlings, b) tillers and c) plants. Responses significant at $P<0.05$.

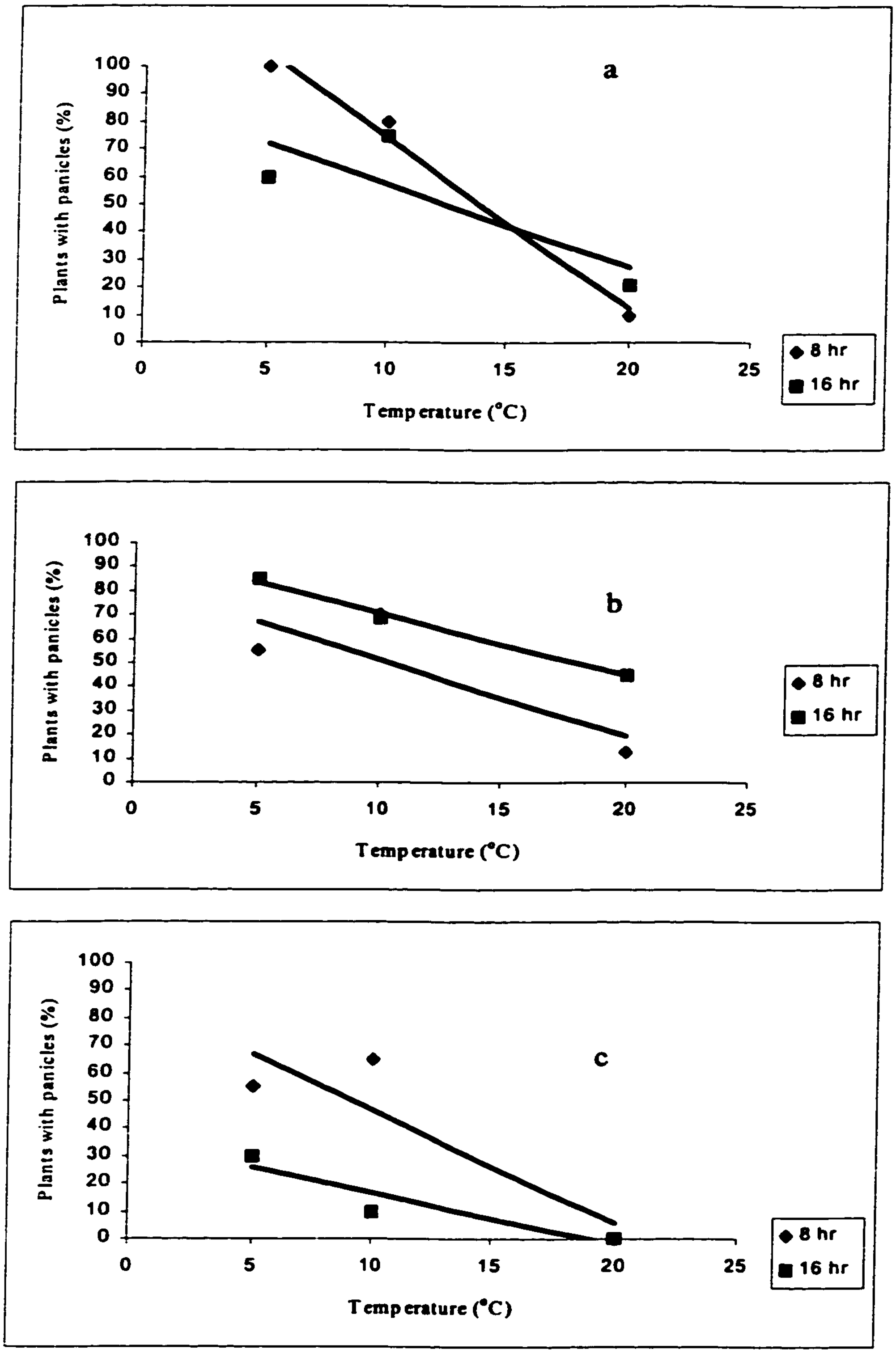


Figure 6.3. The effect of temperature at two daylengths during primary induction on panicle production in Carlton smooth bromegrass a) seedlings, b) tillers and c) plants. Responses significant at $P<0.05$, with the exception of b) 8 hr significant at 0.09.

increased as tiller size increased.

The number of panicles plant^{-1} was often greater than one in these studies, even though only one tiller was present at the start of exposure (data not shown). Havstad (1996a) found that this occurred in meadow fescue as well. This indicates that either little or no juvenility requirement exists, that juvenility is a property of the whole plant rather than the individual tiller, or that florigen, the flowering hormone, is transferable between mother and daughter tillers.

6.3.2 Secondary induction (Exp. 4 and 5)

Floral initiation in meadow bromegrass was not affected by temperature during secondary induction in the range of temperatures tested (data not shown). Flowering occurred in 85% of plants in the temperature trial. A significant linear decline in panicle length occurred with increasing daylength. Slower development was associated with larger panicles in ryegrass (Warringa 1997); however, in this case no significant difference occurred in the rate of development as daylength increased. Heide (1984) found that flowering did not occur without exposure to long days in an American (cv. Manchar) and a Norwegian (cv. Lofar) cultivar of smooth bromegrass. However, floral initiation occurred in autumn in a small percentage (<25%) of a Canadian cultivar ('Carlton') of smooth bromegrass tillers (Clarke and Elliott 1974). Elliott (1966) also found that Carlton smooth bromegrass initiated flowering very early in the spring under field conditions at Beaverlodge, Alberta (latitude 55° 15"). First growth was observed in mid-April (DL=15hr), and initiation was observed May 8-9 (DL=17hr). The mean temperature during

Table 6.1. The effect of stage of development on flowering in Paddock meadow bromegrass and Carlton smooth bromegrass following exposure to different temperatures and daylengths during primary induction (Exp 3).

Species/stage of	Temperature (°C)					
	5		10		20	
	Daylength (hr)					
development	8	16	8	16	8	16
Smooth bromegrass						
Seedlings	100	60	80	75	10	21
Tillers	55	85	70	69	13	45
Plants	55	30	65	10	0	0
Meadow bromegrass						
Seedlings	90	68	25	45	0	30
Tillers	85	72	39	20	0	0
Plants	50	25	40	5	0	0
S.E.	10	12	7	12	5	6
Species	0.57	0.71	0.00	0.01	0.11	0.02
Stage	0.00	0.00	0.95	0.00	0.48	0.00
Species*Stage.	0.15	0.69	0.12	0.20	0.48	0.00

the time between first growth and initiation ranged from 2 to 7° C, with minimum temperatures frequently falling below freezing. Field observations with meadow bromegrass indicate that floral initiation occurs very early in this species as well. This observation, combined with the results of this research, indicate that the response to both primary and secondary induction conditions may be facultative rather than obligate.

7. GENERAL DISCUSSION

The objective of the research presented in this thesis was to determine a) factors responsible for yield decline, b) response to N fertilization and residue removal and c) the mechanism governing flowering in meadow bromegrass. Seed yield of meadow bromegrass declines rapidly after two to three seed crops (Knowles *et al.* 1993). As is the case in other grasses (Meijer and Vreeke 1988a), the decline in yield in meadow bromegrass is often preceded by a decline in panicle production (Knowles *et al.* 1993). Dry conditions in the fall have led to very poor seed production in Saskatchewan seed fields. During the same period, seed production in irrigated fields was normal. In other grass crops, seed yield is highly correlated to fall tiller development (Schoblerlein 1987). Researchers suggest that the key to successful seed production is the development of an optimum number of inducible tillers in the fall when short days or low temperatures prevail (Heide 1994). These conditions are required for the first stage in the floral induction process in many temperate grasses. Induction requirements for meadow bromegrass are not known. In addition, it is not known whether or not tillers must reach a certain size before they are receptive to induction stimuli. Last, but not least, although panicle production is of paramount importance for seed production, panicle production alone does not guarantee good seed production. Silvertop infection can decimate a seed crop by killing many of the panicles.

Several hypotheses were tested. The objective of the first study was to determine whether residue removal and N fertilization could increase and prolong seed production. At the same time, tiller density, development and fertility were studied to determine whether or not seed production is correlated to these earlier developmental events. The impact of silvertop infection on seed yield, as well as the effect of residue removal and N fertilization on silvertop incidence, was also studied. Greenhouse and growth cabinet studies were conducted to determine whether certain temperature and daylength conditions were required to stimulate flowering and to determine whether stage of development (tiller size) and stand age influenced the ability of meadow bromegrass to respond to these conditions.

