ECOLOGICAL RELATIONS OF *BROMUS INERMIS* AND *FESTUCA ALTAICA* SUBSP. *HALLII*

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ABSTRACT

This study was designed to elucidate the ecological relations of *Bromus inermis* and *Festuca altaica* subsp. *hallii*. Germination ecology, water relations and growth following spring or fall burning, glyphosate application on *B. inermis*, *F. hallii* seedling survival, and seedbank composition were studied in a *F. hallii* grassland in central Saskatchewan where *B. inermis* is an agressive invader.

Bromus inermis had greater and more rapid germination over a broader range of temperatures and water stress than *F. hallii*. Germination was lower for *F. hallii* under decreasing temperatures and similar for *B. inermis* under decreasing and increasing temperature regimes. Light did not influence germination in *F. hallii*; however, germination of *B. inermis* was higher under darkness.

Osmotic potentials, relative water content and stomatal conductance were lower for *B. inermis* in Fall burns in 1987, but similar to Control and Spring burns in 1988. Fall burns reduced tiller densities of native graminoids and *F. hallii*. Tiller densities of native graminoids were not affected by spring burning, but *F. hallii* tillered 40% more after spring burns.

There was a burn x glyphosate interaction for the reduction of *B. inermis*; spring burning and glyphosate combined reduced *B. inermis* most. Species richness and diversity were similar between treatments in *F. hallii* and *B. inermis* stands. Tiller densities of *B. inermis* were

higher on burned plots in 1987. In 1988, burning had no impact on tillering and growth of *B. inermis*. Leaf area indices and biomass following burning were generally higher in Spring than in Fall burns and Control.

The seedbank composition was similar between *B. inermis* and *F. hallii* stands averaging 1,900 seeds per m^2. *B. inermis* seeds were found only in *B. inermis* stands, representing less than 1% of the total seedbank.

Seedling survival of *F. hallii* was higher with early spring planting than late spring with vesicular-arbuscular mycorrhizae (VAM) improving survival.

Burning alone did not control *B. inermis* in *F. hallii* grassland. However, spring burning combined with a wicking of glyphosate reduced *B. inermis* and increased tillering of *F. hallii*. *Festuca hallii* should be seeded in the spring when soil temperatures are increasing and soil moisture is favorable. Seedlings of this native perennial should be inoculated with VAM and planted early in the spring. Reduced germination of *B. inermis* under high water stress and in the presence of light suggests that prescribed burning may reduce the availability of "safe sites" for germination.

Bromus inermis is well adapted to grassland dominated by *F. hallii* and it apparently can outcompete the dominant specie. Therefore, if grasslands dominated by *F. hallii* are to be preserved for future generations, proactive management strategies must be employed to limit invasions by *B. inermis* and enhance the vigor of *F. hallii*.

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

1.0 INTRODUCTION

The distribution of the *Festuca* grassland of Western Canada was described by Coupland (1961) as "occupying the black soil between the clumps of *Populus tremuloides* in the aspen grove region north of the Mixed Prairie from central Saskatchewan westward to the foothills of the Rocky Mountains and then extends southward along the foothills contacting the western edge of the Mixed Prairie at least as far southward as the United States boundary". *Festuca* grassland is also found in the Cypress Hills, the southeastern part of Saskatchewan, southwestern Manitoba, northwestern North Dakota, and western Montana (Looman, 1963; Looman, 1969; Blood, 1966; Barker and Whitman, 1988). *Festuca altaica* Trin. subsp. *hallii* (Vasey)(Harms), (Harms, 1985) is the dominant grass of the Black Soil zone, co-dominating with *Stipa spartea* var. *curtiseta* in the more arid Dark Brown Soil zone (Moss and Campbell, 1947; Coupland and Brayshaw, 1953). For the remainder of this thesis *Festuca altaica* subsp. *hallii* will be referred to as *F. hallii*.

Only isolated parcels of *F. hallii* grassland remain because of cultivation and the conversion of this grassland for the production of cereals and forage crops. Overgrazing is also a major cause of the deterioration of the *F. hallii* grassland. Deterioration of the remaining *F. hallii* grassland is occurring because it is being invaded by *Bromus inermis* Leyss., an exotic and long-lived rhizomatous

perennial (Romo et al., 1990). For the remainder of this thesis *Bromus inermis* will be referred as *B. inermis*.

Bromus inermis was introduced to Western Canada in 1896 (Heinrichs, 1969) from Eurasia, where it grows in an environment similar to the parkland region of Western Canada (Looman, 1976). After about 1900 it was widely used for hay and pastures following the extensive settlement of Western Canada. Today it is one of the most widely used forage crops in the Parkland Region of Western Canada (Bittman, 1985).

The wide range of adaptability combined with its reproductive modes enables *B. inermis* to escape from cultivation and form a common grass cover on road sides, railway right-of-ways, abandoned lands, and other disturbed areas (Knowles and White, 1949). In the Brown Soil zone *B. inermis* tends to be restricted to sites with improved moisture regimes such as borrow pits, road sides, flood plains, and areas of snow accumulation. However, in the Dark Brown, Black, and Gray Wooded Soil zones it is less restricted in distribution, growing over a wide range of conditions. Once established in native grassland, it spreads by rhizomes and seed, suppressing the growth and diversity of the native flora (Romo et al., 1990). Eventually, native species are eliminated from the site of invasion and the grassland is dominated by a near monoculture of *B. inermis*. Looman (1969) also noted that as *B. inermis* increases in *F. hallii* grassland the diversity of native plants declines. Wilson (1989) and Wilson and Belcher

(1989) indicated that in a Mixed Prairie in Manitoba *B. inermis* was the most competitive of all introduced species, excluding the native species from the prairie.

Along with changes in the flora of native grasslands are changes in the fauna that inhabit these areas with the invasion of *B. inermis*. Wilson and Belcher (1989) found that on sites invaded by *B. inermis* there was a change in the species of birds that utilize these sites. Driver (1987, unpubl. data) studying bird populations at the Last Mountain Lake National Wildlife Area found that there was a decline in the number of species utilizing these areas from eight to ten to primarily two species.

Invasion of *B. inermis* into *F. hallii* grassland is a growing concern among those responsible for managing this grassland for research, wildlife habitat, ecological reserves, aesthetics and recreation. Aggressive reproduction of *B. inermis*, either through self-seeding or vegetative spread, provides conservation value for establishment of plant cover, but also causes it to be classified as a "weed" in some situations (Newell, 1973). To maintain the integrity of the diverse flora and fauna of the fescue grassland, *B. inermis* must therefore be viewed and managed as a weed or undesirable species.

The objective of the research reported herein was to evaluate the ecological relations of *B. inermis* and *F. hallii* in a *F. hallii* grassland in central Saskatchewan. Specific objectives were to:

1. Determine growth and water relations of *B. inermis* following burning;
2. Determine the effects of the combined application of fall or spring burning and glyphosate for controlling *B. inermis* and releasing the native flora;
3. Ascertain the survival of containerized seedlings of *F. hallii* inoculated with vesicular arbuscular mycorrhizae (VAM) versus nontreated seedlings that were planted in Control plots dominated by *B. inermis* and in plots treated with glyphosate to Control *B. inermis*;
4. Determine the effects of VAM inoculation on the growth of seedlings of *F. hallii*;
5. Determine the composition of the seedbank as a factor influencing possible successional changes following the control of *B. inermis*;
6. Compare germination of *B. inermis* and *F. hallii* under varying temperatures, levels of water stress, and light regimes, and;
7. From these studies propose management strategies for controlling *B. inermis* and re-establishing *F. hallii* on areas previously dominated by the former grass.

2.0 LITERATURE REVIEW

2.1 Ecology of Key Species

To fully understand the purpose of the research conducted and to aid in the interpretation of the results of this research, knowledge of the ecology of *F. hallii* and *B. inermis* are necessary.

2.1.1 *Festuca altaica* subsp. *hallii*

Festuca hallii is a cool season grass, starting growth early in the spring. Johnston and McDonald (1967) found that in Alberta, the closely allied species, *Festuca scabrella* began growing early in May when the soil temperature at the 20 cm depth reached 2^{o}C while Bailey and Anderson (1978) observed that *F. hallii* began growing soon after snow melt in the spring. Stout et al. (1981) found visible growth in *F. scabrella* in mid-April when soil temperature at the 10 cm depth averaged 2.7^{o}C; however, the vegetative shoot apices remained at or near the soil surface.

The initiation of floral primordia begins in late August or early September, and continues over winter until spring (Johnston and McDonald, 1967). The reproductive culms elongate rapidly in late May and emerge from the leaf sheath. Flowering occurs by mid-June and seeds ripen by the end of July or early August (Johnston and McDonald, 1967). Seed production is erratic in *F. hallii* (Toynbee, 1987) and *F. scabrella* (Johnston and McDonald, 1967; Stout et al., 1981). Johnston and McDonald (1967) and Stout et al. (1981)

were unable to explain the factors responsible for the induction and initiation of the floral primordia, except that a combination of environmental factors contribute over a period of undetermined time.

Festuca hallii enters winter dormancy by early October. Stout et al. (1981) stated that the growth cessation in *F. scabrella* is related to the water content of the soil, with limiting soil moisture reduces growth.

Coupland and Brayshaw (1953) studied the distribution of the rooting system of *F. hallii*. Roots extended 120 cm into the soil with 73% of the total weight in the top 15 cm. The weight of roots in the soil contributed by *F. hallii* to a depth of 120 cm averaged 4.1 t ha^{-1}. The large amount of organic matter contributed by *F. hallii* shows how important this species has been in the development of the Black soils of the Parkland Region.

2.1.2 *Bromus inermis*

Ecological literature related to *B. inermis* in native grasslands is limited; most research on this species has focused on its agronomic character.

Bromus inermis is also a cool season species, beginning growth early in the spring. It spreads effectively by seed and rhizomes. *Bromus inermis* seedlings tiller shortly after emergence until late summer (Newell, 1951). Rhizomes form three weeks to six months after emergence. Buds are formed on the rhizomes that can become either aerial shoots or new

rhizomes. This exotic has a deep root system, although a high percentage of the root mass is concentrated in the upper profile of the soil (Newell, 1951).

Heide et al. (1985) found a close relationship between photoperiod and temperature that influences leaf growth. Maximum growth occurred at 15°C with a long day photoperiod. Higher temperatures decreased the rate of leaf growth. Allard (1941) found increases in the daily photoperiod beyond 13 h produced longer stems and leaves.

Flowering in *B. inermis* is also controlled by photoperiod. Heide (1984) found short photoperiods were necessary for primary induction and a transition to long days was required for initiation of floral primordia, culm elongation, and secondary induction of flower development. At optimal temperatures of 15 - 21°C, four to six weeks of 8 to 10 h photoperiods were needed for optimal primary induction. Klebesadel (1970) found that floral initiation occurred in the fall in northern strains of *B. inermis*. This initiation contrasts with southern strains in which initiation occurred in the spring. Because of the photoperiod requirements for floral initiation, flowering usually does not occur during the year of establishment.

Hume and Archibold (1986) examined the influence of a weedy habitat, containing predominantly *B. inermis*, on the seed bank of an adjacent field. There were 32 *B. inermis* seeds/m^2 at a distance of 1 m from the edge of a field. At distances greater than 7 m no *B. inermis* seed was

represented in the seed bank. When they examined the seed rain, there were 107 seeds/m^2 at a distance of 1 m, but at distances greater than 7 m, *B. inermis* was not present.

The higher number of seeds/m^2 in the seed rain than in the seed bank indicates that the persistence of *B. inermis* in the seed bank is low or seeds are moved after their initial dispersal. Rabotnov (1956), (as cited by Harper, 1977), found the seed bank in a Russian meadow dominated by *B. inermis*, contained 280-2,450 seeds/m^2. This number is considered small, for 17,000 seeds/m^2 can be found in grasslands with a diverse species composition (Harper, 1977).

If the seed rain of *B. inermis* is applied to Van der Plank's method of relating the logarithm of seed density to the logarithm of distance from the source (Harper, 1977), the moded of invasion of a habitat by *B. inermis* can be seen. Harper (1977) indicated if the slope of the relationship is as steep or steeper than the inverse square law - "a population will spread into a colonizable territory as an advancing front". According to this statement *B. inermis* invades new habitat as an advancing front.

Small isolated populations also tend to exist when *B. inermis* invades *F. hallii* grasslands. These populations may establish on sites disturbed by rodents or other activity. These isolated groupings in turn function as focis for further advancing fronts (Harper, 1977; Moody and Mack, 1988).

Defoliation of *B. inermis*, either by cutting or grazing can greatly affect plant growth and vigor. The stage of growth when it is defoliated is very important in determining the influence on the plant. A critical time is in the spring during internode elongation and during early heading stages (Carlson and Newell, 1983). Reynolds and Smith (1962) found when most of the shoot apices were removed during internode elongation and early heading stages, there was a reduction in stand density and subsequent regrowth. They attributed this reduction in stand density to low carbohydrate levels and an absence of new tillers. If the first cutting was delayed until the post-anthesis period, carbohydrate reserves were high and there were many new tillers and future yields were not reduced (Eastin et al., 1964). Carlson and Newell (1983) stated that even with high carbohydrate reserves, regrowth is slow because the tiller apices are removed and regrowth must come from buds located on rhizomes.

The regions of major adaptation of *B. inermis* in North America are on sites of favorable soil moisture or where irrigation is available. It is able to survive periods of drought and extreme temperatures by becoming dormant until cool short days and moisture returns in the fall (Carlson and Newell, 1983).

Another limiting factor in the growth of *B. inermis* is a condition that occurs in mature stands. Continued growth of rhizomes which increase tillering causes stands to become

very dense. This "sod-bound" condition was studied by Myers and Anderson (1942) and Benedict (1943); it is not completely clear on what is the actual cause of the sod-bound condition, but it may be associated with concentration of nitrogen in the roots. *B. inermis* fits into a category of plants called "luxury consumers" (Harper, 1977). It tends to accumulate nitrogen in excess amounts in early growth stages, storing it in the roots in forms unavailable for growth at later stages. Application of nitrogen fertilizer generally reduces sod-bound conditions (Alta. Agric., 1987).

Lorenz et al. (1961) examined the effect of nitrogen and phosphorus on forage yields of *B. inermis*. There was no response to the application of phosphorus, but higher yields were realized when nitrogen was applied. This response is highly dependent upon the amount of soil moisture which increases the solubility of nitrogen, allowing greater uptake (Eck et al., 1981).

When nitrogen was applied to a *Bromus-Medicago* mixture, the proportion of legume in the mixture decreased (Wolfe and Smith, 1964). The nitrogen apparently increased the competitive ability of *B. inermis*, crowding out the legume. The availability of nitrogen also alters reproductive activity and seed yield in *B. inermis*. Bueller et al. (1955) found nitrogen applications greatly increased seed yield.

2.2 Effects of Fire on Grassland Vegetation

Vogel (1974) defined grasslands as: "Areas dominated by herbaceous vegetation, particularly grasses or other monocots, and includes those areas that support an open understory of scattered trees or shrubs." Extreme fluctuations in temperature and precipitation are non-conducive for the growth of most trees and shrubs, but help to promote the establishment of grasslands at the expense of the woody vegetation. Thus, climate is a major factor in maintaining grasslands.

Grasslands, because of their high flammability during dry periods, are conducive to the spread of fires. Before European settlers came to North America, fires were a frequently occurring natural force. Fire acted as a natural selective force, favoring vegetation that was tolerant of periodic burning (Daubenmire, 1968). Thus grasslands evolved under fire with climate as the major controlling factor.

Since the west was settled by Europeans in the late 1800's, fire has generally been viewed as undesirable. This resulted in 70 years of no fire in some grassland areas (Nelson and England, 1971). In the absence of fire, forests have extended their boundaries, especially in the more mesic grasslands (Maini, 1960). Bailey and Wroe (1974) also concluded that *F. hallii* grassland is being lost to encroachment by trees.

Prescribed burning is viewed as a possible management tool for managing *F. hallii* grasslands. Prescribed burning

is defined as the skillful application of fire to natural fuel under conditions of weather, fuel moisture, soil moisture, etc., that will allow confinement of the fire to a predetermined area and at the same time produce the intensity of heat and rate of spread required to accomplish certain planned benefits to one or more objectives. (Kayll, 1974).

The effects of fire on *F. hallii* grasslands are complex, depending on several variables. Burning can enhance or depress the growth of selected species through the direct effects of burning (Vallentine, 1971; Wright and Bailey, 1982; Young and Miller, 1985). Plant growth after burning is also related to changes in environmental conditions, competitive relationships, and allocation of resources for growth (Wikeem and Strang, 1983; Old, 1969; Willms and Bailey, 1980; Savage, 1980; Knapp, 1984; Mallik, 1986; Neuenschwander and Wright, 1984; and Sharrow and Wright, 1977).

Bailey and Anderson (1978) found spring burning was more detrimental to *F. hallii* than fall burning in central Alberta. Canopy coverage of *F. hallii* was reduced 26% during the first year and it did not recover to the level of the control for three years. Seed production and canopy cover for *Stipa spartea* var. *curtiseta* were reduced by fall burning, but these parameters were not changed by spring burning. Anderson and Bailey (1980) reported that frequency of *S. spartea* var. *curtiseta* was higher in areas annually

burned, but canopy cover was reduced. Dix (1960) cited both an increase and decrease in *Agropyron dasystachyum* after wildfire, depending on the site. Coupland (1974) reported a 14 to 50% reduction in shoot growth of *A. dasystachyum*, but root-shoot ratios were higher after wildfire in summer.

Bailey and Anderson (1978) found that unlike spring burning, fall burning, after the induction of the floral primordia, did not alter the density of the seed heads. This response is because the initiated growth points elongate rapidly in spring, making them more susceptible to heat injury than in the fall. Sinton and Bailey (1980) found early spring burning decreased the canopy coverage for *F. hallii* by 18%, while at the same time, there was a 17% increase in frequency. They concluded that *F. hallii* was well adapted to early spring burning and annual herbage production was not reduced because tiller numbers increased.

Anderson and Bailey (1980) reported a significant decrease in leaf blade length and canopy cover following burning of *F. hallii*. These decreases were partially attributed to lower moisture in the soil on the burned sites. The decrease in soil moisture was caused by reduced snow catchment and infiltration on the burn that accompany the removal of the vegetation layer (DeJong and MacDonald, 1975). The end result of burning can be the transformation of the site into a more arid microclimate (Old, 1969; Savage, 1980). Antos et al. (1983) found that the soil of a burned fescue grassland was 20^{o}C warmer at a 10 cm depth

than the control. The dark surface of the burn and the lack of a vegetative cover allowed higher rates of absorption of incoming solar radiation in the soil, increasing evaporation.

There is no information available on the water status of *F. hallii* after burning. However, Redmann (1978) concluded that increased water stress on plants growing on a burn site could explain the reduction in primary productivity in Mixed Grass Prairie.

Sinton and Bailey (1980) compared burning and mowing impacts on a *F. hallii* grassland. The results obtained were similar to the results of Bailey and Anderson (1978) where spring burning was more detrimental to *F. hallii* if burned after the plants had initiated active growth. Detrimental impacts were least if burnt early in the spring when plants were still dormant. Burning or mowing at any season reduced herbage yield; the reduction in herbage yield was caused by the decrease in blade length. Burning was least detrimental in early spring or in late fall, but burning or mowing in mid-growing season reduced herbage production for at least two years.

Johnston and McDonald (1967) suggested that the tufted clumps of plant material around *F. scabrella* protected the perenniating buds from damage by fire. Antos et al. (1983) concluded that the this type of protection is only effective when the clump is damp in the spring. Anderson and Bailey (1980) also stated that the least amount of damage from

burning occurred just after snow melts in the spring when the litter is damp and *F. hallii* is still dormant. Antos et al. (1983) found that plants greater than 20 cm in diameter suffered damage to the crowns because they tended to burn down into the crowns, producing higher heat. Plants less than 10 cm in diameter burned quickly and sprouted back rapidly. Long intervals between fires, which allow large clumps and larger fuel loads to develop, may inhibit survival and recovery of *F. hallii*. Antos et al. (1983) suggested a fire cycle of approximately 5 to 10 years would be beneficial to the survival of *F. scabrella*.

Results from studies of burning native grassland show some potential for reducing *B. inermis*. Anderson and Bailey (1980) compared species composition in unburned grasslands and an area that had been burned annually in the spring in central Alberta. Frequency and canopy cover for *B. inermis* were lower in the burned area than in the unburned area. Kirsch and Kruse (1972) reported at least a 50% reduction in canopy cover of *B. inermis* in the year following a spring burn in a Mixed Grass Prairie in North Dakota. In Tallgrass Prairie Old (1969) found the productivity of *B. inermis* was reduced the first growing season following early spring burning, it increased the third growing season and declined thereafter. Hulbert (1986) concluded that where burning is used regularly in Tallgrass Prairie, *B. inermis* is rare except where native grasses have been weakened or are absent following disturbance.

2.3 Control of *Bromus inermis* with Glyphosate

Control of *B. inermis* with herbicides may be possible in native grassland. Waller and Schmidt (1983) reported a significant reduction in *B. inermis* following application of glyphosate. Rodney and Kirby (1991) found that glyphosate, applied nonselectively, controlled *B. inermis*, but it also removed native species such as *Stipa comata*, *Stipa viridula*, *Agropyron smithii*, *Bouteloua gracilis*, *Koeleria pyramidata*, and *Carex* species.

In *F. hallii* grassland *B. inermis* is generally taller than the associated native vegetation. This height differential between *B. inermis* and the native plants is pronounced after burning (Romo unpublished data). Therefore, control maybe possible by using wick applicators so that the herbicide is applied to the *B. inermis* and the lower growing native vegetation is left untreated.

Peters (1981) found that when glyphosate was used in a wicking application to selectively control weeds on rangelands a concentration of 2:1 (water:glyphosate) gave the best control. This control must be timed so that the chances of herbicide application on the native vegetation are minimized and the effectiveness of glyphosate on *B. inermis* is maximized; maximum control of *B. inermis* is expected when it is translocating carbohydrates to the roots and rhizomes. Reynolds and Smith (1962) reported that *B. inermis* shows three stages of growth where carbohydrates

are being translocated downward in the plant. These periods of growth are: 1) just after seedling emergence; 2) after elongation of vegetative shoots following flowering, and; 3) when plants are tillering in the fall. The greatest differential in height of *B. inermis* and associated native flora and the most effective control of *B. inermis* with glyphosate is expected after burning when vegetative shoots begin to elongate in *B. inermis*.

