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THE EFFECT OF SHORT DURATION GRAZING AND REST ON THE SEED BANK AND SEED RAIN ON A TRANSITIONAL MIXED PRAIRIE/FESCUE GRASSLAND

by

ROBIN LYNNE LAGROIX-McLEAN

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE

OF MASTER OF SCIENCE

IN

RANGE SCIENCE

DEPARTMENT OF PLANT SCIENCE

EDMONTON, ALBERTA

SPRING 1990

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DEGREE: MASTER OF SCIENCE

YEAR DEGREE GRANTED: 1990

R Lagroix-McLean

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DATED January 9, 1990

Apprentice yourself to nature.
Not a day will pass without
her opening a new and wondrous
world of experience to learn from
and enjoy.

Richard W. Langer

"Some seeds fell by the way side, . . . some fell upon stony places, . . .
and some fell among thorns; . . . but other fell into good ground."

The Bible
St. Matthew's gospel
Chapt. 13

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled THE EFFECT OF SHORT DURATION GRAZING AND REST ON THE SEED BANK AND SEED RAIN IN A TRANSITIONAL MIXED PRAIRIE/FESCUE GRASSLAND submitted by ROBIN LYNNE LAGROIX-M^CLEAN in partial fulfillment of the requirements for the degree of MASTER OF SCIENCE in RANGE SCIENCE.

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Supervisor

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Date December 15 1989

ABSTRACT

The impact of short duration grazing (Savory Grazing Method; Holistic Resource Management) on seed bank and seed rain was assessed and compared to an ungrazed transitional mixed prairie/fescue grassland in Alberta. Seed bank characteristics including seed density and species number and composition were evaluated in 1985 and 1986; seed rain was assessed in 1986 only. The seed bank was assessed through germination of seeds from soil samples collected from inside and outside five exclosures and placed in the greenhouse for 175 days. Seed rain was determined for each treatment using sticky traps which captured seeds upon contact.

There were no treatment effects on seed density which averaged 395 seeds m^{-2} in 1985 and 1972 seeds m^{-2} in 1986. Seed density significantly increased from 1985 to 1986. In both treatments, in 1985, dicotyledon seed was more abundant than monocotyledon seed, while in 1986 the reverse was observed. Within each treatment, seed density was greater in the 0-2.5 cm soil stratum than the 2.5-5.0 cm soil stratum. Total species number was not significantly different between treatments. Species with the greatest seed density in 1985 in both treatments were *Artemisia frigida* and *Androsace septentrionalis*. In contrast, *Koeleria macrantha*, *Agropyron* sp., and *Poa* sp. were most abundant in 1986. Many species in the above-ground vegetation that were observed producing seed were absent from the soil seed bank.

Total seed rain was not significantly different between grazed and ungrazed treatments and averaged 6009 seeds m^{-2}. Monocotyledon species were dominant in seed rain in both treatments, represented mainly by *Koeleria macrantha*. Patterns of seed rain were slightly different between treatments with one very large peak of dispersal apparent in July in the ungrazed treatment in contrast to five small distinctive peaks in the grazed treatment. Plant species common in the seed rain also occurred in the seed bank but many species in the seed bank did not appear in the seed rain. The implications of this data are that in the management of heavily grazed grasslands the seed bank should not be relied upon to provide seed of desirable forage species for potential revegetation.

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I. INTRODUCTION

GRASSLANDS

Grasslands are plant communities in which graminoid plants are dominant and trees are usually lacking due to a moisture deficit (Brink, 1982). Native (or natural) grasslands have been established since the Tertiary period, occurring under various climatic regimes in every continent (Collinson, 1977; Brink, 1982).

The North American temperate grasslands extend from southern Canada to central Mexico (Coupland, 1979). From north to south the grasslands may be divided into the Northern, Central, and Southern Great Plains and from west to east into the shortgrass, mixed grass, and tallgrass prairies (Wright and Bailey, 1982).

The Canadian Northern Great Plains slope eastward between the Rocky Mountains and the Precambrian Shield (Smoliak, 1988). The boundaries run northwest past Edmonton, Alberta, and southeast through Saskatchewan towards Winnipeg, Manitoba. The main soils of the region are Orthic Brown, Orthic Dark Brown, and Orthic Black Chernozems, although some Orthic Gray Luvisols and a belt of Solonetzic soils occur. The productivity of these native grasslands is most influenced by the variation in amount and timeliness of precipitation from year to year (Barker and Whitman, 1988).

Major plant associations of the Canadian Northern Great Plains include the mixed prairie, tallgrass prairie, fescue grassland, and aspen parkland (Wright and Bailey, 1982). The mixed prairie is the most extensive, reaching to the Rocky Mountains in the west, almost to the Saskatchewan/Manitoba border in the east, and north to a latitude of 52^0 (Wallis, 1982). The mixed prairie borders the fescue grassland on the west and north and a small portion of the tallgrass prairie in the southeast. Topography ranges from flat to strongly rolling. Elevations range from 400 to 915 m (Wright and Bailey, 1982). Annual precipitation averages 300 mm in extreme southeastern Alberta and southwestern Saskatchewan and 400 mm along the western and northern fringes (Wallis, 1982). Two thirds of the annual precipitation falls as rain, peaking in June, with dry summers common. High temperatures and wind speeds in summer result in high potential evapotranspiration.

The Canadian fescue grassland is found in the eastern foothills of the Rocky Mountains in southwestern Alberta and in patches throughout the mixed prairie on northerly facing slopes and at higher elevations (Wright and Bailey, 1982). It can also be observed in the aspen parkland of central Alberta and Saskatchewan extending to southwestern Manitoba. Topography varies from level to sharply rolling with elevations ranging from 365 m in southeastern Manitoba to 2290 m in the Rocky Mountains. Precipitation varies from 360 to 460 mm in the aspen parkland, to 380 to 610 mm in the foothills.

Grasslands were once the most extensive climax vegetative formation on the North American continent (Gartner, 1978) of which there was nearly 388,500 square km in Canada alone (Smoliak, 1988). Human settlement, arable agriculture, alien plants and animals, forestry, overgrazing and accelerated erosion, combined with lack of fire, have changed the climax grassland forever (Coupland, 1979; Brink, 1982; Wright and Bailey, 1982). By 1986, only 129,500 square km remained, providing approximately 50% of the forage necessary to support the estimated 6.0 million cattle in Canada (Smoliak, 1988).

Succession

Succession involves changes in species composition of a plant community through colonization by plants (Horn, 1974). Changes become undetectable or cease altogether as the environment becomes more stable. Grazing animals are the primary factor influencing plant succession in natural grasslands (Ellison, 1960) with successional trends occurring in various directions, related to the intensity of grazing (Grubb, 1977). With persistent overgrazing succession is associated with reduced plant cover leading to less palatable and less productive forage for the grazing animal (Ellison, 1960). Retrogression describes succession from overgrazing if used to indicate movement away from the original undisturbed plant community.

The Northern Great Plains are quite resistant to grazing with moderate continuous or rotational grazing most conducive to the maintenance of vegetative cover and species composition (Hansen et al., 1931; Rogler, 1951; Olson et al., 1985). In the mixed prairie, heavy grazing can cause short grasses and midgrasses to give way to unpalatable shrubs (Larson and Whitman, 1942; Wright and Wright, 1948). Persistent heavy grazing and mowing in the fescue grasslands of Canada increases the proportion of unpalatable forbs and grasses at the expense of *Festuca scabrella* (Moss and Campbell, 1947; Willms et al., 1985).

There are claims of favorable successional trends under moderate and heavy grazing (Eckert and Spenser, 1986; Savory, 1988). Eckert and Spenser (1986) observed that rest-rotation management maintained vegetation in late seral condition and improved those in midseral condition. The effects of trampling may determine the extent to which succession occurs. In sagebrush/bunchgrass vegetation the potential for secondary succession was greatest where trampling was moderate or absent under litter and moss covered surfaces, shrub canopy, and soil cracks (Eckert et al., 1986). Potential for retrogression was greatest with heavy trampling. Howell (1976) observed the establishment of hardy pioneer plants from bare soil due to surface chipping by hooves allowing light, air, and water to enter the soil and expose buried seed to conditions suitable for germination.

The direction of succession is favorable when extended rest occurs after overgrazing although recovery of natural grasslands is slow, especially in arid environments (Smeins et al., 1976; Rice and Westoby, 1978). McLean and Tisdale (1972) found rough fescue and ponderosa pine range took 20 to 40 years to recover to excellent condition under full rest. Anderson and Holte (1981) suggested succession will be slow for approximately ten years of rest, recovering more rapidly with time as the plant populations increase in size and seed production. Savory (1988) contended succession is reversed more by prolonged rest than by low animal impact.

The classical vegetation theory is that vegetation development is directional and predictable, leading to restabilization of a climax community through secondary succession (Stoddart et al., 1975: as cited by Anderson and Holte, 1981). In the mixed prairie, the pattern of recovery of badly or completely denuded grassland has four or five stages of succession, from the inital state of weedy annuals to the fully developed grass stage of native species approaching their previous abundance (Albertson and Weaver, 1944; Costello, 1944). Intermediate stages include weedy grasses and perennial forbs followed by an early native grass stage. However, researchers have concluded that the classical concept of grassland succession does not occur (Smeins et al., 1976; Rice and Westoby, 1978; Anderson and Holte, 1981). Smeins et al. (1976) found vegetation changes over 25 years on Texas native grassland were primarily an adjustment in relative dominance of species developing towards a stable community after each disturbance, rather than species replacement.

Presence or absence of a seed bank may be one of many factors governing the succession of grasslands after disturbance. Succession may be a function of the number and kinds of germinating seeds present in the soil and seed-soil-water relationships (Raynol and Bazzaz, 1973; van der Valk and Davis, 1976). Johnston et al. (1969) stated that seeds found naturally in the soil would assure succession if disturbance eliminated established plants.

THE SEED BANK

The term seed bank denotes reserves of viable seed found in or on the soil (Roberts, 1981). Darwin (1859) first recognized the presence of seeds in the soil when he observed seedlings emerging from a cup of muddy water (Cook, 1980). Since then, viable seeds within the soil have been found in a wide range of habitats including; arable soils (Brenchley, 1918; Archibold, 1981), deserts (Nelson and Chew, 1977), marshes (Milton 1939; van der Valk and Davis, 1976), deciduous and coniferous forests (Oosting and Humphreys, 1940; Olmstead and Curtis, 1947), tundra and subalpine range (McGraw, 1980), European pasturelands (Chippindale and Milton, 1934; Williams, 1984), and natural annual and perennial grasslands in North America (Major and Pyott, 1966; Johnston et al., 1969; Archibold, 1981; Rabinowitz, 1981).

Role Of The Seed Bank

The role and functional significance of the seed bank in vegetation maintenance and regeneration in grasslands is not well documented (Hayashi and Numata, 1971). Many agree the seed bank provides above-ground vegetation with a reserve of dormant individuals that may replenish the natural mature vegetation when losses occur (Major and Pyott, 1966; Baskin and Baskin, 1978; Thompson, 1978; Rabinowitz, 1981). The importance of buried seed may be dependent on the type and severity of disturbance (Moore and Wein, 1977). The seed bank was important for recovery of prairie glacial marshes after the lowering of the water table (van der Valk and Davis, 1976). Rapid recovery was governed by the presence of seed in the soil while floristic composition was related to the species composition of the seed bank. Thompson (1978) suggested the presence of an accumulating seed bank is a viable survival strategy for plant species having high mortality, but only if selection for buried seed is intense under a high disturbance rate, or if the seed bank is sustained through seed production from the above-ground vegetation.

In theory, unstable environments in herbaceous plant communities favor seed production for local recruitment (Abrahamson, 1980). As successive maturity of a habitat increases, there is decreasing sexual reproduction and an increase in the importance of vegetative reproduction for perennial herbs. In order to colonize a site, herbaceous species of mature habitats may reproduce almost exclusively by vegetative means (Salisbury, 1942). Salisbury (1942) noted vegetative reproduction occurring in two-thirds of perennial species common in most countries. Vegetative propagation of perennials on grazed ecosystems has also been documented (Archibold, 1981) and may be most important for grasslands in good to excellent condition where plant mortality is low and competive dominance strong (Johnston et al., 1969).

Thompson and Grime (1979), in determining types of seed banks in European grasslands, suggested transient seed banks, in which seeds are present in a viable state for no more than one year, are adapted to exploit gaps which occur in the vegetation due to plant mortality and seasonally-predictable damage. Persistent seed banks, in which seeds are present in a viable state for more than one year, provide seedlings for plant regeneration after temporary disturbances in established vegetation or for spatially unpredictable damage.

Seed banks may also be important in maintaining the floristic diversity within communities by enhancing genetic diversity of the flora or in serving as evolutionary filters damping out varying conditions of sequential years (Baskin and Baskin, 1978; Templeton and Levin, 1979; Roberts, 1981).

What then is the role and significance of seed banks in grasslands and how important is the seed bank to recovery of grasslands after disturbance? Is the seed bank the cause of retrogression seen on heavily grazed grasslands supplying seed of undesirable, less palatable species? Does the role and significance of the seed bank lessen with increased vegetative propagation in grasslands? These and many other questions have yet to be answered. Recognizing circumstances in which a plant population survives in the absence of a seed bank (Templeton and Levin, 1979) and understanding seed fate and mortality (Cavers, 1983) would give some insight into the significance of the seed bank in grazed ecosystems .

Problems In Studying Seed Banks

Various techniques have been employed to determine the presence of seed in the soil (Major and Pyott, 1966; Roberts, 1981). The most widely used method in grasslands is soil sampling in a defined area and to a specific depth. Samples are subjected to suitable environmental conditions for seed germination. This procedure is considered the most exact (Hayashi and Numata, 1971) although it is time consuming, and dormancy and death of seeds during germination should be considered.