7.1 *Does residue removal and N fertilization increase and/or prolong seed production?*

Residue removal increases seed production in many grass seed crops (Knowles 1966, Canode and Law 1978, Nordestgaard 1980, Meijer and Vreeke 1988b, Thompson and Clarke 1989). This is due, in part, to the control of insect and disease pests, however; it is also due to a direct impact on reproductive development (Chilcote *et al.* 1980). In the present study, removing residue after harvest and fertilizing with N increased second year seed yield in meadow bromegrass by approximately 200 to 450 kg ha^{-1} compared to not removing residue and not fertilizing with N. Residue removal increased third year seed yield by 30 to 90 kg ha^{-1}. Yields for all treatments were considerably reduced in the third, compared to the second crop. N fertilization was only effective in increasing third year seed yield at one of the two sites. The range in seed yield (200 to 450 and 30 to 90 kg ha $^{-1}$) represents the difference in response at the two locations. The greater response occurred at the rainfed site in the second year seed crop and at the irrigated site in the third year seed crop. In terms of total seed production over the three yr of the study, removing residue after harvest and adding 100 kg ha^{-1} N increased seed yield by 500 to 560 kg ha^{-1} compared to the untreated control. At the current price for meadow bromegrass seed of approximately CAN $2.50 kg^{-1} , this would provide a return of $1,250 to $1,400 ha^{-1} on an investment of approximately $200 ha^{-1}.

7.2 *Was seed production correlated to panicle production?*

In Kentucky bluegrass and creeping red fescue, increases in seed yield following residue removal were proportional to increases in the number of fertile tillers (Meijer and Vreeke 1988b). In the present study, a significant ($P \leq 0.01$) positive correlation was observed between panicle production and seed yield at both sites in both years; however, it did not account for much of the variability in seed yield ($r^2=0.14$ to 0.59). Seed yield per fertile tiller was much lower in the third year than in the second year, and it was lower in treatments that produced the most panicles and the highest seed yield. This indicates that competition among fertile tillers may be limiting production in certain cases. In addition, the increase in panicle density, which resulted when residue was removed after harvest and N was added, was generally accompanied by an increase in the number of panicles affected by silvertop. The magnitude of the increase in panicles was greater than the magnitude of the increase in silvertop. Hence, the percentage of panicles affected by silvertop was lower in plots where the residue was removed after harvest. Although this treatment reduced the percentage of panicles affected by silvertop, silvertop incidence (%) was high enough to cause significant seed yield reductions. Further research is required to determine the causal agent and develop more effective control strategies for silvertop.

7.3 *Do tiller size and age of stand influence flowering in meadow bromegrass?*

A strong positive correlation was reported between flowering and leaf number at the time of induction in orchardgrass, meadow fescue and timothy (Schoberlein 1987, Havstad 1996a). In the present study, a linear increase in panicle production occurred as tiller size (basal diameter) increased from one to three mm. Tiller size did not interact with the age of stand from which the tillers originated in terms of panicle production. Tillers from a four-yr-old stand produced fewer flowers than tillers from a two-yr-old stand regardless of their size. It was observed that large-sized tillers were less abundant in older stands. Flowers originated from tillers that were farther from the center of the row in plants from ten-yr-old stands compared to plants from two-yr-old stands. These results indicate that, although competition is a factor in seed yield decline in meadow bromegrass, other factors are involved. Further research is required to determine these factors.

7.4 Does meadow bromegrass require exposure to certain temperatures and daylengths during primary and secondary induction to stimulate flowering?

Exposure to short days or low temperatures followed by long days promotes flowering in smooth bromegrass (Heide 1984). It has been observed, however, that under field conditions in northern Alberta, Carlton smooth bromegrass will initiate floral primordia in the fall (Elliott 1966). In the present study, 35% of plants from tillers of meadow bromegrass dug in September produced panicles when exposed to long days. This percentage increased to 70% for tillers dug in mid-November. This indicates that meadow bromegrass has a facultative rather than an obligate requirement for short days or low temperature during primary induction. In terms of the percentage of plants that formed inflorescence, and the percentage of fertile tillers on flowering plants, both Paddock meadow bromegrass and Carlton smooth bromegrass responded in an inverse linear fashion to increasing temperature (5, 10 and 20 °C), regardless of daylength. Short days increased the percentage of flowering tillers (compared to long days), but not the percentage of plants that flowered in this study. This is a divergence from Heide's (1984) finding that smooth bromegrass responded to short daylength rather than low temperature during primary induction. It is possible that the difference in response is due to the difference in the background of the smooth bromegrass cultivars used in the two studies.

8. CONCLUSIONS

1. Residue removal after harvest and fertilization with up to 100 kg ha^{-1} N significantly and consistently increased second year seed yield of Paddock meadow bromegrass. However, third year seed yield declined dramatically, irrespective of treatment, especially under rainfed conditions. High seed yield was associated with higher panicle production and lower levels of silvertop infestation.

2. The percentage of plants that flowered and the percentage of fertile tillers increased as tiller size increased and decreased as the stand aged. This indicates that competition among tillers can reduce flowering and seed yield. However, significantly fewer panicles were produced from large tillers from a four-yr-old stand than from the same-sized tillers from a two-yr-old stand, indicating that it is not competition alone that limits flowering.

3. Paddock meadow bromegrass has a facultative requirement for low temperature and no daylength requirement during primary induction. Carlton smooth bromegrass apparently has a facultative response to low temperature and showed no response to daylength during primary induction. Temperature in the range of 5 to 20°C or daylength in the range of 10 to 16 hr day^{-1} had no effect on secondary induction in Paddock meadow bromegrass.

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10. APPENDIX

Table A1. Growing season precipitation at Saskatoon and Outlook and irrigation at Outlook, 1994-1997.

		Saskatoon	Outlook	
Year	**Month**	**Precipitation (mm)**	**Precipitation (mm)**	**Irrigation (mm)**
1994	April	7.8	16.5	
	May	116.4	71.4	Details
	June	54.3	50.6	not available
	July	42.5	18.6	
	August	63.6	59.4	
	September	0.8	4.8	
	October	21.2	30.4	
	Total	306.6	251.7	150
1995	April	34.3	18.8	
	May	15.0	22.2	Details
	June	32.8	50.4	not available
	July	81.7	46.0	
	August	82.4	107.1	
	September	0.6	2.8	
	October	34.7	24.4	
	Total	281.5	271.7	225

Table A1 (cont.). Growing season precipitation at Saskatoon and Outlook and irrigation at Outlook, 1994-1997.

		Saskatoon	Outlook	
Year	Month	Precipitation (mm)	Precipitation (mm)	Irrigation (mm)
1996	April	25.1	37.8	
	May	58.9	67.4	
	June	100.8	61.5	6.25
	July	118.1	60.8	100
	August	18.3	6.4	
	September	39.2	55.7	
	October	5.1	8.2	
	Total	365.5	297.8	106.3
1997	April	27.6	23.2	25
	May	25.4	28.2	50
	June	53.7	64.2	144
	July	24.9	6.6	50
	August	48.2	29.2	50
	September	46.2	30.4	
	October	21.1	15	
	Total	247.1	196.8	319

Table A2. Analysis of variance for seed yield in Paddock meadow bromegrass at two sites with three N rates and four residue removal treatments. Sites considered fixed effects.

		Second crop (1996)			Third crop (1997)			Total yield (1996 and 1997)		
Source of variation	Df	MS	F	P>F	MS	F	P>F	MS	F	P>F
Site	1	685971	14.2	0.03	211782	29.1	0.01	135450	2.0	0.25
Rep	3	27031	0.6	0.68	8115	1.1	0.47	39219	0.6	0.67
Rep (Site)	3	48162	6.8	0.01	7277	2.6	0.10	67505	9.3	0.00
N	2	170333	24.1	0.00	16949	6.1	0.01	266357	36.7	0.00
Site*N	2	104004	14.7	0.00	30478	11.1	0.00	46019	6.3	0.01
Rep*N (Site)	12	7070	1.01	0.46	2758	1.3	0.23	7265	0.8	0.61
Res	3	296236	42.1	0.00	27715	13.4	0.00	496171	57.7	0.00
Site*Res	3	101865	14.5	0.00	6044	2.9	0.04	59933	7.0	0.00
N*Res	6	13133	1.87	0.10	838	0.4	0.87	19284	2.2	0.05
Site*N*Res	6	37844	5.4	0.00	3243	1.6	0.17	38641	4.5	0.00
Residual	54	7035			2063			8606		

Table A2 (cont.). Analysis of variance for seed yield in Paddock meadow bromegrass at two sites with three N rates and four residue removal treatments. Sites considered fixed effects

Contrasts:										
N linear (NL)	1	319790	45.2	0.00	26285	9.5	0.01	529438	72.9	0.00
N quadratic (NQ)	1	20875	3.0	0.11	7613	2.8	0.12	3275	0.5	0.51
Res 1 (+ vs -)	1	553089	78.6	0.00	65673	31.8	0.00	999934	116.2	0.00
Res 2 (1 vs 2)	1	40301	5.7	0.02	9669	4.7	0.03	89451	10.4	0.00
Res 3 (early vs late)	1	295317	42.0	0.00	7803	3.8	0.06	399128	46.4	0.00
NL*Res 1	1	17787	2.5	0.12	1088	0.5	0.47	27672	3.2	0.08
NQ*Res 1	1	19670	2.8	0.10	106	0.1	0.82	22663	2.6	0.11
NL*Res 2	1	22971	3.3	0.08	1080	0.5	0.47	34013	4.0	0.05
NQ*Res 2	1	5913	0.8	0.36	455	0.2	0.64	9649	1.1	0.29
NL*Res 3	1	2794	0.4	0.53	300	0.2	0.70	1263	0.2	0.70
NQ*Res 3	1	9660	1.4	0.25	1998	1.0	0.33	20446	2.4	0.13

Table A2a. Analysis of variance for seed yield in Paddock meadow bromegrass with three N rates and four residue removal treatments at Saskatoon and Outlook, 1997.