2.4 Grassland Restoration

In grasslands where the desired vegetation has been depleted, artificial seeding or revegetation via natural processes are necessary to restore vegetation (Vallentine, 1971). Natural revegetation is possible only if the competing species are reduced, if the environmental conditions are conducive to proliferation of native species, and if plants are available to inhabit the site. In many areas where *B. inermis* has established and persisted, the abundance of native grasses has declined (Looman, 1969). This decline in native plants together with usually low numbers of *F. hallii* seeds in the seed bank (Johnston et al., 1969) may necessitate artificial revegetation if native grassland is to be perpetuated. Artificial revegetation can take the form of seeding or planting of containerized seedlings. Whether direct seeding or containerized seedlings are used depends on the extent and nature of the area to be revegetated, availability of seeds, and economics. Wallace

et al. (1986) concluded the ecological and financial advantages of using containerized seedlings were greater than direct seeding. Bland (1970) reported that planting seedlings was superior to direct seeding for 30 prairie grasses and forbs. Russel (1979) evaluated transplanting of 34 grass species in Alberta, with survival ranging from 76 to 88%.

Planting containerized seedlings also minimizes the degree of disturbance on the site. Use of containerized seedlings may be extremely critical since Smoliak and Johnston (1968) found that *B. inermis* germinated faster and in higher amounts, and grew more rapidly over a wider range of temperatures than the native grasses. Erratic seed production in *F. scabrella* (Johnston and MacDonald, 1967) also favors the use of containerized seedlings because of scarcity of seed. Therefore, planting containerized seedlings may have advantages over direct seeding.

2.4.1 Mycorrihizal Considerations

Molina et al. (1978) found vesicular-arbuscular mycorrhizae (VAM) were associated with *F. hallii*. VAM grow into the cortical cells of the host roots, and out of the root system into the surrounding soil (Trappe, 1981). Within the root cortex, nutrients absorbed by VAM are dissolved and used by the host plant with photosynthates being extracted by the fungi (Ho and Trappe, 1974). The mycorrhizal mycelia thus act as a highly efficient extension of the root system

and may play an important role in maximizing productivity in native grasslands.

One of the best known benefits of VAM is in the uptake of P (Cooper and Tinker, 1978; Hall et al., 1984; Hayman and Mosse, 1972; Nielsen and Jensen, 1983; and Rhodes and Gerdemann, 1978). Other nutrients in the soil including K, Ca, S, Zn, Cu and Sr are also absorbed by VAM (Cooper and Tinker, 1978; Nielsen and Jensen, 1983; Rhodes and Gerdemann, 1978). VAM are efficient in absorbing nutrients from cation exchange sites in the soil because they produce many different exogenous enzymes capable of breaking down these nutrients allowing for uptake and metabolism (Trappe, 1981; Trappe and Fogel, 1977). Cooper and Tinker (1978) suggested that the transport of P by the hyphae, and other nutrients, is controlled by the host plant demand rather than by the amount of absorbing mycelium.

VAM also apparently increase the uptake of N from the soil (Bagyaraj et al., 1979; Barea et al., 1987; Hall et al., 1984; Ho and Trappe, 1975; Trappe and Fogel, 1977). Ho and Trappe (1975) found that VAM were capable of reducing nitrate to nitrite and therefore contain the nitrate reductase system.

VAM can also alter water transport in the host plant. Allen et al. (1981) found that *Bouteloua gracilis* inoculated with VAM had transpiration rates 100% greater, and leaf resistances to water vapor diffusion 20-50% lower than plants that were not inoculated. Leaf xylem water potentials

were not different between mycorrhizal and non-mycorrhizal plants, indicating that whole-plant resistance to water transport was reduced. Bildusas et al. (1986) found similar results for *B. inermis*. They attributed the increased efficiency of water uptake and reduced resistance to water flow through the plant to: 1) increased absorbing surface in the soil from the extensive network of mycorrhizal mycelia; 2) reduced development of vapor gaps between soil particles and roots, and; 3) functioning of fungi as a low-resistance pathway for water to the cortex. They concluded that mycorrhizal symbiosis may therefore play an important role in the adaptation of *B. inermis* to drier sites.

The effects of VAM on plant growth are highly variable (Bildusas et al., 1986; Daft and Nicolson, 1966; Hetrick et al., 1988). Hetrick et al. (1988) found that when C_3 and C_4 grasses where inoculated with VAM, C_4 grasses grew faster than C_3 grasses. They concluded that C_4 species are dependent upon VAM because their root systems are not as diffuse as C_3 grasses. Bildusas et al. (1986) found that growth decreased when *B. inermis* was inoculated with VAM.

Safir and Dunway (1982) stated that there is high variability on the effect VAM has on plants because of the differences in the host plant, the symbiotic fungus, and the environment. However, Daft and Nicolson (1966) suggested that the greatest benefit from mycorrhizal fungi can be obtained where plants are grown under conditions of low soil fertility and poor soil moisture. Therefore, the recognized

ability of VAM to increase uptake of nutrients and water suggests that they may play an important role in grassland restoration.

2.4.2 Germination and Seedling Recruitment

The establishment of a seedling from a seed is highly complicated, depending on a timely series of events. Whether a given seed will germinate depends on the availability of what Harper (1977) termed a "safe site". Therefore, the established seedling density depends on the frequency and availability of safe sites. Harper (1977) defined a safe site as a place where a seed may find itself which provides: (1) the stimuli for breaking seed dormancy; (2) the conditions for germination to proceed; (3) the resources which are consumed in the process of germination, and; (4) the lack of hazards such as predators, competitors, toxic soil constituents, and pathogens.

Smoliak and Johnston (1968) studied the effects of soil temperatures of 7, 13, 18, and 27^{o}C on the germination and early seedling growth of several native and introduced grasses. For *B. inermis* there was equally high germination at all four soil temperatures. Emergence was highest at 13 and 18^{o}C, averaging 85%. When total emergence was considered with speed of germination, 18^{o}C was the optimal. *B. inermis* had both a faster and higher rate of emergence than *F. scabrella* at all soil temperatures.

In regards to seedling growth, Smoliak and Johnston

(1968) found *B. inermis* had the most leaves at 13°C, while *F. scabrella* had the most leaves at 18°C at the end of 90 days. The size of *B. inermis* increased as the root zone temperature increased from 7 to 27°C, but growth of *F. scabrella* increased to 18°C and then decreased. Root development was greater in *B. inermis* and showed an increase with increasing temperature. Root development of *F. scabrella* was best at 7°C and poorest at higher temperatures. Masiunas and Carpenter (1984) examined the effects of temperature on radicle growth in *B. inermis*. Radicle growth increased as temperatures rose from 12 to 27°C. At temperatures greater than 27°C, radicle growth was reduced. *Bromus inermis* put a higher percentage of total growth into leaves than *F. scabrella* (Smoliak and Johnston, 1968).

Plummer (1943) studied the germination of *B. inermis*. Four temperature conditions were tested to determine the effect on germination: (1) alternating temperature (30°C - 6 hours; 20°C - 18 hours); (2) constant temperature (30°C); (3) room temperature (mean temperature of 21°C with a range of 19 to 23°C), and; (4) greenhouse temperature (mean temperature of 14°C with a range from 10 to 40°C). Total germination was high under all treatments with the highest occurring with the alternating temperature regime.

Wilson et al. (1974) examined cold tolerance of *B. inermis* seed by storing them in cotton bags in the soil over winter and incubating them at 10°C. *Bromus inermis*

suffered a slight decrease in germination after exposure to winter temperatures with germination of 67% as compared to 74% in control.

McGinnies (1960) found that *B. inermis* germinated over a broad range of temperatures and water stress. At the end of 28 days, the optimal germinating temperature was 20°C; the rate of germination was high to -1.0 MPa of stress. Total germination was 30% at moisture stress of -1.5 MPa and 20°C, but no germination occurred at this level of moisture stress at 10 or 30°C.

3.0 STUDY AREA DESCRIPTION

The field work of this research was conducted at the University of Saskatchewan's Kernen Prairie, located approximately 1 km east of Saskatoon. Kernen Prairie, a 130 ha tract of a relict *F. hallii* grassland, is found in the transitional zone between the Mixed Prairie to the south and the *F. hallii* grassland of the Parkland Region to the north (Coupland, 1961; Coupland and Brayshaw, 1953; Rowe and Coupland, 1984). Kernen Prairie is found on a glacial melt water lake formed from a receding Wisconsin glacier approximately 12,000 years ago (Christiansen, 1979). Glaciolacustrine deposits were laid down over glacial till, and formed the parent material for the soils of Kernen Prairie.

Soils of Kernen Prairie are predominantly sandy Bradwell loam on a ridge running north-south through the Prairie which gently slopes to the east and west at 1 - 1.5^{o} where a Sutherland clay soil is found (Souster, 1979).

Vegetation of Kernen Prairie is documented by Baines (1973) and Pylypec (1986). It is characteristic of grasslands that fall in the transitional zone between the Mixed Prairie to the south and the *F. hallii* grassland to the north because it contains plant species common to both grassland types. Clay textured soils are dominated by *F. hallii* while on the coarser textured soils it co-dominates with *Stipa curtiseta* and *Agropyron dasystachyum* (Baines, 1973; Pylypec, 1986).

There is no record of Kernen Prairie being burned since 1917, however prior to this time circular fireguards were established with mouldboard-ploughs to protect haystacks (Baines, 1973). Therefore, fire may have been common in the area before 1917. From 1917 to 1967 portions of Kernen Prairie were grazed or mowed periodically (Baines, 1973; Pylypec, 1986).

Kernen Prairie is very important ecologically. Very little *F. hallii* grassland remains in Saskatchewan because of cultivation, over grazing and urban expansion. Kernen Prairie is a remnant patch of *F. hallii* grassland surrounded by cultivation. Road allowances encompass Kernen Prairie on the north, east and south sides. A general practice for revegetating road allowances has been to seed *B. inermis* after construction. This has therefore probably been a main source of genetic material for the invasion of *B. inermis* into the prairie. *B. inermis* appears to be invading the prairie from the road allowances which surround it. Scattered stands of *B. inermis* also occur throughout the prairie. It is this problem of *B. inermis* invasion that is the basis for the initiation of this research.

4.0 MATERIALS AND METHODS

4.1 Germination

Seeds of *F. hallii* and *B. inermis* were collected by hand stripping seeds from plants at Kernen Prairie in July 1987 and 1988. After seeds were collected they were hand threshed, screened, and stored in the laboratory at room temperature in paper envelopes. Germination tests were conducted four to six months following collection.

4.1.1 Temperature and Water Stress

Solutions were prepared to depress osmotic potentials to -0.3, -0.6, -0.9, -1.2, and -1.5 MPa by adding Polyethylene Glycol (PEG) (M.W. 20,000) to distilled water. Distilled water was used as the control (0.0 MPa). Osmotic potentials of these PEG solutions were determined using a Wescor vapor pressure osmometer.

Mean osmotic potentials and standard errors (n=4) for the PEG solutions used for the 1987 collections were -0.20 $\pm$0.02, -0.05 $\pm$0.01, -0.81 $\pm$0.02, -0.90 $\pm$0.03, and -1.17 $\pm$0.02 MPa. They were -0.29 $\pm$0.01, -0.68 $\pm$0.02, -0.99 $\pm$0.22, -1.27 $\pm$0.03, and -1.64 $\pm$0.05 MPa for the 1988 collections.

A randomized complete block design with 50 seeds in each of four replications was used with temperature and osmotic potentials factorially applied within collections. Seeds were incubated in closed petri dishes on 1 mm thick germination paper that was moistened by adding 7 mL of distilled water or PEG solution (Romo et al., 1991). These

petri dishes were enclosed and sealed in polyethylene bags to prevent desiccation. Seeds were incubated at 5, 10, 15, 20, and 25°C in darkness for 400 degree days. The length of the incubation period was based on a set number of degree days using 0°C as the base temperature. This was done because germination is a temperature sensitive process, and the use of degree days integrates both time and temperature (Johnson and Thornley, 1985).

Germination counts were made at 2-day intervals; a seed was considered germinated when the plumule and radicle were both at least 5 mm long (Romo et al., 1991). Germination results may be lower than in section 4.1.4 because of more restricted criteria for germination. Germinated seeds were removed from petri dishes, and after completing the incubation period the ungerminated seeds were dissected to determine seed fill. Germination data are thus expressed as a percentage of florets that had fully developed caryopses.

Total germination (%) and germination rate (%/degree day) (Maguire, 1962) were subjected to factorial analysis of variance using temperature and osmotic potentials as main effects (Snedecor and Cochran, 1980). The best fit polynomial regression equations were then developed for total germination and germination rate at $P \leq 0.05$ (Steele and Torrie, 1980).

4.1.2 Ascending and Descending Temperature

The effects of osmotic potential and temperatures decreasing 25 to 10°C or increasing from 10 to 25°C, were studied. Temperatures were increased or decreased at a rate of 0.5°C per day, but the actual change in degree days depended on temperature. A randomized complete block design with 50 seeds in each of four replications was used.

Seeds were incubated in closed petri dishes on 1 mm thick germination paper that was moistened by adding 7 mL of distilled water or PEG solution. Mean osmotic potentials and standard errors (n=4) were -0.22 ±0.02, -0.71 ±0.02, -1.50 ±0.05, and -1.64 ±0.06 MPa for the 1987 collections and -0.34 ±0.01, -0.58 ±0.01, -0.78 ±0.03, -0.95 ±0.02, and -1.08 ±0.04 MPa for the 1988 collections. Petri dishes were enclosed and sealed in polyethylene bags to limit desiccation. Seeds were incubated for 600 degree days and germination was tallied using the procedures described above.

Total germination (%) and germination rate (%/degree day) were subjected to factorial analysis of variance using temperature regime and osmotic potentials as main effects (Snedecor and Cochran, 1980). The best fit polynomial regression equations were then developed for total germination and germination rate at $P \leq 0.05$ (Steel and Torrie, 1980).

4.1.3 Light

The effects of light, osmotic potential, and temperature on germination were evaluated by incubating seeds at 10 or 20°C for 400 degree days under light and dark treatments. A photoperiod of 24 h for the light treatment was maintained with Philips Cool White florescent tubes with a photon flux of 56-64 umol $m^{-2}s^{-1}$. Mean osmotic potentials and standard errors (n=4) were -0.58 ±0.01, and -0.95 ±0.02 MPa for both the 1987 and 1988 collections. A randomized complete block design with 50 seeds in each of four replications was used. Seeds were incubated in closed petri dishes on 1 mm thick germination paper that was moistened by adding 7 mL of distilled water or PEG solution. Germination was then tallied using the procedure described in section 4.1.1.

Total germination (%) and germination rate (%/degree day) were subjected to factorial analysis of variance using light, temperature and osmotic potentials as main effects (Snedecor and Cochran, 1980). Tukey's honestly significant difference (Tukey's HSD) was calculated for mean comparisons at $P \leq 0.05$ (Petersen, 1985).

4.1.4 Constant and Alternating Temperature

Seeds of the 1987 and 1988 collections were sent to the U.S. Department of Agriculture, Agriculture Research Service Laboratory, Reno, Nevada where germination response to 55 temperature regimes was investigated in dark germinators

(Evans et al., 1982). A randomized complete block design with 25 seeds in each of four replications was used in germination tests. Seeds were incubated in closed petri dishes on 1 mm thick germination paper that was kept moist with water. Seeds were incubated for four weeks in dark germinators at 55 constant and alternating temperatures. Constant temperature regimes were 0, 2, 5, and 5 degree increments through 40°C. Alternating temperature regimes consisted of a 16 h cold period and an 8 h warm period, at all possible higher temperatures each 24 h interval. For example, 2°C (cold period) was alternated with 5, 10, 15, 20, 25, 30, 35, and 40°C (warm period), and 25°C (cold period) was alternated only with 30, 35, and 40°C (warm period). Germination was recorded after 1, 2, and 4 weeks of incubation. Seeds were considered germinated when the radicle was at least 5 mm long.

Germination parameters from the temperature-germination regression equations are defined as: (1) Mean germination - the average germination of the 55 temperature regimes; (2) Mean of regimes with some germination - the average germination of those temperature regimes showing germination (regimes with 0% germination are excluded); (3) Percentage with maximum germination - the percentage of the 55 temperature regimes in which some germinated; (4) Percentage with maximum germination - the highest germination of the 55 temperature regimes; (5) Germination at optimum temperatures - the average germination of the regimes with optimal

germination, and; (6) Maximum germination - the percentage of the 55 temperature regimes with germination not lower than the maximum germination minus one-half its confidence interval. The frequency of maximum is the percentage of the time that each temperature regime supports maximum germination. This value is determined across the germination profiles, providing an estimate of the maximum temperatures for germination. Details of the statistical procedures used are provided by Evans et al. (1982).

4.2 Prescribed Burn Treatments

Prior to initiating the burn treatments ten 2 ha blocks were delineated in a completely randomized block design (Appendix A1). Blocks were burned with headfires on each of the following dates: October 17, 1986 (one block); October 22, 1986 (one block); April 28, 1987 (one block); May 6, 1987 (one block); October 14, 1987 (two blocks); and April 20, 1988 (two blocks). Two unburned blocks were left as controls. Spring burn treatments were timed to minimize damage to *F. hallii* and fall burn treatments were timed to correspond with dormancy before winter. Redmann et al. (unpublished manuscript) provided the details of the fuel loads and burn conditions (Appendix A2 and A3).

4.3 Water Relations

Prior to burning, one stand of *B. inermis* in a community dominated by *F. hallii* was selected for water

relations and soil moisture measurements in each of the 10 experimental blocks.

Water relations during the first year of growth following burning were determined on June 9, June 26, July 3, July 14, July 21, July 28 and August 31 of 1987 for Fall 1986 and Spring 1987 burns, and on May 27, June 9, June 27, July 26, August 9, and August 24 of 1988 for Fall 1987 and Spring 1988 burns. Water relations were also studied in the second growing season of the Fall of 1986 and Spring 1987 burns on the same dates in 1988.

Xylem water potentials were determined on the uppermost fully expanded leaves of six different tillers within each *B. inermis* stand. Xylem water potentials of separate leaves were measured before dawn and another leaf at midday (1200 - 1400 h) using a portable pressure chamber in which a moist sponge was placed to maintain a humid environment (Ritchie and Hinckley, 1975).

Stomatal conductance was determined on the upper leaf surfaces on the uppermost fully expanded leaves of six different tillers within each *B. inermis* stand. Measurements were made at midday (1200-1400 h) using a Li-Cor 1600 steady state porometer equipped with a 2 cm^2 cuvette.

At the same time that midday xylem water potentials were determined, four leaves were collected from the same plants (n=6), immediately inserted into 5 mL disposable syringes, placed in plastic bags in a cooler and transported to the laboratory where they were stored at -80^{o}C. Later

leaves were thawed at room temperature, cell sap was forced from the leaves using a mechanical syringe compressor and the sap was collected on filter paper discs. Osmotic potentials of these paper discs were immediately determined with a Wescor vapor pressure osmometer after calibration using standard NaCl solutions (Turner, 1981).

Relative water content was measured at midday. The uppermost fully expanded leaf of six different *B. inermis* tillers were loosely rolled and enclosed in 20 mL scintillation vials (n=6). Samples were stored in a cooler until they were brought back to the laboratory where fresh weights were immediately determined. Approximately 10 mL of distilled water were added to the vials, and the vials were placed in darkness at 5°C for approximately 12 h. Leaves were then removed, quickly blotted dry with tissue paper and hydrated weight determined. The leaves were then oven dried at 80°C for 24 hours and weighed. Relative water content was calculated as follows (Kramer, 1983):

$$RWC = \frac{(FW - DW)}{DW} \times 100$$

where: RWC = relative water content
FW = fresh weight
DW = dry weight

Soil moisture in the upper 30 cm of the soil was determined throughout the same time frame as the plant water relations. Using a hand held 2.5 cm diameter soil probe, two

soil samples were collected from each *B. inermis* stand used in the plant water relations. Samples were placed in soil cans, and transported to the laboratory where they were immediately weighed and oven dried at 80°C for at least 48h. Soil moisture (%) was determined as follows (Kramer, 1983):

$$\text{Soil Moisture (\%)} = \frac{\text{(wet weight - dry weight)}}{\text{dry weight}} \times 100$$

Soil moisture and water relations data were analyzed with split-plot analysis of variance in a completely randomized design with subsamples. Tukey's HSD was calculated for mean comparisons at $P \leq 0.05$.

4.4 Population Dynamics

In each replication burned in Fall 1987, Spring 1988, and the unburned Control one stand of *B. inermis* was selected in a area dominated by *F. hallii* (Appendix A1). These *B. inermis* stands were established to study the effects of burning and glyphosate on *B. inermis* and associated flora; and for testing the survival of seedlings of *F. hallii* that were planted as containerized plants. These *B. inermis* stands were approximately 3 m in diameter and fit the description of a focus as defined by Harper (1977).

Each stand was then split in half with a steel plate that was 4 mm thick X 0.25 m X 5 m. The plate was driven

into the ground 25 cm, while care was taken to minimize disturbance to the surrounding vegetation. The purpose of the plate was to split the plot underground so *B. inermis* and other plant species would not spread by rhizomes to the other treatment side. Seed bank composition was also determined in both the *F. hallii* and *B. inermis* stand prior to treatment.

4.4.1 Effects of Burning and Glyphosate on *Bromus inermis* and Native Flora

Each side of the split plot contained a *F. hallii* stand and a *B. inermis* stand. Within each of these subplots, three permanent circular 0.10 m^2 microplots were established (Figure 4.1). Stem densities were determined for each plant species in these microplots before and during the two years after burning and glyphosate application. Plants were identified and classified (Looman and Best, 1979). The plant species were categorized into six different groupings including: (1) native graminoids; (2) *F. hallii*; (3) *B. inermis*; (4) native forbs; (5) exotic forbs, and; (6) shrubs.