Concerns arise regarding the appropriate size and number of samples necessary to obtain statistically valid conclusions (Roberts, 1981) although the intensity of sampling needed may be impractable (Champness, 1949). Problems arise from the way seeds are dispersed over grasslands. The majority of studies dealing with seed banks have been criticised for using very large samples over small areas to determine seed numbers in the soil (Major and Pyott, 1966; Whipple,

1978) although Forcella (1984) felt some of this criticism has been too harsh. Bigwood and Inouye (1988), through comparing various methods of sampling, also contended that soil sampling techniques result in imprecise estimates of seed. They suggested the most precise method is to subsample large units by taking very small subunits along transects. Forcella (1984) found that aggregates of soil cores greater than 200 cm^2 from clover pasture resulted in a decreased rate of detecting new species. He therefore recommended that single cores or combined cores should have a surface area of 200 cm^2 and within any treatment, surface areas of replications should be approximately 1000 cm^2 to determine species numbers and their seed in the soil. Whipple (1978) argued that the number of samples taken and a specific sample size should be assigned to vegetation type to ensure complete species representation and to add similarity to studies for comparison. This has yet to be accomplished although Hayashi and Numata (1971) and Forcella (1984) have attempted to do so on some grasslands.

Determination of seed density and species composition of seed banks through germination studies may fail to detect some species as a result of inappropriate germination conditions. Under different germination conditions, the same samples differ in the amounts and types of seed detected (Roberts, 1981). Certain seeds may require special treatment for germination such as scarification while others may need months or even years to ensure high germination rates (Brenchley and Warrrington, 1930). Short germination treatments may be acceptable for determining the presence of species from year to year (Thompson and Grime, 1979). Stirring soil samples during germination treatment is often neglected, yet increases emergence by exposing seeds to environmental conditions that initiate germination (Forcella 1984). Forcella (1984) recommended at least four periods of stirring and drying to enhance germination. Other considerations should be depth of soil in greenhouse containers, period of dry storage, and timing of sampling (Roberts, 1981).

Seed Bank Dynamics

Seed bank dynamics are complex (Keeley, 1977; Rabinowitz, 1981) and are interconnected with, but still independent, from the above-ground vegetation (Harper, 1977). The annual potential gain to the soil is from dispersed seed (seed rain) produced in the area or blown in (Harper, 1977) and is dependent on current plant abundance and seed production (Howe and Chancellor, 1983). Seed production, in turn, is influenced by predation, grazing, and the environment. After dispersal, the seed may remain *in situ* or be removed through an agent of long distance dispersal. If burial occurs the seed has three basic alternatives (Cavers, 1983). The seed may remain ungerminated but viable becoming part of the dormant seed bank, die through predation, decay or old age, or germinate. The relationship between these seed bank components is shown in Figure 1.1.

Theoretical models attempt to define the relationship between the seed population of the soil and the components previously described. The models consider: potential return to the seed bank through seeds produced by a germinating seedling (Cohen, 1966), loss of seed through germination and emergence, germination and death in the soil, physiological aging, predators and pathogens, seeds initially inviable, and the fraction of seed in innate, induced, and enforced dormancy (Cook, 1980).

Seed rain

Seed rain is the composition and abundance of dispersing plant propagules arriving on a surface (Foster Huenneke and Graham, 1987), forming the potential source of colonists for recruitment to a habitat or for plant regeneration after disturbance (Harper, 1977). Seed rain is a function of seed production per unit area and seed dispersal (van der Valk and Davis, 1979).

Methods used to study seed rain are diverse, varying from the use of plastic or cheese cloth to capture seed from around the base of the plant to tracking individual seeds from the mother plant to the point of landing (Levin and Kerster, 1969; Platt, 1975). These procedures are time consuming, limited to larger seeds, and focus on seed rain of individual species.

Total seed rain for a community has rarely been measured due to difficulties in obtaining adequate representation of all species (Werner, 1975; Rabinowitz and Rapp, 1980) although it has been attempted for a radiation damaged forest (Wagner, 1965), a mature forest understory (Falinska, 1968), the base of a retreating glacier (Ryvarden, 1971), and a North American tallgrass prairie (Rabinowitz and Rapp, 1980).

In grasslands, measurement of seed rain is possible through the use of sticky traps. Designed by Werner (1975), these traps consist of a petri dish and filter paper mounted on a wooden rod inserted into the ground to various depths. Adhesives applied to the filter paper include petroleum jelly (Verkaar et al. 1983), or a non-drying substance "Tacky-toes" (Werner, 1975). Termed effective and unbiased by Werner (1975), traps are efficient in seed capture, remaining sticky for up to five months with only the slightest seed contact required for capture. Foster Huenneke and Graham (1987) suggested traps are still cumbersome and show differences in effectiveness of capture due to seed size, morphology, and plant dispersal modes. Awned seeds show the greatest capture rate while small round seeds bounce off the traps. Seed capture is influenced by height of seed release as fewer seeds are caught as plant height increases. Sticky traps such as these can be effective in grasslands, especially those with plants of low stature.

Estimates of total seed rain range from 166 seeds m^{-2} in a weedy forest understory (Wagner, 1965) to 19,726 seeds m^{-2} in a tallgrass prairie (Rabinowitz and Rapp, 1980). Species richness ranges from 12 species (Wagner, 1965) to 57 species captured per study (Ryvarden, 1971). Seed rain is generally dominated by a few species. Of 30 species captured on the tallgrass prairie, 9 species contributed 92% of the seeds while 21 contributed less than 50 seeds each to the seed rain (Rabinowitz and Rapp, 1980). The number of trapped species was small and was attributed to the vegetation, which closed as the season progressed, impeding seed fall to the ground.

Seasonal peaks of seed rain, usually represented by one or two species, represent highs and lows in the levels of seed production of grassland species. In tallgrass prairie, grasses, rushes and sedges produced an early summer peak. Warm season grasses produced the late September and early October peak while Composites, mainly *Aster* and *Solidago* species, represented the late October and November peak (Rabinowitz and Rapp, 1980). Maximum and average wind speed influenced seed rain patterns.

Seed production

Seed production is expressed as seed productivity or seed yield. Seed productivity is described by plant characteristics such as number of fertile shoots per plant, number of flowers per shoot, and the percentage of fertile flowers and number of seeds per flower (Rabotnov, 1969). Seed yield is expressed as the average number of seeds produced by a single species per unit area. The importance of each yield characteristic is dependent on the environment and year and varies considerably for a given species (Rabotnov, 1969). The number of seeds a plant produces is dependent on the amount of annual assimilated energy and the proportion directed towards seed production (Harper et al., 1970). Seed production per plant varies due to the integration of such factors as climatic and edaphic conditions, age, stress, species density and density of other species, predation, parasitism, grazing, and management of the habitat (Harper and White, 1974; Sagar and Mortimer, 1976).

The seed productivity of various British habitats has been generalized on the basis of the plant life cycle (Harper and White, 1974). Seed output, greater than 2 $x10^4$ seeds per plant, is characteristic of intermittent habitats such as wood clearings and exposed mud banks which are comprised of annuals and biennials. Biennials, which after two seasons of growth have a "big-bang" of seed production, generally have very high seed output (Harper and White, 1974). Permanent open, semiclosed, and closed unshaded habitats such as grasslands have seed productivity of 5 $x10^3$ seeds per plant and are largely comprised of perennial species. In more shaded habitats there are rarely more than 3 to 4 $x10^2$ seeds per plant. Differences in seed production are partially attributed to the successional stage of the plant population (Harper et al., 1970). High reproductive output is typical of early successional environments while in more stable environments plants direct more energy towards their vegetative organs.

Variation in annual seed production has been attributed to seasonal differences in precipitation and the amount of precipitation received in the previous year (Field-Dogdson, 1976; Keeley, 1977; Schirman, 1981). Spotted and diffuse knapweed show reduced numbers of viable seed per head in dry years while an increase in precipitation increased seed production (Schirman, 1981).

Seed production for a population, species, or individual plant is not constant (Rabotnov, 1969). Seed production of a species can vary from population to population within a limited area, fluctuate from year to year, and change with altitude. Some species do not produce seed at all while others produce seed infrequently.

Reduced seed production is observed in plant species, especially grasses, with increased age (Harper and White, 1974; Harper, 1977). *Poa pratensis* showed an age-associated decrease in seed production after the first two years of seed production (Harper and White, 1974).

Reduction in seed output per unit area may occur due to stress. At high plant densities, some perennials and biennials fail to flower (Sagar and Mortimer, 1976). Seed production of *Avena fatua* is largely influenced by the density of the companion crop, and to a lesser degree, its own density. *Papaver rhoeas* had limited seed production (1 capsule; 4 seeds) until enhanced with high fertilizer rates producing 400 capsules with 800 to 900 seeds in each (Harper and White, 1974).

Animal grazing affects seed production through consumption of seed stalks prior to seed dispersal although only very intense grazing will result in total consumption. Grazing also produces changes in seed productivity since reduced plant vigor and basal area may lead to reduced and/or delayed seed maturation and loss of seed viability (Sampson, 1914). The ability of plants to tolerate grazing varies with species although most show reduced seed production with grazing (Rabotnov, 1969). Some herbaceous forbs are able to withstand up to 50% utilization although increased utilization often results in weak and spindly flower stalks that are unable to produce seed (Julander, 1968).

Seed production on overgrazed grasslands tends to be delayed (Sampson, 1914; Collins and Atkins, 1970). Sampson (1914) found seed production was 40 to 47 days later on overgrazed grasslands than on moderately grazed grasslands. Delayed seed maturation resulted in decreased seed viability, especially for the more palatable species. In contrast, other studies have shown seeds from grazed ranges having the same viability as seeds from ungrazed sites (Hanson and Stoddard, 1940) although the requirements for breaking dormancy may not be as stringent (Harper, 1977).

The proportion of mature seed on ungrazed plants is generally greater than on grazed plants. Hanson and Stoddart (1940) found 14% more mature seed on ungrazed than grazed plants in mixed prairie. The more severely plants are grazed, the fewer seed heads are produced. This is true even with rest-rotation grazing systems due to periodic heavy use (Eckert and Spenser, 1987).

Timing of defoliation is the most important factor involved in determining the response of the plant to grazing (Harper, 1977). Defoliation prior to inflorescence formation may result in the inflorescence not being formed or the production of a smaller inflorescence. Leaves defoliated after the inflorescence is formed generally results in aborted seed production or smaller seeds (Womack and Thurman, 1962; Harper, 1977).

Dispersal

Dispersal is the scattering or spreading of seeds from the parent plant and may be aided by distributing agents such as wind, water and animals. It is a mechanism for maintaining established and stabilized populations and for expanding the range and population size of invading species (Harper, 1977; Rabinowitz and Rapp, 1981). Dispersal can result in loss of seed from the community although there may be an influx of seed which may balance the loss (Sagar and Mortimer, 1976). Dispersal and seed distribution is a function of seed morphology, characteristics of the distributing agents, height and distance from seed source, concentration of the seed source, terminal velocity (the rate of seed fall through the air), microtopographic features, and foraging (Harper, 1977; Rabinowitz and Rapp, 1981;

Verkaar et al. 1983; Reichman, 1984). Factors affecting seed dispersal and distribution vary simultaneously, making it difficult to determine the importance and contribution of each (Augspurger and Franson, 1987).

Wind-dispersed seeds tend to be small and light in weight (Reichman, 1981). Dispersal by wind depends on height of seed release, speed and turbulence of wind between the ground and point of release, and wind direction (Cremer, 1965). Prairie species with similar terminal velocities will not have the same fall movements due to differences in morphology (Rabinowitz and Rapp, 1981). Small flattened seeds, irregularily shaped seeds, and winged seeds tumble and glide during dispersal, resulting in lateral movement away from the mother plant (Burrows, 1973; Rabinowitz and Rapp, 1981). Dispersal structures, such as pappi, keep propagules airborne longer by lowering the terminal velocity (Sheldon and Burrows, 1973).

Rabinowitz and Rapp (1980) found distribution distance may be enhanced by wind although others suggest there is little effect (Burrows, 1973; Werner, 1975). Instead, distance of seed distribution varies with location, propagule abundance, rate and production regime of parent plants (Rabinowitz and Rapp. 1981; Reichman, 1984), and height of release (Sheldon and Burrows, 1973; Harper, 1977). Seeds of sparse species show greater maximum lateral movement than do seeds of common species and are influenced more by inflorescence height (Rabinowtiz and Rapp, 1981). The main determining factor of enhanced dispersal and distribution in species with long stemmed inflorescences was height of the inflorescence while with short stemed inflorescences wind profile and vegetation density became more important (Verkaar et al., 1983). Greatest differences in seed density across microsites were observed when seed production was greatest, while differences disappeared with low levels of seed production (Reichman, 1984).

Seeds with no adaptation for wind dispersal or ejaculation from the plant have dispersal linked to animal behavior (Harper, 1977). Seed content, color, size, and general morphology have been related to specific types of animal dispersers. Adhesive dispersal occurs through hooks, spines, barbs, and sticky substances. Dispersal through this method is, however, rare in British flora with only 10% of species containing adhesive fruits (Sevensen, 1986). Few forage plants appear to be well adapted to transport by animals since many have large, soft, late developing seeds that shatter easily and fall to the ground (Ellison, 1960). Animals may eat and digest seeds causing loss of seed although some may pass through the animal undamaged in a viable state (Harper, 1977). Cows grazing a weedy field consumed 89,000 seeds per day of *Plantago* species of which 85,000 were voided with 58% still viable (Hanson, 1911: as cited by Harper, 1977).

Seed distribution is complex due to the variability of dispersal agents within a community (Janzen, 1971). Seeds are generally dispersed in an uneven pattern (Harper, 1977). In many species, seeds are concentrated around the parent plant and do not disperse very far (Salisbury, 1942; Verkaar et al., 1983). With increased distance, seed density declines steeply. Exceptions are winged and plumed seeds which can disperse far from the parent plant (Sheldon and Burrows, 1973). Lack of seed around the parent is characteristic of plants in isolation. Species with specialized mechanisms of wind dispersal tend to colonize as isolated individuals over a great distance while seeds having no specific adaptation for wind dispersal often drop seeds close to the parent plant (Harper, 1977). For a single grassland species, dispersal may be in a random pattern in space or may be clumped, depending on the pattern of the inflorescences in the vegetation (Rabinowitz and Rapp, 1981). For the whole population seed is usually distributed in a clumped and spatially patchy pattern.