		Saskatoon			Outlook		
Source of variation	Df	MS	F	P>F	MS	F	P>F
N	2	1193	0.8	0.49	46233	11.4	0.00
Rep	3	3453	2.3	0.17	11939	3.0	0.12
Rep*N	6	1474	0.9	0.48	4042	1.6	0.19
Res	3	4382	2.8	0.06	29377	11.5	0.00
N*Res	6	1630	1.0	0.42	2451	1.0	0.47
Residual	27	1561			2566		
Contrasts:							
N linear (NL)	1	703	0.5	0.52	65432	16.2	0.01
N quadratic (NQ)	1	1683	1.1	0.33	27035	6.7	0.04
Res 1 (+ vs -)	1	7921	5.1	0.03	74757	29.1	0.00
Res 2 (1 vs 2)	1	2211	1.4	0.24	8472	3.3	0.08
Res 3 (early vs late)	1	3015	1.9	0.18	4902	1.9	0.18
NL*Res 1	1	22	0.0	0.91	2636	1.0	0.32
NQ*Res 1	1	780	0.5	0.49	179	0.1	0.79
NL*Res 2	1	326	0.2	0.65	809	0.3	0.58
NQ*Res 2	1	7877	5.1	0.03	3432	1.3	0.26
NL*Res 3	1	716	0.5	0.50	2627	1.0	0.32
NQ*Res 3	1	59	0.0	0.85	5023	2.0	0.17

Table A3. Analysis of variance for tiller survival in Paddock meadow bromegrass at two sites with three N rates and four residue removal treatments. Sites considered fixed effects.

		1996			1997		
Source of variation	Df	MS	F	P>F	MS	F	P>F
Site	1	12437	8.0	0.07	392451	4.8	0.12
Rep	3	16706	10.8	0.04	79191	1.0	0.51
Rep (Site)	3	1547	0.3	0.83	82226	4.2	0.03
N	2	7895	1.5	0.27	29910	1.5	0.25
Site*N	2	737	0.1	0.87	15647	0.8	0.47
Rep*N (Site)	12	5332	1.6	0.09	19462	2.5	0.00
Res	3	13238	4.0	0.01	32997	4.3	0.01
Site*Res	3	43709	13.2	0.00	11156	1.4	0.23
N*Res	6	4427	1.3	0.24	7923	1.0	0.41
Site*N*Res	6	2655	0.8	0.57	7032	0.9	0.49
Residual	342	3311			7697		
Contrasts:							
N linear (NL)	1	8746	1.6	0.22	51307	2.6	0.13
N quadratic (NQ)	1	7048	1.3	0.27	8526	0.4	0.52
Res 1 (+ vs -)	1	15033	4.5	0.03	30235	3.9	0.05
Res 2 (1 vs 2)	1	23869	7.2	0.01	29242	3.8	0.05
Res 3 (early vs late)	1	660	0.2	0.66	40134	5.2	0.02
NL*Res 1	1	2583	0.8	0.38	13574	1.8	0.19
NQ*Res 1	1	17592	5.3	0.02	6625	0.9	0.35
NL*Res 2	1	4624	1.4	0.24	6960	0.9	0.34
NQ*Res 2	1	1012	0.3	0.58	1794	0.2	0.63
NL*Res 3	1	262	0.0	0.78	18225	2.4	0.12
NQ*Res 3	1	583	0.2	0.67	791	0.1	0.75

Table A3a. Analysis of variance for tiller survival (%) in Paddock meadow bromegrass with three N rates and four residue removal treatments at Saskatoon and Outlook, Spring 1996.

		Saskatoon			Outlook		
Source of variation	Df	MS	F	P>F	MS	F	P>F
N	2	1385	2.3	0.18	2256	0.5	0.61
Rep	3	2820	4.7	0.05	226	0.1	0.98
Rep*N	6	602	1.2	0.36	4203	1.0	0.44
Res	3	792	1.5	0.23	10469	2.5	0.08
N*Res	6	347	0.7	0.67	2549	0.6	0.72
Residual	27	520			4135		
Contrasts:							
N linear (NL)	1	2757	4.6	0.08	4255	1.0	0.35
N quadratic (NQ)	1	13	0.0	0.89	257	0.1	0.81
Res 1 (+ vs -)	1	4	0.0	0.93	16813	4.1	0.05
Res 2 (1 vs 2)	1	1531	2.9	0.10	3799	0.9	0.35
Res 3 (early vs late)	1	840	1.6	0.21	10795	2.6	0.12
NL*Res 1	1	0	0.0	1.00	106	0.0	0.87
NQ*Res 1	1	1296	2.5	0.13	5556	1.3	0.26
NL*Res 2	1	184	0.4	0.56	1151	0.3	0.60
NQ*Res 2	1	87	0.2	0.69	213	0.1	0.82
NL*Res 3	1	400	0.8	0.39	1040	0.3	0.62
NQ*Res 3	1	114	0.2	0.64	7228	1.8	0.20

Table A4. Analysis of variance for harvest index in Paddock meadow bromegrass at two sites with three N rates and four residue removal treatments. Sites considered fixed effects.

		1996				1997		
Source of variation	Df	MS	F	P>F	Df	MS	F	P>F
Site	1	0.0173	36.8	0.01	1	0.0028	4.9	0.09
Rep	3	0.0014	3.0	0.20	3	0.0012	2.2	0.27
Rep (Site)	3	0.0005	0.7	0.57	3	0.0006	1.5	0.27
N	2	0.0001	0.1	0.90	2	0.0013	3.2	0.06
Site*N	2	0.0003	0.5	0.65	2	0.0000	0.1	0.95
Rep*N (Site)	12	0.0007	1.5	0.15	12	0.0004	0.5	0.88
Res	3	0.0043	9.6	0.00	3	0.0033	4.8	0.01
Site*Res	3	0.0015	3.4	0.02	3	0.0006	0.9	0.46
N*Res	6	0.0008	1.8	0.12	6	0.0003	0.4	0.87
Site*N*Res	6	0.0003	0.7	0.67	6	0.0002	0.3	0.93
Residual	51	0.0005			43	0.0007		
Contrasts:								
N linear (NL)	1	0.00005	0.1	0.79		0.00253	6.9	0.02
N quadratic (NQ)	1	0.00009	0.1	0.72		0.00029	0.8	0.39
Res 1 (+ vs -)	1	0.01102	24.6	0.00		0.00292	4.2	0.05
Res 2 (1 vs 2)	1	0.00046	1.0	0.31		0.00265	3.8	0.06
Res 3 (early vs late)	1	0.00136	3.0	0.09		0.00406	5.9	0.02
NL*Res 1	1	0.00002	0.0	0.85		0.00002	0.04	0.85
NQ*Res 1	1	0.00041	0.9	0.35		0.00008	0.1	0.74
NL*Res 2	1	0.00207	4.6	0.04		0.00019	0.3	0.61
NQ*Res 2	1	0.00215	4.8	0.03		0.00053	0.8	0.39
NL*Res 3	1	0.00007	0.2	0.69		0.00050	0.7	0.40
NQ*Res 3	1	0.00000	0.0	0.96		0.00026	0.4	0.54

Table A4a. Analysis of variance for harvest index in Paddock meadow bromegrass with three N rates and four residue removal treatments at Saskatoon and Outlook, 1996.