One side of each split plot was randomly chosen for a wicking application of glyphosate at a rate of 2:1 (water:glyphosate) on June 10, 1988 when *B. inermis* was in the boot stage. Care was taken to apply glyphosate only to *B. inermis*. The height to the upper leaf of *B. inermis* and the associated native flora was measured before glyphosate application.

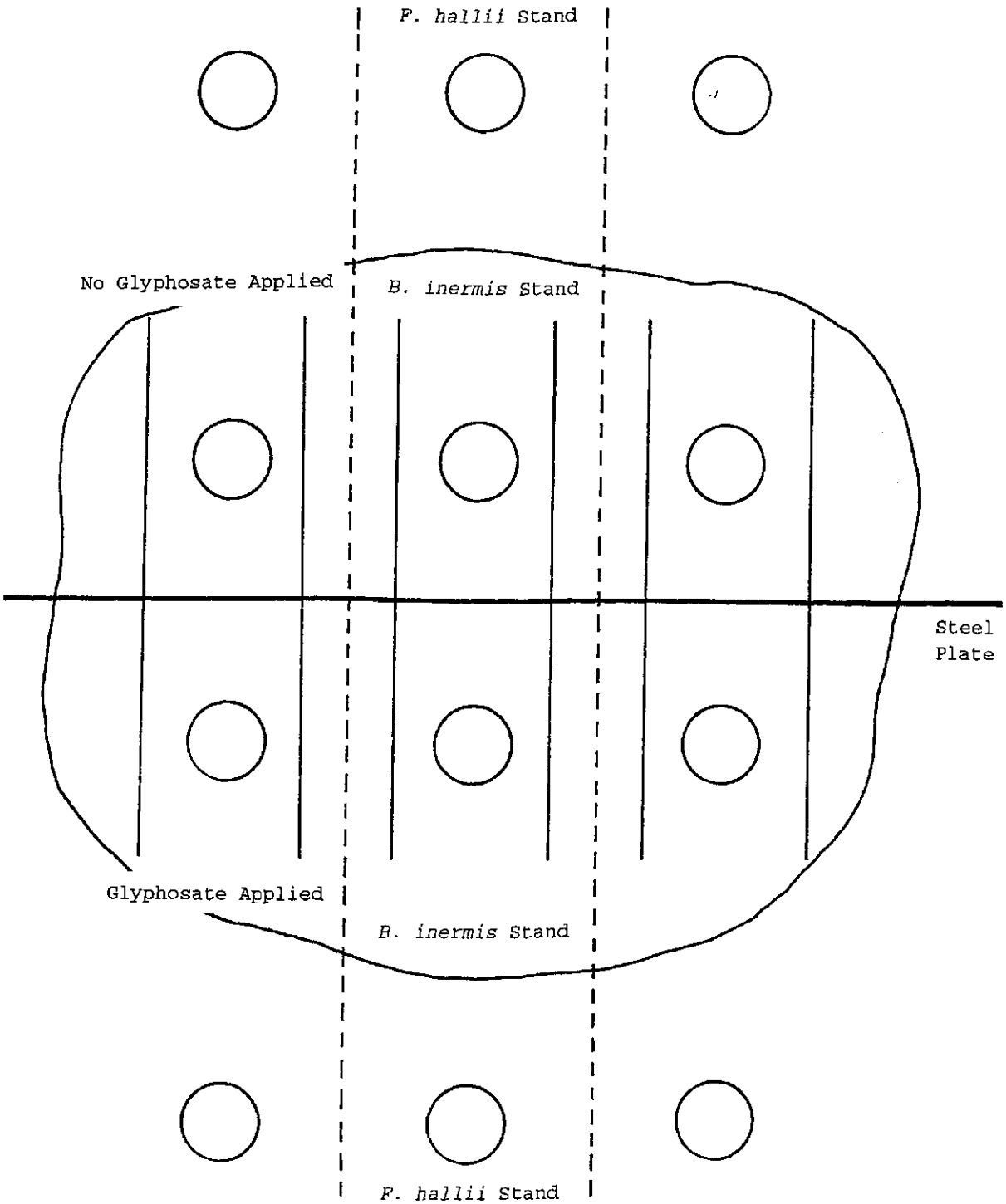

Figure 4.1 General layout of a burn plot for the population dynamics study showing *B. inermis* stand, *F. hallii* stand, glyphosate application and steel plate. Locations of permanent quadrats are indicated by circles, solid lines indicate transects where seedlings were planted and dashed lines indicate transects for seedbank sampling.

Stem density of plants and Simpson's diversity indices (Barbour et al., 1987) were analyzed with split-split-plot analysis of variance in a completely randomized design. Stem densities of *B. inermis* were analyzed with split-plot analysis of variance in a completely randomized design. Tukey's HSD was calculated for mean comparisons at $P \leq 0.05$.

4.4.2 Effects of Burning on Growth of *Bromus inermis*

Prior to burning, one stand of *B. inermis* in a native grassland community dominated by *F. hallii* was selected in each of the 10 blocks. Growth of *B. inermis* was studied in these stands.

Responses of *B. inermis* to burning were ascertained on a unit area basis by randomly selecting four 0.10 m^2 circular quadrats in each stand. Periodically, following burning, tillers of *B. inermis* were clipped at ground level and stem number, inflorescence number and number of leaves per stem were recorded. Leaves were stripped from tillers and leaf area was determined with a Li-Cor 3100 area meter. Samples were oven dried at 80°C for 48 h and weighed. Samples were taken on June 8 and July 13, 1987 for the first growing season of the Fall 1986 and Spring 1987 burns; and on June 21, July 21 and August 10, 1988 for the first growing season of the Fall 1987 and Spring 1988 burns and the second growing season of the Fall 1986 and Spring 1987 burns.

Data were analyzed with split-plot analysis of variance

in a completely randomized design with subsamples. Tukey's HSD was calculated for mean comparisons at $P \leq 0.05$.

4.4.3 Seed Bank Composition

Seed bank composition was determined on plots burned in Fall 1987, Spring 1988, and Control, prior to treatment. Cores of litter and soil (8 cm diameter X 10 cm deep) were removed from plots and placed in plastic bags. Five soil cores were taken along two transects from both the *B. inermis* stand and the *F. hallii* stand (Figure 4.1). Samples were taken to the laboratory where the material was spread in 10 X 25 cm germination trays to a depth of approximately 4 cm. These samples were incubated in a growth chamber with temperatures set at 8 h/10^{o}C dark period and 16 h/20^{o}C light period. Florescent and incandescent lights were used to provide the 16 h photoperiod with photon flux rates averaging 214 umol $m^{-2}s^{-1}$. Tap water was used to keep the samples moist. Seedlings were counted and identified when 600 degree days (base temperature = 0^{o}C) had accumulated (Looman, 1982). Species were grouped according to the following categories for data analyses: (1) native graminoids; (2) *B. inermis;* (3) native forbs, and; (4) exotic forbs.

The data from each stand type were averaged and analyzed with split-plot analysis of variance in a completely randomized design. Tukey's HSD was calculated for mean comparisons at $P \leq 0.05$.

4.4.4 Establishment of *Festuca altaica* subsp. *hallii* Seedlings

Festuca hallii seedlings were grown in Spencer-Lamaire seedling trays with 100 cells measuring 4 cm^2 X 12 cm deep. In 1988, 20 trays (2000 cells) were filled with a sandy loam soil. Soil that was collected from the Kernen Prairie Research area and stored at 4°C was used as a source of the VAM inoculum by placing a 2 cm layer on top of one-half of the trays. The soil inoculum presumably included, in addition to spores, infected root segments and hyphal fragments which however, were not quantified. Other soil microorganisms were not controlled. Four seeds of *F. hallii* that had been collected at Kernen Prairie in 1987 were placed in each cell. Cells were thinned to one seedling 21 days after emergence. The trays were randomized on a greenhouse bench and kept moist with water. Seedlings were preconditioned in a growth chamber with temperatures of 5°C night and 25°C day for 21 days before planting in the field.

Seedlings were transplanted into the split plots described in section 4.4 on May 5 or May 30, 1988. Soil temperatures at 10 cm were recorded at noon on each planting date. Six parallel transects were established through the *B. inermis* stand (Figure 4.1). Three of the transects were randomly chosen for early planting and three for late planting. Ten seedlings of each VAM seedling treatment were randomly planted along each transect in each glyphosate

treatment.

In 1989 the experiment was repeated but the sandy loam soil potting mixture was first steam-sterilized to kill VAM. The early planting date was May 1, 1989 and late planting date was June 6, 1989.

Festuca hallii seedling survival was assessed in late August of the first growing season; and percentage survival was averaged for the transects for analyses. Data were analyzed with split-split-plot analysis of variance in a completely randomized design. Tukey's HSD was calculated for mean comparisons at $P \leq 0.05$.

Festuca hallii seedlings from the establishment experiment were used to determine the percentage of roots colonized by VAM. The assay procedure for the quantification of VAM was described by Kormanik and McGraw (1982). The main procedures used were:

1) Two plants from each of the 10 trays were removed and the roots washed to remove all soil. The sample, approximately 2 grams (fresh weight), was placed into Tissue-Tek plastic capsules and labeled. This technique allowed all the samples to be processed at the same time.

2) The capsules were then rinsed with distilled water and placed in a beaker and covered with a 10% KOH solution for clearing. Specimens were heated at 90^{o}C for 15 to 20 minutes.

3) The KOH solution was poured off and the specimens were rinsed several times with distilled water until no brown

color appeared in the rinse water.

4) The specimens were covered with 1% HCl for three to four minutes and the solution was decanted. This step acidified the specimens for proper staining.

5) The samples were covered with 0.01% acid fuchsin-lactic acid staining solution and heated for 20 minutes at 90°C. The lactic-acid solution consisted of 875 mL of laboratory grade lactic acid, 63 mL of glycerin, 63 mL of distilled water, and 0.05% Trypan Blue.

A non-systematic procedure developed at the Institute for Mycorrhizal Research and Development, USDA Forest Service, Athens, Georgia was used to quantify the percentage of roots colonized by VAM (Kormanik and McGraw, 1982). A root sample was spread uniformly in a petri dish, and the root sample was examined under a dissecting microscope at 100X magnification by carefully rotating on the stage. The colonization was categorized into classes of percentage of colonization. The classes are: Class 1, 0-5%; Class 2, 6-26%;, Class 3, 27-50%; Class 4, 51-75%; Class 5, 76-100%. An assay of 100 random positions in the petri dish was used to classify infection. No attempt was made to identify the fungal species that colonized the *F. hallii* roots. Data were subjected to analysis of variance in a randomized complete block design with subsamples at the $P \leq 0.05$.

Seedlings that remained after the transplant survival experiment were placed in the greenhouse and evaluated for plant response to the colonization by VAM fungi when

seedlings were eight months old. Five plants were randomly selected from each of the ten seedling trays. Number of tillers, leaves per tiller, and plant height were determined. Data were subjected to analysis of variance in a randomized complete block design with subsamples at $P \leq 0.05$.

5.0 RESULTS

5.1 Germination

5.1.1 Temperature and Water Stress

Within species and years of collection, germination was not significantly different between temperatures ranging from 5 to 25°C. As osmotic potentials declined total germination for the 1987 collections decreased linearly (Figure 5.1). No seeds germinated at osmotic potentials lower than -0.9 MPa for *F. hallii* while *B. inermis* had some germination at -1.0 MPa (Figure 5.1). For the 1988 collection, total germination of *F. hallii* was much lower than the 1987 collection while *B. inermis* germination remained high in both years (Figure 5.2). *Bromus inermis* had higher germination at all levels of water stress than *F. hallii*, but total germination of both species declined with osmotic potential to -1.4 MPa after which no further germination occurred.

Festuca hallii germinated slower at all temperatures and osmotic potentials than *B. inermis* for the 1987 collections (Figure 5.3). Osmotic potential controlled germination rate of *F. hallii* while germination rate of *B. inermis* was a product of interacting effects of temperature and osmotic potential. As temperatures declined from 25°C the speed of germination for *B. inermis* decreased and the effect of osmotic potential was greater.

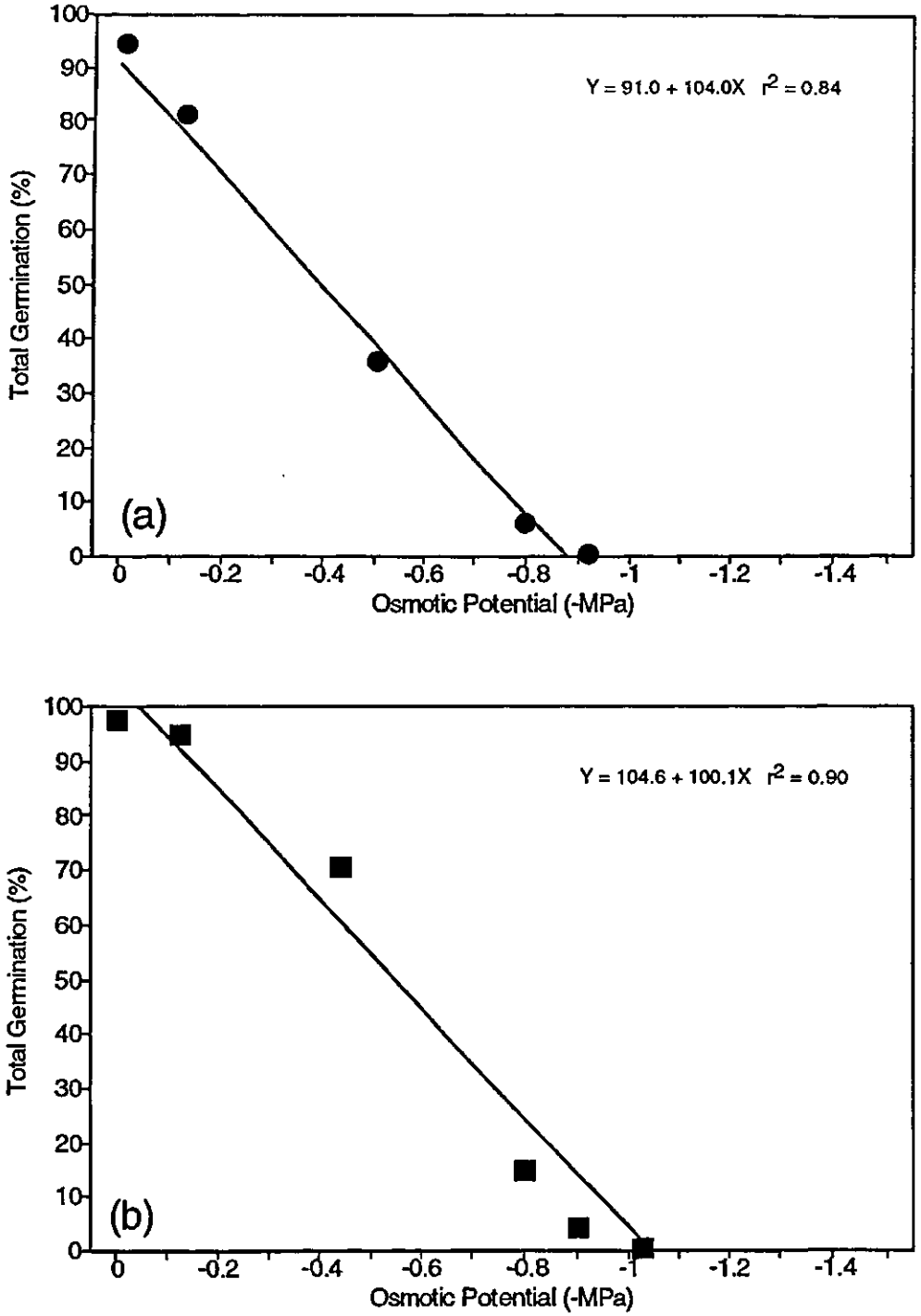

Figure 5.1 Total germination (Y) (%) for the 1987 collection of (a) *Festuca altaica* subsp. *hallii* [●] and (b) *Bromus inermis* [■], for the temperature (Z) and osmotic potential (X) interaction for seed incubated for 400 degree days (base temperature equals 0°C) at temperatures between 5 and 25°C in a gradient of osmotic potentials.

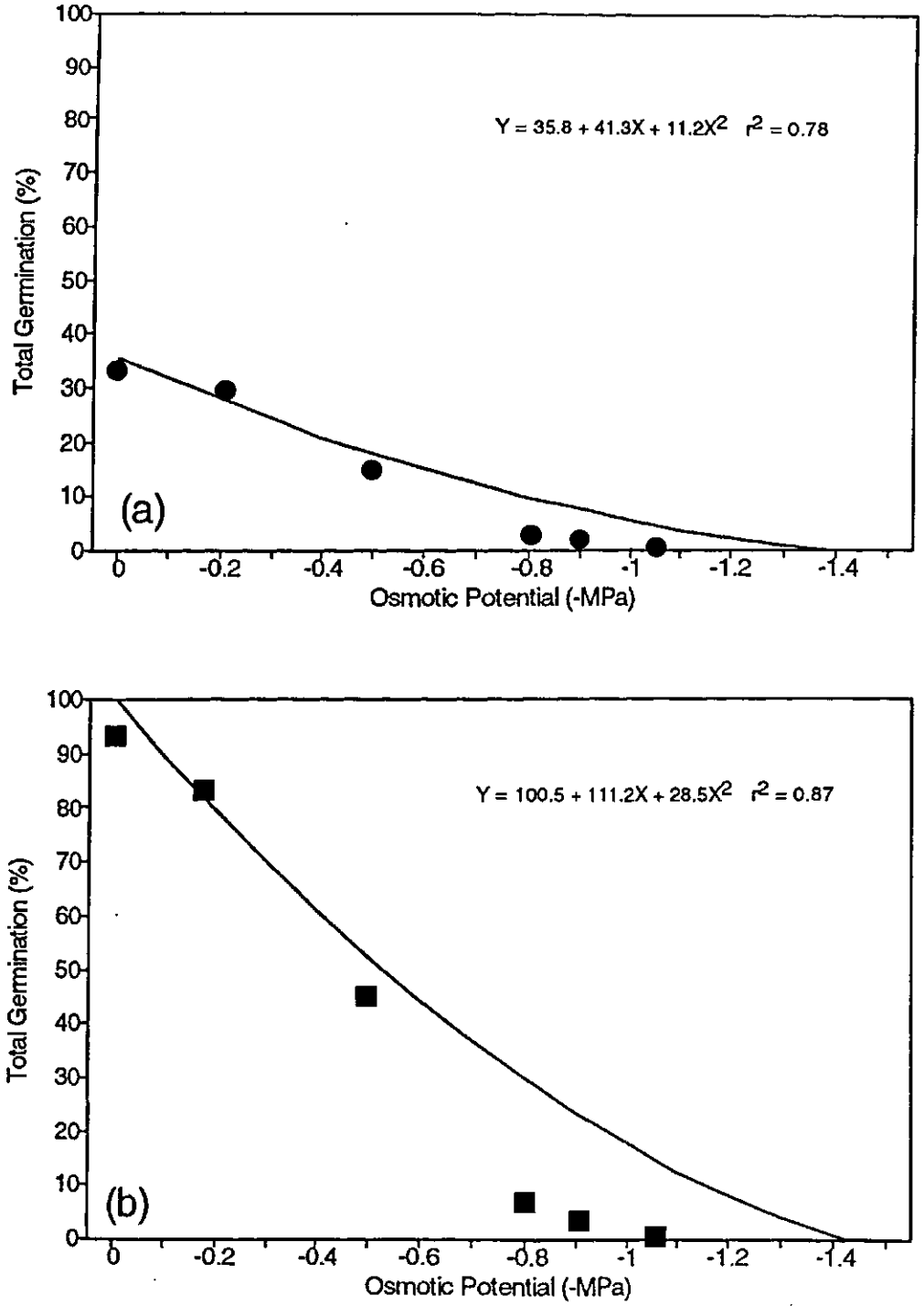

Figure 5.2 Total germination (Y) (%) for the 1988 collection of (a) *Festuca altaica* subsp. *hallii* [●] and (b) *Bromus inermis* [■], for the temperature (Z) and osmotic potential (X) interaction for seed incubated for 400 degree days (base temperature equals 0°C) at temperatures between 5 and 25°C in a gradient of osmotic potentials.

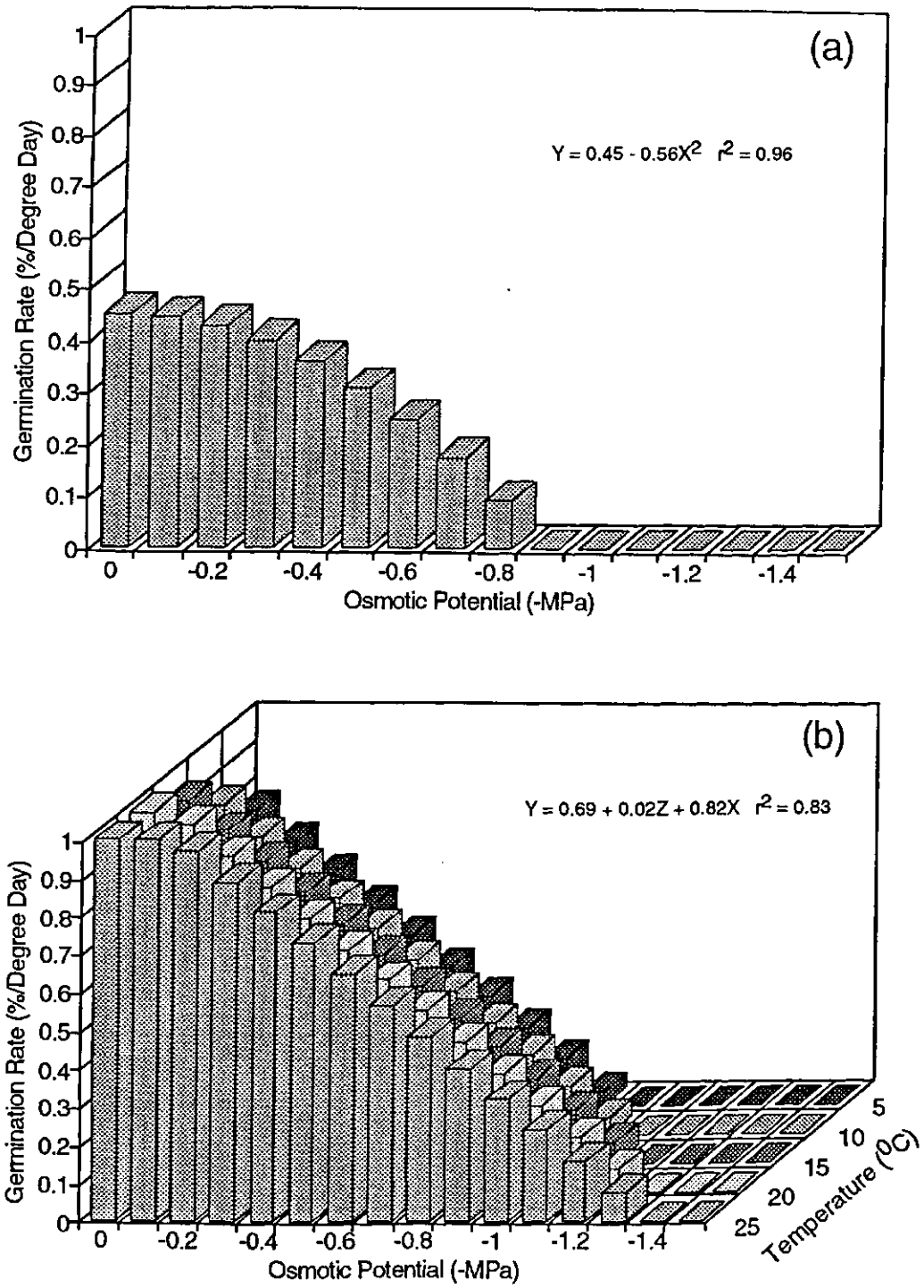

Figure 5.3 Germination rate (Y) (%/ Degree Day) for the 1987 collection of (a) *Festuca altaica* subsp. *hallii* and (b) *Bromus inermis*, for the temperature (Z) and osmotic potential (X) interaction for seed incubated for 400 degree days (base temperature equals 0°C) at temperatures between 5 and 25°C in a gradient of osmotic potentials.