Patchy and clumped seed patterns may result from animal dispersers and seed predators (Janzen, 1971). Seeds may be locally aggregated in soil by birds and small rodents such as mice, creating the potential for dense localized seedling populations or patchy seed shadow. Large ruminants may distribute seeds in local concentrations and move seeds away from the parent plant (Harper, 1977).

Surface topography and roughness influence seed distribution (Thompson and Grime, 1979). Seeds may move across the soil surface and into the soil. Depressions in soil cause wind speed to decrease resulting in seed being trapped in these microsites until the sites are full (Reichman, 1981). Seed morphology, such as hygroscopic awns and pappus, and plant distribution also influence seed distribution on the soil (Harper, 1977). Vegetation may influence seed distribution by impeding blowing seeds (Osman et al., 1987).

Flowering and seed ripening have short time spans in northern temperate regions with seed dispersal either long or short. Seed may be released as it ripens, be held on the plant and then released in sudden bursts, or slowly dispersed over a long time (Harper, 1977). Seeds may be released early in the season in very large amounts, at a constant rate over the whole season, or twice during one season (Falinska, 1968). In disturbed habitats, characteristic plant species possess a long flowering and seed ripening period with dispersal occurring nearly as soon as ripening occurs. Species in arable land concentrate flowering, ripening and seed release into a narrower time span (Harper, 1977). In grasslands, many C_3 species flower and disperse early while C_4 species disperse later in the season (Rabinowitz and Rapp, 1981).

Time of dispersal may influence seed viability, emergence, and mortality (Lacey, 1982). Dispersal time affects seed viability through variation in seed quality or changes in the environment and propagules (Baskin and Baskin, 1978; Lacey and Pace, 1983). There may be a seasonal advantage to early dispersal with seed produced and sown earlier also geminating earlier. However, Roach (1986) found dispersal time had no effect on emergence, plant size, and fecundity in species of *Geranium*.

Timing of seed release through natural selection may optimize survival. Seeds released over a short time may saturate predator demands which may be the optimal strategy for leaving survivors. A more constant release of seed over time may be advantageous in maximizing opportunities for the seed to find a favorable environment and germinating quicky to escape predation (Harper, 1977). Species of poppy which retain seed until harvested by man suffer heavy losses to bird predation. Natural species of poppy have quick release as soon as ripening occurs or long release facilitated by spines on capsules that reduce seed predation (Harper, 1977).

Incorporation of seed into the soil

Burial is a frequent fate of seed after dispersal (Sagar and Mortimer, 1976) although plant species usually produce more seed than is found in the soil indicating there is not a steady accumulation of buried seed (Keeley, 1977). The mechanism of seed burial is not fully understood although soil processes, animal activity, and seed morphology are involved. Percolating rainwater moves small seeds down the soil profile (Harper, 1977). Seeds deposited on litter are distributed in the soil by soil physical processes, soil organisms, movement of organic matter, or successive piling of litter (Moore and Wein, 1977). Soil cavities and cracks also create traps for seeds.

Seed shape and the presence of awns influence burial (Harper et al. 1970; Harper, 1977). Rounded seeds roll into crevices while reticulate seeds stay *in situ* upon landing. Awnless seeds mostly remain horizontal on the soil surface. Curved awns often cause the seed to curl around soil crumbs while straight awns penetrate the soil deeply. Awn length may influence the depth of burial (Harper et al., 1970). Species with self-burial mechanisms, such as awns, are mainly weedy species commonly found in disturbed habitats (Harper, 1977).

Burying actions by birds and rodents, and seed ingestion by earthworms buries seed (McRill, 1974; Harper, 1977). Animal trampling can aid seed burial (Rabotnov, 1956) although Major and Pyott (1966) suggested sheep inhibited seed burial through increased soil compaction. Theoretically, there should be higher seed densities in grazed sites since grazing can uproot plants and reduce surface litter facilitating the incorporation of seed into the soil (Archibold, 1981). However, Golubeva (1962) observed litter did not impede the incorporation of seed into the soil.

Seed density and species composition

There is considerable variation in the density of seeds found in the soil. From Great Britain, examples of seed density range from 430 seeds m^{-2} in permanent pasture (Douglas, 1965) to 70,000 seeds m^{-2} in a formerly arable pasture (Chippindale and Milton, 1934). Although fewer studies have dealt with seed banks of natural grasslands, Harper (1977) suggested rarely more than 5000 seeds m^{-2} will be found.

Seed density in soil from short and mixed grass prairies range from 300 to 800 seeds m^{-2} (Weaver and Mueller, 1942; Lippert and Hopkins, 1950), while Rabinowitz (1981) found 6470 seeds m^{-2} on a productive tallgrass praire. From mixed prairie/fescue grassland in southern Alberta and Saskatchewan 204 to 12,842 seeds m^{-2} were observed (Johnston et al., 1969; Archibold, 1981).

In grasslands, the majority of seeds are found in the upper 2.5 cm of soil and decrease in abundance with depth (Chippindale and Milton,1934; Major and Pyott, 1966; Harper, 1977; Williams, 1984). Williams (1984) observed 30 to 40% of all grass seeds in the top 2 cm of soil and 13% in the next 2 cm, with seed numbers decreasing further with depth. Density of seed was still appreciable at 30 to 50 cm in European grasslands (Chippindale and Milton, 1934) and observed down to 3 m in meadow steepes in Russia (Rabotnov, 1969). Seeds observed at deeper depths of soil are assumed to be older than those found near the soil surface (Moore and Wein, 1977).

Although species diversity of seed banks in grasslands is high, they are generally dominated by one or two species. Milton (1936) found that in grasslands *Calluna vulgaris* represented over half the seed population in the soil. Species commonly dominating seed banks of mixed prairie and fescue grassland in Canada are *Artemisia frigida* and *Androsace septentrionalis* (Johnston et al., 1969; Archibold, 1981).

A consistent feature of seed banks of grasslands is the presence of dicotyledon species in appreciable numbers (Chippindale and Milton, 1934; Major and Pyott, 1966; Rabinowitz, 1981). Dicotyledon species are especially common in previously cultivated grasslands or those seasonally flooded (Rabotnov, 1969). On native perennial grasslands most dicotyledon species are weedy annual forbs (Johnson et al., 1969; Rabinowitz, 1981). Dicotyledons which rely heavily on vegetative propagation have little, if any, seed in the soil (Chippindale and Milton, 1934; Major and Pyott, 1966).

Seed of some monocotyledons, other than rush or sedge, can form an appreciable percentage of the total seed bank (Major and Pyott, 1966; King, 1976; Chancellor, 1979). The majority are weedy annual grasses. Certain species, such as *Poa annua* and *Poa trivialis* have persistently large seed banks while others, such as *Festuca rubra*, do not persist well in the soil (Roberts, 1981). Seeds of dominant perennial grasses are rarely found in the seed bank (Grime et al., 1981). Most grass seeds persist less than one year in the soil (Rabinowitz, 1981) and have higher decay rates than dicotyledon seed (Rampton and May Ching, 1966; Williams, 1984). Williams (1984) found that with seed shed prohibited, monocotyledons decreased in the soil by 27% and their presence was exhausted within three years while dicotyledons decreased by only 10%. Seed banks dominated by grass seed tend to be transient due to the short life-span of the seed (Rabinowitz, 1981).

Species of rush (*Juncaceae*) and sedge (*Cyperaceae*) often represent a significant proportion of the seed bank in British grasslands (Chippindale and Milton, 1934; Williams, 1984), meadows in the USSR (Rabotnov, 1969) and in North American native grasslands (Rabinowitz, 1981). *Juncus* species are plentiful in the soil perhaps as a result of their prolific seed production, estimated as high as 700,000 seeds per plant (Salisbury, 1961) and their long life span of 60 years or more (Major and Pyott, 1966). *Juncus* species may lack the opportunity to germinate because of inadequate light which becomes less available as succession proceeds. The presence of such species in the soil, although rarely observed in the vegetation, indicates the seed bank is likely a reflection or memory of past successional stages (Rabinowitz, 1981). These seed banks may represent survival mechansims for the species should environmental conditions again become favorable (Williams, 1984).

Seed density of leguminous species observed in seed banks are appreciably less than those of herbs, grasses, or grass-like species although numbers are greater in wet soils and flooded meadows (Roberts, 1981) and in calcareous rather than acidic conditions (Milton, 1943). In European grasslands, *Trifolium repens* may be found under tame pastures (Champness and Morris, 1948; van Altena and Minderhoud, 1972: as cited by Roberts, 1981). In natural grasslands, legumes represent little if any of the seed bank (Major and Pyott, 1966; Roberts, 1981). Where present, buried seeds of leguminous species are of high value in maintaining and increasing the legume content of pastures (Charlton, 1977).

Variability in seed density and species composition

Management influences seed density and species composition of seed banks in grasslands (Chippindale and Milton, 1934; Zelenchuck, 1968; Johnston et al., 1969; Jones and Jones, 1978; Roberts, 1981; Howe and Chancellor, 1983). Zelenchuck (1968: as cited by Roberts, 1981) found the greatest abundance of seed in soil under mown meadows although greater numbers of legume and grass seed were present when grazed. Golubeva (1962: as cited by Major and Pyott, 1966) found little difference in seed density between mown and unmown sites. Mueggler (1956) observed that burning reduced the amount of seed present in the upper 6 mm of soil with no significant change in seed density at a depth of 12 to 25 mm of soil. In mixed prairie, density of grass seed was greatest for ungrazed sites and lowest for very heavily grazed sites, while the opposite was true for forbs and shrubs (Johnston et al., 1969). In contrast, Major and Pyott (1966) found no significant difference in soil seed density between grazed and ungrazed sites. Grazing and trampling may create conditions or microsites within the soil conducive to seed viability of certain species (Harper, 1977). Conversely, higher seed density under grazing may be a result of enforced seed dormancy in the faeces (Harper, 1977), and unpalatable species and short statured plants benefitting from grazing due to reduced competition (Archibold, 1981).

Variability in seed density and species compositon are due to site differences even though histories and management may be similar (Jalloq, 1975). Jalloq (1975) found upland pastures in Wales had twice the seed density of dicotyledon and perennial species than in lowland sites. In contrast, lowland pastures showed greater species diversity with many more annuals, rush, and sedge species present.

Changes in seed density in the soil throughout the season are significant, especially in annual grasslands (Bartolome, 1979). Varying seed density and species composition in the seed bank are related to seasonal changes reflecting seed production and seed rain of certain plant species. On sagebrush semi-desert grassland, seed density in the soil was lowest in March and June due to lack of seed rain and depletion of seeds due to seed germination, decomposition, and predation while seed density increased from June through September (Hassan and West, 1986). Hayashi and Numata (1971) found changes only in floristic compositon between seasons while seed density was similar.

Density of seed in the soil of grassland communities decreases as sward age increases (Milton, 1936; Douglas, 1965; Howe and Chancellor, 1983). In permanent but originally cultivated grasslands in England, seed numbers declined with increasing sward age due to a corresponding loss of arable weeds, especially dicotyledons.

Thompson (1978) suggested variations in seed density in the seed bank occur as a result of disturbance and stress with large seed banks promoted by increased levels of disturbance and decreased levels of stress. Milton (1939) observed a decrease in seed density within the soil with increasing elevation which Thompson (1987) suggested was a result of corresponding increased levels of stress. Seed density and disturbance both increase as stress decreases going from late to early successional stages of vegetation (Thompson, 1987). This pattern was observed by Archibold (1981) who found 758 seeds m^{-2} on native prairie, 803 seeds m^{-2} on grazed pasture, 1205 seeds m^{-2} on wheat stubble, and 2674 seeds m^{-2} on summerfallow.

The dormant seed

Longevity

The life span of buried seeds varies among species with some seed remaining viable for centuries. Viable seeds of species from the *Nelumbo* genus date back 150 to 1040 years (Exell, 1931; Libby, 1951) while seed of *Chenopodium album* were viable for 1700 years (Odum, 1965). Optimum conditions for longevity appear to be moderately moist soil deficient in oxygen.

Longevity of seeds of arable weeds, grasses, and cereals has been observed in long term studies where seeds were artificially buried in jars or bags of sand. Weed seeds, especially those native to an area and having a hard seed coat, show the greatest longevity (Lewis, 1973). *Chenopodium album* was persistent even after 20 years in the soil. Least persistent in the soil are grasses and crop seeds, which often lose viability within a year (Toole and Brown, 1946; Darlington and

Steinbauer, 1961). Exceptions are *Trifolium* and *Poa* species which remained viable for as long as 39 years (Toole and Brown, 1946).

Seed longevity can be categorized according to habitat type and seed size (Harper, 1977; Grime et al. 1981). Smaller seeds have greater longevity than larger seeds as the palea is more effective in covering the embryo and endosperm in some species. Plants having long-lived seeds tend to be from disturbed habitats and are annuals and biennials with very small seeds (Harper, 1977). In contrast, seeds of species from stable habitats, such as tropical or temperate forests, tend to be very short-lived and are very large in size.

Seed preservation may be aided by acidic soil conditions (Milton,1939, 1943) although Brown and Oosterhuis (1981) found otherwise. Large numbers of seeds under acidic soil conditions may be due to the species common to these sites which are also prolific seed producers (Harper, 1977).

Conditions which encourage germination, such as light, moderate temperatures, moisture, and increased oxygen, decrease the longevity of seed in the soil. Buried seeds retain viability better than those near the surface, likely a result of improved conditions for preservation within the soil (Brown and Oosterhuis, 1981). Although seed longevity increases with a corresponding increase in soil depth there is a corresponding decrease in seed number with depth which may be offset by improved conditions for preservation and linked to those conditions which promote seed dormancy (Weaver and Cavers, 1979).

Dormancy

The ability of seeds to remain viable in the soil for many years is related to dormancy, defined as a "state in which viable seeds, spores, or buds fail to germinate under conditions of moisture, temperature and oxygen favorable to vegetative growth" (Amen, 1968). Dormancy is opportunistic, allowing members of the population to remain insulated from recruitment or unpredictable environmental hazards to which the growing plant is not adapted, ensuring continuation of a plant population (Ratchke and Lacey, 1985). For a complete review of dormancy see Roberts (1972) and Villiers (1972).