		Saskatoon			Outlook		
Source of variation	Df	MS	F	P>F	MS	F	P>F
N	2	0.00008	0.1	0.93	0.00031	1.0	0.42
Rep	3	0.00098	0.9	0.48	0.00086	2.8	0.13
Rep*N	6	0.00106	3.3	0.02	0.0003	0.5	0.78
Res	3	0.00466	14.7	0.00	0.00078	1.4	0.27
N*Res	6	0.00010	0.3	0.92	0.00101	1.8	0.14
Residual	27	0.00032			0.00057		
Contrasts:							
N linear (NL)	1	0.00014	0.1	0.73	0.00053	1.7	0.24
N quadratic (NQ)	1	0.00002	0.0	0.90	0.00008	0.3	0.62
Res 1 (+ vs -)	1	0.01323	41.7	0.00	0.00085	1.5	0.23
Res 2 (1 vs 2)	1	0.00002	0.1	0.80	0.00067	1.2	0.29
Res 3 (early vs late)	1	0.00056	1.8	0.20	0.00082	1.4	0.24
NL*Res 1	1	0.00000	0.0	0.94	0.00005	0.1	0.77
NQ*Res 1	1	0.00006	0.2	0.67	0.00048	0.8	0.37
NL*Res 2	1	0.00005	0.2	0.69	0.00130	2.3	0.14
NQ*Res 2	1	0.00003	0.1	0.75	0.00067	1.2	0.29
NL*Res 3	1	0.00001	0.0	0.90	0.00226	4.0	0.06
NQ*Res 3	1	0.00045	1.4	0.24	0.00130	2.3	0.14

Table A5. Analysis of variance for tiller density in Paddock meadow bromegrass at two sites with three N rates and four residue removal treatments. Sites considered fixed effects.

		Fall 1995			Spring 1996		
Source of variation	Df	MS	F	P>F	MS	F	P>F
Site	1	141067	0.1	0.77	6299651	2.0	0.25
Rep	3	3489746	2.6	0.22	1979594	0.6	0.65
Rep (Site)	3	1319036	2.7	0.10	3182701	2.6	0.10
N	2	3238003	6.5	0.01	319371	0.3	0.77
Site*N	2	10371	0.2	0.98	563979	0.5	0.64
Rep*N (Site)	12	496631	1.1	0.35	1211940	0.8	0.66
Res	3	1326282	3.0	0.04	5628881	3.6	0.02
Site*Res	3	1052178	2.4	0.08	2656074	1.7	0.17
N*Res	6	422600	1.0	0.45	913710	0.6	0.74
Site*N*Res	6	432842	1.0	0.44	547346	0.4	0.90
Residual	54	435145			1545695		
Contrasts:							
N linear (NL)	1	6441444	13.0	0.00	256	0.0	0.99
N quadratic (NQ)	1	34561	0.1	0.80	638485	0.5	0.48
Res 1 (+ vs -)	1	284761	0.7	0.42	5047724	3.3	0.08
Res 2 (1 vs 2)	1	741895	1.7	0.20	1504711	1.0	0.33
Res 3 (early vs late)	1	2952192	6.8	0.01	10334208	6.7	0.01
NL*Res 1	1	428652	1.0	0.33	1843968	1.2	0.28
NQ*Res 1	1	157344	0.4	0.55	2940082	1.9	0.17
NL*Res 2	1	629856	1.5	0.23	285144	0.2	0.67
NQ*Res 2	1	7524	0.0	0.90	68204	0.0	0.83
NL*Res 3	1	332928	0.8	0.39	5000	0.0	0.95
NQ*Res 3	1	979296	2.3	0.14	339864	0.2	0.64

Table A5 (cont.). Analysis of variance for tiller density in Paddock meadow bromegrass at two sites with three N rates and four residue removal treatments. Sites considered fixed effects.

		Fall 1996			Spring 1997		
Source of variation	Df	MS	F	P>F	MS	F	P>F
Site	1	1278960	3.7	0.15	3782616	2.5	0.21
Rep	3	1247157	0.4	0.79	3578527	2.4	0.25
Rep (Site)	3	3420711	4.3	0.03	1506093	2.3	0.13
N	2	1369923	1.7	0.22	5389448	8.1	0.01
Site*N	2	1055544	1.3	0.30	2318616	3.5	0.06
Rep*N (Site)	12	801846	3.1	0.00	663902	0.9	0.53
Res	3	561653	2.2	0.10	12315267	17.2	0.00
Site*Res	3	2031676	7.8	0.00	2592330	3.6	0.02
N*Res	6	193155	0.7	0.62	696317	1.0	0.45
Site*N*Res	6	153556	0.6	0.74	615871	0.9	0.53
Residual	54	260655			716036		
Contrasts:							
N linear (NL)	1	2402500	3.0	0.11	10471696	15.8	0.00
N quadratic (NQ)	1	337345	0.4	0.53	307200	0.5	0.51
Res 1 (+ vs -)	1	1233497	4.7	0.03	30994689	43.3	0.00
Res 2 (1 vs 2)	1	231682	0.9	0.35	1867778	2.6	0.11
Res 3 (early vs late)	1	219781	0.8	0.36	4083333	5.7	0.02
NL*Res 1	1	19521	0.1	0.79	34992	0.1	0.83
NQ*Res 1	1	11520	0.0	0.83	2844	0.0	0.95
NL*Res 2	1	729411	2.8	0.10	1348056	1.9	0.18
NQ*Res 2	1	4481	0.0	0.90	747457	1.0	0.31
NL*Res 3	1	233928	0.9	0.35	1598472	2.2	0.14
NQ*Res 3	1	160067	0.6	0.44	446083	0.6	0.43

Table A5a. Analysis of variance for tiller density in Paddock meadow bromegrass with three N rates and four residue removal treatments at Saskatoon and Outlook, Fall 1996.

		Saskatoon			Outlook		
Source of variation	Df	MS	F	P>F	MS	F	P>F
N	2	14309	0	0.98	2411157	2.8	0.14
Rep	3	4111908	5.5	0.04	555961	0.7	0.61
Rep*N	6	748745	3.6	0.01	854947	2.7	0.03
Res	3	232199	1.1	0.36	2361131	7.6	0.00
N*Res	6	58668	0.3	0.94	288043	0.9	0.50
Residual	27	208772			312538		
Contrasts:							
N linear (NL)	1	27848	0.0	0.85	4101248	4.8	0.07
N quadratic (NQ)	1	771	0.0	0.98	721067	0.8	0.39
Res 1 (+ vs -)	1	406194	2.0	0.17	4875264	15.6	0.00
Res 2 (1 vs 2)	1	110137	0.5	0.47	1025312	3.3	0.08
Res 3 (early vs late)	1	180267	0.9	0.36	1182816	3.8	0.06
NL*Res 1	1	168003	0.8	0.38	369024	1.2	0.29
NQ*Res 1	1	854	0.0	0.95	32768	0.1	0.75
NL*Res 2	1	152325	0.7	0.40	668352	2.1	0.16
NQ*Res 2	1	12247	0.1	0.81	256	0.0	0.98
NL*Res 3	1	16	0.0	0.99	473344	1.5	0.23
NQ*Res 3	1	18565	0.1	0.77	184512	0.6	0.45

Table A5b. Analysis of variance for tiller density in Paddock meadow bromegrass with three N rates and four residue removal treatments at Saskatoon and Outlook, Spring 1997.

		Saskatoon			Outlook		
Source of variation	Df	MS	F	P>F	MS	F	P>F
N	2	4048912	7.8	0	3659152	4.5	0.06
Rep	3	4842772	9.3	0	241849	0.3	0.83
Rep*N	6	518345	0.9	0.5	809460	1.0	0.46
Res	3	2061758	3.4	0	12845838	15.5	0.00
N*Res	6	813492	1.3	0.3	498697	0.6	0.72
Residual	27	604087			827986		
Contrasts:							
N linear (NL)	1	6904328	13.3	0.01	3797768	4.7	0.07
N quadratic (NQ)	1	1193496	2.3	0.18	3520536	4.4	0.08
Res 1 (+ vs -)	1	4602455	7.6	0.01	32809984	36.6	0.00
Res 2 (1 vs 2)	1	26296	0.0	0.84	3135008	3.8	0.06
Res 3 (early vs late)	1	1556523	2.6	0.12	2592523	3.1	0.09
NL*Res 1	1	1868184	3.1	0.09	1215000	1.5	0.24
NQ*Res 1	1	18689	0.0	0.86	45000	0.1	0.82
NL*Res 2	1	702768	1.2	0.29	645888	0.8	0.38
NQ*Res 2	1	140375	0.2	0.63	719104	0.9	0.36
NL*Res 3	1	1904400	3.2	0.09	166464	0.2	0.66
NQ*Res 3	1	246533	0.4	0.53	200725	0.2	0.63

Table A6. Analysis of variance for tiller development (leaf number tiller $^{-1}$) in Paddock meadow bromegrass at two sites with three N rates and two residue removal treatments. Sites considered fixed effects.