Germination rate for the 1988 collection of *F. hallii* was the product of the interacting effects of temperature and osmotic potential while only osmotic potential influenced the rate of germination in *B. inermis* (Figure 5.4). The rate of germination for *F. hallii* declined with increasing temperatures and decreasing osmotic potentials. As water stress increased, germination rate remained highest at intermediate temperatures. Germination rate for *B. inermis* declined linearly with decreasing osmotic potentials. *Bromus inermis* germinated more rapidly than *F. hallii* over the majority of temperatures and osmotic potentials.

Total germination and germination rate for the 1987 and 1988 collections of *F. hallii* and *B. inermis* were the product of the interacting effects of temperature and osmotic potential. However, 90 and 94% of the variation in total germination for *F. hallii* and *B. inermis*, respectively was accounted for by osmotic potential. In 1988, 76 and 91% of the variation in total germination was attributed to osmotic potential in *F. hallii* and *B. inermis*. The combined effect of temperature and the interacting effects of temperature and osmotic potential accounted for only 9 and 15% for *F. hallii* and 4 and 9% of the variation in total germination for *B. inermis* in 1987 and 1988, respectively.

The total variation in germination rate accounted for by osmotic potential was 91 and 72% for *F. hallii* and 48 and

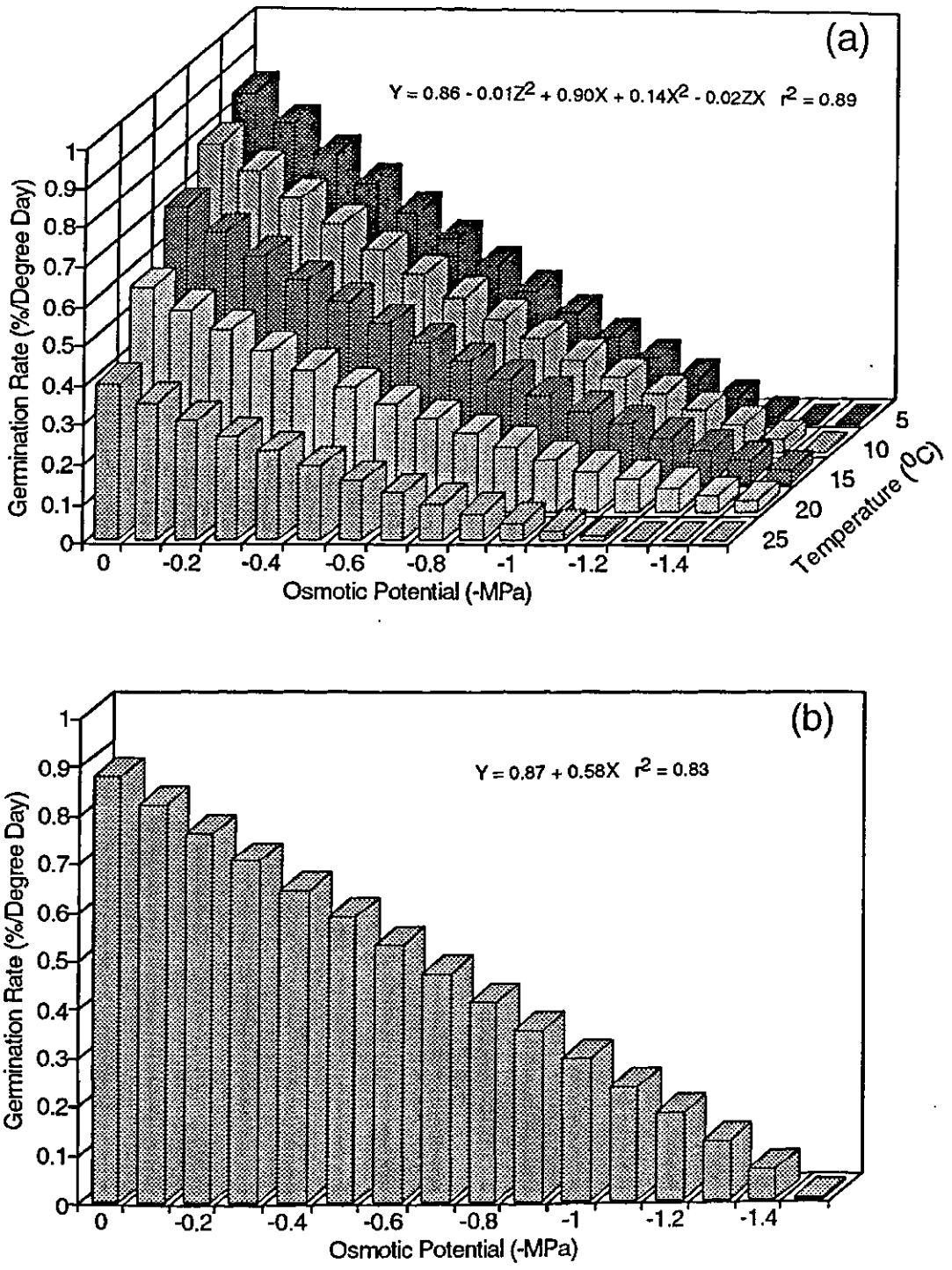

Figure 5.4 Germination rate (Y) (%/ Degree Day) for the 1988 collection of (a) *Festuca altaica* subsp. *hallii* and (b) *Bromus inermis*, for the temperature (Z) and osmotic potential (X) interaction for seed incubated for 400 degree days (base temperature equals 0°C) at temperatures between 5 and 25°C in a gradient of osmotic potentials.

76% for *B. inermis* in 1987 and 1988. The combined effect of temperature and the interacting effects of temperature and osmotic potential accounted for only 7 and 19% of the variation in germination rate for *F. hallii* and 10 and 13% for *B. inermis* in the 1987 and 1988 collections. Thus water stress was the most important factor controlling germination when seeds were germinated for an equal number of degree days at different temperatures.

5.1.2 Ascending and Descending Temperature

When germinated under a regime of temperatures ascending from 10 to 25°C or descending from 25 to 10°C, germination declined linearly as osmotic potentials declined for the 1987 and 1988 collections of *F. hallii* and *B. inermis* (Figures 5.5 and 5.6). *Festuca hallii* had higher germination over all osmotic potentials when incubated under ascending temperatures than under descending temperatures. Total germination and the range of osmotic potentials where germination occurred in the 1988 collection of *F. hallii* was lower than the 1987 collection (Figures 5.5 and 5.6). *Bromus inermis* had higher germination and germinated over a broader range of osmotic potentials than *F. hallii* in both 1987 and 1988. In 1987, *B. inermis* had slightly higher germination under the descending temperature regime at low osmotic potentials, but as osmotic potentials decreased this relationship reversed with germination greater under

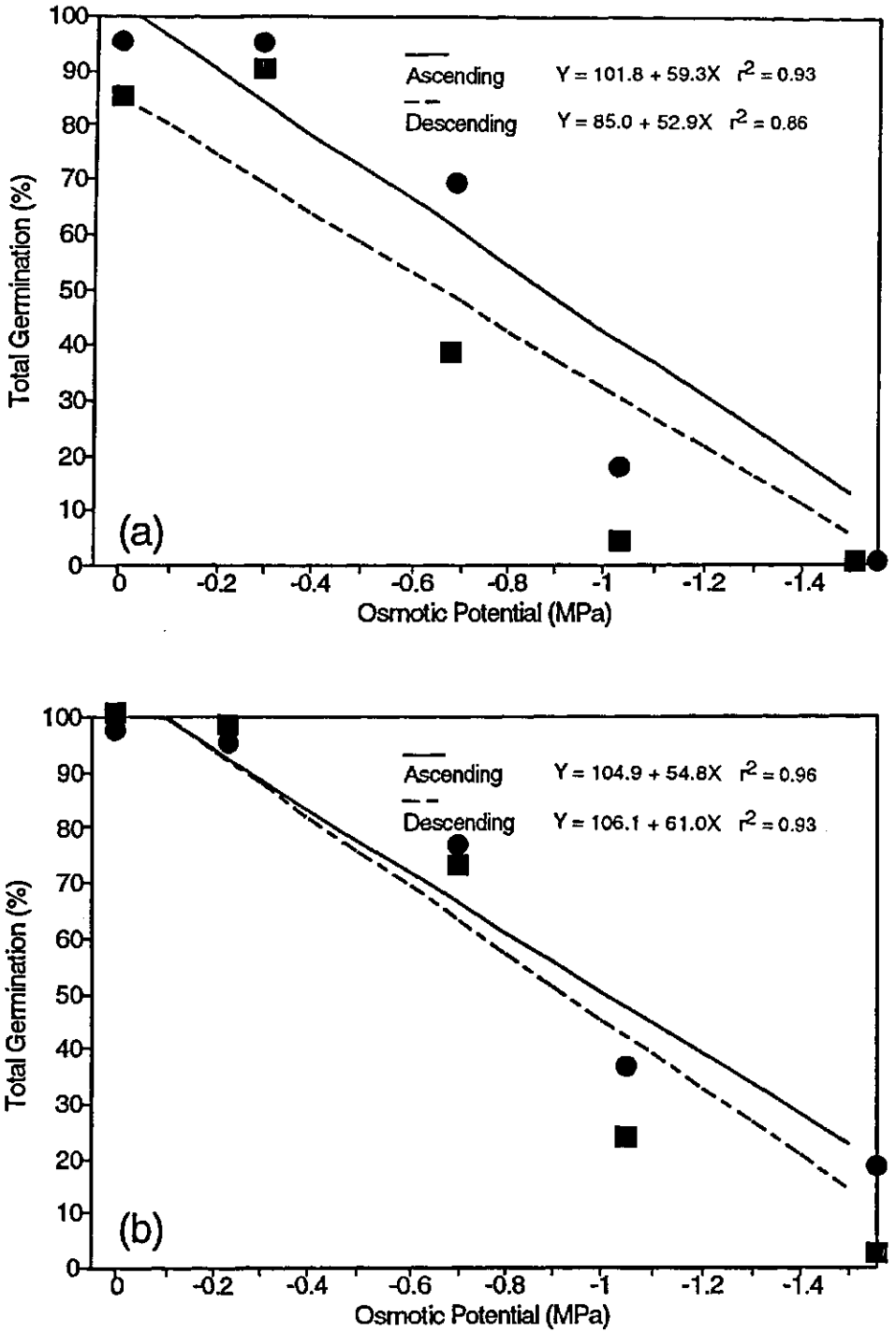

Figure 5.5 Total germination (Y) (%) for the 1987 collection of (a) *Festuca altaica* subsp. *hallii* and (b) *Bromus inermis*, incubated in a gradient of osmotic potentials (X) with temperatures ascending [●] from 10 to 25°C and descending [■] from 25 to 10°C for a total of 600 degree days (base temperature equals 0°C).

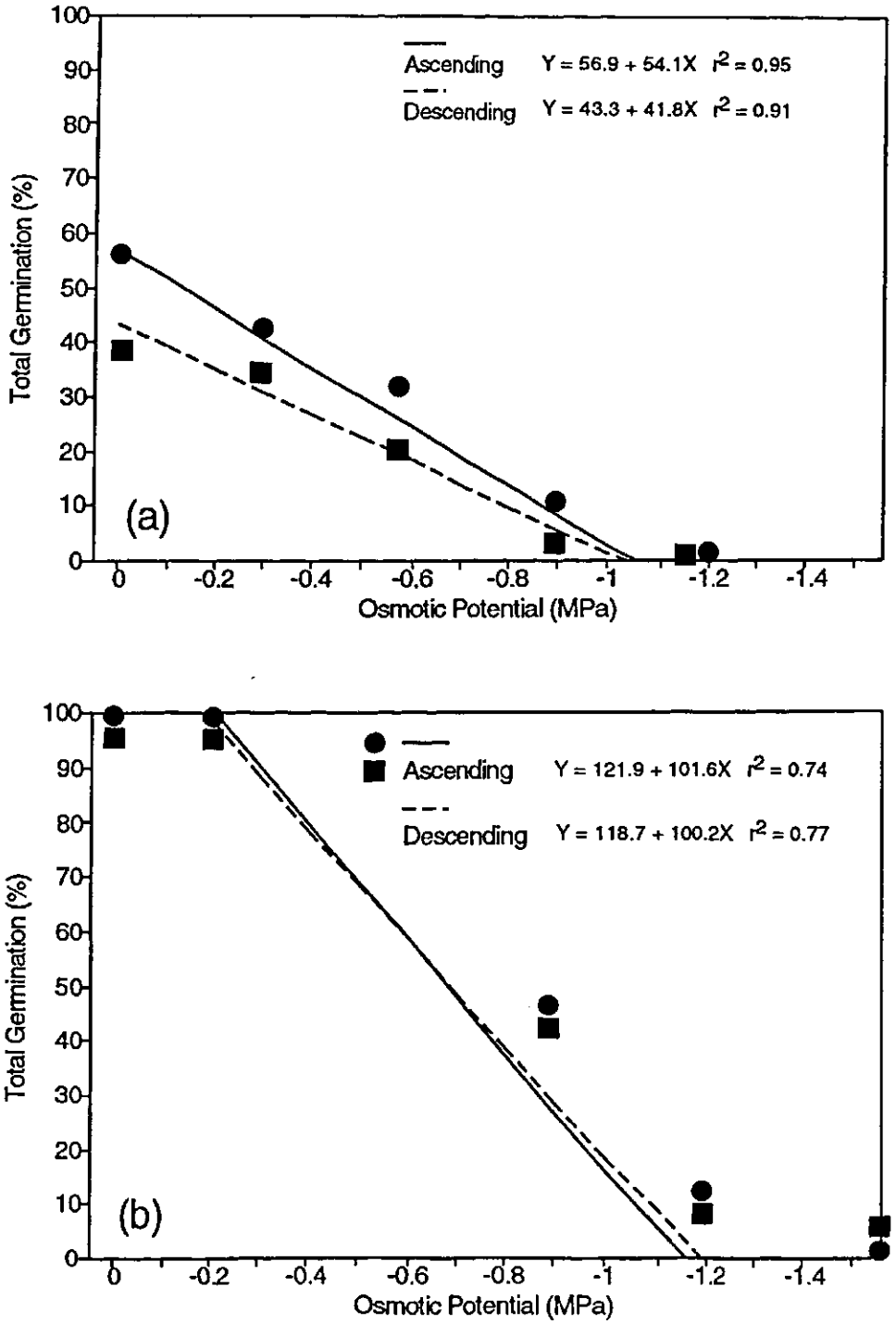

Figure 5.6 Total germination (Y) (%) for the 1988 collection of (a) *Festuca altaica* subsp. *hallii* and (b) *Bromus inermis*, incubated in a gradient of osmotic potentials (X) with temperatures ascending [●] from 10 to 25°C and descending [■] from 25 to 10°C for a total of 600 degree days (base temperature equals 0°C).

ascending temperatures. However, germination of *B. inermis* was similar under the two regimes in 1988.

Seeds of *B. inermis* germinated more rapidly over a broader range of osmotic potentials than *F. hallii* in both years and temperature regimes (Figures 5.7 and 5.8). In both species, year of collection, and temperature regime, the rate of germination declined linearly as osmotic potentials declined. Germination was more rapid for both species in 1987 than in 1988. *Festuca hallii* germinated more rapidly under ascending than descending temperatures in both 1987 and 1988. Germination rate for the 1987 collection of *B. inermis* was greater at high osmotic potentials under descending temperatures, but at low osmotic potentials the rate was greater under ascending temperatures. In 1988 a reversed relationship was observed.

Water stress was the major factor contributing to variation in total germination and germination rate. Ninety-five and 87%, and 97 and 98% of the variation in total germination was attributed to osmotic potential for the 1987 and 1988 collections of *F. hallii* and *B. inermis*, respectively. The total variation in germination rate attributed to osmotic potential in 1987 and 1988 was 88 and 78% for *F. hallii* and 93 and 97% for *B. inermis*. The combination of temperature and the interacting effects of temperature and osmotic potential accounted for only 9 and 4% of the variation for *F. hallii* and 5 and 1% for *B. inermis* in the 1987 and 1988 collections.

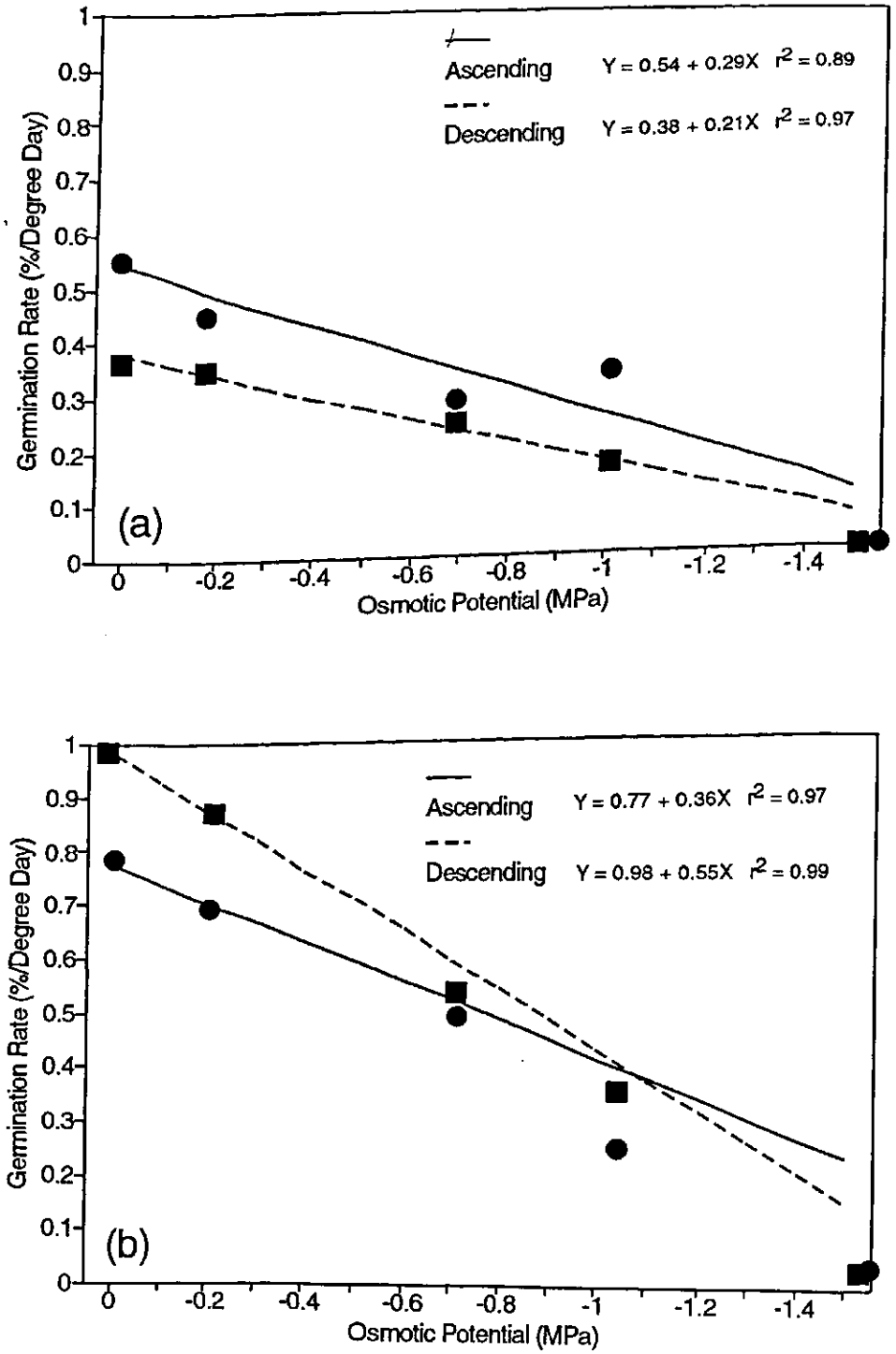

Figure 5.7 Germination rate (Y) (%/Degree Day) for the 1987 collection of (a) *Festuca altaica* subsp. *hallii* and (b) *Bromus inermis*, incubated in a gradient of osmotic potentials (X) with temperatures ascending [●] from 10 to 25°C and descending [■] from 25 to 10°C for a total of 600 degree days (base temperature equals 0°C).