Common constituents of grassland seed banks, such as *Carex*, *Juncus*, and *Poa* species, show natural dormancy in the soil (Chippindale and Milton, 1934). Harper (1959) suggested some seeds are born dormant, others achieve dormancy, and some have dormancy forced upon them. Innate, induced, and enforced dormancy may all be displayed by a single seed at some point in time.

Innate dormancy is established during seed maturation by nearly all species (Cook, 1980). Although the dormancy period varies from plant to plant, it rarely lasts longer than two years. A cue, such as chilling, is necesssary before dormancy is released. Innate dormancy may be a temporary measure to prevent immediate post-dispersal germination under favorable conditions and allow seeds to come to equilibrium with the environment of the seed bank. The chilling requirement in temperate species is presumably a mechanism to inhibit autumn germination (Harper, 1977).

Innate dormancy is replaced by induced dormancy at some point after dispersal even when there are favorable environmental conditions (Ratchke and Lacey, 1982). The seed may be imbibed but germination is prevented by an environmental inhibitory factor, such as decreased red- to far-red light which occurs beneath the leaf canopy in grasslands. Induced dormancy is capable of persisting even after the limiting environmental conditions are removed (Cook, 1980).

Seed burial extends innate dormancy into enforced dormancy due to lack of light (Brown and Oosterhuis, 1981) although temperature, nutrient availability (Thompson et al., 1977) and light quality (Silvertown, 1980) may be involved. Roberts (1972) found most seeds in the soil are in a state of enforced dormancy. On grasslands, Brown and Oosterhuis (1981) found a third to half of seeds of *Poa* species showing enforced dormancy due to burial. Induced light requirements through burial on initially light independent seeds also maintains enforced dormancy (Wesson and Wareing, 1969). The large number of *Poa* species often found in the seed bank may be partially explained by the dormancy mechanism. The persistence of seeds of some very old arable weed species under grasslands indicates that seeds move out of enforced dormancy infrequently (Chippindale and Milton, 1934; Champness and Morris, 1948). Enforced dormancy may be broken by correction of a limiting factor such as light (Wesson and Wareing, 1969).

The role of seed size and morphology in dormancy is unclear although seeds with the greatest longevity in soil are small (Cook, 1980). Bhat (1973) found larger seeds broke dormancy much quicker than small seeds which may be partially related to hard seededness which decreases as seed weight increases (Halloran and Collins, 1974).

Losses in the seed bank

Harper (1977) suggested buried seeds have a "continuous and constant death risk". Some studies on weed seeds have implied that the loss to the soil is constant with the number of seeds decreasing exponentially and increasing with disturbance (Roberts, 1970; Roberts and Feast, 1973). Much of the loss of seed is attributed to the breakdown of dormancy although losses due to pathogens and predation cannot be ignored.

Decay, old age, and senescence

Losses in the seed bank may occur through decay, old age and senescence. Old age leads to a loss of seed viability Roberts (1960) while Kjellsson (1985) noted mortality of seeds of *Carex* species due to pathogens and physiological aging. Loss of viability in crop species due to soil pathogens results in accelerated death (Leach, 1947; Tadros, 1957).

Seed survival is influenced by interactions between the environment and soil microflora (Harper, 1977). Seed death was high in early spring and during the hot, dry summer when germination was delayed (Harper et al., 1955). The ability of the microflora to cause seed decay was in itself constantly changing (Harper, 1977). Changing environmental conditions of temperature and moisture in the soil, and management practices which change the microclimate will indirectly influence longevity of seed in the soil (Sagar and Mortimer, 1976; Harper, 1977).

Predation

Predation by insects, birds, and small mammals can result in enormous annual losses from the seed bank of tame pastures (Janzen, 1971; Harper, 1977; Cavers, 1983; Kjellsson, 1985) and natural grasslands (Nelson et al., 1970; Pullian and Brand, 1975; Everett et al. 1978; Whitford, 1978). Consumption by seed foragers prior to dispersal has been recorded at between 10 and 90% of total seed in natural habitats (Sagar and Mortimer, 1976). Insect larvae may consume the total contents of a seed capsule or inflorescence (Randall, 1982) or foragers may move from one seed to another (Harper et al., 1970). Success in finding buried seed varies between 0 and 57% for various North American rodents (John and Jorgensen, 1981). Harvester ants in the Sonoran desert removed and destroyed up to 15 million seeds per acre annually (Harper et al., 1970).

Seed predation depends upon species, size, chemistry and characteristics of the seed; plant behavior, and dispersal mechanisms; seed burial; and predator species, size, and age (Janzen, 1971; John and Jorgensen, 1981). Seeds of some plant species are preferred over others, although rodents increase the variety of seed consumed when seed becomes scarce (Sullivan and Sullivan, 1982). Ants in the Sonoran desert choose 90% of their seed source from species which contribute only 8% of the seed production per year, avoiding seed of the most prolific seed producer (Harper et al., 1970). Seed structures aiding the seed against predation include a hard seed coat, enlarged or thickened calyx, spines, long hair, or toxic compounds (Kjellsson, 1985). Seed size does not cause avoidance by predators (Harper et al., 1970) although Thompson (1987) suggests otherwise. The seed bank should provide some safety to seeds from predation as the potential predator will not be able to locate all the seed (Harper, 1977; De Steven, 1983). Small seeds, between 1 to 3 mg, may find refuge from predation through burial, especially if not aggregated in the soil (Campbell, 1982; Kjellsson, 1985). Plants having a large and fast ripening seed crop, with a short dispersal period, should suffer less seed loss through predation. Seed selection varies among foragers; ants and beetles can find buried seed while rodents are restricted to seed on the soil surface (Reichman, 1979; Abramsky, 1983).

Positive effects of seed predation may be to move the seed away from the parent plant, removing the potential for competition, and making seed less available to other predators (Harper, 1977; Heithaus, 1981; Kjellsson, 1985). Predation may influence the rate at which plant succession proceeds by the preference for certain seeds over others, changing their relative abundance in the soil (Janzen, 1971). The overall effect of seed predation on the composition and size of the seed bank may be significant as Inouye et al. (1980) observed loss of seed influenced the species composition of the plant community.

Germination

Germination occurs when the viable seed contacts and absorbs water, initiating metabolic activites, resulting in emergence of the embryo and the production of a normal plant (Bewley and Black, 1978). Three stages of germination are the "awakening or activation" of the seed, the "phase of water content and respiration", and the "phase of cell division and growth characterized by a continuous decrease in fresh water and respiration" (Ching, 1972). A relationship exists between seed germination and environmental parameters with germination occurring when risk is minimal under favorable conditions and when potential adult competition is low (Solbrig, 1980). In an unstable environment the seed germination is staggered (Cohen, 1966; Solbrig, 1980).

Germination is influenced by seed morphology including the seed coat, weight, size, shape, and presence of appendages. The seed coat inhibits the early germination stages due to interference with the uptake of water and gases required for metabolic activity, inhibition of radicle protrusion, and lack of outward diffusion of endogenous germination inhibitors (Harper et al., 1970; Ballard, 1973). Families associated with grasslands such as *Gramineae, Compositae,* and *Juncaceae* have shown increased germination following removal of the seed coat (Ballard, 1973). Although there is enough pressure from within the seed to break the seed coat, environmental conditions, such as light, may weaken the seed coat or increase the thrust force of the embryo (Mayer and Shain, 1974).

Germination is influenced by seed size (Harper et al., 1970; Sheldon, 1974; Grime et al., 1980; Roach, 1986), with seeds less than 0.1 mg having a greater germination percentage than large seeds due to greater surface to volume ratio enabling them to extract sufficient water from soil (Grime et al., 1980). An increase in seed weight, which increases the surface to volume ratio provided the seed shape remains constant (Harper, 1977), results in a decrease in lifespan (Grime et al., 1980). In contrast, Breman et al. (1980) determined seed weight did not influence germination.

Seed shape influences germination (Peart, 1979; Grime et al., 1980). Cylindrical and tadpole shaped seeds, commonly found in the *Gramineae* family, and coneshaped seeds often of the *Compositae* family, have a very strong response for immediate germination (Griswold, 1936). Flat seeds have enhanced seed germination as the seed lies in close contact with the soil more readily obtaining water (Harper, 1977).

The presence of hygroscopic awns in *Gramineae* species, pappus in the *Compositae*, and antrose hairs present in both families is directly correlated with a high incidence of germination by orientating the seed to optimize the contact between the seed surface and available moisture (Grime et al., 1980). Mucilaginous seed coats increase the area of the seed to soil enhancing water uptake while large spiny seeds have poor water uptake (Harper, 1977).

Soil moisture in the extreme upper soil profile is a major factor controlling seed germination of native prairie grass species (Blake, 1935; Raynol and Bazzaz, 1973). Moisture stress causes germination delay or interruption although small seeds may be able to germinate before large seeds due to their size (Roach, 1986). Optimum water content of praire soils for germination of grass seed is at two-thirds saturation (Blake, 1935). McGinnies (1960) noted a significant drop in germination in six cool season range grasses when water dropped from 7.5 atm to 15 atm or to the permanent wilting point. Too much water also reduces the germination percentage as water is held by the soil with a greater force (Janssen, 1973).

Temperature requirements for germination of seeds are not constant and may change with time or environmental conditions

(Heady, 1954). Most herbs in temperate climates will germinate in spring with rising temperatures although pulses of germination may be observed throughout the season (Ratchke and Lacey, 1982; Williams, 1983). Annual and perennial grass species are capable of germination over a wide temperature range (Grime et al., 1980) although the greatest germination occurs at 18 ^{o}C for *Koeleria pyrimadata* and *Agropyron cristata*, 27 ^{o}C for *Festuca rubra*, *Poa pratensis* and *Danthonia parryi*, and 7 ^{o}C for *Elymus junceus* (Julander, 1968). Plummer (1943) observed most native grasses germinate better at a constant temperature although *Agropyron* and *Poa* species respond to fluctuations in temperature. Species characteristic of wetland and disturbed sites, mostly annuals, show greater germination responses to fluctuating temperatures than grassland species (Thompson et al., 1977; Bazzaz, 1979). Species least sensitive to temperature are those in which water is the most important factor for germination.

Some grass species having large and persistent seed banks in European grasslands require either exact temperature conditions or diurnal temperature fluctuations for germination (Williams, 1983). Those having the more transient and less frequent seed banks were able to germinate under a wide range of temperature conditions.

Most germination occurs in air at 20% oxygen levels (Wilkins, 1969) and 0.03% carbon dioxide levels in the atmosphere (Went, 1949; Mayer and Poljakaff-Mayber, 1975). The ratio of carbon dioxide to oxygen may be the most important factor rather than the direct concentration of either in regulating germination.

Seeds of pasture species may require full light for germination, germinate independent of light, or have an induced light requirement maintaining them in an enforced state of dormancy (Wesson and Wareing, 1969). Having a light requirement for germination is ecologically advantageous and likely adaptive for a species since it may be a safeguard against germination at great depths and during unfavorable conditions for seedling establishment (Mayer and Poljakaff-Mayber, 1975; Grime et al., 1980). Factors influencing light penetration into the soil are soil type, moisture, and amount of vegetation.

Seeds of early successional species are especially sensitive to light (Bazzaz, 1979). Species may become light requiring after burial due to gaseous inhibitors produced by the seeds (Wesson and Wareing, 1969). Seeds sensitive to light tend to be small, characteristic of open disturbed habitats and marshlands, and are most persistent in the seed bank (Smith 1972; Thompson and Grime, 1979). Seed of grassland species, especially perennial grasses, germinate better in darkness than those species from woodlands, disturbed areas, and marshlands.

Recruitment From Buried Seed

In grasslands, the relationship between seed reserves in the soil and the fraction recruited into seedlings annually is unclear. It is possible that buried viable seed contributes only minimally to the recruitment of new plants with germination of seeds from the soil surface more frequent than from within the soil (Harper, 1977). The presence of large numbers of dormant seed in the soil may support this theory. Roberts (1970) suggested most seeds in the soil die without germinating. It should be possible, using the parameters of seed rain, soil bank, recruitment rates and expected mortality, to predict size of potential seedling populations (Harper, 1977). This has been attempted on cultivated soils (Naylor, 1972) although information concerning natural grassland habitats appear to be scarce.

An extra effort is required by the germinating seed to emerge from beneath the soil. Experiments suggest only species with extensive energy reserves are likely to form established seedlings from deeply buried seeds with succcess related to soil characteristics, seed depth, seed size, and species involved (Black and Wilkinson, 1963; Harper, 1977). Variation in the soil microtopography determines the proportions of seed established (Harper et al., 1970) as well as the existing vegetation which limits regeneration of new plants (Sagar and Mortimer, 1976).

It is thought that seed populations in the soil are composed of younger age groups with a progressively lower representation of seeds which are older (Harper, 1977). Evidence suggests a seedling population is not recruited evenly from all age groups from within the soil with the majority of seedlings coming from very new seed. Naylor (1972) estimated for *Alopecurus myosuroides* on a cropland that between 62 and 71% of the seedling population was derived from seed less than one year old. There was greater chance of regeneration from a newly arrived seed than from one already dormant in the soil. Jalloq (1975) observed that in tame pastures in Wales, most of the seeds in the soil had the capacity for germination only within the first few months of burial.

The fraction of dormant viable seed in natural soil which fails to emerge after germination is unclear. Thompson (1987) suggests the decay rate of seeds *in situ* is negligible over the short term as many of the seeds of long-lived species have evolved successful mechanisms to prevent germination. In contrast, Cook (1980) and Roberts (1970) argue the main cause of death following burial is premature germination at an unsuitable depth.