		Fall 1995			Fall 1996		
Source of variation	Df	MS	F	P>F	MS	F	P>F
Site	1	1.432	61.8	0.00	0.368	6.0	0.09
Rep	3	0.027	1.2	0.45	0.296	4.8	0.11
Rep (Site)	3	0.023	0.4	0.79	0.061	0.4	0.76
N	2	0.011	0.2	0.85	0.131	0.9	0.45
Site*N	2	0.039	0.6	0.57	0.036	0.2	0.79
Rep*N (Site)	12	0.065	2.0	0.09	0.153	1.7	0.16
Res	1	1.384	42.9	0.00	1.548	17.0	0.00
Site*Res	1	0.809	25.1	0.00	0.052	0.6	0.46
N*Res	2	0.110	3.4	0.06	0.125	1.4	0.28
Site*N*Res	2	0.068	2.1	0.15	0.047	0.5	0.60
Residual	18	0.032			0.091		
Contrasts:							
N linear (NL)	1	0.000	0.0	0.96	0.245	1.6	0.23
N quadratic (NQ)	1	0.021	0.3	0.58	0.017	0.1	0.75
Res 1 (+ vs -)	1	1.384	42.9	0.00	1.548	17.0	0.00
NL*Res 1	1	0.063	2.0	0.18	0.001	0.0	0.92
NQ*Res 1	1	0.157	4.9	0.04	0.248	2.7	0.12

Table A6 (cont.). Analysis of variance for tiller development (leaf number tiller $^{-1}$) in Paddock meadow bromegrass at two sites with three N rates and four residue removal treatments. Sites considered fixed effects.

		Spring 1996				Spring 1997		
Source of variation	Df	MS	F	P>F	Df	MS	F	P>F
Site	1	1.153	5.6	0.10	1	1.107	1.1	0.37
Rep	3	0.269	1.3	0.42	3	0.480	0.5	0.72
Rep (Site)	3	0.205	1.8	0.20	3	1.005	19.2	0.00
N	2	0.067	0.6	0.57	2	0.162	3.1	0.08
Site*N	2	0.009	0.1	0.92	2	0.001	0.0	0.98
Rep*N (Site)	12	0.112	1.9	0.06	12	0.052	0.8	0.65
Res	3	0.638	10.8	0.00	3	0.173	2.6	0.06
Site*Res	3	0.246	4.1	0.01	3	0.335	5.1	0.00
N*Res	6	0.115	1.9	0.09	6	0.072	1.1	0.38
Site*N*Res	6	0.148	2.5	0.03	6	0.054	0.8	0.56
Residual	49	0.059			47	0.066		
Contrasts:								
N linear (NL)	1	0.127	1.1	0.31		0.250	4.8	0.05
N quadratic (NQ)	1	0.006	0.1	0.82		0.074	1.4	0.26
Res 1 (+ vs -)	1	0.982	16.6	0.00		0.465	7.1	0.01
Res 2 (1 vs 2)	1	0.215	3.6	0.06		0.002	0.0	0.86
Res 3 (early vs late)	1	0.715	12.1	0.00		0.053	0.8	0.37
NL*Res 1	1	0.058	1.0	0.33		0.068	1.0	0.31
NQ*Res 1	1	0.084	1.4	0.24		0.034	0.5	0.48
NL*Res 2	1	0.026	0.4	0.51		0.006	0.1	0.76
NQ*Res 2	1	0.313	5.3	0.03		0.077	1.2	0.28
NL*Res 3	1	0.002	0.0	0.87		0.238	3.6	0.06
NQ*Res 3	1	0.207	3.5	0.07		0.010	0.2	0.70

Table A6a. Analysis of variance for tiller development (leaf number tiller $^{-1}$) in Paddock meadow bromegrass with three nitrogen rates and two residue removal treatments at Saskatoon and Outlook, Fall 1995.

		Saskatoon			Outlook		
Source of variation	Df	MS	F	P>F	MS	F	P>F
N	2	0.041	2.9	0.13	0.009	0.1	0.93
Rep	3	0.032	2.3	0.18	0.018	0.2	0.92
Rep*N	6	0.014	0.5	0.82	0.116	3.4	0.05
Res	1	0.038	1.3	0.29	2.154	62.8	0.00
N*Res	6	0.026	0.9	0.45	0.151	4.4	0.05
Residual	27	0.030			0.034		
Contrasts:							
N linear (NL)	1	0.009	0.6	0.45	0.013	0.1	0.75
N quadratic (NQ)	1	0.072	5.1	0.06	0.004	0.0	0.86
Res 1 (+ vs -)	1	0.038	1.3	0.29	2.154	62.9	0
NL*Res 1	1	0.006	0.2	0.68	0.185	5.4	0.1
NQ*Res 1	1	0.047	1.6	0.24	0.118	3.4	0.1

Table A6b. Analysis of variance for tiller development (leaf number tiller $^{-1}$) in Paddock meadow bromegrass with three N rates and four residue removal treatments at Saskatoon and Outlook, Spring 1996.

		Saskatoon			Outlook		
Source of variation	Df	MS	F	P>F	MS	F	P>F
N	2	0.049	0.5	0.65	0.027	0.2	0.81
Rep	3	0.260	2.5	0.16	0.214	1.8	0.25
Rep*N	6	0.104	2.3	0.07	0.120	1.7	0.17
Res	3	0.644	13.9	0.00	0.240	3.3	0.03
N*Res	6	0.125	2.7	0.04	0.138	1.9	0.11
Residual	27	0.046			0.072		
Contrasts:							
N linear (NL)	1	0.098	0.9	0.37	0.036	0.3	0.60
N quadratic (NQ)	1	0.000	0.0	0.96	0.017	0.1	0.72
Res 1 (+ vs -)	1	1.511	32.6	0.00	0.030	0.4	0.53
Res 2 (1 vs 2)	1	0.279	6.0	0.02	0.016	0.2	0.64
Res 3 (early vs late)	1	0.141	3.0	0.09	0.673	9.3	0.01
NL*Res 1	1	0.114	2.5	0.13	0.000	0.0	0.99
NQ*Res 1	1	0.137	3.0	0.10	0.002	0.0	0.89
NL*Res 2	1	0.151	3.3	0.08	0.380	5.3	0.03
NQ*Res 2	1	0.184	4.0	0.06	0.131	1.8	0.19
NL*Res 3	1	0.107	2.3	0.14	0.146	2.0	0.17
NQ*Res 3	1	0.054	1.2	0.29	0.169	2.4	0.14

Table A6c. Analysis of variance for tiller development (leaf number tiller $^{-1}$) in Paddock meadow bromegrass with three N rates and four residue removal treatments at Saskatoon and Outlook, Spring 1997.

		Saskatoon			Outlook		
Source of variation	Df	MS	F	P>F	MS	F	P>F
N	2	0.092	2.4	0.17	0.071	1.1	0.40
Rep	3	1.412	37.5	0.00	0.074	1.1	0.42
Rep*N	6	0.038	0.6	0.69	0.067	0.9	0.50
Res	3	0.463	8.0	0.00	0.045	0.6	0.61
N*Res	6	0.046	0.8	0.58	0.079	1.1	0.40
Residual	27	0.058			0.073		
Contrasts:							
N linear (NL)	1	0.147	3.9	0.10	0.105	1.6	0.26
N quadratic (NQ)	1	0.036	1.0	0.36	0.038	0.6	0.48
Res 1 (+ vs -)	1	1.042	17.9	0.00	0.003	0.0	0.84
Res 2 (1 vs 2)	1	0.052	0.9	0.35	0.085	1.2	0.29
Res 3 (early vs late)	1	0.295	5.1	0.03	0.048	0.7	0.43
NL*Res 1	1	0.034	0.6	0.45	0.033	0.5	0.50
NQ*Res 1	1	0.029	0.5	0.49	0.008	0.1	0.74
NL*Res 2	1	0.122	2.1	0.16	0.056	0.8	0.39
NQ*Res 2	1	0.083	1.4	0.24	0.011	0.2	0.70
NL*Res 3	1	0.009	0.2	0.70	0.354	4.9	0.04
NQ*Res 3	1	0.000	0.0	0.93	0.014	0.2	0.66

Table A7. Analysis of variance for fertile tiller density in Paddock meadow bromegrass at two sites with three N rates and four residue removal treatments. Sites considered fixed effects.