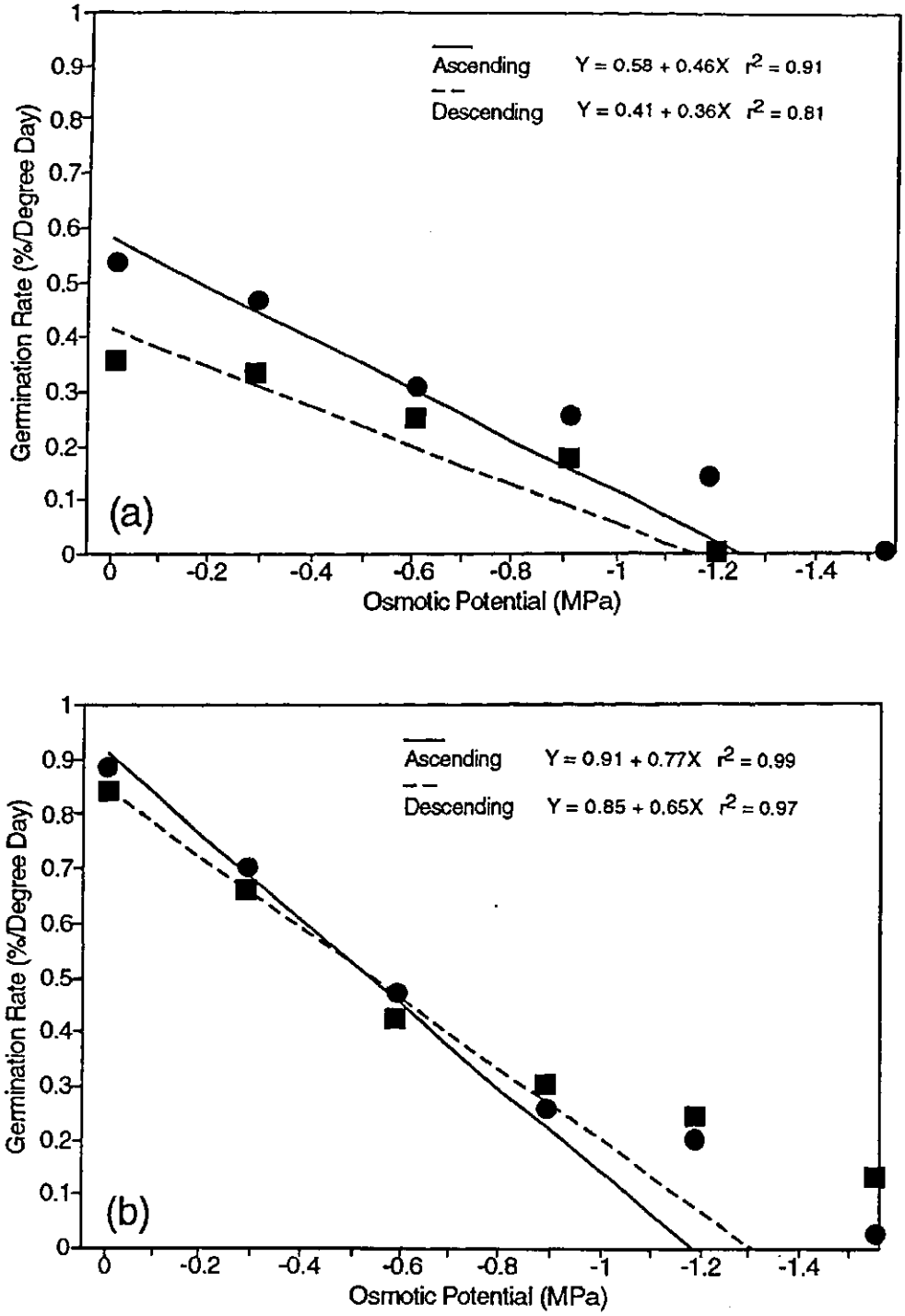

Figure 5.8 Germination rate (Y) (%/Degree Day) for the 1988 collection of (a) *Festuca altaica* subsp. *hallii* and (b) *Bromus inermis*, incubated in a gradient of osmotic potentials (X) with temperatures ascending [●] from 10 to 25°C and descending [■] from 25 to 10°C for a total of 600 degree days (base temperature equals 0°C).

5.1.3 Light

Total germination was the product of the interacting effects of light, temperature and osmotic potential for the 1987 collections of *F. hallii* and *B. inermis* (Table 5.1). Maximum germination for *F. hallii* was highest at 10°C in light or darkness with no water stress. Germination of *B. inermis* was highest at 10 and 20°C with no water stress under light or darkness. No seeds germinated at -0.95 MPa for *F. hallii* except at 10°C under darkness. Total germination was generally higher for *B. inermis* under darkness. Total germination was greater for *B. inermis* than *F. hallii* at osmotic potentials lower than 0.0 MPa in light and darkness.

For the 1988 collection of *F. hallii*, light, temperature and osmotic potential interacted to influence total germination (Table 5.2). Germination was greatest with light at 20°C and no water stress. Germination of *B. inermis* was the product of temperature x osmotic potential, light x osmotic potential, and light x temperature interactions. Germination was generally higher under darkness than light for *B. inermis*.

Germination rate for *F. hallii* in 1987 was the product of interacting effects of temperature and osmotic potential; light did not influence germination rate (Table 5.3). Germination of *F. hallii* was most rapid at 10°C with no water stress. A light x temperature x osmotic potential interaction occurred for the germination rate in the 1987

Table 5.1 Mean total germination (%) for the light, temperature and osmotic potential interaction for the 1987 seed collection of *Festuca altaica* subsp. *hallii* and *Bromus inermis* incubated for 400 degree days (base temperature equals 0°) under light and dark photoperiods, 10 and 20° and a gradient of osmotic potentials.

Temperature (°C)	Osmotic Potential (MPa)	Light Treatment			
		F. hallii		*B. inermis*	
		Light	Dark	Light	Dark
10	0.00	97.5 a[1]	96.0 a	94.5 ab	98.5 a
	-0.58	52.0 c	53.5 c	79.0 c	87.5 b
	-0.95	0.0 e	0.5 e	0.0 e	15.0 d
20	0.00	71.5 b	80.0 ab	98.5 a	99.0 a
	-0.58	43.5 cd	30.0 d	88.0 b	92.5 ab
	-0.95	0.0 e	0.0 e	7.0 de	6.5 e
Standard Error		3.4		1.7	

[1] A different letter within a species indicates significant ($P \leq 0.05$) differences among means by Tukey's HSD.

Table 5.2 Mean total germination (%) for the light, temperature and osmotic potential interaction for the 1988 seed collection of *Festuca altaica* subsp. *hallii* and *Bromus inermis* incubated for 400 degree days (base temperature equals 0^{o}) under light and dark photoperiods, 10 and 20^{o}C and a gradient of osmotic potentials.

		Light Treatment			
		F. hallii		*B. inermis*	
Temperature (^{o}C)	Osmotic Potential (MPa)	Light	Dark	Light	Dark
10	0.00	69.0 ab[1]	77.5 a	94.0 a	97.0 a
	-0.58	56.5 bc	59.4 bc	45.5 d	67.0 c
	-0.95	0.0 e	0.50 e	0.0 e	3.5 e
20	0.00	81.0 a	59.5 bc	98.0 a	98.0 a
	-0.58	43.5 cd	36.0 d	66.5 c	83.5 b
	-0.95	0.0 e	0.0 e	3.0 e	2.5 e
Standard Error		3.3		1.5	

[1] A different letter within a species indicates significant ($P \leq 0.05$) differences among means by Tukey's HSD.

Table 5.3 Mean germination rate (%/degree day) for the light, temperature and osmotic potential interaction for the 1987 seed collection of *Festuca altaica* subsp. *hallii* and *Bromus inermis* incubated for 400 degree days (base temperature equals 0°C) under light and dark photoperiods, 10 and 20°C and a gradient of osmotic potentials.

		Light Treatment			
		F. hallii		*B. inermis*	
Temperature (°C)	Osmotic Potential (MPa)	Light	Dark	Light	Dark
10	0.00	0.67 a[1]	0.72 a	1.20 a	1.21 a
	-0.58	0.36 cd	0.34 d	0.48 c	0.70 b
	-0.95	0.00 e	0.07 e	0.00 e	0.30 d
20	0.00	0.46 bc	0.49 b	1.14 a	1.19 a
	-0.58	0.31 d	0.30 d	0.53 c	0.62 b
	-0.95	0.00 e	0.00 e	0.27 d	0.30 d
Standard Error		0.02		0.02	

[1] A different letter within a species indicates significant ($P \leq 0.05$) differences among means by Tukey's HSD.

collection of *B. inermis* (Table 5.3). Germination rate was greatest under light and darkness at 10 and 20°C with no water stress. Germination at 10 and 20°C was generally faster in darkness at -0.58 and -0.95 MPa. Germination rates for the 1988 collection of *B. inermis* were similar to 1987 (Table 5.4). The temperature x osmotic potential interaction and light influenced germination rate in 1988 collection of *F. hallii* (Table 5.4). Germination rates were greater at 10°C for *F. hallii* and declined with decreasing osmotic potential.

Water stress was the major factor contributing to total germination and germination rate for both *F. hallii* and *B. inermis* with 88 to 98% of the total variation accounted for by osmotic potential.

5.1.4 Constant and Alternating Temperature

Total germination over the 55 constant and alternating temperatures was nearly five-fold greater in 1987 than in 1988 for *F. hallii* (Table 5.5). Total germination of *B. inermis* averaged 5% higher in 1987 than in 1988.

Seeds of *F. hallii* germinated in 82% of the temperature regimes in both 1987 and 1988 with total germination at these temperatures averaging five times greater in 1987 than in 1988 (Table 5.5). *Bromus inermis* germinated over a wider range of temperatures and had a higher average total germination than *F. hallii*. In both 1987 and 1988 *B. inermis*

Table 5.4 Mean germination rate (%/degree day) for the light, temperature and osmotic potential interaction for the 1988 seed collection of *Festuca altaica* subsp. *hallii* and *Bromus inermis* incubated for 400 degree days (base temperature equals 0°C) under light and dark photoperiods, 10 and 20°C and a gradient of osmotic potentials.

Temperature (°C)	Osmotic Potential (MPa)	Light Treatment			
		F. hallii		*B. inermis*	
		Light	Dark	Light	Dark
10	0.00	0.75 a[1]	0.80 a	1.04 a	1.11 a
	-0.58	0.40 bcd	0.45 bc	0.48 b	0.54 b
	-0.95	0.00 e	0.07 e	0.00 c	0.41 b
20	0.00	0.51 b	0.51 b	1.10 a	1.20 a
	-0.58	0.31 d	0.34 c	0.40 bc	0.44 bc
	-0.95	0.00 e	0.00 e	0.21 d	0.27 cd
Standard Error		0.03		0.03	

[1] A different letter within a species indicates significant ($P \leq 0.05$) differences among means by Tukey's HSD.

Table 5.5 Germination parameters for 1987 and 1988 collections of *Festuca altaica* subsp. *hallii* and *Bromus inermis* incubated in 55 temperature regimes.

Germination parameter	Seed Collection			
	F. hallii		*B. inermis*	
	1987	1988	1987	1988
Mean (%)[1]	36	7	71	66
Mean with some germination (%)[2]	44	9	73	72
Percentage with some germination[3]	82	82	98	91
Percentage with maximum germination[4]	7	9	42	27
Germination at Optimum temperatures (%)[5]	82	20	99	98
Maximum Germination (%)[6]	85	21	100	100
Seed fill (%)	95±2	78±1	99±1	98±1

[1] Mean germination is the average germination of the 55 temperature regimes tested.

[2] Mean of regimes with some germination excluding regimes with no germination.

[3] Percentage with some germination is the percentage of the 55 temperature regimes in which some seeds germinated.

[4] Percentage with maximum germination is the percentage of the 55 temperature regimes having maximum germination.

[5] Germination at optimum temperatures is the average germination of the temperature regimes with maximum germination.

[6] Maximum germination is the highest germination observed in the 55 temperature regimes.

germinated in more than 90% of the temperature regimes with total germination averaging over 70%.

Maximum germination of *F. hallii* was observed in 7 to 9% of the regimes with germination at optimum temperatures for the 1987 collection approximately four-fold greater than the 1988 collection (Table 5.5). The 1987 and 1988 collections of *B. inermis* germinated in 42 and 27% of the regimes with mean germination nearly 100% in the optimum temperatures.

The maximum germination of *F. hallii* in the 55 temperature regimes was 85% for the 1987 and 21% for the 1988 collections (Table 5.5). Maximum germination of 100% was observed for both the 1987 and 1988 collections of *B. inermis*.

Complete germination responses are presented for the 1987 and 1988 collections of *F. hallii* and *B. inermis* (Tables 5.6 and 5.7). Year-to-year variability is reflected in total germination for both species with the highest and lowest total germination occurring in 1987 and 1988 respectively; however the range of optimal temperatures varied little. *Bromus inermis* had higher total germination and germinated over a broader range of temperatures than *F. hallii*. Optimal temperature regimes for *F. hallii* were 15/15, 15/20, 20/20 and 20/25^{o}C in 1987 and 15/15, 15/20, 20/20, 20/25 and 25/25^{o}C in 1988. In the 1987 collection, *B. inermis* germinated in all of the temperature regimes except 0/0^{o}C; but the number of regimes was reduced to 49 in

Table 5.6 Estimated total germination (%) and confidence interval for the 1987 and 1988 collections of *Festuca altaica* subs. *hallii* seeds incubated for 4 weeks in darkness at 55 constant and alternating temperatures.[1]

Cold-period temperature (°C)	Warm-period temperature (°C) 8-hr									
16-hr	0	2	5	10	15	20	25	30	35	40
					1987					
0	0(7)	0(6)	0(5)	0(4)	1(5)	2(5)	0(5)	0(5)	0(5)	0(8)
2		8(6)	12(5)	16(4)	18(4)	18(4)	15(4)	11(4)	5(4)	0(7)
5			33(5)	37(3)	39(3)	39(4)	36(4)	32(3)	25(4)	16(6)
10				64(5)	65(4)	65(3)	62(3)	57(3)	50(4)	41(5)
15					<u>81(6)</u>	<u>80(4)</u>	77(4)	72(4)	65(4)	55(6)
20						<u>85(6)</u>	<u>82(4)</u>	76(3)	68(4)	59(6)
25							75(6)	69(4)	61(4)	51(6)
30								52(6)	44(4)	33(6)
35									15(7)	4(7)
40										0(6)
					1988					
0	0(3)	0(3)	0(2)	2(2)	3(2)	3(2)	2(2)	1(2)	0(2)	0(3)
2		2(3)	3(2)	5(2)	6(2)	6(2)	5(2)	3(2)	0(2)	0(3)
5			8(2)	10(1)	10(1)	10(1)	8(1)	6(1)	3(1)	0(2)
10				16(2)	16(2)	15(1)	13(1)	11(1)	7(2)	3(2)
15					<u>20(2)</u>	<u>19(2)</u>	17(1)	14(1)	10(2)	5(2)
20						<u>21(2)</u>	<u>19(2)</u>	15(1)	11(2)	5(2)
25							<u>19(2)</u>	15(2)	10(2)	4(2)
30								13(2)	8(2)	1(2)
35									4(3)	0(3)
40										0(4)

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

Table 5.7 Estimated total germination (%) and confidence interval for the 1987 and 1988 collections of *Bromus inermis* seeds incubated for 4 weeks in darkness at 55 constant and alternating temperatures.[1]

Cold-period temperature (°C)	Warm-period temperature (°C) 8-hr									
16-hr	0	2	5	10	15	20	25	30	35	40
					1987					
0	0(9)	19(6)	45(6)	78(5)	99(6)	100(6)	100(6)	87(6)	58(7)	17(10)
2		20(7)	46(6)	79(4)	100(5)	100(5)	100(5)	90(5)	61(5)	20(8)
5			47(6)	81(4)	100(4)	100(4)	100(4)	93(4)	65(4)	24(7)
10				82(6)	100(4)	100(4)	100(4)	97(4)	69(4)	30(6)
15					100(7)	100(5)	100(4)	99(4)	72(5)	33(7)
20						100(7)	100(5)	98(4)	73(5)	34(7)
25							100(7)	96(5)	71(5)	34(7)
30								92(7)	68(5)	31(7)
35									62(8)	26(8)
40										20(12)
					1988					
0	0(8)	0(7)	23(6)	57(5)	77(6)	86(6)	83(6)	67(5)	39(6)	0(9)
2		0(7)	27(5)	61(4)	83(5)	93(5)	90(5)	76(5)	49(5)	10(8)
5			30(6)	66(4)	89(4)	100(4)	100(4)	87(4)	62(4)	24(7)
10				67(6)	94(4)	100(4)	100(4)	100(4)	77(4)	42(6)
15					91(7)	100(5)	100(4)	100(4)	85(5)	53(7)
20						100(7)	100(5)	100(4)	86(5)	57(7)
25							96(7)	94(4)	80(4)	53(7)
30								77(7)	66(5)	42(7)
35									45(8)	24(8)
40										0(11)

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

1988. Optimal temperature regimes for *B. inermis* were 0-15/15, 0-20/20, 0-25/25, and 5-25/30°C in 1987 and 10/15, 2-20/20, 5-25/25, and 10-25/30°C in 1988. Part of the variation in total germination between collections of *F. hallii* can be attributed to seed fill (Table 5.5), but it was not important for *B. inermis*. Dormancy cannot be ruled out as a contributor to this yearly variation in germination of both species.

5.2 Water Relations

Precipitation from September 1986 through August 1987 totaled 281mm, 22% below the longterm average of 360mm for Saskatoon. During the same period in 1987-1988, precipitation was 275mm, 24% below normal. For the periods of May through August of 1987 and 1988 precipitation for all months except July and August 1988 were below the longterm average. Average monthly temperatures were 3-5°C above normal for May and June of both 1987 and 1988 and at or below normal in July and August.

Analysis of variance revealed that soil moisture, predawn xylem water potential, midday xylem water potential, osmotic potential, osmotic potential at full turgor, relative water content, and stomatal conductance at midday reflected the interacting influence of season of burning and sampling date during the first and second years after burning.

In 1987 soil moisture was higher in Control than in the

plots that had been burned (Table 5.8) However, in the second year after burning there was no significant difference between treatments. Plots burned in Fall 1987 or Spring 1988 had soil moisture similar to Control.

In 1988 predawn and midday xylem water potentials of plants were lowest in the Fall 1986 burn and higher in the Spring 1987 burn and Control (Table 5.8). This pattern was reversed in 1988 where predawn and midday xylem water potentials of plants in the Fall 1986 plots were higher than the Control and Spring burn. In 1988 predawn xylem water potentials of plants burned in Fall 1987 or Spring 1988 were equal to Control, but plants burned in the Fall had the highest midday xylem water potentials, Control was lowest and it was intermediate in Spring burns.

Osmotic potentials were lower for plants in the Fall burn than Control or Spring burn in 1987 (Table 5.8). In the second growing season osmotic potentials were lowest for Spring burns and highest for Fall burns. Osmotic potentials were similar among treatments for Control and those burned in Fall 1987 or Spring 1988.

In 1987 osmotic potential at full turgor was lowest for plants in the Fall burns and highest in the Spring burns (Table 5.8). There were no differences among treatments in 1988.

Relative water content of leaves in 1987 was higher in the Control and Spring 1987 burns than in the Fall 1986 burn

Table 5.8 Soil moisture and plant water relations characteristics averaged over the growing seasons and standard error for means for *Bromus inermis* following burning in fall or spring.

Parameters	Burn Treatments			S.E.
	Control	Fall86	Spring87	
--------- 1987 ---------				
Soil Moisture (%)	15.7a[3]	11.1b	12.0b	0.4
Predawn (MPa)[1]	-0.81b	-1.68a	-0.75b	0.08
Midday (MPa)[2]	-2.56b	-3.22a	-2.16b	0.12
Osmotic Potential (MPa)	-2.34b	-3.11a	-1.96b	0.13
Osmotic Potential at Full Turgor (MPa)	-1.99ab	-2.26a	-1.67b	0.10
Relative Water Content (%)	85.0a	73.5b	84.5a	1.4
Midday Stomatal Conductance (cm s-1)	0.22a	0.10b	0.18a	0.02
	Control	Fall86	Spring87	
--------- 1988 ---------				
Soil Moisture (%)	13.4a	12.7a	12.1a	1.1
Predawn (MPa)[1]	-1.44a	-0.73b	-1.87a	0.17
Midday (Mpa)[2]	-3.49a	-2.49b	-3.83a	0.12
Osmotic Potential (MPa)	-2.47ab	-2.09b	-2.61a	0.13
Osmotic Potential at Full Turgor (MPa)	-1.68a	-1.68a	-1.62a	0.09
Relative Water Content (%)	71.0a	80.7b	67.2a	1.7
Midday Stomatal Conductance (cm s-1)	0.12a	0.14a	0.11a	0.01
	Control	Fall87	Spring88	
--------- 1988 ---------				
Soil Moisture (%)	13.5a	13.7a	13.1a	0.7
Predawn (MPa)[1]	-1.44a	-1.22a	-1.54a	0.13
Midday (Mpa)[2]	-3.49a	-2.97b	-3.30ab	0.15
Osmotic Potential (MPa)	-2.47a	-2.18a	-2.55a	0.14
Osmotic Potential at Full Turgor (MPa)	-1.68a	-1.65a	-1.70a	0.10
Relative Water Content (%)	71.0a	77.1a	72.1a	2.0
Midday Stomatal Conductance (cm s-1)	0.12a	0.11a	0.09a	0.01

[1] Predawn xylem water potential.
[2] Midday xylem water potential.
[3] A different letter within a parameter and year indicates significant ($P \leq 0.05$) differences among means by Tukey's HSD.

(Table 5.8), but in 1988, the second growing season, it was highest in the Fall burns. Relative water content was similar among treatments in the first growing season of the Fall 1987 and Spring 1988 burns.

In 1987 midday stomatal conductance for plants was approximately two-fold higher in Control and the Spring burn than in the Fall burn (Table 5.8). In 1988 there were no significant differences between treatments.

5.3 Population Dynamics

5.3.1 Effects of Burning and Glyphosate on *Bromus inermis* and Native Flora

Stem densities for all vegetation categories were similar in all treatments before burning except for differences in the dominant species between *B. inermis* and *F. hallii* stands (Table 5.9). There were on average 107 native graminoids per 0.10 m^2 in the *F. hallii* stand and 93 in the *B. inermis* stand. In the *F. hallii* stand there were on average 127 *F. hallii* tillers but only 29 in the *B. inermis* stand. There were no *B. inermis* tillers found in any plots in the *F. hallii* stand.