Correspondence Between The Seed Bank and Vegetation

Although first recognized by Chippindale and Milton (1934), many researchers have commented on the lack of correspondence between the seed bank and the above-ground vegetation in pastures (Champness and Morris, 1948; Jalloq, 1975; Williams, 1984) and native grasslands (Major and Pyott, 1966, Johnson et al., 1969; Rabinowitz 1981). Only a few studies show good correlation between the two (Prince and Hodgdson, 1946; Hayashi and Numata, 1971, 1975). Rabinowitz (1981) stated comparisons should not be made between the seed bank and vegetation because the counting units are not equivalent. Instead, comparisons between seed rain and seed bank should be made.

Species present in the soil are not always found in the above-ground vegetation and vice versa. Swards dominated by perennial grasses have few seeds in the soil (Chippindale and Milton, 1934; Champness and Morris, 1948; Milton 1936, 1939, 1943; Major and Pyott, 1966; Hassan and West, 1986). Lack of perennial seed in the soil has been accounted for by differences in seed dormancy, rapid germination, lack of mechanisms and adaptations which would encourage extended preservation of viability and survival within the soil, variation in seed production, and predation (Harper, 1977; Cook, 1980; Roberts, 1981).

Dormant seeds may be produced only by species which have a potential risk for periodic extinction such as annuals (Silvertown, 1981) which would account for the lack of perennial seed present in soil of many perennial grasslands. Absence of some species in the seed bank may be due to germination of seed soon after dispersal. Other species may lack the germination inhibitory mechanism so germination occurs even when environmental conditions are not suitable for survival (Rabotnov, 1969; Brown and Oosterhuis, 1981).

Absence of some species suggest they do not survive long in the soil (Williams, 1984). Short-lived seeds may require continual input into the soil to maintain some sort of seed density (Fyles, 1988) while viability of certain seeds may decrease too rapidly for them to even become incorporated into the soil (Brown and Oosterhuis, 1981).

If practices of good grass management are followed, high seed populations should be characteristic of the soil. Johnston et al. (1969) suggested the lack of seed from perennial species may be due to the lack of opportunity to set seed although Champness and Morris (1948) and Chippindale and Milton (1934) observed a lack of perennial seed even when seed production was evident. Lack of correlation between the seed bank and above-ground vegetation in natural Australian topsoils of heaths occurred even when pods of fruiting species were found on the ground (Barbour and Lange, 1967). Predation, known to significantly reduce the amount of seed present of some species (Janzen, 1971), may have influenced the amount of seed present in the soil.

Seed of certain species may not be present in the soil due to timing of seed production and germination. Seeds from the *Umbelliferea* family lack seed in the seed bank as seed is produced in autumn and germinates early in spring (Thomson and Grime, 1979). Certain species may not be present in the soil in the form of seeds as vegetative propagation is more important for survival than seed production (Archibold, 1981).

OBJECTIVES

Studies dealing with seed banks in Alberta natural grasslands are few. Although some proponents of short duration grazing claim improved grassland condition from natural seed in the soil and seed production, the importance of this seed for revegetation in the event of disturbance or for improved successional trends is unclear. Further studies are necessary to understand seed bank dynamics and the implications to management.

The objective of this study was to compare seed density, number of species and their composition in the seed bank of a ungrazed site with those under short duration grazing (Savory Grazing Method; Holistic Resource Management) in a transitional mixed prairie/fescue grassland. Factors related to the seed bank such as seed yield and seed rain were compared between treatments as were the relationships between these factors and the seed bank. The efficiency of sampling techniques and the implications of this data in the role of the seed bank for revegetation, potential succession, and management of natural grasslands were considered.

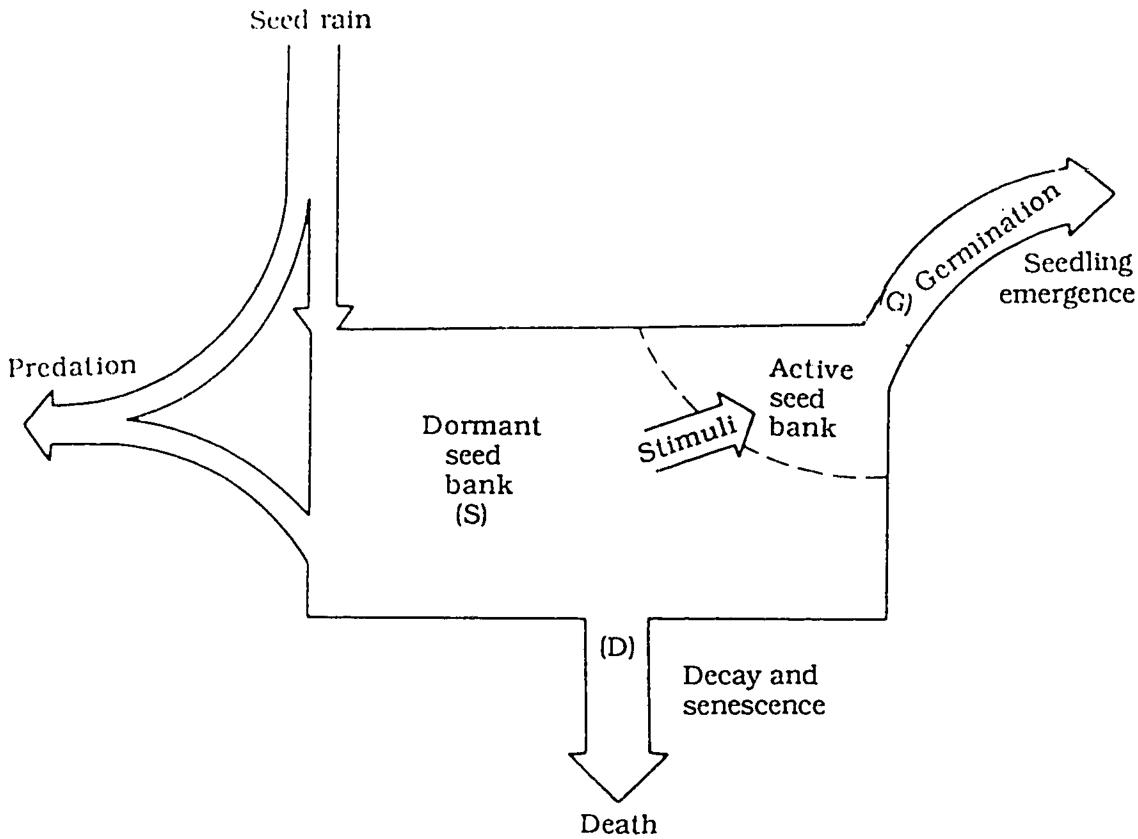

Figure 1.1 Flow chart for the dynamics of seed populations in the soil with G=Germination, S=Dormant seed bank, and D=Decay and senescence. Reprinted with permission from Harper (1977: Academic Press, Ltd. London. Pp. 84).

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II. THE EFFECT OF SHORT DURATION GRAZING AND REST ON SEED BANK DENSITY AND SPECIES COMPOSITION IN A TRANSITIONAL MIXED PRAIRIE/ROUGH FESCUE GRASSLAND IN ALBERTA

INTRODUCTION

The term seed bank denotes reserves of viable seed found in or on the soil (Roberts, 1981). Seed banks are well recognized in a variety of habitats from deserts to forests (Milton, 1939; Oosting and Humphreys, 1940; Olmstead and Curtis, 1947; van der Valk and Davis, 1976; Nelson and Chew, 1977; McGraw, 1980) although the most extensive work has been on agricultural soils (Brenchley, 1918; Brenchley and Warrington, 1930: Archibold, 1979). Numerous studies conducted on European pastures have determined species composition and abundance of seeds in the soil (Chippindale and Milton, 1934; Champness and Morris, 1948; Williams, 1984). Less work has been carried out on naturally occurring grasslands in North America (Lippert and Hopkins, 1950; Major and Pyott, 1966; Rabinowitz, 1981) with even fewer focusing on Canadian grasslands (Johnston et al., 1969; Archibold, 1981).

Seed density in soil varies widely among natural grassland communities from 300 to 800 seeds m^{-2} on short and mixed grass prairie sites (Weaver and Mueller, 1942; Lippert and Hopkins, 1950) to 6470 seeds m^{-2} on productive tallgrass prairie (Rabinowitz, 1981). In southern Alberta and Saskatchewan on mixed prairie and rough fescue grassland, seed density ranges from 204 to 12,842 seeds m^{-2} (Johnston et al., 1969; Archibold, 1981). Seed density is greatest in the upper 2.5 cm of soil and decreases with depth (Chippindale and Milton, 1934; Milton, 1939; Williams, 1984).

Many species found in seed banks of grasslands are weedy annual dicotyledons and are generally more abundant than grasses (Johnston et al., 1969; Rabinowitz, 1981). Although species diversity may be high, grassland seed banks are generally dominated by one or two species (Milton, 1939; Rabinowitz, 1981). In Canadian natural grasslands, *Artemisia frigida* and *Androsace septentrionalis* (Moss, 1983) often represent a significant proportion of the seed bank

(Johnston et al., 1969; Archibold, 1981). *Juncus* species are also common (Major and Pyott, 1966; Rabinowitz, 1981) likely reflecting past successional stages and their longevity, persistence, and accumulation in the soil (Rabinowitz, 1981).

Seed density and species composition of the seed bank may be influenced by variation in grassland management. In mixed prairie and rough fescue grassland in Alberta *Festuca scabrella* had reduced seed density under heavy and very heavy grazing while forbs such as *Artemisia frigida* and shrubs had increased seed numbers (Johnston et al., 1969). In contrast, Major and Pyott (1966) found seed density and species composition were not significantly different between grazed and ungrazed treatments. Soil seed density and composition is also related to season and sampling time, reflecting dispersal periods of various plant species (Harper and White, 1974; Bartolome, 1979), sward age (Cook, 1980), and differing levels of stress and disturbance (Thompson, 1978).

Lack of correlation between the seed bank and above-ground vegetation has been well documented (Major and Pyott, 1966; Johnston et al., 1969; Rabinowitz, 1981; Williams, 1984). Seed bank composition and its correlation with above-ground vegetation is influenced by differences between species in seed dormancy and persistence (Roberts, 1981), yearly variations in fruiting, and lack of mechanisms and adaptations which encourage extended seed viability and permanency in the seed bank (Golubeva, 1962: as cited by Major and Pyott, 1966; Williams, 1984). Limited opportunity for species to set seed may explain the absence of some seed in the soil (Johnston et al., 1969) although Chippindale and Milton (1934) noted a lack of correlation with observed seed production. The emphasis on vegetative reproduction for some perennials is also important (Archibold, 1981).

The functional significance of seed banks may be for maintenance and regeneration of vegetation by providing a reserve of dormant seed in the soil (Thompson, 1979; Rabinowtiz, 1981). Some proponents of short duration grazing systems claim natural seed in the soil may provide plants for regeneration (Kingsberry, personal communication, 1987). The relationship between the seed bank and that fraction recruited to above-ground vegetation is not well documented, although the importance of seed banks to recovery of prairie glacial marshes has been noted (van der Valk and Davis, 1976).

This study was undertaken to assess the impact of grazing on the seed bank in a transitional mixed prairie/rough fescue grassland. It was hypothesized that seed density and the number of species and their composition would differ significantly between grazed and ungrazed treatments, and between the upper and lower soil strata within each treatment. Seed density and species number and composition from two soil strata were determined under short duration grazing (Savory Grazing Method) and compared to an ungrazed treatment. The efficiency of sampling technique and implications of this data in the role of the seed bank in potential succession were also considered.

MATERIALS AND METHODS

Site Description

The study site was northwest of Fort Macleod, Alberta on the edge of the Porcupine Hills (49° 47' N Lat, 113° 39' W). The area is transitional between the mixed prairie and the rough fescue grassland associations with *Koeleria macrantha*, *Agropyron dasystachyum* var. *dasystachyum*, *Stipa curtiseta* and forbs such as *Artemisia frigida* common elements of the flora (Moss and Campbell, 1947).

Soils are predominantly Orthic Black Chernozems (Agriculture Canada, 1977). Topography is gently undulating to very severely sloped. Rock outcrops and exposed till are evident. The area has a continental prairie climate with dry summers and cold winters. Annual precipitation averages 450 mm and from 1982 to 1986 was 408, 322, 367, 423, and 435 mm, respectively (Dormaar et al., 1989). Growing season precipitation from 1982 to 1986 was 193, 77, 160, 247, and 280 mm, respectively (Shipwheel Grasslands, 1987). Chinook winds are frequent with average wind velocities of 50 km h^{-1} but occasionally as high as 100 km h^{-1} causing extreme temperature changes (Agriculture Canada, 1977). High summer temperatures, low precipitation, and strong winds result in high potential evapotranspiration and often a moisture deficit, while low winter temperatures, little snowfall, and strong winds combine to provide a harsh winter climate for vegetation.

Grazing Treatment

Since 1982, the 960 hectare study area has been managed under short duration grazing as pertaining to the Savory Grazing Method (Holistic Resource Manag[illegible] Seventeen permanent fields radiate from a central cell wher[illegible] handling facilities are located (Figure I.1; Appendix [illegible] rate from 1982 to 1986 averaged 277 cow/calf pairs per gra[illegible] season and in 1985 and 1986 were 235 and 250 cow/calf pairs, respectively (Shipwheel Grasslands, 1987), approximately twice that recommended under continuous grazing (Wroe et al., 1988).

Cattle grazed from early May to as late as November in some years. Grazing regime is dependent on plant growth and varies each year, with movement timed to prevent overgrazing. In general, three rotations are interspersed with two rests. Grazing periods in early spring average 2.5 days in each field, extending to 4 to 5 days by the third rotation. Rest increases from 40 to 60 days as the season progresses to facilitate recovery of forage after grazing. Grazing occurred from May 6 to October 30 in 1985 and from April 29 to November 13 in 1986 (Mary Holtman, personal communication, 1986).