		1996				1997		
Source of variation	Df	MS	F	P>F	Df	MS	F	P>F
Site	1	994560	17.4	0.03	1	166667	3.1	0.18
Rep	3	105779	1.8	0..31	3	29372	0.5	0.69
Rep (Site)	3	57196	0.9	0.48	3	54005	2.5	0.11
N	2	131044	2.0	0.17	2	150675	6.9	0.01
Site*N	2	13622	0.2	0.81	2	18435	0.8	0.45
Rep*N (Site)	12	64457	1.5	0.16	12	21774	1.2	0.31
Res	3	477195	11.0	0.00	3	426044	23.3	0.00
Site*Res	3	115845	2.7	0.06	3	6418	0.4	0.79
N*Res	6	109644	2.5	0.03	6	12666	0.7	0.66
Site*N*Res	6	32042	0.7	0.62	6	14527	0.8	0.58
Residual	53	43575			54	18322		
Contrasts:								
N linear (NL)	1	217376	3.4	0.09		300304	13.8	0.00
N quadratic (NQ)	1	47859	0.7	0.41		1045	0.1	0.83
Res 1 (+ vs -)	1	634783	14.6	0.00		850208	46.4	0.00
Res 2 (1 vs 2)	1	104837	2.4	0.13		138384	7.6	0.01
Res 3 (early vs late)	1	695205	16.0	0.00		289541	15.8	0.00
NL*Res 1	1	25	0.0	0.98		44165	2.4	0.13
NQ*Res 1	1	36326	0.8	0.37		256	0.0	0.91
NL*Res 2	1	69847	1.6	0.21		8971	0.5	0.49
NQ*Res 2	1	369433	8.5	0.01		11552	0.6	0.43
NL*Res 3	1	173571	4.0	0.05		5408	0.3	0.59
NQ*Res 3	1	6372	0.2	0.70		5643	0.3	0.58

Table A8. Analysis of variance for tiller fertility (percentage fertile tillers) in Paddock meadow bromegrass at two sites with three nitrogen rates and four residue removal treatments. Sites considered fixed effects.

		1996, based on Fall 1995				1997, based on Fall 1996		
Source of variation	Df	MS	F	P>F	Df	MS	F	P>F
Site	1	2522	60.9	0.00	1	1	0.0	0.91
Rep	3	151	3.7	0.16	3	92	1.1	0.48
Rep (Site)	3	41	0.6	0.65	3	86	1.8	0.21
N	2	132	1.8	0.21	2	149	3.1	0.08
Site*N	2	13	0.2	0.85	2	0	0.0	0.99
Rep*N (Site)	12	74	0.8	0.61	12	49	1.3	0.26
Res	3	796	9.0	0.00	3	692	18.1	0.00
Site*Res	3	336	3.8	0.02	3	105	2.7	0.05
N*Res	6	268	3.0	0.01	6	26	0.7	0.68
Site*N*Res	6	58	0.7	0.68	6	15	0.4	0.89
Residual	53	88			54	38		
Contrasts:								
N linear (NL)	1	17	0.2	0.64		298	6.1	0.03
N quadratic (NQ)	1	249	3.3	0.09		1	0.0	0.92
Res 1 (+ vs -)	1	1359	15.4	0.00		1391	36.4	0.00
Res 2 (1 vs 2)	1	718	8.2	0.01		289	7.6	0.01
Res 3 (early vs late)	1	292	3.3	0.07		397	10.4	0..00
NL*Res 1	1	5	0.1	0.82		59	1.5	0.22
NQ*Res 1	1	168	1.9	0.17		2	0.0	0.84
NL*Res 2	1	71	0.8	0.37		1	0.0	0.87
NQ*Res 2	1	10998876	12.5	0.00		32	0.8	0.36
NL*Res 3	1	163	2.1	0.15		6	0.2	0.69
NQ*Res 3	1	71	0.8	0.37		54	1.4	0.24

Table A8a. Analysis of variance for tiller fertility (percentage fertile tillers) in Paddock meadow bromegrass with three N rates and four residue removal treatments at Saskatoon and Outlook, 1996.

		Saskatoon			Outlook		
Source of variation	Df	MS	F	P>F	MS	F	P>F
N	2	53	1.4	0.31	92	0.8	0.48
Rep	3	48	1.3	0.36	138	1.2	0.37
Rep*N	6	37	0.6	0.75	111	1.0	0.45
Res	3	919	14.0	0.00	207	1.9	0.16
N*Res	6	167	2.6	0.04	157	1.4	0.25
Residual	27	66			111		
Contrasts:							
N linear (NL)	1	30	0.8	0.40	0	0.0	0.97
N quadratic (NQ)	1	75	2.0	0.21	185	1.7	0.25
Res 1 (+ vs -)	1	1863	28.4	0.00	82	0.7	0.40
Res 2 (1 vs 2)	1	889	13.6	0.00	67	0.6	0.44
Res 3 (early vs late)	1	5	0.1	0.78	466	4.2	0.05
NL*Res 1	1	1	0.0	0.89	3	0.0	0.86
NQ*Res 1	1	33	0.5	0.49	159	1.4	0.24
NL*Res 2	1	16	0.3	0.62	250	2.2	0.15
NQ*Res 2	1	711	3.7	0.07	410	3.7	0.07
NL*Res 3	1	240	3.7	0.07	17	0.2	0.70
NQ*Res 3	1	2	0.0	0.86	108	1.0	0.33

Table A8b. Analysis of variance for tiller fertility (percentage fertile tillers) in Paddock meadow bromegrass with three N rates and four residue removal treatments at Saskatoon and Outlook, 1997.

		Saskatoon			Outlook		
Source of variation	Df	MS	F	P>F	MS	F	P>F
N	2	79	1.9	0.23	70	1.3	0.35
Rep	3	108	2.6	0.15	70	1.3	0.37
Rep*N	6	42	1.1	0.39	56	1.5	0.23
Res	3	645	16.8	0.00	153	4.0	0.02
N*Res	6	25	0.7	0.68	15	0.4	0.88
Residual	27	38			38		
Contrasts:							
N linear (NL)	1	158	3.8	0.10	140	2.5	0.16
N quadratic (NQ)	1	1	0.0	0.89	0	0.0	0.99
Res 1 (+ vs -)	1	1100	28.7	0.00	384	10.1	0.00
Res 2 (1 vs 2)	1	425	11.1	0.00	12	0.3	0.58
Res 3 (early vs late)	1	408	10.6	0.00	63	1.7	0.21
NL*Res 1	1	53	1.4	0.25	13	0.3	0.57
NQ*Res 1	1	0	0.0	0.95	2	0.1	0.83
NL*Res 2	1	24	0.6	0.44	40	1.1	0.31
NQ*Res 2	1	17	0.5	0.51	15	0.4	0.54
NL*Res 3	1	20	0.5	0.47	1	0.0	0.87
NQ*Res 3	1	37	1.0	0.34	19	0.5	0.49

Table A9. Analysis of variance for silvertop incidence (density and %) in Paddock meadow bromegrass at two sites with three N rates and four residue removal treatments. Sites fixed. Only treatments that produced heads were included in the analysis.

		1996					
		Silvertop density (# m^{-2})			Silvertop incidence (%)		
Source of variation	Df	MS	F	P>F	MS	F	P>F
Site	1	97465	33.1	0.01	396	1.3	0.33
Rep	3	3589	1.2	0.44	206	0.7	0.62
Rep (Site)	3	2969	0.8	0.51	298	0.3	0.81
N	2	1919	0.5	0.60	933	1.0	0.39
Site*N	2	1234	0.3	0.42	917	1.0	0.39
Rep*N (Site)	12	3708	1.3	0.23	918	1.2	0.30
Res	3	2501	0.9	0.45	1822	2.4	0.08
Site*Res	3	3332	1.2	0.32	41	0.1	0.98
N*Res	6	4541	1.6	0.16	870	1.1	0.35
Site*N*Res	6	3272	1.2	0.33	167	0.2	0.97
Residual	50	2772			760		
Contrasts:							
N linear (NL)	1	2921	0.8	0.39	853	0.9	0.35
N quadratic (NQ)	1	887	0.2	0.63	959	1.1	0.33
Res 1 (+ vs -)	1	1318	0.5	0.49	3198	4.2	0.05
Res 2 (1 vs 2)	1	3	0.0	0.97	960	1.3	0.27
Res 3 (early vs late)	1	6298	2.3	0.14	1223	1.6	0.21
NL*Res 1	1	14168	5.1	0.03	680	0.9	0.35
NQ*Res 1	1	521	0.2	0.67	179	0.2	0.63
NL*Res 2	1	7404	2.7	0.11	4116	5.4	0.02
NQ*Res 2	1	354	0.1	0.72	90	0.1	0.73
NL*Res 3	1	2814	1.0	0.32	270	0.4	0.55
NQ*Res 3	1	3724	1.3	0.25	52	0.1	0.79

Table A9 (cont.). Analysis of variance for silvertop incidence (density and %) in Paddock meadow bromegrass at two sites with three N rates and four residue removal treatments. Sites fixed. Only treatments that produced heads were included in the analysis.