In May, 1988 native graminoids, *F. hallii* and *B. inermis* densities reflected burning impacts (Table 5.9). Densities of native forbs, exotic forbs and shrubs were not significantly affected by burning in this study. Tiller density of native graminoids decreased 8% in the Control, and 43 and 5% in the Fall and Spring burns, respectively, in

Table 5.9 Stem densities (0.25 m^2) for broad vegetation categories for the burn, glyphosate and stand type sampled on: D_1 (August 1987 - preburn); D_2 (May 1988 - postburn); D_3 (September 1988 - postglyphosate; and D_4 (August 1989).

Treatment	Vegetation Categories																							
	Native Graminoids				*F. hallii*				*B. inermis*				Native Forbs				Exotic Forbs				Shrubs			
	D_1	D_2	D_3	D_4	D_1	D_2	D_3	D_4	D_1	D_2	D_3	D_4	D_1	D_2	D_3	D_4	D_1	D_2	D_3	D_4	D_1	D_2	D_3	D_4
No Glyphosate																								
F. hallii Stand																								
Spring Burn	136	129ab[1]	142	137ab	107	142	143	128	0	0	0	0	12	11	14	19	0	0	0	0	0	0	0	0
Fall Burn	135	74ab	113	136ab	186	72	117	191	0	0	0	0	4	4	8	9	0	0	0	0	0	0	0	0
Control	67	64b	73	83ab	119	115	117	111	0	0	0	0	3	3	4	10	0	0	0	0	1	1	1	1
B. inermis Stand																								
Spring Burn	92	99ab	98	122ab	20	43	15	18	32a	34a	35a	33a	1	3	1	2	0	0	0	0	0	0	0	0
Fall Burn	148	85ab	135	147ab	6	2	4	7	21a	14b	24b	22b	1	1	1	5	0	0	0	0	0	0	0	0
Control	55	50b	52	52ab	62	51	46	52	14b	14b	15bc	17bc	1	1	1	0	0	0	0	0	0	0	0	0
Glyphosate Applied																								
F. hallii Stand																								
Spring Burn	195	186a	154	222a	18	33	34	27	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Fall Burn	57	36b	18	27ab	187	116	143	208	0	0	0	0	3	2	1	2	0	0	0	0	0	0	0	0
Control	54	47b	42	62ab	143	141	67	84	0	0	0	0	0	0	0	1	0	0	0	0	2	2	2	1
B. inermis Stand																								
Spring Burn	104	113ab	10	22ab	3	1	0	0	32a	38a	0e	1de	3	2	9	26	0	0	0	2	0	0	0	0
Fall Burn	117	74ab	13	15b	66	18	56	29	27a	19ab	7ce	9cd	1	0	2	6	0	0	1	3	0	0	0	1
Control	39	36b	1	10b	15	10	8	8	19a	18b	10cd	13c	1	1	2	7	0	0	0	1	2	2	2	2
Standard Error	33	21	24	30	59	52	39	126	3	3	1	1	3	2	5	9	0	0	0	1	1	1	1	0

[1] A different letter within a sampling date and vegetation category indicates significant ($P \leq 0.05$) differences among means by Tukey's HSD. No letter indicates no significant differences.

the *F. hallii* stand. In the *B. inermis* stand density of native graminoids decreased 40% in the Fall burn and 9% in Control, while tiller densities increased 8% in the Spring burns. Tiller densities of *F. hallii* in *F. hallii* and *B. inermis* stands decreased 2 and 21% in Control and 50 and 70% after fall burning in the *F. hallii* and *B. inermis* stands. Following spring burning *F. hallii* tiller density increased 40% in the *F. hallii* stand and 91% in the *B. inermis* stand. *Bromus inermis* tiller densities decreased 31% following fall burning while they increased 13% with spring burning. There was a 3% increase in tiller density of *B. inermis* in the Control.

The effects of the glyphosate application on stem densities are reflected in the third sampling in September, 1988. Tiller densities of native graminoids and *F. hallii* were reduced by glyphosate application in the *B. inermis* stand. These plants apparently received glyphosate during the wicking application, probably killing some tillers. At the time of the glyphosate application the average height of *B. inermis* and the associated native flora was 67 and 51 mm for Fall burns, 146 and 75 mm for Spring burns and 105 and 84 for Control, respectively.

Control of *B. inermis* was a product of the interacting effects of burning and glyphosate application. After glyphosate application, tiller densities of *B. inermis* declined 45% in Control, 100% in the Spring burned plots and 71% in plots burned in the fall (Table 5.10). Following

Table 5.10 Percentage change in tiller density for *Bromus inermis* in May, 1988 (post-burn); September, 1988 (post-glyphosate) and August 1989, and standard errors for means. Values are relative to preburn densities.

Treatment	Change in Tiller Density (%)		
	May 1988	Sept 1988	Aug 1989
No Glyphosate			
Spring Burn	6.5a[1]	11.0a	4.5a
Fall Burn	-29.5a	16.0a	7.5a
Control	0.0a	7.5a	19.5a
Glyphosate Applied			
Spring Burn	18.5a	-100.0b	-98.5b
Fall Burn	-33.5a	-76.0bc	-69.0c
Control	-8.5a	-45.0c	-34.0d
Standard Error	6.5	5.3	4.1

[1] A different letter within a sampling date indicates significant ($P \leq 0.05$) differences among means by Tukey's HSD.

burning the number of *B. inermis* tillers increased 11 and 16% for Spring and Fall, while tiller densities increased 8% in Control.

In August 1989, the second growing season following treatments there was a burn x glyphosate interaction for percentage change in tiller densities of *B. inermis*. Spring burns with glyphosate applied had 98.5% fewer *B. inermis* tillers compared to 69 and 34% reductions in the Fall burn and Control (Table 5.9 and 5.10). *Bromus inermis* tiller densities in plots that had been burned but not receiving glyphosate were 4.5 and 7.5% higher than pretreatment densities.

Tiller densities for the native graminoids in the *F. hallii* stand where no glyphosate was applied were similar to pretreatment (Table 5.9). In the *B. inermis* stand with no glyphosate applied, native graminoid densities in the Fall burn and Control plots were similar to pretreatment densities; however, native graminoid densities were 33% higher than pretreatment densities in Spring burns. With the glyphosate treatment, tiller densities of native graminoids in the *F. hallii* stand were 53% lower and 14% higher than pretreatment in the Fall and Spring burned plots, respectively; tiller densities were 15% greater in Control. Tiller densities of native graminoids in the *B. inermis* stand were greatly reduced from pretreatment densities but had increased from September 1988 densities.

Species richness and Simpson's diversity indices for

the tiller data were not significantly different between treatments on all sampling dates (Table 5.11). Fewer than ten species were found in *F. hallii* and *B. inermis* stands, while Simpson's diversity indices ranged from 0.29 to 0.77.

5.3.2 Effects of Burning on Growth of *Bromus inermis*

Average stem densities for the Spring and Fall burns were nearly two-fold greater than Control in 1987 (Table 5.12). Stem densities in Fall burns were significantly higher than Control, but similar to the Spring burn. In the second growing season stem densities were similar among treatments. Similarily in the first growing season of the 1988 burns, there were no differences in stem densities between treatments.

The number of leaves per stem was not significantly different for the first growing season following both the 1987 and 1988 burns (Table 5.12). However, in the second growing season there were significantly fewer leaves on the August sampling for Spring burns (Table 5.12).

The number of inflorescences in the burns were not significantly different in the first growing season of 1987 and 1988 and the second growing season following the 1987 burn (Table 5.12). The number of inflorescence in 1988 was nine- to 19-fold greater than in 1987.

Leaf area indices for the first growing season of the

Table 5.11 Species richness and diversity indices for the burn, glyphosate, community type interaction for stem densities on: D_1 (August 1987 - preburn); D_2 (May 1988 - postburn); D_3 (September 1988 - postglyphosate application; and D_4 (August 1989).

Treatment	Parameter							
	Species Richness				Diversity Indices			
	D_1	D_2	D_3	D_4	D_1	D_2	D_3	D_4
No Glyphosate								
F. hallii Stand								
Spring Burn	7	7	7	8	0.64	0.60	0.64	0.69
Fall Burn	5	5	6	6	0.57	0.59	0.58	0.57
Control	6	6	6	7	0.55	0.55	0.58	0.63
B. inermis Stand								
Spring Burn	5	5	5	5	0.54	0.52	0.51	0.51
Fall Burn	6	6	6	7	0.59	0.65	0.65	0.66
Control	6	6	5	5	0.59	0.62	0.62	0.59
Glyphosate Applied								
F. hallii Stand								
Spring Burn	6	6	6	6	0.75	0.70	0.72	0.74
Fall Burn	6	6	5	6	0.41	0.42	0.34	0.36
Control	5	5	5	5	0.51	0.48	0.57	0.59
B. inermis Stand								
Spring Burn	5	5	4	5	0.48	0.46	0.39	0.48
Fall Burn	4	4	4	6	0.34	0.50	0.29	0.51
Control	6	6	4	7	0.62	0.62	0.56	0.77
Standard Error					0.11	0.15	0.16	0.12

Table 5.12 Average growth characteristics and standard errors for means for *Bromus inermis* the first and second growing season following the 1987 and first growing season following the 1988 burning.

Growth Parameter	Burn Treatment	First Growing Season 1987				First Growing Season 1988					Second Growing Season 1988				
		June	July	Mean	S.E.	June	July	August	Mean	S.E.	June	July	August	Mean	S.E.
Stem Number (m^2)	Control	158	165	161b[1]	27	223	221	241	228	31	223	221	241	228	18
	Fall Burn	338	320	329a		223	275	376	295		221	213	246	227	
	Spring Burn	350	283	316ab		305	338	371	338		231	255	218	335	
Leaves/Stem	Control	4.3	5.3	4.8	0.7	4.1	3.6	3.9	3.9	0.7	4.1ab	3.6ab	3.9ab	3.9	0.5
	Fall Burn	3.5	3.3	3.4		4.5	4.0	5.4	4.6		3.8ab	3.5ab	3.8ab	3.7	
	Spring Burn	4.0	7.3	5.6		5.0	4.8	4.4	4.7		5.6ab	3.8ab	3.0c	4.1	
Inflorescence Number	Control	0.0	7.5	3.8	2.7	60.0	38.8	38.8	45.8	29.5	60.0	38.8	38.8	45.8	32.1
	Fall Burn	0.0	5.0	2.5		23.8	15.0	28.8	22.5		30.0	37.5	33.8	33.8	
	Spring Burn	0.0	7.5	3.8		20.0	26.3	22.5	22.9		136.3	102.5	91.3	110.0	
Leaf Area Index	Control	0.48bc	0.52bc	0.50	0.14	0.43	0.34	0.28	0.34	0.14	0.43	0.34	0.28	0.34	0.09
	Fall Burn	0.66bc	0.34c	0.50		0.26	0.30	0.45	0.33		0.22	0.23	0.23	0.29	
	Spring Burn	0.85ab	1.14a	0.99		0.53	0.54	0.38	0.48		0.36	0.30	0.19	0.28	
Specific Leaf Weight (g/m^2)	Control	46.8	56.6	51.7b	1.6	56.6	65.6	86.3	69.5	27.5	56.6	65.6	86.3	69.5	9.1
	Fall Burn	53.9	68.9	61.4a		59.2	138.0	42.2	79.8		62.7	58.3	70.5	63.8	
	Spring Burn	44.7	52.6	48.7b		57.1	230.7	60.9	116.2		58.3	80.5	147.4	95.4	
Total Biomass (g/m^2)	Control	40.8d	70.0c	55.4	15.7	62.1	54.8	43.5	53.5	22.5	62.1	54.8	43.5	53.5	18.4
	Fall Burn	68.8c	53.7cd	61.2		28.8	54.0	45.0	42.2		28.7	25.3	30.0	28.0	
	Spring Burn	68.2c	118.0a	93.1		63.6	112.2	43.9	73.2		57.0	55.6	37.8	50.1	

[1] A different letter within a parameter indicates significant ($P \leq 0.05$) differences among means by Tukey's HSD. No letter indicates no significant differences.

1987 burn were the product of burn x date interaction (Table 5.12). The leaf area index was greatest in the Spring burns and least in the Fall burns and Control. In the second growing season, leaf area indices of the 1987 burns were lower, but similar among treatments. Leaf area indices for the Spring and Fall burns were similar to Control in the first growing season following the 1988 burns.

In the first growing season following the 1987 burn, specific leaf weights averaged over the growing season were lower for Control and the Spring burn than the Fall burn (Table 5.12). There were no differences in specific leaf weight for *B. inermis* during the 1988 growing season for the 1987 and 1988 burns.

The effect of burning on total biomass in *B. inermis* was a product of the interacting effects of burning and time of sampling in 1987. On the June sample date Control had lower total biomass than the Fall and Spring burns. In July, biomass in Control and Fall burn were lower than the Spring burn. There was no carryover effect of burning on total production in the second year, nor did burning have an effect on biomass production for the first growing season following burning in 1988.

5.3.3 Seed Bank Composition

Twenty five species were identified from the seedlings in the seed bank taken from the preburn plots with the number of seedlings ranging from 1,400 to 2,500 per m^2 for

the *F. hallii* stand and from 1,500 to 1,600 per m^2 for the *B. inermis* stand (Table 5.13 and Appendix A8). There were no significant differences in the number of seedlings between plots and stand types. *Bromus inermis* seed was not found in the *F. hallii* stands and it represented less than 1% of the seedlings from the Fall burn in the *B. inermis* stand. The remaining seedlings were primarily native forbs and native graminoids. The native graminoids and forbs were nearly equal in their contribution in the *F. hallii* stand. Exotic forbs contributed the least amount to the seedbank but they were a significant proportion of the total number of seedlings in all samples.

5.3.4 Establishment of *Festuca altaica* subsp. *hallii* Seedlings

For the 1988 growing season there was a significant difference in survival of seedlings between planting dates (Table 5.14). Seedling survival for the May 5 planting ranged from 2.8% on Control with glyphosate applied to *B. inermis* to 16.9% on the Spring burn with no glyphosate. Survival was generally higher on plots that were not treated with glyphosate. Soil temperatures at noon on May 5 were $10.9 \pm 0.5^{o}C$ at the 10 cm soil depth. No seedlings survived for the May 30 planting; soil temperatures at noon at a 10 cm depth were $29.5 \pm 1.2^{o}C$.

In 1989 seedling survival was the product of a burn x glyphosate interaction. There were no significant

Table 5.13 Percentage of seed bank composition for broad vegetation categories. Actual number of seeds per square meter are given in parentheses.

Plots	Vegetation Category			
	Native Graminoids	*B. inermis*	Native Forbs	Exotic Forbs
F. hallii Stand				
Spring Burn	47.8a[1] (816)	0.0b (0)	33.8c (567)	18.4d (289)
Fall Burn	41.7a (1035)	0.0b (0)	51.1c (1423)	7.2d (189)
Control	38.8a (714)	0.0b (0)	48.5c (975)	12.7d (229)
B. inermis Stand				
Spring Burn	29.3a (507)	0.0b (0)	58.1c (945)	12.6d (219)
Fall Burn	37.8a (726)	0.6b (10)	53.4c (1025)	8.2d (159)
Control	28.8a (567)	0.0b (0)	60.9c (1015)	10.3d (209)
Standard Error	13.6	0.5	19.4	10.9

[1] A different letter within a vegetation category indicates significant ($P \leq 0.05$) differences among means by Tukey's HSD.

Table 5.14 Percentage seedling survival for the burn, glyphosate, inoculation, and planting date interactions for the 1988 and 1989 plantings of *Festuca altaica* subsp. *hallii* in *B. inermis* stands.

Treatments	Inoculated		Not Inoculated		S.E.
	Early Planting	Late Planting	Early Planting	Late Planting	
No Glyphosate			1988		
Spring Burn	28.4a[1]	0.0b	5.5b	0.0b	6.6
Fall Burn	8.4b	0.0b	24.2a	0.0b	
Control	13.9a	0.0b	11.0a	0.0b	
Glyphosate Applied					
Spring Burn	8.3b	0.0b	0.0b	0.0b	
Fall Burn	22.4a	0.0b	8.4b	0.0b	
Control	0.0b	0.0b	5.5b	0.0b	
No glyphosate			1989		
Spring Burn	66.7a	55.7a	83.4a	37.5bc	13.6
Fall Burn	48.7ac	75.0a	50.0ac	33.5bc	
Control	64.0a	26.4bc	15.2bc	19.5bc	
Glyphosate Applied					
Spring Burn	33.4bc	47.2ac	13.9bc	20.5bc	
Fall Burn	66.7a	65.2a	47.2ac	58.4a	
Control	23.7bc	26.8bc	22.2bc	21.9bc	

[1] A different letter within a year indicates significant ($P \leq 0.05$) differences among means by Tukey's HSD..

differences between planting dates. Inoculation with VAM improved seedling survival. When averaged over the plots and both planting dates 50% of the seedlings inoculated with VAM survived compared to 35% for non-inoculated seedlings. The highest rate of survival was 75% for inoculated seedlings planted early in Spring burns and not receiving glyphosate. The minimum survival averaged 23% in Control with and without glyphosate for both the early and late planting dates. Survival was higher on burned plots than in Control, with more seedlings living in the Fall burns treated with glyphosate than in the Spring burns. When no glyphosate was applied seedling survival was greater in the Spring burns. Soil temperatures at the 10 cm planting depth for May 1 planting date were $8.0 \pm 1.7^{o}C$ and for the June 6 planting date were $14.3 \pm 0.7^{o}C$.

The difference in survival between 1987 and 1988 can be explained by environmental factors. After the 1988 planting temperatures reached $35^{o}C$ and no rain was received. In 1989 temperatures were more moderate and rainfall was more plentiful.

Evaluation of characteristics for *F. hallii* grown in the greenhouse in 1989 revealed increased growth when inoculated with VAM (Table 5.15). There were no significant differences in growth characteristics for the 1988 seedlings. This difference could be explained by the degree of infection. The soil used for the non-inoculated seedlings in 1988 had not been sterilized to kill soil organisms. This

Table 5.15 Average growth characteristics for 1988 and 1989 seedlings of *Festuca altaica* subsp. *hallii* inoculated with VAM, grown in a greenhouse.

Parameters	VAM Treatment		S.E.
	Not Inoculated	Inoculated	
----- 1988 ------			
Leaf Height	15.2	15.5	0.7
Leaves/Tiller	4.5	4.5	0.2
Tillers	7.4	7.8	0.3
----- 1989 ------			
Leaf Height	14.1a[1]	16.4b	0.7
Leaves/Tiller	4.6	4.8	0.2
Tillers	5.1a	8.6b	0.4

[1] A different letter within a parameter indicates significant ($P \leq 0.05$) differences among means by Tukey's HSD. No letter indicates no significant differences.

was shown when the seedling roots were analyzed for degree of infection. Although there was a statistical difference in the degree of infection, the non-inoculated seedlings had a VAM infection of 2.5 compared to 4.3 for seedlings grown on inoculated soils. The degree of infection for the 1989 seedlings where the non-inoculated soil had been sterlized averaged 1.2 compared to 4.4 for VAM inoculated. Inoculated seedlings in 1989 had significantly more tillers and were taller than non-inoculated seedlings. There was no significant difference for the number of leaves per tiller for inoculated and non-inoculated seedlings.

6.0 DISCUSSION

6.1 Germination

Harper (1977) stated that the number of individuals in a population depends not only on the availability of seed but on the frequency of "safe sites" that provide the exact conditions for germination and seedling establishment. Understanding the responses of germination under controlled conditions gives a better idea of the limitations to germination of *F. hallii* and *B. inermis* that are imposed by abiotic factors in the field.

Germination of *F. hallii* and *B. inermis* was primarily reduced by osmotic potential. Temperature does not severely restrict the germination of these two species because germination occurred over a broad range of temperatures. This was evident through partitioning the variance of germination where osmotic potential accounted for the largest percentage. Regression analysis for the temperature and osmotic potential interaction for total germination in both *F. hallii* and *B. inermis* showed that germination was primarily controlled by osmotic potential. Romo et al. (1991) also found that water stress severely reduced germination of *F. hallii* especially at the upper and lower limits of the temperatures tested. McGinnies (1960) reported that at -1.5 MPa of water stress *B. inermis* had 30% germination at 20^{o}C. However, at 10 and 30^{o}C and -1.5 MPa of water stress no seeds germinated. Knipe (1973) reported a significant interrelationship in the effect of temperature

and water stress on *Agropyron smithii* germination; an increase in temperature increased the limitations of moisture stress and decreased germination. Romo et al. (1991) concluded that this strong limitation imposed by water stress is an adaptation in *F. hallii* which limits germination to periods of extended available moisture and protects it from germinating under low or transient soil moisture. Harris (1967) also stated that adaptations that enable seedlings of cool season grasses to emerge at a time of the year when there is more favorable moisture is very important for successful establishment. Since the germination of both *F. hallii* and *B. inermis* is restricted primarily by available soil moisture, this explains why *B. inermis* is so well adapted at invading areas that are occupied by *F. hallii*.

Maximum germination for *F. hallii* in this study occurred at 15/15, 15/20, 20/20 and 20/25°C. Romo et al. (1991) reported that maximum germination occurred at 15/15 and 15/20°C for *F. hallii*. In a closely related species, Johnston (1961) found maximum germination for *F. scabrella* was at 13, 18 and 24°C. Young and Evans (1982) also studied *F. scabrella* and found that maximum germination occurred from 15/15 through 20/30.

Maximum germination for *B. inermis* occurred over a much broader range of temperatures than *F. hallii*. Optimal temperatures were 0-15/15, 0-20/20, 0-25/25, and 5-25/30°C. Smoliak and Johnston (1968) evaluated germination for

B. inermis at 7, 13, 18, and 27°C and found germination was equally high at all temperatures with germination most rapid at 18°C. Using alternating temperatures Plummer (1943) found that maximum germination in *B. inermis* occurred at 20/30°C. The range of temperatures for optimal germination in both *F. hallii* and *B. inermis* is similar to that of the *F. hallii* grassland in July and August (Johnston et al. 1971). If moisture conditions are suitable, *B. inermis* is likely to germinate earlier than *F. hallii* because of the ability to germinate at higher temperatures. *Bromus inermis* can also germinate more rapidly than *F. hallii*. Furthermore, if intermittent precipitation is received seeds may germinate and seedlings of *B. inermis* may establish where *F. hallii* may not be able to exploit temporarily favorable moisture conditions.