Seed Bank Sampling

Five fields, in which a 10 by 30 m exclosure was erected in each, were randomly selected for another study in 1982 by Dormaar et al. (1989). From each of these five exclosures cylindrical core samples (10 cm diameter by 5 cm depth) were taken of soil and litter in mid June, 1985 and early July, 1986. Concurrently, samples were collected from a marked unfenced 10 by 30 m grazed area adjacent to and generally upwind of the exclosure. Six 5 m transects were randomly selected along a 30 m length in each treatment and subsamples taken at five 1 m intervals along each transect. For each subsample vegetation was cut to approximately 1 cm above the soil surface. Subsamples were divided into two 2.5 cm layers referred to as the upper and lower soil strata. The five subsamples representing a soil strata from each transect were then pooled and bagged, later air-dried, and stored in a refrigerator in the dark at 5 ^{o}C for 3 months. Following storage, samples were crumbled and sieved to remove litter, rocks, and roots. Dry weight of each sample was determined.

Three 200 ml subsamples of each sample were spread on a base of perlite in plastic seed trays to a depth of approximately 0.5 cm. Germination tests were conducted in the greenhouse at 18 ^{o}C with a 14 hour photoperiod for 175 days. Samples were generally watered every second day and sprayed with "No-Damp" fungicide weekly for two months. Subsamples were surficially stirred at 75 day intervals to enhance germination. Species frequency and germination were recorded daily for the first eight weeks and then every two to three days. Species not identifiable at the seedling stage were maintained until identification was possible. A small number of plants were not identified due to premature deaths. Botanical names are from Moss (1983) with some common names adapted from Looman (1982) and Vance et al. (1984).

Above-ground Species Composition

Above-ground species composition of the study site was determined over the two seasons. Botanical names are from Moss (1983) with some common names adapted from Looman (1982) and Vance et al. (1984).

Statistical Analyses

Seed bank parameters for data analyses were seed density (seeds m^{-2}) and species number. Raw data represented subsamples of samples. The data was analyzed as seed m^{-2} after applying a conversion factor related to the original soil volume.

Data were analyzed using a split-split plot model. All parameters were analyzed with an SPSS.X analysis of variance program. Data were tested for homogeneity of variance using the Bartlett-Box test. Lack of homogeneity in most data sets resulted in transformation of all data using the natural log. Upon comparison of transformed data with raw data, tests of significance were similar enough to present untransformed data as the results (Dr. R. Hardin, personal communication, 1989). Data were separately analyzed for each year. Analysis were performed at the 0.05% level of significance.

Species found in the seed bank in each treatment within soil strata and year were ranked in order of their abundance according to their mean seed density by the Dominance Hierarchy Curve.

RESULTS

Seedling Emergence Patterns

Patterns of seedling emergence were similar between treatments within soil strata in each year, and between soil strata in 1986. In all comparisons in both years, with the exception of treatments within the lower soil stratum in 1985, seedling emergence was apparent by day 5 (Figure 2.1). The largest flush of seedling emergence occurred between days 5 and 15 with at least half the total seedlings emerged by day 25. In 1985, emergence rate after the first 30 days was slow and sporadic with the majority of seedlings not emerged until approximately day 100. In 1986, the majority of seedlings were observed within the first month. In the lower soil stratum in 1985, initial emergence occurred by approximately day 15 in both treatments and was very sporadic without the characteristic flush of seedlings within the first 20 days (Figure II.1, Appendix II). Emergence of half the seedlings took up to three times longer than that cited for the other comparisons. Seedling emergence was observed no later than day 156 in 1985 and day 147 in 1986. No apparent enhancement of germination occurred after stirring in either treatment, soil stratum, or year. Although the total number of seedlings emerged were slightly greater in grazed treatments than ungrazed treatments in both soil strata in 1985 and in the lower soil stratum in 1986 there were no significant differences (Table 2.1). In both years, total seedlings emerged were significantly greater for treatments in the upper soil stratum than in the lower soil stratum.

Seed Density

There were no significant treatment effects within either soil stratum or year for dicotyledon, monocotyledon, and total seed density (seed m^{-2}) (Table 2.1) although slightly more seed was found in grazed treatments than ungrazed treatments in each soil stratum in both years (Table 2.2). Exceptions were monocotyledon and total seed density in the upper soil stratum in 1986. Seed density in the upper soil stratum was at least twice that in the lower soil stratum in 1985 with the differences less pronounced in 1986. Differences in either treatment between soil strata within years were significant for all comparisons with the exception of monocotyledons in 1985 and dicotyledons in 1986 (Table 2.1).

Within a given soil stratum and year, the proportion of dicotyledon seed was similar between grazed and ungrazed treatments; this was also true for monocotyledon seed (Table II.1, Appendix II). In 1985, dicotyledon seed density was triple the monocotyledon seed density in each treatment in the upper soil stratum, and double the monocotyledon seed density in each treatment in the lower soil stratum (Table 2.2). In 1986, in both soil strata, monocotyledon seed density was twice as great as dicotyledon seed density in grazed treatments, and three times as great in ungrazed treatments.

In each treatment within a given soil stratum, dicotyledon, monocotyledon, and total seed density were significantly greater in 1986 than in 1985 (Table II.2, Appendix II). The increased total seed density was largely a result of increased monocotyledon seed density (Table 2.2). The degree of change in annual seed density was less extreme in treatments within the upper soil stratum than in the lower soil stratum, and was much greater for monocotyledon seed than dicotyledon seed within soil strata. Dicotyledon seed, which represented over two-thirds of the seed in each treatment within soil strata in 1985, comprised a maximum of 31% of the total seed in 1986 (Table II.1, Appendix II).

Differences in seed density across fields were significant in 1985 and 1986 for all comparisons with the exception of monocotyledon seed in 1985 (Table 2.1). Field variability (Tables II.3 and II.4, Appendix II) was also apparent from various field interactions.

Species Composition

Seeds present in the seed bank in both treatments, soil strata, and years represented 16 families, 37 genera, and 54 species (Table 2.3). The most frequently represented dicotyledon and monocotyledon families were the *Compositae* and *Gramineae*, respectively. Species included 31 forbs, 1 shrub, and 22 grass or grass-like species represented by annuals, biennials, and perennials of which the latter were most abundant (66%). All monocotyledon species present were perennials. Thirty-four species were observed in the seed bank in 1985; 22 dicotyledons and 12 monocotyledons. In 1986 an increase to 54 species was observed; 32 dicotyledons and 22 monocotyledons.

Treatment effects on dicotyledon, monocotyledon, and total species number were not significant within soil stratum or year (Table 2.1). In 1985, in both soil strata, species present in grazed treatments were present in ungrazed treatments, and vice versa, with the exception of two to three species (Table 2.3). Differences in species composition between treatments in both soil strata were slightly greater in 1986 than 1985. Seed of species observed in only one treatment within a given soil stratum or year was present in very small amounts (Table II.5, Appendix II).

The upper soil stratum had more total species in each treatment than the lower soil stratum in both years (Table 2.3). Differences were significant with the exception of monocotyledon species in both treatments in 1985 (Table 2.1). In 1985, in the upper soil stratum, nearly one quarter of all species observed in the grazed treatment, and slightly more in the ungrazed treatment, were not present in the lower soil stratum (Table 2.3). These differences were slightly greater in 1986 than in 1985. In both years, all species present in the lower soil stratum were present in the upper soil stratum with the exception of one to three species.

Changes in species number between 1985 and 1986 were significant (Table II.2, Appendix II). These changes were more pronounced for each treatment in the upper soil stratum than in the lower soil stratum and for monocotyledon and total species (Table 2.3). A few dicotyledon species were absent from the upper soil stratum in both treatments in 1985 while present in 1986 even though they were absent from the above-ground vegetation. The most conspicuous change in the upper soil stratum between years was the presence of *Koeleria macrantha* and additional species of *Agropyron* and *Poa* not observed in the above-ground vegetation.

In 1985, in each treatment in the upper soil stratum, *Artemisia frigida* was the most abundant species (Table 2.4) comprising approximately 40% of the total seed (Table II.5, Appendix II). Together with *Juncus* species and *Androsace septentrionalis* these species comprised nearly three-quarters of the total seed in each treatment. Similarily, these species dominated each treatment in the lower soil stratum although *Androsace septentrionalis* was most abundant representing approximately 34% of the total seed in each. In 1986, unlike 1985, the majority of seed in the upper soil stratum in both treatments was represented by monocotyledon species, with one dicotyledon making a significant contribution in the ungrazed treatment (Table 2.5). In grazed treatments *Koeleria macrantha* (27%), *Agropyron* species, and *Poa* species represented over half the total seed in the soil (Table II.5, Appendix II). In the ungrazed treatment, *Koeleria macrantha* (37%), *Poa* species, and *Artemisia frigida* represented 61% of the total seed. In 1986, in the lower soil stratum, total seed was represented largely by *Agropyron* species (40%), *Koeleria macrantha*, and *Androsace septentrionalis* in the grazed treatment, while in the ungrazed treatment *Agropyron* species (42%), *Juncus* species, and *Carex* species were most abundant.

Species numbers were significantly different between fields, with the exception of monocotyledon species in 1985 and dicotyledon species in 1986 (Table 2.1). Field variability was also apparent from various field interactions.

Comparison of the Seed Bank and Above-ground Vegetation

There were 145 species from 109 genera and 27 families observed in the above-ground vegetation (Table 2.6). They were comprised of forbs (69%), shrubs (8%), and grass or grass-like monocotyledons (23%). The *Compositae* family was most frequently observed followed by *Leguminosae*, *Cruciferecae*, *Rosaceae*, and *Gramineae* families.

Eighty-three percent of the species observed were perennials. All monocotyledon species, except *Bromus mollis*, were perennial.

Of 54 species present in the seed bank over both treatments, soil strata, and years, 29 were observed in the vegetation of which 79% were perennials (Table 2.6). Seventeen of the 32 dicotyledon species and 12 of the 22 monocotyledon species present in the seed bank were observed in the vegetation. All of these species were observed producing seed during the study period, and at least two-thirds were observed producing seed in the monitored quadrats (Chapter 3).

The correspondence between species in the seed bank and those in the vegetation was similar between 1985 and 1986 (56% and 53%, respectively) (Table 2.6). Of the 34 species present in the seed bank in 1985, 11 dicotyledons and 8 monocotyledons were found in the vegetation. In 1986, of the 54 species observed in the seed bank, 17 dicotyledons and 12 monocotyledons were found in the vegetation.

Of 145 species in the vegetation, only 28 species were present in the soil, the majority of which were perennials. Only 17 of the 111 dicotyledon species in the vegetation were present in the seed bank. Representation by monocotyledons was better than dicotyledons with 12 of the 34 monocotyledon species in the vegetation present in the soil. Conspicuously absent from the seed bank, although present in the vegetation, was *Festuca scabrella*. Results were similar from year to year.

DISCUSSION

Emergence Patterns

Different patterns of seedling emergence observed between years and soil strata likely reflect the type of seed present in the soil and their response to optimum germination conditions. The slow, sporadic emergence in 1985 in the upper soil stratum may reflect the high proportion of dicotyledon to monocotyledon seed, while the quicker, less sporadic emergence in 1986, in both soil strata, reflects the large proportion of monocotyledon seed. Dicotyledon species germinate more slowly than monocotyledon species (Major and Pyott, 1966) which may account for the differences seen in this study.

Absence of any pattern in the lower soil stratum in 1985, although perhaps related to the large proportion of dicotyledon seed, may also reflect the small numbers of total seed. Enhancement of seedling emergence from soil stirring every 75 days may not have been observed because many seedlings emerged within the first 25 days, or germinated and failed to emerge. Lack of response from stirring is in contrast to Forcella's (1984) work where stirring at 60 day intervals enhanced germination.

Seed Density

There were no statistically significant differences in seed density between treatments, which is similar to Major and Pyott's (1966) work in California grasslands. With grazing and trampling reducing litter on the soil surface, uprooting plants and chipping the soil surface, seed incorporation into the soil should theoretically be enhanced resulting in significantly greater seed density in the grazed treatment. However, Golubeva (1962: as cited by Major and Pyott, 1966) found litter accumulation did not impede seed penetration. Enhanced seed incorporation into the soil from the grazed treatment is likely offset by very severe grazing and trampling, observed in areas around the exclosures in this study, reducing seed yield and hence, seed available for incorporation into the soil. As well, soil compaction from animal impact likely impedes, rather than aids seed burial, as noted by Major and Pyott (1966).

In 1985 in the ungrazed treatment, where monocotyledon species were more abundant than dicotyledon species in the above-ground vegetation (Willms, unpublished data), the presence of a dicotyledon dominated seed bank may indicate the longevity of dicotyledon seed in the soil. Slightly less dicotyledon seed in the ungrazed treatment than in the grazed treatment in 1985, although not significantly different, may indicate a progressive reduction in density of dicotyledon seed in the soil over time as a result of reduced seed production. Dicotyledon seed density in soil from the ungrazed treatment would theoretically continue to decrease with further dominance of monocotyledon species in the vegetation. Density of dicotyledon seed in soil from the grazed treatment would likely increase slightly over time or remain constant, as shorter less palatable dicotyledon species continue to increase in abundance as range condition deteriorates. In time, under these conditions, differences in density of dicotyledon seed between treatments would likely become significant.

Most monocotyledon seed, with the exception of *Juncus* sp., will likely never be present in the soil in extremely large amounts even with prolonged rest, as in the ungrazed treatment, due to high seed decay rates (Rampton and May Ching, 1966; Williams, 1984). Large numbers of seed though may be found in the soil directly after seed dispersal as was observed by Williams (1984). Slightly greater monocotyledon seed density in the ungrazed treatment in 1986, in comparison to the grazed treatment, may reflect the absence of grazing. Density of monocotyledon seed in the ungrazed treatment though is likely underestimated as dense vegetation can intercept the seed rain, as observed by Rabinowitz (1981), reducing the amount of seed reaching the soil.

Significant yearly differences in seed density were likely a result of seed production, influenced by precipitation, and sampling date, or a combination of these effects. Lack of seed production was noted in 1985 in both treatments and was likely related to severe moisture deficits in years preceding 1985. Increased density of seed in the soil in 1986 was likely influenced by improved moisture conditions in 1985 and 1986 as plants, especially monocotyledon species, were observed producing seed. This is supported by Johnston et al. (1969) who observed a 70% reduction in seed density from 1966 to 1968, following a lower than average moisture supply in 1967 with fewer species observed producing seed. Also contributing to enhanced seed density in 1986 was sampling which occurred two weeks later than in 1985, and coincided with the onset of seed dispersal of various grass species (Chapter 3). Bartolome (1979) observed seasonal changes in the seed bank of an annual grassland which were related to the flowering period of certain species. Seed densities observed in both years in this study are similar to those observed by Johnston et al. (1969) and Archibold (1981) on Canadian natural grasslands.