		1997					
		Silvertop density (# m^{-2})			Silvertop incidence (%)		
Source of variation	Df	MS	F	P>F	MS	F	P>F
Site	1	9136	0.6	0.48	18499	39.8	0.01
Rep	3	2071	0.1	0.93	1237	2.6	0.23
Rep (Site)	3	14079	3.4	0.05	481	1.2	0.36
N	2	35702	8.8	0.00	2522	6.2	0.01
Site*N	2	22435	5.6	0.02	1811	4.5	0.03
Rep*N (Site)	12	4160	1.4	0.22	414	1.3	0.27
Res	3	43478	14.3	0.00	1455	4.5	0.01
Site*Res	3	7954	2.6	0.06	543	1.7	0.19
N*Res	6	1878	0.6	0.72	465	1.4	0.23
Site*N*Res	6	4762	1.6	0.18	335	1.0	0.42
Residual	47	3050			327		
Contrasts:							
N linear (NL)	1	71382	17.2	0.00	4107	9.9	0.01
N quadratic (NQ)	1	54	0.0	0.91	1093	2.6	0.13
Res 1 (+ vs -)	1	74068	24.3	0.00	2715	8.3	0.01
Res 2 (1 vs 2)	1	24731	8.1	0.01	784	2.4	0.13
Res 3 (early vs late)	1	30141	9.9	0.00	867	2.7	0.11
NL*Res 1	1	3931	1.3	0.26	1934	5.9	0.02
NQ*Res 1	1	294	0.1	0.76	201	0.6	0.44
NL*Res 2	1	5933	2.0	0.17	468	1.4	0.23
NQ*Res 2	1	126	0.0	0.84	1	0.7	0.39
NL*Res 3	1	355	0.1	0.73	242	0.7	0.39
NQ*Res 3	1	506	0.2	0.69	30	0.1	0.76

Table A10. Analysis of variance for seed yield per fertile tiller in Paddock meadow bromegrass at two sites with three N rates and four residue removal treatments. Sites fixed.

		1996			1997		
Source of variation	Df	MS	F	P>F	MS	F	P>F
Site	1	28.64	3.6	0.15	6.26	18.5	0.00
Rep	3	8.68	1.1	0.48	2.13	8.2	0.06
Rep (Site)	3	8.15	7.1	0.00	0.26	0.3	0.83
N	2	0.06	0.1	0.95	0.55	0.6	0.56
Site*N	2	0.20	0.2	0.84	1.83	2.0	0.17
Rep*N (Site)	12	1.13	0.8	0.70	0.90	0.9	0.58
Res	3	5.18	3.4	0.02	1.24	1.2	0.32
Site*Res	3	3.21	2.1	0.11	0.66	0.6	0.59
N*Res	6	1.99	1.3	0.27	0.82	0.8	0.58
Site*N*Res	6	0.84	0.6	0.76	1.05	1.0	0.43
Residual	54	1.51			1.03		
Contrasts:							
N linear (NL)	1	0.03	0.0	0.88	0.04	0.1	0.83
N quadratic (NQ)	1	0.09	0.1	0.78	1.04	1.2	0.30
Res 1 (+ vs -)	1	0.80	0.5	0.47	0.24	0.2	0.63
Res 2 (1 vs 2)	1	4.78	3.2	0.08	0.53	0.5	0.48
Res 3 (early vs late)	1	10.02	6.6	0.01	2.95	2.9	0.10
NL*Res 1	1	6.31	4.2	0.05	0.94	0.9	0.35
NQ*Res 1	1	0.65	0.4	0.52	0.10	0.1	0.75
NL*Res 2	1	0.06	0.0	0.84	1.39	1.3	0.25
NQ*Res 2	1	2.03	1.3	0.25	0.02	0.0	0.90
NL*Res 3	1	1.56	1.0	0.31	2.17	2.1	0.15
NQ*Res 3	1	1.69	1.1	0.29	0.38	0.4	0.55

Table A11. Analysis of variance for tiller and panicle development in individual tillers (Exp 1&2) of Paddock meadow bromegrass.

Source of Var'n	Df	Flowering plants (%)			Inflorescence (no. plt⁻¹)[6]			Tiller (no.plt⁻¹)			Fertile tillers (%)[1]			Rate of floral dev'ment (days to first flower)[1]		
		MS	F	P>F	MS	F	P>F	MS	F	P>F	MS	F	P>F	MS	F	P>F
Exp. 1																
Age	1	25.7	3.40	0.08	1.80	4.4	0.1	4.2	0.4	0.53	174.7	7.8	0.01	4864	18.1	0.00
Rep	2	7.0	0.90	0.42	0.58	1.4	0.26	2.5	0.2	0.79	37.2	1.7	0.21	314	1.2	0.33
Error	22	7.6			0.41			10.5			22.4			269		
Exp. 2																
Age	1	113.1	38.50	0.00	0.00	0.7	0.41	0.6	1.1	0.31	2.3	0.0	0.87	1377	1.3	0.27
Size	2	68.3	23.2	0.00	0.00	0.3	0.74	3.1	5.2	0.01	72.4	0.9	0.42	10579	9.8	0.00
Rep	8	7.1	2.4	0.03	0.01	1.0	0.45	1.1	1.8	0.12	68.4	0.9	0.57	332	0.3	0.96
Age* Size	2	3.6	1.2	0.31	0.00	0.3	0.77	1.0	1.7	0.20	55.1	0.7	0.51	4242	4.0	0.03
Error	35	2.9			0.01			0.6			80.4			1075		

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[6] Flowering plants only; error df=24.

Table A11 (cont.). Analysis of variance for tiller and panicle development in individual tillers (Exp 1&2) of Paddock meadow bromegrass.

		Flowering plants (%)			Inflorescence (no. plt^{-1}) [7]			Tiller (no.plt^{-1})			Fertile tillers (%)[1]			Rate of floral dev'ment (days to first flower)[1]		
Source of Variation	Df	MS	F	P>F	MS	F	P>F	MS	F	P>F	MS	F	P>F	MS	F	P>F
Contrasts: Exp. 2																
Age (young vs old)		113.1	38.5	0.00	0.00	0.7	0.41	0.6	1.1	0.31	2.3	0.0	0.87	1377	1.3	0.27
Size linear		1.1	37.1	0.00	0.00	0.0	0.94	5.6	9.3	0.00	137.1	1.7	0.20	17806	16.6	0.00
Size quad.		0.1	3.8	0.06	0.00	0.1	0.47	1.5	2.5	0.12	7.1	0.1	0.76	1142	1.1	0.31
Age* Size L		0.0	1.1	0.30	0.00	0.0	0.98	1.0	1.6	0.21	0.3	0.0	0.95	8481	7.9	0.01
Age *Size Q		0.1	1.8	0.20	0.00	0.4	0.53	0.7	1.2	0.28	93.8	1.2	0.29	202	0.2	0.67

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[7] Flowering plants only; error df=24.

Table A12. Analysis of variance for tiller and panicle development in potted plants (Exp 3&4) of Paddock meadow bromegrass.

		Flowering plants (%)			Inflorescence (no. plt ^{1})			Tiller (no.plt $^{-1}$)			Fertile tillers (%)			Rate of floral dev'ment		
Source of var'n	Df	MS	F	P>F	MS	F	P>F	MS	F	P>F	MS	F	P>F	MS	F	P>F
Exp. 3																
Treatment	2	8.44	13.8	0.02	27.11	9.2	0.03	1327.4	78.3	0.00	2.30	0.3	0.77	1147	37	0.00
Rep	2	4.78	7.8	0.04	3.44	1.2	0.40	37.4	2.2	0.23	3.13	0.4	0.71	122	3.9	0.11
Error	4	0.06			2.94			16.9			8.35			31		
Contrasts:																
Age (young vs old - res removed (RR))		0.17	27.3	0.01	54.00	18.3	0.01	2521.5	149.0	0.00	3.12	0.4	0.57	1959	63.2	0.00
RR vs intact (RI) (new)		0.03	4.4	0.11	10.67	3.6	0.13	1232.7	73.0	0.00	3.76	0.5	0.54	39	1.3	0.32
Exp. 4																
Treatment	3	17.99	15.7	0.00	91.42	43.9	0.00	165.6	9.1	0.01	374.42	29.3	0.00	332	1.3	0.35
Rep	2	14.40	12.6	0.01	1.08	0.5	0.62	25.0	1.4	0.32	13.96	1.1	0.39	276	1.1	0.39
Error	6	1.14			2.08			18.2			12.80			250		
Contrasts:																
Young vs old (RR)		42.70	37.3	0.00	192.70	92.5	0.00	368.2	20.2	0.00	742.15	58.0	0.00	833	3.3	0.12
N vs no N (old RR)		20.20	17.6	0.01	1.50	0.7	0.43	10.7	0.6	0.47	0.85	0.1	0.81	609	2.4	0.17
RR vs RI (old)		10.90	9.6	0.02	1.50	0.7	0.43	8.2	0.5	0.53	4.23	0.3	0.59	9	0	0.86

Table A13. Analysis of variance for tiller and panicle development in row sgements (Exp. 5 & 6) of Paddock meadow bromegrass.