The reduced germination of *F. hallii* under descending temperatures and declining osmotic potentials relative to the ascending temperatures is an adaptive response to fall conditions in the *F. hallii* grassland. This same response was found for several collections of *F. hallii* (Romo et al. 1991). A lower rate of germination in the fall allows some of the seed to enter the seedbank and possibly germinate in the future when soil moisture conditions and an ascending temperature regime are more favorable for germination and growth of young seedlings.

Bromus inermis did not respond differently to ascending and descending temperature regimes. This difference may

allow high germination in the fall when moisture conditions are favorable. Eddleman and Romo, (1988) stated that for *Centaurea maculosa* the ability to germinate in the fall may give it an competitive advantage by occupying open niches, gaining dominance on the site. This fall germination may be an important competitive strategy for *B. inermis* allowing it to germinate sooner and more rapidly than *F. hallii* and establish and compete with *F. hallii* for available resources. If seeds of *B. inermis* do not germinate in the fall they will pass into the seed bank and they may be available to germinate in the spring. Wilson et al. (1974) noted only a 7% decrease in the germination of *B. inermis* seed stored at winter temperatures and then germinated at 10^{o}C.

In the spring *B. inermis* probably can germinate more rapidly at colder temperatures than *F. hallii*. Wilson et al. (1974) noted that the ability of a species to germinate rapidly at low temperatures gives it a competitive advantage when faced with water stress or competition from other species. Smoliak and Johnston (1968) found that root development in seedlings of *F. scabrella* was best at low temperatures while *B. inermis* had an increase in growth with increasing temperatures. Therefore if spring conditions are cool, seedlings of *F. hallii* will probably establish, but if temperatures become too high, *B. inermis* will have the competitive advantage.

Germination of *F. hallii* was not limited by light.

However, germination in *B. inermis* was higher under darkness than light. Knipe (1973) found that germination of *Agropyron smithii* was independent of light. Other research has shown that germination is increased in the presence of light (Williams, 1983 and Danielson and Toole, 1976). Protected *F. hallii* grassland characteristically has a heavy buildup of dead plant material (Johnston and MacDonald, 1967). Therefore, for optimal germination of *B. inermis* to occur, seed must get under this layer of dead plant material and into darkness. This safe site requirement together with the inability of *B. inermis* to germinate at low osmotic potentials may be an adaptive strategy ensuring that adequate moisture is available and seeds are near the soil surface for germination and seedling establishment. The layer beneath the humus has more available moisture and less fluctuation in temperatures than open bare ground (Johnston et al. 1971). Evans and Young (1970) found that accumulations of humus was a requirement for the establishment of *Bromus tectorum*, an alien invader of native grasslands. On bare ground *B. tectorum* failed to germinate and establish. They concluded that the humus layer modifies the microenvironment of the soil surface within the requirements for germination and seedling establishment of *B. tectorum*. *Bromus inermis's* production of an abundance of highly germinable seed, as compared to *F. hallii* which rarely produces seed (Toynbee, 1987), combined with less restrictive inherent requirements for germination gives

B. inermis a competitive advantage over *F. hallii*.

It may be possible that the competitive germination ability of *B. inermis* could be reduced or minimized with prescribed burning, grazing management, or other means. Burning or grazing can remove the heavy buildup of dead plant material creating a drier microclimate with more light, making it less conducive for the germination of *B. inermis*. Early spring burning of *F. hallii* would increase tillering and improve its competitive ability (Sinton and Bailey, 1980). Hulbert (1986) concluded that where fire is used regularly *B. inermis* is rare in native grassland except where native grasses have been weakened or are absent following fire. Whisenant and Uresk (1990) found that spring burning reduced the potential for germination of *Bromus japonicus* which is also dependent on litter accumulations for germination.

When *F. hallii* seed is available and if *B. inermis* has been eliminated from a site of invasion, Romo et al. (1991) recommended seeding early in the spring when seedbed temperatures are increasing and available soil moisture is optimal.

6.2 Water Relations

No information was found in a review of the literature on the effects of burning on the water relations of *B. inermis*. However, there are results from work on native grasses. Redmann (1978) found that burning in *Agropyron-*

Koeleria faciation of the mixed grass prairie reduced soil moisture and increased water stress in *Agropyron dasystachyum* and *Koeleria cristata*. White and Currie (1983) also noted that soil moisture was less on burned plots than in control.

Soil moisture in this study was reduced by burning following the 1987 burn and was equal to control following the 1988 burn and during the second growing season of the 1987 burn. In the first growing season of 1987 differences in soil moisture may be attributed to reduced snow trap because of a lack of standing dead material on fall burned plots. DeJong and Stewart (1973) and Trlica and Schuster (1969) also reported lower soil moisture on burned areas and attributed this to lower snow cover. However, soil moisture in Spring burned plots was also lower than Control, but were higher than Fall burn. Reduced soil moisture on Spring burns was probably the result of changes in the microclimate with burning (Old, 1969 and Savage, 1980); reduced soil moisture in the Fall burn may have been a function of both lack of snow catchment and microclimatic changes.

Predawn xylem water potentials can be used as an indicator of the impact of burning on water balance because it measures the water status of a plant at a time when it is at equilibrium with available soil moisture (Ritchie and Hinckley, 1975). In the first growing season following the 1987 burn, predawn xylem water potentials were lower for plants in Fall burns than on Spring burns and Control.

Predawn xylem water potentials were also lower for plants in the Fall burn than in Spring burn suggesting that fall burning was even more detrimental to the water status of *B. inermis*. In the second growing season on the 1987 burn no differences in soil moisture were found, however, plants in Control exhibited greater levels of water stress than those that had been burned. Similar relationships were observed for the first growing season of the 1988 burn. Svejcar and Browning (1988), and Knapp (1985) found lower midday xylem water potentials in burned than unburned *Andropgon gerardii*. They concluded that the increase in water stress through the growing season was the result of greater leaf area and higher transpirational demand on burned plots. The present study found slightly higher leaf area indices in burned plots indicating that the transpiring leaf surface was higher than Control early in the growing season (See Sec. 5.3.2).

Midday stomatal conductance was lower in plants that had been burned than those that were not burned. In contrast, Knapp (1985) found that burning increased stomatal conductance in *Andropogon gerardii*. He concluded this was the result of a greater internal-to-external leaf area ratio caused by increased leaf thickness with burning. In this study the decrease in stomatal conductance with burning was probably the result of a decrease in available soil moisture with changes in the microclimate with burning.

No consistent differences were found in soil moisture

or plant water relations parameters between Spring and Fall burns. Therefore, no statements can be made as to whether fall or spring burning of *B. inermis* alters its water status in a positive or negative manner; responses to burning expressed in water relations are unique to each site, burn, year, and time elapsed since burning.

6.3 Population Dynamics

6.3.1 Effects of Burning and Glyphosate on *Bromus inermis* and Native Flora

The effects of fire on *Festuca* grasslands are highly complex and depend on several variables (Bailey, 1978). Bailey and Anderson (1978) found that spring burning was more detrimental to *F. scabrella* than fall burning in central Alberta. Canopy cover of *F. scabrella* was reduced by 26% in Spring burns and 6% in Fall burns. The Spring burn was conducted when *F. scabrella* had 10 cm of green growth. Sinton and Bailey (1980) concluded that mid-spring burning after *F. scabrella* had initiated growth was more detrimental than burning after snow melt.

The present study found that fall burning was more detrimental to *F. hallii* than spring burning. Spring burns were conducted in the spring when *F. hallii* was still dormant and the humus layer was still moist. There may have been minimal effect of the fire on the crowns of *F. hallii* at this time. Fall burns were conducted after *F. hallii* was dormant. The lack of snow cover on Fall burn plots during

the winter may have exposed crowns to low temperature damage, and soil moisture may have been low early in the spring. Anderson and Bailey (1980) found that early spring burning reduced canopy coverage of *F. scabrella* by 18%, but frequency increased by 17%. They concluded that overall production of *F. scabrella* was not reduced because of the increase in tillering. Antos et al. (1983) concluded that the effect of fire on *F. scabrella* depended upon the size of clumps of dead plant material. Plants with large clumps burned slower with higher temperatures and more damage was done to the crown than smaller clumps.

Tiller densities for the native graminoids were severely reduced with fall burning as compared to spring burns. Similar results have been reported in other studies. Bailey and Anderson (1978) found that canopy coverage was reduced in *Agropyron trachycaulum* and *A. subsecundum* when burned in the spring when plants were actively growing. Bailey and Anderson (1978) also found that cover for *Stipa spartea* was reduced by fall burning, but it was not altered by spring burning. Anderson and Bailey (1980) reported that frequency of *S. spartea* was higher in annually burned areas, but cover was reduced. Spring burning was more detrimental to *Carex spp.* than fall burning (Bailey and Anderson, 1978). Canopy cover of *Carex spp.* was reduced 10% as compared to fall burning. After a wildfire in August in an *Agropyron-Koeleria* faciation of the mixed prairie association, Coupland (1973) found that the productivity of *Agropyron*

dasystachyum was reduced by 19%, *Carex* spp. increased by 36% and *Stipa viridula* increased by 45% the year following burning.

Fire did not affect stem densities for both native and exotic forbs in this study. However, Bailey and Anderson (1978) found that *Geum triflorum*, *Astragalus striatus*, *Achillea millefolium* and *Antennaria nitida* increased in frequency and cover with spring burning. The differences are in part the result of differences in criteria used to evaluate plant responses.

Burning alone did not reduce tiller densities of *B. inermis* in this study. Other research has shown different results on the effect of burning on *B. inermis*. Kirsch and Kruse (1972) reported at least a 50% reduction in cover of *B. inermis* following a spring burn in the mixed grass prairie in North Dakota. Anderson and Bailey (1980) compared species composition in unburned grasslands and an area that was burned annually in the spring in central Alberta. Frequency and canopy cover for *B. inermis* were lower in the burned area than in the unburned area. In the present study the different effect of burning on *B. inermis* can be explained by different timing of burns, different environmental factors and also different methods in the measurement of the data.

Glyphosate is effective for controlling *B. inermis* (Waller and Schmidt, 1983 and Rodney and Kirby, 1991); however, Rodney and Kirby (1991) showed that when glyphosate

was applied nonselectively it killed many native graminoids. The wicking application of glyphosate in this study was effective in applying glyphosate to *B. inermis* and minimizing effects on the native species in the stand.

There are several possible explanations for the greater control of *B. inermis* with the combination of spring burning and application of glyphosate. First, spring burning increased the height differentiation between *B. inermis* and the associated native species allowing for more glyphosate to be applied to *B. inermis* and less to the native species. Secondly, plants in the spring burns had higher leaf area indices at the time of the glyphosate application resulting in a better leaf to wick contact and a higher rate of glyphosate application. Thirdly, in the spring burns *B. inermis* was also more actively growing than in Fall burns and Control resulting possibly in a better translocation of the glyphosate throughout the plant. Fourthly, spring burning may have physiologically weakened the plant because of a reduction in carbohydrates used in initiating the rapid early growth after burning and, fifthly, a combination of two or more of the above reasons. Fall burns and Control were also slower in activating growth in the spring than the Spring burns. Therefore there may have been tillers of *B. inermis* that did not receive glyphosate resulting in poorer control. Growth in Fall burns was slower because of lower available moisture early in the spring because of lack of snow cover in winter while Control plots were insulated

from incoming solar radiation because of an accumulation of dead plant material (Wright and Bailey, 1982).

Results of this study suggest that early spring burning is recommended over fall burning for managing *F. hallii* grassland because it increased the effectiveness of the glyphosate application for controlling *B. inermis* and was less detrimental to the associated native flora than fall burning.

When species richness and diversity indices are considered there was no difference between *F. hallii* and *B. inermis* stands. Apparently when *B. inermis* invades and colonizes a *F. hallii* stand it tends to suppress *F. hallii* and displaces it in the stand. According to Gause's principle of "Competitive Exclusion" if two species cannot coexist then they are complete competitors (Forman and Godron, 1986; Harper, 1977). Therefore *F. hallii* and *B. inermis* appear to occupy the same ecological niche and are in competition for the same resources. This ecological overlap explains why *B. inermis* invasions are so detrimental to the *F. hallii* grassland. Furthermore, *B. inermis* is more capable of displacing *F. hallii* when plants of *F. hallii* are weakened by a buildup in dead plant material and death of tillers or other disturbances.

6.3.2 Effects of Burning on Growth of *Bromus inermis*

Limited research had been done on the effect of burning on the growth of *B. inermis*. Old (1969) found that the

productivity of *B. inermis* was reduced the first growing season following early spring burning, it increased by the third growing season, declining thereafter. One possible explanation for different results from the present study is that Old's work was done in the tall grass prairie which is dominated by warm season grasses. *Bromus inermis* is a cool season grass, therefore if the area was burned in spring the warm season grasses have not begun growing and they are given a competitive advantage over *B. inermis*. On a mixed grass prairie in North Dakota, Kirsch and Kruse (1972) reported that there was a 50% reduction in the canopy coverage of *B. inermis* following spring burning.

Changes in the growth of *B. inermis* in this study can be explained by the indirect effects of burning which change the microclimate of the site. Unburned areas have a dense accumulation of dead plant material which insulates the crown of grasses from incoming solar radiation (Old, 1969; Penfound and Kelting, 1950; and Peet et al., 1975). Burning blackens the soil surface, increases incoming soil radiation and as result soil temperatures are higher than on unburned areas (Old, 1969 and Ehrenreich and Aikman, 1963). The increase in solar radiation and soil temperature with burning promoted earlier and greater growth of *B. inermis*. Differences in growth between treatments later in the growing season were less, possibly because available soil moisture on burned plots was quickly depleted both through plant use and increased evaporation.

Burning did not adversely affect the growth of *B. inermis* in this study. Generally there were increased stem densities, higher leaf area indices, and higher biomass production with burning early in the growing season, with differences between burn treatments becoming less pronounced through the growing season. However, in the second year of burning no differences were found over the growing season. Results from this study suggest that a single spring burn may enhance the spread and dominance of *B. inermis* in *F. hallii* grasslands and that other control measures must be incorporated.

6.3.3 Seed Bank Composition

The seedlings from the seed bank did not closely match the plant population from which they were taken. Such dissimilarities have also been noted by Archibold (1981), Chippendale and Milton (1934), and Major and Pyott (1966). A possible explanation for this is that in perennial grasslands vegetative reproduction is a more important mode of maintenance than by regeneration from seed. Other factors such as induced dormancy and loss of viability are also important (Harper, 1977). Harper (1977) states that the buried seed populations in a climax community tend to reflect the earlier successional stages of that system. The cultivated land that surrounds the study site may also have had an impact on seed bank composition, particularly with exotic forbs. Archibold (1981) found that in cultivated

lands 60% of the seed in the seed bank was composed of exotic forbs.

Archibold (1981) found an average of 1,500 seeds per m^2 in a *F. hallii* grassland in Saskatchewan. In a mixed grass prairie of the Great Plains, Lippert and Hopkin (1950) reported low seed banks of 300 to 800 seed per m^2. An average of 40 seeds per m^2 of *F. hallii* seeds were found in the seed bank in the present study. This number is very low, however, but because *F. hallii* infrequently produces seed (Johnston and MacDonald, 1967; Toynbee 1987) this could be considered high and important in the maintenance of this species. Johnston et al. (1969) found that the seedbank for the closely allied *F. scabrella* averaged 846 seeds per m^2.

Rabotonov (1956) found that in a Russian grassland dominated by *B. inermis* the seed bank contained 280-2450 seed per m^2. The relatively low number of *B. inermis* seeds found in the seed bank indicates that this species, with its high seed production, is a minor component of the seed bank. The seeds either germinate, decompose or are predated. However, in most landscapes there is extremely high potential for the continual import of *B. inermis* seed from surrounding areas because it is grown extensively for forage production and for road side revegetation (Romo et al., 1990). With an average of 1,600 seeds per m^2 of native species in *B. inermis* stands, the seed bank is an important component for successional changes towards a desirable vegetation cover after *B. inermis* is controlled.

6.3.4 Establishment of *Festuca altaica* subsp. *hallii* Seedlings

No literature was found on the effect of VAM on the growth of *F. hallii,* except that VAM is present (Molina et al., 1978). The increase in tillering and plant height in this study may be explained by the potential for increased uptake of P and N and by improved water relations. *Festuca ovina* seedlings were better able to take P up when seedlings possessed mycorrhizae (Whittingham and Read, 1982). The increase in the uptake of P enabled a three-fold increase in biomass production over nonmycorrhizal plants. It has also been demonstrated that VAM can increase the uptake of N from the soil into the plant and therefore increase growth of the host plant (Bagyaraj et al., 1979; Barea et al., 1987; Hall et al., 1984; Ho and Trappe, 1975; Trappe and Fogel, 1977). Ho and Trappe (1975) found that when *Festuca occidentalis* was inoculated with VAM it was capable of reducing nitrate to nitrite. Allen et al. (1981) found that *Bouteloua gracilis* inoculated with VAM had transpiration rates that were 100% greater and 20-50% lower leaf resistances to water vapor diffusion. Bildusas et al. (1986) also found that VAM improved the water status of *B. inermis*. Goodwin (1992) concluded that the improved water relations of plants associated with VAM is probably one of the most important benefits especially on rangelands where water is the most limiting factor.

Allen and Allen (1984) found that mycorrhizae improved the competitive ability of *Agropyron smithii* and *Bouteloua gracilis* when grown with *Salsola kali*, a nonmycorrhizal species. Biomass production for the grasses increased nearly 25% and stomatal conductances were three times higher than plants without mycorrhiza, while *S. kali* had reduced biomass and stomatal conductance.

If seedlings could develop a mycorrhizal association with nearby mature plants, then assimilates from the mature plant could pass via mycorrhizae to the developing seedlings and subsidize the growth requirements of seedlings (Goodwin, 1992). VAM then would help improve the success of establishment of grasses.

It is very difficult to make comparisons with other research when looking at the effects of VAM on plants because of differences in the host plant, the symbiotic fungus and, the environment. However, it is apparent at least for one year, VAM improved survival and there was improved growth in the greenhouse for *F. hallii*.

7.0 SUMMARY AND CONCLUSIONS

This study was designed to elucidate the ecological relations of *B. inermis* and *F. hallii* in a *F. hallii* grassland in central Saskatchewan. The objectives were to: 1) determine growth and water relations of *B. inermis* following burning; 2) determine the effects of the combined application of fall or spring burning and glyphosate for controlling *B. inermis* and releasing the native flora; 3) ascertain the survival of containerized seedlings of *F. hallii* inoculated with vesicular arbuscular mycorrhizae (VAM) versus nontreated seedlings that were planted in Control plots dominated by *B. inermis* and plots treated with glyphosate to control *B. inermis*; 4) determine the effects of VAM inoculation on the growth of *F. hallii* seedlings; 5) determine the composition of the seedbank as a factor influencing successional changes following the control of *B. inermis*; 6) compare germination of *B. inermis* and *F. hallii* under varying temperatures, levels of water stress, and light regimes, and; 7) from these studies propose management strategies for controlling *B. inermis* and re-establishing *F. hallii* on areas previously dominated by the exotic perennial.

Seeds of *F. hallii* and *B. inermis* collected from the study site in 1987 and 1988 were subjected to different levels of temperature and water stress, ascending and descending temperatures in a gradient of osmotic potentials,

light and darkness, and 55 constant and alternating temperature regimes. Total germination and rate of germination of *F. hallii* were highest at temperatures near 15°C with low levels of water stress. Germination was severely restricted by water stress. *B. inermis* had greater and more rapid germination over a broader range of temperatures and water stress than *F. hallii*. Total germination and germination rate were reduced for *F. hallii* under temperatures decreasing from 25 to 5°C than under temperatures ascending from 5 to 25°C. Generally, there was no difference in germination of *B. inermis* for ascending and descending temperature regimes. Light did not adversely affect germination in *F. hallii*, however germination was higher for *B. inermis* in dark than in light.

Predawn and midday xylem water potentials, osmotic potentials, relative water content and soil moisture were measured throughout the growing season on *B. inermis* stands on Spring and Fall burns and Control in 1987 and 1988. In 1987 soil moisture was lower on burned plots than in Control. In 1988 there were no differences in soil moisture between treatments. Predawn and midday xylem water potentials were lower for plants in Fall burns than spring burns and Control in 1987. In 1988 this was reversed where plants in spring burns had lower xylem water potentials than in Fall or Control. Osmotic potentials, relative water content and stomatal conductances were lower for Fall burns in 1987 and in the second growing season this was reversed.

In 1988 osmotic potentials, relative water content and stomatal conductances were similar among treatments.

Stem densities were determined in permanent microplots prior to treatment in both *F. hallii* and *B. inermis* stands to determine the effects of burning and glyphosate on population dynamics. No differences were found prior to treatment. Densities of native forbs, exotic forbs and shrubs were not affected by burning or application of glyphosate. Generally fall burning reduced tiller densities of native graminoids and *F. hallii*. Tiller densities of native graminoids did not change significantly following spring burning but there was an increase in tiller densities of *F. hallii* with spring burning. Tiller densities of native graminoids and *F. hallii* were slightly reduced following glyphosate application in all plots. There was a burn x glyphosate interaction for the reduction of tiller densities of *B. inermis*. Following spring burning and glyphosate application tiller numbers for *B. inermis* were reduced most followed fall burning combined with glyphosate.

Burning did not adversely affect the growth of *B. inermis*, but the effects of burning were dependent upon year of burn. In 1988 burning had no impact on growth of *B. inermis*. Stem densities in the 1987 burns were generally higher on burned plots than Control the first growing season following burning. Leaf area indices following burning were generally higher on spring burns than on Fall burns and Control. Biomass production was greatest for spring burns

and there was no carryover effect of burning on growth in the second growing season.