Increased seed density in 1986, in comparison to 1985, may indicate only a temporary increase in the size of the seed bank. Many seeds present in 1986, especially monocotyledon seeds, are likely transient residents of the soil. Williams (1984) found temporary increases in seed density in the soil after seed shed, with only 20% of the seeds becoming permanently incorporated into the soil. Using Williams' results, if only 20% of the additional seed present in 1986 became permanently incorporated into the soil, the seed bank would still double in size from 1985. With fall sampling, one might find seed density, especially monocotyledon seed density, reduced or similar to those found in 1985.

In periods of enhanced seed production, as in 1986, dicotyledon seed density in the soil increases slightly. Less extreme yearly changes in dicotyledon seed density in the seed bank, in comparison to monocotyledon seed density, may indicate that some difficulty exists in incorporation of these seeds into the soil but that seed is more persistent over time. Conversely, monocotyledon seed may be more easily incorporated in the soil but represent a transient short-lived seed bank due to the high decay rate of most monocotyledon seed.

It was not surprising to find the majority of seed in the upper few cm of soil and decreasing with depth. This pattern has been found on natural grasslands by Major and Pyott (1966) in similar depths of soil. Incorporation of seed into the soil is related to soil processes, animal activity, and seed morphology. It is assumed deeper seeds have been in the soil for longer periods of time than the more shallowly buried seed (Moore and Wein, 1977). If moisture deficits prior to 1985 restricted the amount of seed present on the site, the low seed density in the lower soil stratum in 1985 may indicate that the seeds observed were older than those in the upper soil stratum.

Differences in seed density between soil strata were not as extreme in 1986, as in 1985, due to increased seed density, especially of monocotyledon seed. Greater seed density was observed in the lower soil stratum in 1986 than in 1985 which was unexpected as processes involved in burial appear to be long-term (Harper, 1977). The processes by which seeds are incorporated into greater soil depths are rather obscure (Harper, 1977) although rather quick incorporation of some seed may be due to movement of seeds down the soil profile by percolating rain water, and the falling of seeds down soil cavities and cracks caused by root decay and wetting-drying cycles in the soil. Some seed may also become incorporated into greater depths of soil (>5.0 cm) over time, due to these processes, and the action of seeds with self burial mechanisms (e.g. awns), piling of successive stages of litter, the burying action of earthworms, and caching activities of rodents. If it is assumed much of the additional seed in the soil is transitory, due to the short life-span of most monocotyledon seed and the low efficiency of seed incorporation into the soil (Williams, 1984), the seed density in the lower soil stratum will likely rapidly decrease over time due to lack of dormancy and mechanisms for extended viability.

Differences in seed density among fields were likely related to species composition of each, although they were initially considered vegetationally similar. Due to different locations, the potentially changing microclimate and varying grazing periods, differences may have occurred in the timing of seed production and dispersal affecting the fate of the seed.

Species Composition

Species observed in the seed bank of each treatment were similar. Most abundant were many weedy dicotyledon species. The presence of these species in the soil likely reflects the vast amount of seed produced by each of these species which is easily transported and accumulated in the soil (Archibold, 1981). Seed of weedy species is especially abundant in non-virgin soil, lying dormant for long periods of time (Chippindale and Milton, 1934). The abundance of dicotyledon species, especially *Artemisia frigida* and *Androsace septentrionalis*, has been noted in seed banks of other natural grasslands (Johnston et al., 1969; Archibold, 1981).

Although the seed bank was comprised of many species only a few were well represented in the soil having similar seed densities between treatments. In 1985, the presence of *Artemisia frigida* seed in both treatments was not unexpected as this species was observed in the above-ground vegetation, although to a lesser extent in the ungrazed treatment where seed density was also slightly less.

Androsace septentrionalis was rarely observed in the vegetation of the ungrazed treatment and occurred in patches throughout the grazed treatment indicating its seed must be persistent in the soil, especially since it was most abundant in the lower soil stratum where seed is assumed to be old as suggested by Moore and Wein (1977). Lack of abundance of these two species in the above-ground vegetation of the ungrazed treatment, in comparison to the grazed treatment, suggests seeds may have been blown in from the surrounding vegetation or are remnants of past vegetations and persist well in the soil. Both species have small seeds which are commonly most abundant in seed banks. The results found here contrast with Johnston et al. (1969) who observed more seed of weedy dicotyledon species, such as *Artemisia frigida*, when going from ungrazed to heavily grazed sites.

Lack of significant differences in species composition between treatments, and the presence of dicotyledon species and absence of many monocotyledon species in the seed bank in 1985, may indicate that the seed bank in the ungrazed treatment is not representative of an ungrazed situation, due to the short time since the establishment of the exclosures. Athough species composition of the above-ground vegetation reflects lack of grazing, many years may have to pass before the seed in the soil also resembles an ungrazed situation. This is likely if one considers the small amount of seed which becomes permanently incorporated into the soil each year (Williams, 1984), and that monocotyledon seeds are rarely persistent in the soil for longer than one year (Rampton and May Ching, 1966; Lewis, 1973). The ungrazed treatment used by Johnston et al. (1969), where differences between grazed and ungrazed treatments were observed, was nearly 20 years old. Lack of long-term persistence of monocotyledon seed in the soil may indicate that the seed bank under an ungrazed treatment may never truely reflect the abundance of monocotyledon species in the vegetation.

The presence of *Juncus* species in the seed bank of both treatments but not in the above-ground vegetation likely indicates the seed bank is a reflection or "memory" of past successional stages. Studies have indicated the longevity of seed from Seed of *Juncus* sp. in the soil (at least 70 years), their persistence, and progressive accumulation over time (Chippindale and Milton, 1934; Rabinowitz, 1981). The presence and abundance of *Juncus* species has been noted in seed banks of other natural grasslands (Rabinowitz, 1981; Archibold, 1981) and European pastures (Chippindale and Milton, 1934; Williams, 1984) where *Juncus* sp. are no longer evident in the vegetation. *Juncus* species were however, more abundant in the upper soil stratum than in the lower soil stratum. This is unexpected since seed of *Juncus* sp. should have been more numerous in the lower soil stratum if present for many years in the soil, as has been observed by Williams (1984), and especially if the species observed in the seed bank are no longer present in the vegetation. It is possible small localized areas of *Juncus* sp. exist on the site, or nearby, which were not observed in the vegetation survey, and through wind dispersal seed is distributed. When considering the massive amounts of seed produced and seed persistence, these small populations may be enough to supplement the soil with seed of *Juncus* sp., even if infrequently, to ensure its presence in the seed bank.

The change in species compositon and their abundance from 1985 to 1986 reflects seed production and the ability of seed to become incorporated into the soil. Greater species diversity in the upper soil stratum was accentuated in 1986 by the vast amount of seed produced on the site. The magnitude of change in the lower soil stratum from 1985 to 1986 was puzzling as other researchers indicate that seeds are not easily incorporated into the soil (Harper, 1977). Differences in seed morphology and mechanisms for extended longevity in the soil may determine how deeply seeds penetrate the soil and how long they persist. Nearly all species present in the lower soil stratum were also found in the upper soil statum. The reverse was not true, supporting the assumption that seeds found at greater depths are older seeds that have, over time, moved downward in the soil. Differences in species composition between two soil strata has been noted by Major and Pyott (1966).

Species observed in 1985 were present in 1986, indicating these are species which persist within the soil for long periods of time with constant losses and gains creating a persistent seed bank. Additional species observed in 1986, many of which were observed in the vegetation, represented only a small proportion of the seed in soil (excluding *Koeleria macrantha*, *Agropyron* and *Poa* sp.) suggesting they may only be periodic guests of the seed bank when the opportunity arises. These species may lack mechanisms for long-term persistence or have difficulty in becoming buried in the soil. The absence of some species in the soil may indicate lack of dormancy mechanisms, wind dispersed species, or a reflection of sampling and the clumped distribution of seed in the soil.

The most significant change in species composition of the seed bank from 1985 to 1986 was the presence of many grass species and their increased abundance. Most interesing was the presence of *Koeleria macrantha*, absent in 1985, and the additional species and increased seed density of *Agropyron* and *Poa* species, which together represented over half the seed bank in each treatment. These monocotyledon species may be present in the soil only during the summer and otherwise make little or no contribution to the seed bank (Thompson and Grime, 1979; Grime et al., 1981). In European grasslands, *Koeleria macrantha* has a transient seed bank during the summer with the functional significance being to exploit grasslands subjected to seasonally-predictable damage by drought (Thompson and grime, 1979). This data is in contrast to other studies on natural grasslands which have found monocotyledon species represent a very small part of the seed bank (Johnston et al., 1969; Archibold, 1981; Rabinowitz, 1981).

The absence of *Festuca scabrella* in the seed bank in any given treatment, soil stratum, or year in this study was unexpected as Johnston et al. (1969) observed *Festuca scrabrella* in fairly large quantities in an ungrazed treatment in rough fescue grassland and also in grazed treatments, although in smaller quantities. Lack of *Festuca scabrella* seed in the soil of this study may reflect its absence in the above-ground vegetation, especially in the grazed treatment due to very heavy grazing pressure. However, seed should have occurred in the ungrazed treatment where plants were observed producing and dispersing seed. The absence of *Festuca scabrella* seed in the ungrazed treatment may be related in part to a high seed decay rate and its inability to survive in the soil. Roberts (1981) has shown low rates of persistence for other species of *Festuca*. Also, *Festuca scabrella* is an erratic seed producer with many years having no appreciable seed production (Johnston and MacDonald, 1967). Considering seed persistence and frequency of seed production, it may take many years for seed of this species to occur in the soil in appreciable quantities. In Johnston's study soil was sampled in 1966, an important year in seed production for this species (Johnston and MacDonald, 1967), which likely accounts for the presence of *Festuca scabrella* in the soil. Seed production of *Festuca scabrella* shown by Johnston and MacDonald (1967) was far superior to that observed in this study (Chapter 3) perhaps suggesting that 1986 was not a good year for seed production of *Festuca scabrella*.

The absence of large numbers of seed of other grass species such as *Stipa* sp., *Helictotrichon hookeri*, and *Danthonia parryi* is likely related to low levels of seed production, but also to a short-life span in the soil related to seed size and morphology since these species are common constituents of the vegetation. Grass species commonly lacking in seed banks are those in which the seeds are large and accentuated with awns or hairs which likely applies to the species discussed here (Grime et al., 1981).

In contrast to other research (Champness and Morris, 1948; Major and Pyott, 1966; Rabinowitz, 1981), seed from perennial species was more abundant in the seed bank in both 1985 and 1986 than from annual species. This may reflect the abundance of perennial species on this grassland and on other Canadian grasslands since Johnston et al. (1969) and Archibold (1981) both observed the presence of some perennial species in the seed bank. Presence of seed from perennial species in the soil was unexpected since theoretically vegetative propagation by rhizomes and stolons is more important than seed production, as was observed by Archibold (1981). Silvertown (1981) contends dormant seeds may be produced only by species which have a high potential risk of periodic extinction, such as annuals. Fyles (1988) noted that short-lived seeds in the soil may require continual input of seed into the soil to maintain seed bank populations and may be true for perennial species on this site. Perhaps in years of improved moisture conditions following drought, perennial grass species may be able to supplement the seed bank, through increased seed production even though only a small percentage of seed will be permanently incorporated into the soil.

Comparison of the Seed Bank and Above-ground Vegetation

The variety of species in the seed bank in both years was, in part, a reflection of species present on the site and their seed yield. Correlation between species observed in the seed bank with species in the above-ground vegetation is poor but somewhat better than in most studies (Chippindale and Milton, 1934; Dore and Raymond, 1942; Major and Pyott, 1966; Rabinowitz, 1981) although Prince and Hodgdon (1946) showed better correlation between the vegetation and seed bank.

The discrepencies between the seed bank and vegetation have been attributed to the inability of some species to set seed (Johnston et al., 1969) and occurrence of vegetative regeneration for perennial grass and grass-like species (Archibold,1981). Together these factors may account for differences. Even with seed production observed in 1986, the seed bank did not contain seed of all seed producing plants. This lack of correlation was also noted by Chippindale and Milton (1934). Seeds reaching the surface may not be present in the soil due to *in situ* germination, and death due to predation (Janzen, 1971) or fungal pathogens (Moore and Wein, 1977). Absence of seed of some species in the soil is largely related to lack of seed dormancy mechanisms and seed morphology which encourage extended preservation of viability (Golubeva, 1962: as cited by Major and Pyott, 1966; Roberts, 1981). Other factors such as depth of burial (Archibold, 1981), moisture stress (Blake, 1935), long distance dispersal and sampling may also determine the presence or absence of seed of various species in the soil. The presence of seed in the soil of some species which are absent from the vegetation is likely related to the extended seed longevity of these species from earlier successional stages, such as previously cultivated grasslands in which weedy species are common and persistent in the soil (Milton, 1943). It appears that in years of enhanced seed production, correspondance between the seed bank and the above-ground vegetation is not greatly improved.

Similarities between the seed bank and vegetation may lack accuracy in part since vegetation data is based on the whole site rather than the flora directly in the area of sampling (Rabinowitz, 1981). However, since some seeds are dispersed by wind one would expect some input from the surrounding vegetation. A closer relationship would be expected when comparisons are made between seed rain and the seed bank as seed rain is a more accurate representation of the seeds coming in contact with the soil (Rabinowitz, 1981).

Implications for Secondary Succession

Presence of seed in the soil, mostly from early successional species having special mechanisms designed for longevity, may assure the success of secondary plant succession should disturbance occur (Johnston et al., 1966). Seeds of these species are opportunistic and only germinate and emerge under special conditions. Since seeds of many early successional species require light to grow, conditions conducive to germination are bare ground and lack of competition from other light inhibiting plants. Data shown here suggests the seed observed in the soil in 1985 is persistent and likely most characteristic of the seed bank during dry years. If the seed bank provides species to exploit gaps that occur during these periods of moisture deficit, the abundance of dicotyledon species in the soil, many of which are early sucessional species, suggests plant succession would be undesirable, progressing towards a lower level of succession.