Source of variation	Df	Inflorescence (no. plt $^{-1}$)			Distance from mid-row			Rate of floral dev'ment (days to first flower)			Panicle length (cm)		
		MS	F	P>F	MS	F	P>F	MS	F	P>F	MS	F	P>F
Exp. 5													
Treatment	2	789	2.2	0.17	138.9	23.5	0.00	7.47	3.5	0.08	11.7	1.9	0.21
Rep	5	149	0.4	0.83	6.2	1.1	0.45	6.83	3.2	0.07	3.5	0.6	0.72
Error	8	361			5.9			2.13			6.2		
Contrasts:													
Age (young vs old - res removed (RR))		1369	3.8	0.09	222.8	37.8	0.00	1.60	0.8	0.41	22.8	3.7	0.09
RR vs intact (RI) (new)		960	2.7	0.14	1.1	0.2	0.68	14.40	6.8	0.03	9.0	1.5	0.26
Exp. 6													
Treatment	3	2002	10.1	0.00	9.0	1.8	0.21	33.55	0.3	0.81	10.1	0.7	0.58
Rep	4	152	0.8	0.57	9.1	1.8	0.20	84.03	0.8	0.55	18.9	1.3	0.33
Error	11	199			5.0			104.74			14.6		
Contrasts:													
Young vs old (RR)		2190	11.0	0.01	5.5	1.1	0.32	3.60	0.0	0.86	10.4	0.7	0.42
N vs no N (old RR)		137	0.7	0.42	2.2	0.4	0.52	40.00	0.4	0.55	4.8	0.3	0.58
RR vs RI (old)		315	1.6	0.23	13.8	2.7	0.13	95.71	0.9	0.36	9.0	0.6	0.45

Table A14. Analysis of variance for flowering in Paddock meadow bromegrass tillers exposed to different conditions during primary induction (Exp. 1 & 2).

Source of variation	Df	Flowering plants (%) MS	F	P>F
Exp. 1				
Date	10	14.10	2.7	0.03
Rep	2	161.45	31.1	0.00
Error	20	5.19		
Contrasts:				
Dates linear	1	42.19	8.1	0.01
Dates quadratic	1	0.62	0.1	0.73
Dates cubic	1	12.62	2.4	0.13
Dates quartic	1	2.36	0.5	0.51
Exp. 2				
Temperature	2	8889.63	12.50	0.00
Daylength	1	431.72	0.6	0.44
Temp * Daylength	2	667.13	0.9	0.40
Rep	1	65.49	0.1	0.76
Error	29	712.91		
Contrasts:				
Temp linear	1	17615.90	24.7	0.00
Temp quadratic	1	163.37	0.2	0.64
Daylength (8 vs 16)	1	431.72	0.6	0.44
Temp lin * daylength	1	464.15	0.7	0.43
Temp quad *daylength	1	870.11	1.2	0.28

Table A15. Analysis of variance for flowering in Paddock meadow bromegrass (MB) and Carlton smooth bromegrass (SB) seedlings, tillers and plants in two daylengths exposed to three temperatures during primary induction (Exp. 3).

		Flowering plants (%)					
		8 hr day			16 hr day		
Source of variation	Df	MS	F	P>F	MS	F	P>F
MB seedlings							
Temperature	2	8633	45.7	0.00	1425	1.60	0.27
Rep	3	122	0.7	0.61	586	0.70	0.60
Error	6	189			869		
Contrasts:							
Temp linear	1	14117	74.7	0.00	2593	3.00	0.13
Temp quadratic	1	3150	16.7	0.01	257	0.30	0.61
MB tillers							
Temperature	2	7244	109.8	0.00	5484	15.3	0.00
Rep	3	74	1.1	0.41	180	0.5	0.70
Error	6	66			360		
Contrasts:							
Temp linear	1	13662	207.1	0.00	8976	25.0	0.00
Temp quadratic	1	825	12.5	0.01	1992	5.5	0.06
MB plants							
Temperature	2	2800	12.6	0.01	700	4.2	0.07
Rep	3	222	1.0	0.45	133	0.8	0.54
Error	6	222			167		
Contrasts:							
Temp linear	1	5486	24.7	0.00	1050	6.3	0.05
Temp quadratic	1	114	0.5	0.50	350	2.1	0.20

Table A15 (cont.). Analysis of variance for flowering in Paddock meadow bromegrass (MB) and Carlton smooth bromegrass (SB) seedlings, tillers and plants in two daylengths exposed to three temperatures during primary induction (Exp. 3).

		Flowering plants (%)					
		8 hr day			16 hr day		
Source of variation	Df	MS	F	P>F	MS	F	P>F
<u>SB seedlings</u>							
Temperature	2	8933	28.7	0.00	3077	4.5	0.06
Rep	3	44	0.1	0.93	330	0.1	0.71
Error	6	311			688		
Contrasts:							
Temp linear	1	17610	56.6	0.00	4150	6.0	0.05
Temp quadratic	1	257	0.8	0.40	2004	2.9	0.14
<u>SB tillers</u>							
Temperature	2	2725	3.3	0.12	1618	3.1	0.12
Rep	3	272	0.3	0.81	69	0.1	0.94
Error	6[8]	830			519		
Contrasts:							
Temp linear	1	3799	4.6	0.09	3216	6.2	0.05
Temp quadratic	1	2112	2.5	0.17	22	0.0	0.84
<u>SB plants</u>							
Temperature	2	4900	21.0	0.00	933	4.2	0.07
Rep	3	533	2.3	0.18	89	0.4	0.76
Error	6	233			22		
Contrasts:							
Temp linear	1	7736	33.2	0.00	1610	7.2	0.04
Temp quadratic	1	2064	8.9	0.02	257	1.2	0.32

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[8] df for error 8 hr day =5, for 16 hr day=6

Table A16. Analysis of variance for flowering in Paddock meadow bromegrass and Carlton smooth bromegrass exposed to different conditions during primary induction (Exp. 3).

Source of variation	Df	Flowering plants (%) MS	F	P>F
Temp 5°C, 8 hr day				
Species (MB, SB)	1	1.5	0.3	0.57
Stage (seedling, tiller, plant)	2	36.5	8.3	0.00
Species * stage	2	9.5	2.2	0.15
Rep	3	5.1	1.2	0.36
Error	15	4.4		
Temp 5°C, 16 hr day				
Species (MB, SB)	1	0.8	0.1	0.72
Stage (seedling, tiller, plant)	2	54.9	9.7	0.00
Species * stage	2	2.2	0.4	0.69
Rep	3	5.0	0.9	0.47
Error	15	5.6		
Temp 10°C, 8 hr day				
Species (MB, SB)	1	82.5	40.8	0.00
Stage (seedling, tiller, plant)	2	0.1	0.1	0.95
Species * stage	2	5.0	2.5	0.12
Rep	3	2.3	1.1	0.37
Error	15	2.0		
Temp 10°C, 16 hr day				
Species (MB, SB)	1	46.8	8.7	0.01
Stage (seedling, tiller, plant)	2	58.1	10.9	0.00
Species * stage	2	9.6	1.8	0.20
Rep	3	2.6	0.5	0.69
Error	15	5.3		

Table A16 (cont.). Analysis of variance for flowering in Paddock meadow bromegrass and Carlton smooth bromegrass exposed to different conditions during primary induction (Exp. 3).

		Flowering plants (%)		
Source of variation	Df	MS	F	P>F
Temp 20°C, 8 hr day				
Species (MB, SB)	1	3.21	2.9	0.11
Stage (seedling, tiller, plant)	2	0.85	0.8	0.48
Species * stage	2	0.85	0.8	0.48
Rep	3	2.46	2.3	0.13
Error	14	1.09		
Temp 20°C, 16 hr day				
Species (MB, SB)	1	8.76	6.6	0.02
Stage (seedling, tiller, plant)	2	15.64	11.8	0.00
Species * stage	2	16.64	12.5	0.00
Rep	3	1.09	0.8	0.50
Error	15	1.33		