Seed bank composition was determined for both the *F. hallii* and *B. inermis* stands in all plots prior to burning in 1987. *B. inermis* seed was found only in the *B. inermis* stand of the Fall burn where it represented less that 1% of the total seedbank. The seedbank was composed primarily of native graminoids and forbs. An average of 1,700 native seeds per m^2 were found in the soil. The number of seeds in the seedbank was generally equal between stand types. Exotic forbs were also represented in the seedbank, presumably coming from the surrounding cultivated lands.

Seeds of *F. hallii* collected from the study site in 1987 were used to produce seedlings in the greenhouse to study the effect of VAM inoculation and planting date on seedling survival when transplanted to sites previously dominated by *B. inermis*. Seedling survival was highest from the early spring planting in 1988. In 1989 seedlings inoculated with VAM had a better survival; survival was also generally better on burned plots than on Control. Seedlings grown in the greenhouse had more tillers and were taller when inoculated with VAM.

It must be kept in mind when drawing conclusions from this and other studies that examining the effect of burning and herbicides on flora that many factors can affect plant responses. The degree of invasion of *B. inermis*, the ecological condition of the native grassland, timing of

burns, fuel loads, environment and the method and accuracy that herbicides are applied and their interactions can all affect the final response.

Conclusions derived from this study are:

1. A single burn cannot be viewed as a single method for controlling *B. inermis* in *F. hallii* grassland.
2. The combined use of spring burning and wicking application of glyphosate can control *B. inermis* where it has recently invaded *F. hallii* grasslands. Follow up applications of glyphosate will probably be needed to completely control the vegetative reproduction in *B. inermis*.
3. Spring burning is less detrimental to the native flora than fall burning.
4. Spring burning promoted tillering of *F. hallii* while tillering was reduced following fall burning.
5. *Festuca hallii* seedlings inoculated with VAM had greater survival, more tillers and were taller than non-inoculated seedlings.
6. The seedbank in a grassland invaded by *B. inermis* contained a sufficient supply of native propagules to aid in successional changes toward a native grassland community following the control of *B. inermis*.
7. Temperatures near 15^{o}C appear to be the optimal for germination of *F. hallii* under low levels of water stress; high temperatures and high levels of water stress greatly

reduce the rate of germination.

8. A higher rate of germination in *F. hallii* can be expected in the spring when seedbed temperatures are warming rather that in autumn when they are cooling; soil moisture is also generally more favorable in the spring. Therefore spring seeding of *F. hallii* is recommended for revegetation.

9. The low number of *B. inermis* seeds in the seedbank indicates that new seeds readily germinate, reducing the need for extended years of control once the vegetative growth is controlled.

10. The higher and more rapid rate of germination of *B. inermis* over a broader range of temperatures at higher levels of water stress indicates that it has the competitive advantage over *F. hallii* when establishing from seed.

11. Sources of *B. inermis* seed around *F. hallii* grasslands which are being preserved should be reduced with mowing or other means to restrict seed production or the *B. inermis* should be removed with glyphosate and desirable native grasses seeded.

12. Spring burning can be used to improve the vigor of *F. hallii* grasslands that have a heavy buildup of plant litter and are being threatened with invasion by *B. inermis*. The burning will help stimulate tillering in *F. hallii* and reduce the moist conditions that exist under the humus layer, reducing the chance for germination of *B. inermis* because of increased light and increased water stress.

13. Proactive management strategies must be employed to

limit invasions by *B. inermis* and enhance the vigor of *F. hallii* to preserve *F. hallii* grasslands for future generations.

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APPENDIX

Table A1 General layout of burn plots and *B. inermis* stands for the population dynamics study at Kernen Prairie.

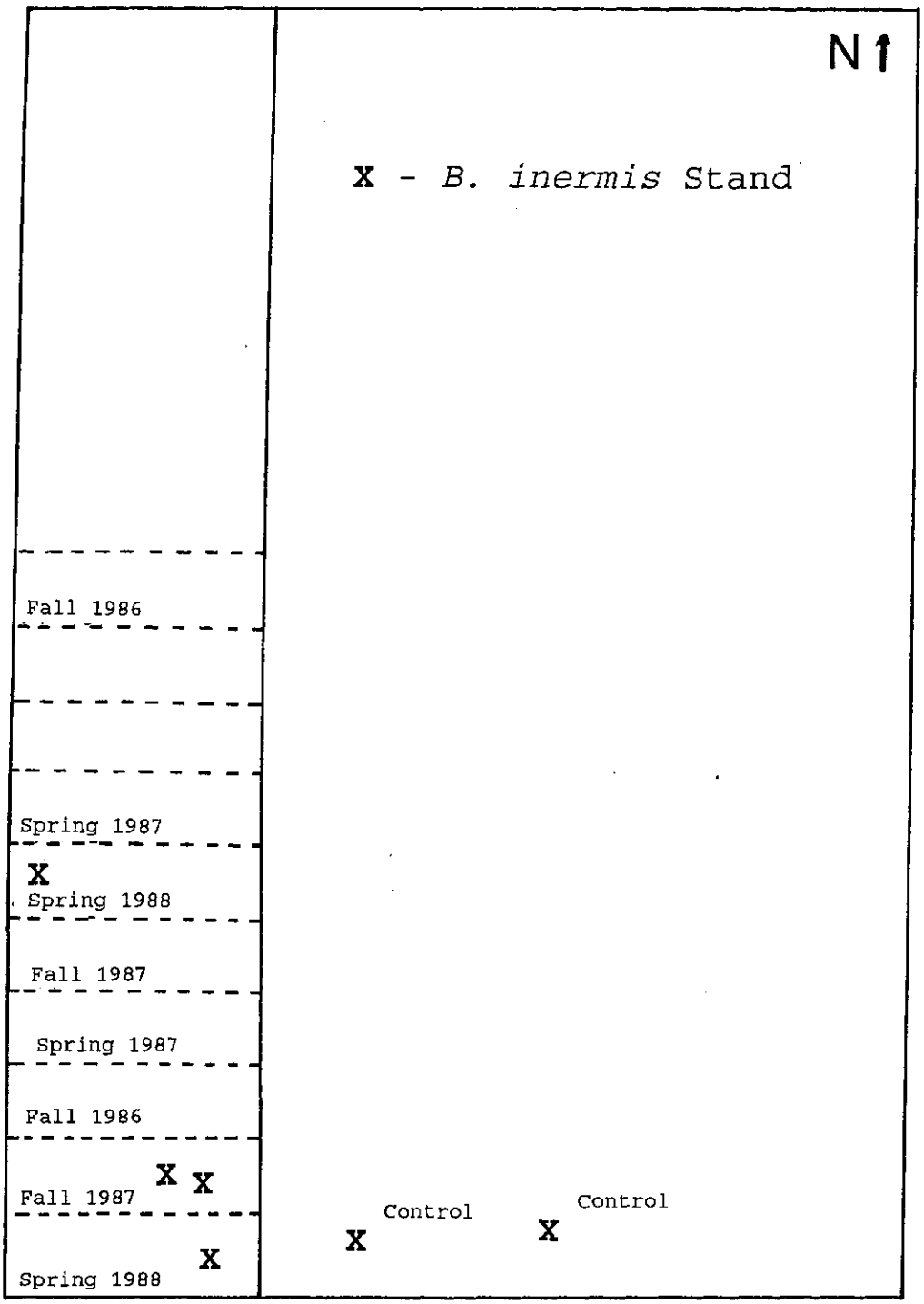

Table A2 Meteorological conditions in the hour preceding experimental burns at Kernen Prairie (Source: Redmann unpubl. manuscript).

Date	Time C.S.T.	Temp ^{o}C	R.H. %	Wind Speed km h^{-1}	Wind Direction deg
1986 October 17	15:10	20	37	15	180
1986 October 22	15:25	15	51	6	150
1987 April 28	13:30	23	23	15	360
1987 May 6	10:30	15	39	4	270
1987 October 14	14:40	8	46	7	110
1987 October 14	17:50	9	40	20	110
1988 April 20	16:10	5	28	11	010
1988 April 20	17:40	6	24	13	090

Table A3 Fuel supply determined from total aboveground biomass harvested from control plots on spring or fall dates close to dates of experimental burns. Mean (g m^{-2}) and standard deviation of eight quadrats clipped in each grassland type. (Source: Redmann unpubl. manuscript).

Harvest Date	F. Hallii	Stipa-Agropyron
October 1986	---	298 ±114
May 1987	379 ±68	317 ±71
September 1987	510 ±169	324 ±99
May 1988	489 ±144	339 ±74
Mean	459	320

Table A.4 Stem densities (0.10 m^2) for the burn, glyphosate and stand type sampled on August, 1987 - Preburn.

Species	Treatments											
	No Glyphosate						Glyphosate Applied					
	F. hallii Stand			*B. inermis* Stand			*F. hallii* Stand			*B. inermis* Stand		
	Spring	Fall	Control	Spring	Fall	Control	Spring	Fall	Control	Spring	Fall	Control
Native Graminoids												
Agropyron albicans	2	0	0	0	0	0	0	0	0	0	0	0
Agropyron dasystachyum	37	51	7	5	13	4	67	33	14	6	9	3
Agropyron smithii	0	4	1	1	4	1	3	3	4	1	2	1
Agropyron subsecundum	5	1	0	1	0	1	1	1	1	0	0	1
Carex spp.	81	67	32	80	77	25	109	35	23	84	94	19
Helictotrichon hookeri	0	0	0	0	0	0	0	3	0	1	0	1
Koeleria cristata	0	0	0	0	0	0	3	1	0	2	0	0
Poa cusickii	3	0	0	0	0	0	17	0	0	0	0	0
Stipa curtiseta	37	19	40	6	21	17	53	28	31	15	7	9
F. hallii												
Festuca altaica subsp. *hallii*	107	186	119	20	6	62	18	187	143	3	66	15
B. inermis												
Bromus inermis	0	0	0	32	21	14	0	0	0	32	27	19

Table A.4 (*Concluded*)

Species	Treatments											
	No Glyphosate						Glyphosate Applied					
	F. hallii Stand			*B. inermis* Stand			*F. hallii* Stand			*B. inermis* Stand		
	Spring	Fall	Control	Spring	Fall	Control	Spring	Fall	Control	Spring	Fall	Control
Native Forbs												
Achillea millefolium	1	1	2	0	0	0	0	1	0	1	0	1
Androsace septentrionalis	0	0	0	0	0	0	0	0	0	0	0	0
Anemone patens	0	1	1	0	0	1	0	1	1	0	0	0
Artemisia frigida	0	0	1	0	0	0	0	0	0	1	4	1
Artemisia ludovinciana	2	1	1	1	1	1	1	1	3	1	1	0
Aster ericoides	0	1	2	0	1	0	0	0	0	0	1	0
Galium boreale	11	1	1	1	1	0	0	3	0	0	0	0
Geum triflorum	0	1	0	0	0	0	0	0	0	0	4	0
Heuchera richardsonii	0	0	0	0	0	0	0	0	0	0	0	0
Selaginella densa	0	0	0	0	0	0	0	0	0	2	0	0
Solidago missouriensis	1	0	0	0	1	0	0	0	0	0	0	0
Exotic Forbs												
Descurainia sophia	0	0	0	0	0	0	0	0	0	0	0	0
Salsola kali	0	0	0	0	0	0	0	0	0	0	0	0
Thalspi arvense	0	0	0	0	0	0	0	0	0	0	0	0
Shrubs												
Rosa arkansana	0	0	1	0	0	1	0	1	1	0	1	1
Symphoricarpos occidentalis	1	0	0	0	0	0	0	0	0	0	0	0

Table A.5 Stem densities (0.10 m^2) for the burn, glyphosate and stand type sampled on May, 1988 - Postburn.

Species	Treatments											
	No Glyphosate						Glyphosate Applied					
	F. hallii Stand			*B. inermis* Stand			*F. hallii* Stand			*B. inermis* Stand		
	Spring	Fall	Control	Spring	Fall	Control	Spring	Fall	Control	Spring	Fall	Control
Native Graminoids												
Agropyron albicans	1	0	0	0	0	0	0	0	0	0	0	0
Agropyron dasystachyum	34	32	6	4	9	5	61	19	10	4	4	3
Agropyron smithii	0	3	1	1	2	1	2	3	4	2	1	1
Agropyron subsecundum	4	1	0	1	0	1	1	1	1	0	0	0
Carex spp.	63	39	37	85	39	23	108	24	20	82	54	17
Helictotrichon hookeri	0	0	0	0	0	0	0	2	0	1	0	0
Koeleria cristata	0	0	0	0	0	0	2	1	0	1	0	0
Poa cusickii	2	0	0	0	0	0	9	0	0	0	0	0
Stipa curtiseta	31	17	36	4	16	16	38	21	27	15	10	7
F. hallii												
Festuca altaica subsp. *hallii*	142	72	115	43	2	51	33	116	141	1	18	10
B. inermis												
Bromus inermis	0	0	0	34	14	14	0	0	0	38	19	18

Table A.5 (*Concluded*)

Species	Treatments											
	No Glyphosate						Glyphosate Applied					
	F. hallii Stand			*B. inermis* Stand			*F. hallii* Stand			*B. inermis* Stand		
	Spring	Fall	Control	Spring	Fall	Control	Spring	Fall	Control	Spring	Fall	Control
Native Forbs												
Achillea millefolium	1	0	0	0	0	0	0	1	0	1	0	1
Androsace septentrionalis	0	0	0	0	0	0	0	0	0	0	0	0
Anemone patens	0	0	1	0	0	1	0	1	1	0	0	0
Artemisia frigida	0	0	1	0	0	0	0	0	0	1	2	1
Artemisia ludovinciana	2	1	1	2	1	1	1	1	2	2	1	0
Aster ericoides	0	1	2	0	1	0	0	0	0	0	0	0
Galium boreale	11	1	1	2	1	0	0	1	0	0	0	0
Geum triflorum	0	1	0	0	0	0	0	0	0	0	4	0
Heuchera richardsonii	0	0	0	0	0	0	0	0	0	0	0	0
Selaginella densa	0	0	0	0	0	0	0	0	0	1	0	0
Solidago missouriensis	1	0	0	0	1	0	0	0	0	0	0	0
Exotic Forbs												
Descurainia sophia	0	0	0	0	0	0	0	0	0	0	0	0
Salsola kali	0	0	0	0	0	0	0	0	0	0	0	0
Thalspi arvense	0	0	0	0	0	0	0	0	0	0	0	0
Shrubs												
Rosa arkansana	0	0	1	0	0	1	0	1	1	0	1	1
Symphoricarpos occidentalis	1	0	0	0	0	0	0	0	0	0	0	0

Table A.6 Stem densities (0.10 m^2) for the burn, glyphosate and stand type sampled on September, 1988 - Postglyphosate.

Species	Treatments											
	No Glyphosate						Glyphosate Applied					
	F. hallii Stand			*B. inermis* Stand			*F. hallii* Stand			*B. inermis* Stand		
	Spring	Fall	Control	Spring	Fall	Control	Spring	Fall	Control	Spring	Fall	Control
Native Graminoids												
Agropyron albicans	1	0	0	0	0	0	0	0	0	0	0	0
Agropyron dasystachyum	34	48	7	5	14	7	34	5	6	1	1	1
Agropyron smithii	0	4	1	1	3	1	2	2	1	2	1	0
Agropyron subsecundum	4	1	0	1	0	1	1	2	1	0	0	1
Carex spp.	72	51	42	87	60	22	93	10	17	7	7	0
Helictotrichon hookeri	0	0	0	0	0	0	0	1	0	0	0	1
Koeleria cristata	0	0	0	0	0	0	2	1	0	2	0	0
Poa cusickii	2	0	0	0	0	0	5	0	0	0	0	0
Stipa curtiseta	28	22	43	5	24	17	44	6	13	9	0	0
F. hallii												
Festuca altaica subsp. *hallii*	143	117	117	15	4	46	34	143	67	0	56	8
B. inermis												
Bromus inermis	0	0	0	35	24	15	0	0	0	0	7	10

Table A.6 (*Concluded*)

Species	Treatments											
	No Glyphosate						Glyphosate Applied					
	F. hallii Stand			*B. inermis* Stand			*F. hallii* Stand			*B. inermis* Stand		
	Spring	Fall	Control	Spring	Fall	Control	Spring	Fall	Control	Spring	Fall	Control
Native Forbs												
Achillea millefolium	1	0	3	0	0	0	0	1	0	1	0	0
Androsace septentrionalis	0	0	0	0	0	0	1	0	0	1	1	2
Anemone patens	0	0	1	0	0	1	0	0	1	0	0	0
Artemisia frigida	0	0	1	0	0	0	0	0	0	4	1	1
Artemisia ludovinciana	2	2	1	2	1	1	1	1	5	3	1	0
Aster ericoides	0	2	2	0	1	0	0	1	0	0	0	0
Galium boreale	12	1	1	2	1	0	0	1	0	0	0	0
Geum triflorum	0	1	0	0	0	0	0	0	0	0	1	0
Heuchera richardsonii	0	0	0	0	0	0	0	0	0	0	2	2
Selaginella densa	0	0	0	0	0	0	0	0	0	1	0	0
Solidago missouriensis	1	0	0	0	1	0	0	0	0	0	0	0
Exotic Forbs												
Descurainia sophia	0	0	0	0	0	0	0	0	0	0	1	2
Salsola kali	0	0	0	0	0	0	0	0	0	0	0	0
Thalspi arvense	0	0	0	0	0	0	0	0	0	0	0	1
Shrubs												
Rosa arkansana	0	0	1	0	0	1	0	1	1	0	1	1
Symphoricarpos occidentalis	1	0	0	0	0	0	0	0	0	0	0	0

Table A.7 Stem densities (0.10 m^2) for the burn, glyphosate and stand type sampled on August, 1989.

Species	Treatments											
	No Glyphosate						Glyphosate Applied					
	F. hallii Stand			*B. inermis* Stand			*F. hallii* Stand			*B. inermis* Stand		
	Spring	Fall	Control	Spring	Fall	Control	Spring	Fall	Control	Spring	Fall	Control
Native Graminoids												
Agropyron albicans	2	0	0	0	0	0	0	0	0	0	0	0
Agropyron dasystachyum	35	53	6	5	12	5	48	9	9	2	1	2
Agropyron smithii	0	4	1	1	4	2	2	4	3	5	1	0
Agropyron subsecundum	7	2	0	0	0	1	2	2	1	1	0	1
Carex spp.	87	64	50	97	64	22	100	13	23	15	8	2
Helictotrichon hookeri	0	0	0	0	0	0	0	2	0	2	0	5
Koeleria cristata	0	0	0	0	0	0	2	1	0	2	0	0
Poa cusickii	2	0	0	0	0	0	10	0	0	2	0	0
Stipa curtiseta	39	22	43	5	24	17	57	7	20	15	1	0
F. hallii												
Festuca altaica subsp. *hallii*	128	191	111	18	7	52	27	208	84	0	29	8
B. inermis												
Bromus inermis	0	0	0	33	22	17	0	0	0	1	9	13

Table A.7 (*Concluded*)

Species	Treatments											
	No Glyphosate						Glyphosate Applied					
	F. hallii Stand			*B. inermis* Stand			*F. hallii* Stand			*B. inermis* Stand		
	Spring	Fall	Control	Spring	Fall	Control	Spring	Fall	Control	Spring	Fall	Control
Native Forbs												
Achillea millefolium	1	0	4	0	0	0	0	1	0	3	0	1
Androsace septentrionalis	0	0	0	0	0	0	1	0	0	2	2	1
Anemone patens	0	0	2	0	0	1	0	1	1	0	1	0
Artemisia frigida	0	0	2	0	0	0	1	0	2	13	6	5
Artemisia ludovinciana	3	4	1	2	3	2	1	1	5	8	2	0
Aster ericoides	0	4	5	0	1	0	0	2	0	0	0	0
Galium boreale	12	1	2	2	1	0	0	2	0	0	0	0
Geum triflorum	0	1	0	0	0	0	0	0	0	0	7	0
Heuchera richardsonii	0	0	0	0	0	0	0	0	0	0	2	3
Selaginella densa	0	0	0	0	0	0	0	0	0	1	0	0
Solidago missouriensis	1	0	0	1	2	0	0	0	0	1	0	0
Exotic Forbs												
Descurainia sophia	0	0	0	0	0	0	0	0	0	1	1	9
Salsola kali	1	0	0	0	0	0	0	0	0	1	0	1
Thalspi arvense	0	0	0	0	0	0	1	0	0	1	0	0
Shrubs												
Rosa arkansana	0	0	1	0	1	1	0	1	1	0	1	1
Symphoricarpos occidentalis	1	0	0	0	0	0	0	0	0	0	0	0

Table A.8 Mean number of seedlings per square meter in seedbank.

	Vegetation Categories					
	F. halli Stand			*B. inermis* Stand		
	Spring	Fall	Control	Spring	Fall	Control
Native Graminoids						
Agropyron dasystachyum	55	18	7	0	9	40
Agropyron smithii	66	9	27	9	27	20
Agropyron subsecundum	0	9	7	0	0	0
Agrostis scabra	11	0	33	0	0	299
Carex spp.	88	235	192	81	90	40
Festuca altaica subsp. *hallii*	11	54	106	0	18	0
Helictotrichon hookeri	0	0	7	9	0	0
Koeleria cristata	0	9	0	0	0	20
Muhlenbergia richardsonis	254	9	13	289	0	20
Poa cusickii	11	525	20	9	434	40
Stipa curtiseta	111	100	106	18	36	
Exotic Graminoids						
Bromus inermis	0	0	0	0	9	0
Native Forbs						
Achillea millefolium	22	27	0	0	0	0
Androsace septentrionalis	343	1121	869	705	579	637
Artemisia frigida	117	127	226	116	137	219
Astragalus flexuosus	0	0	0	0	9	0
Erysimum inconspicuum	11	27	13	36	9	0
Geum triflorum	0	0	7	0	0	0
Sonchus oleraceus	66	63	93	18	63	100
Exotic Forbs						
Amaranthus retroflexus	11	18	0	18	0	0
Capsella bursa-pastoris	11	0	7	9	0	0
Chenopodium album	33	0	0	18	0	0
Descurainia sophia	188	163	126	163	100	179
Stellaria media	0	9	0	0	0	0
Thalspi arvense	22	0	0	0	0	0
Total	1411	2532	1859	1498	1520	1614