In periods of favorable moisture conditions with improved species composition in the seed bank, as in 1986, monocotyledon species may be able to exploit gaps that occur during the grazing season. If monocotyledon species germinate faster than dicotyledon species, as was suggested from data shown in this study, these species may be able to exploit gaps more effectively than dicotyledon species. Although plant succession will never proceed through the seed banks towards a successional level where *Festuca scabrella* is dominant, as indicated from data found here, in seasons with enhanced seed production succession may be able to proceed in a favorable direction.

Sampling Procedure

The presence in the seed bank in 1986 of some species which were absent in the seed bank in 1985 and in the above-ground vegetation suggests germination treatments may fail to detect seed of some species. It is unlikely any germination treatment would be adequate for all species in the sward which was also suggested by Johnston et al. (1969). Certain seeds may require special treatment, such as scarification for germination, while others may need months and even years to ensure germination of all species (Brenchley and Warrington, 1930) since it is likely some of the seed would exhibi dormancy. No attempts were made to extract seed from the soil after germination to determine ungerminated seeds. This may have resulted in an underestimation of the seed bank. Moore and Wein (1977) found a greater number of seeds present in forest soil after germination than the number that germinated. In contrast, Archibold (1981) found only 3% of the seeds did not germinate under laboratory conditions.

To minimize sampling error, samples were taken over very large units, along transects, with subsamples pooled. For the purpose of this study, this procedure was suitable for determining species composition and to give an estimation of seed density between treatments, soil strata, and years. Bigwood and Inouye (1988) found spatial distribution of seed was largely governed by environmental conditions, and to a lesser degree, biological factors. It is presumed here that changes seen in the seed bank over the two years were a result of improved moisture conditions, especially during the growing season, in 1985 and 1986 compared to 1982 through 1984. This perhaps resulted in changes in the spatial distribution of the seed in the soil from enhanced seed production, which was not considered at the time of sampling, and perhaps neccesitated a change in the intensity of soil sampling. For these reasons, the intensity of sampling used here may be criticized by others. The majority of previous studies dealing with seed banks have been criticized for using very small numbers of large samples resulting in imprecise estimates of seed in the soil and statistically invalid conclusions (Champness, 1949; Roberts, 1981).

CONCLUSIONS

Seed bank density and species number were not found to be significantly influenced by grazing treatment or rest in this study. These components of the seed bank are significantly different between soil strata with the majority of seed present in the upper soil stratum. Yearly differences were observed with seed density being much greater in 1986 largely due to the presence of monocotyledon species. Dicotyledon species, especially *Artemisia frigida* and *Androsace septentrionalis*, were more abundant in the soil in 1985 while *Koeleria macrantha*, *Agropyron* and *Poa* species were more abundant in 1986 due to increased seed production. Lack of similarity between the above-ground vegetation and seed bank suggest many species are remnants of past successional stages, but also that seed of many species is not accumulative in the soil. Absence of *Festuca scabrella* seed in the soil is probably related to poor seed persistence and intermittent seed production. Some species are likely only periodic guests of the soil occurring when environmental conditions are suitable for seed production.

Table 2.1. Significant effects ($P<0.05$) from transformed data shown for seed density (seeds m^{-2}) and species number in the seed bank in 1985 and 1986 for dicotyledon (D), monocotyledon (M), and total (T) seed.

Parameters[1]		Degrees of freedom	Seed m^{-2} 1985			Seed m^{-2} 1986			Species number 1985			Species number 1986		
			D	M	T	D	M	T	D	M	T	D	M	T
	L	1	*	NS	*	NS	*	*	*	NS	*	*	*	*
error	FL	4												
	T	1	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
error	FT	4												
	TL	1	NS	NS	NS	NS	*	NS	NS	NS	NS	NS	NS	NS
error	FTL	4												
	F	4	*	NS	*	*	*	*	*	NS	*	NS	*	*
	FT	4	*	NS	NS	*	*	*	NS	NS	NS	NS	*	*
error	S(F,T)	50												
	FL	4	NS	NS	NS	*	NS	NS	NS	NS	NS	NS	NS	NS
	FTL	4	NS	NS	NS	*	NS	NS	NS	NS	NS	*	NS	*
	S(F,T)	50	NS	NS	NS	*	*	*	NS	NS	NS	NS	NS	NS
	LS(F,T)	50	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
error	LS(F,T)	50												

[1]Parameters consist of L=soil stratum (0-2.5cm and 2.5-5.0 cm);T=treatment (ungrazed and grazed);F=fields; S=samples.

Table 2.2. Dicotyledon (D), monocotyledon (M), and total (T) mean seed density (seeds m^{-2} (+/- SE)) of the seed bank in 1985 and 1986 in grazed and ungrazed treatments in the upper (0-2.5 cm) and lower (2.5-5.0 cm) soil strata.

	1985			1986		
Treatment	D	M	T	D	M	T
<u>Upper soil stratum</u>						
Grazed	499 (37)	158 (30)	657 (49)	685 (71)	1496 (208)	2181 (235)
Ungrazed	465 (49)	134 (22)	599 (59)	560 (60)	1953 (149)	2513 (164)
<u>Lower Soil Stratum</u>						
Grazed	117 (21)	58 (10)	175 (27)	572 (71)	1264 (189)	1836 (225)
Ungrazed	103 (25)	43 (13)	146 (27)	343 (36)	1024 (98)	1367 (108)
Treatment mean						
Grazed	308	108	416	625	1380	2004
Ungrazed	284	89	373	451	1489	1940

Between years seed density was significantly different for all comparisons (P<0.05).
Within year seed density was significantly different between soil strata for all comparisons; exceptions were monocotyledon seed density in 1985, and dicotyledon seed density in 1986 (P<0.05).
Within year and soil stratum seed density did not differ significantly between treatments (P<0.05).

Table 2.3. Species composition of the seed bank in 1985 and 1986 in grazed (G) and ungrazed (Un) treatments in the upper (U: 0-2.5 cm) and lower (L: 2.5-5.0 cm) soil strata.

	1985				1986			
	Treatments							
	G		Un		G		Un	
Species	U	L	U	L	U	L	U	L
Dicotyledons								
Achillea millefolium	-	-	-	-	+	-	-	-
Amaranthus retroflexus	+	-	+	-	+	-	-	-
Androsace septentrionalis	+	+	+	+	+	+	+	+
Anemone patens	-	-	-	-	+	-	+	-
Antennaria parvifolia	+	+	+	-	+	+	+	-
Arabis holboellii var. *retrofracta*	-	-	-	-	+	-	+	-
Artemisia cana	+	-	+	-	+	+	+	-
Artemisia frigida	+	+	+	+	+	+	+	+
Aster ericoides subspp. *pansus*	+	-	+	-	+	+	+	+
Campanula rotundifolia	-	-	-	-	-	+	-	+
Chenopodium album	+	+	+	+	-	+	-	-
Cirsium arvense	+	-	+	-	+	-	-	-
Delphinium nutallianum	-	-	-	-	+	-	+	-
Draba nemorosa	+	+	-	-	+	+	+	+
Draba sp. (1)[1]	+	+	+	-	+	+	-	+
Epilobium angustifolium and *Epilobium ciliatum*[2]	+	+	+	+	+	+	+	+
Galeopis tetrahit	-	-	-	-	+	-	-	-
Galium boreale	+	-	+	-	+	+	+	+
Geum sp. (2)[1]	+	-	+	+	+	+	+	+
Huechera richardsonii	-	-	-	-	-	-	+	-
Lepidium densiflorum	+	+	+	+	+	+	+	+
Linum silcatum	-	-	-	+	+	+	+	+
Malva rotundifolia	+	+	+	+	+	+	+	+
Potentilla sp. (1)[1]	+	+	+	+	+	+	+	+
Ranunculus cymbalaria and *Ranunculus pusillus*[2]	+	+	+	-	+	+	+	+
Solidago missouriensis	-	-	-	-	+	+	-	-
Taraxacum officinale	+	-	-	-	+	-	-	+
Unidentified X1	-	-	-	-	-	-	+	-
Unidentified X2	-	-	-	-	-	-	+	-
Subtotal	21	13	19	11	27	21	23	18

Table 2.3 cont'd

<u>Monocotyledons</u>								
Agropyron sp. (4)[3]	+	+	+	+	+	+	+	+
Bouteloua gracilis	-	-	-	+	+	+	+	-
Carex sp. (1)[1]	-	-	-	-	+	+	+	+
Cyperus schweinitzii	-	-	-	-	+	-	-	-
Danthonia parryi	-	-	-	-	+	-	+	-
Festuca rubra	-	-	-	-	+	-	+	-
Helictotrichon hookeri	+	+	+	+	+	-	+	+
Juncus bufonius, Juncus tenuis, and Juncus torreyi[2]	+	+	+	+	+	+	+	+
Koeleria macrantha	-	-	-	-	+	+	+	+
Muhlenbergia cuspidata	+	-	-	-	+	-	-	-
Poa sp. (6)[4]	+	+	+	+	+	+	+	+
Stipa sp. (1)[1]	-	-	-	-	-	-	+	-
Subtotal	11	10	10	11	21[5]	12	20[5]	12
TOTAL	32	23	29	22	48	33	43	30

[1] Number of unidentified species.

[2] Species grouped together in which identification separating each was not always possible.

[3] *Agropyron* species present in 1985 in both soil strata included *Agropyron dasystachyum* var. *dasystachyum*, *Agropyron pectiniforme*, and *Agropyron smithii*. Also present in 1986 in the upper soil stratum was *Agropyron repens*. Presence of each species in each treatment was not determined due to the large number of emerged seedlings.

[4] *Poa* species present in 1985 in both soil strata included *Poa compressa*, *Poa pratensis*, and *Poa sandbergii*. Also present in 1986 in the upper soil stratum only was *Poa cusickii*, *Poa nevadensis*, and *Poa puccinella*. Presence of each species in each treatment was not determined due to the large number of emerged seedlings.

[5] Assuming all *Agropron* and *Poa* species were present in both treatments within the upper soil stratum.

Table 2.4. Ranking of species in the seed bank in 1985 by the Dominance Hierarchy Curve.

	Soil Strata							
	Upper (0-2.5 cm)				Lower (2.5-5.0 cm)			
	Treatment							
Species	Grazed		Ungrazed		Grazed		Ungrazed	
Dicotyledons								
Amaranthus retroflexus	18[5]	(13)[6]	15	(11)				
Androsace septentrionalis	3	(2)	2	(2)	1	(1)	1	(1)
Anemone patens								
Antennaria parvifolia	11	(9)	11	(8)	13	(9)		
Artemisia cana	10	(8)	13	(10)				
Artemisia frigida	1	(1)	1	(1)	3	(2)	3	(2)
Aster ericoides subssp. *pansus*	6	(4)	16	(12)				
Campanula rotundifolia								
Chenopodium album	19	(14)	19	(15)	9	(6)	13	(9)
Cirsium arvense	20	(15)	20	(16)				
Draba nemorosa	21	(16)			6	(4)		
Draba sp. (1)[1]	22	(17)	17	(13)	14	(10)		
Epilobium angustifolium and *Epilobium ciliatum*[2]	4	(3)	4	(3)	10	(7)	4	(3)
Galium boreale	13	(11)	8	(6)	12	(8)	9	(5)
Geum sp. (2)[1]	9	(7)	7	(5)			7	(6)
Lepedium densiflorum	12	(10)	9	(7)	15	(11)	8	(7)
Linum silcatum							11	(8)
Malva rotundifolia	16	(12)	6	(4)	5	(3)	14	(10)
Potentilla sp. (1)[1]	7	(5)	12	(9)	16	(12)	6	(4)
Ranunculus cymbalaria and *Ranunculus pusillus*[2]	8	(6)	18	(14)	7	(5)		
Solidago missouriensis								
Taraxacum officinale	23	(18)						

Table 2.4. cont'd

<u>Monocotyledons</u>								
Agropyron sp. (4)[3]	5	(1)	5	(1)		(4)	10	(3)
Bouteloua gracilis							15	(5)
Helictrichon hookeri	17	(5)	14	(4)		(2)	5	(2)
Juncus bufonius, *Juncus tenuis*, and *Juncus torreyi*[2]	2	(2)	3	(2)	2	(1)	2	(1)
Muhlenbergia cuspidata	14	(3)						
Poa sp. (6)[4]	15	(4)	10	(3)	8	(3)	12	(4)

[1] Number of unidentified species.
[2] Species grouped together in which identification separating each was not always possible.
[3] *Agropyron* species present in 1985 in both treatments and soil strata included *Agropyron dasystachyum* var. *dasystachyum*, *Agropyron pectiniforme*, and *Agropyron smithii*.
[4] *Poa* species present in 1985 in both treatments and soil strata included *Poa compressa*, *Poa pratensis*, and *Poa sandbergii*.
[5] Ranking of species overall species.
[6] Ranking of species within dicotyledon and monocotyledon groups.

Table 2.5. Ranking of species in the seed bank in 1986 by the Dominance Hierarchy Curve.

	Soil Strata							
	Upper (0-2.5 cm)				Lower (2.5-5.0 cm)			
	Treatment							
Species	Grazed		Ungrazed		Grazed		Ungrazed	
Dicotyledons								
Achillea millefolium	35[5]	(24)[6]						
Amaranthus retroflexus	25	(17)						
Androsace septentrionalis	6	(2)	7	(2)	3	(1)	4	(1)
Anemone patens	21	(14)	23	(16)				
Antennaria parvifolia	8	(3)	12	(7)	15	(10)	18	(12)
Arabis holboellii var. *retrofracta*	9	(4)	8	(3)				
Artemisia cana	16	(11)	14	(9)	19	(14)		
Artemisia frigida	4	(1)	3	(1)	4	(2)	8	(3)
Aster ericoides subssp. *pansus*	12	(7)	16	(11)	11	(6)	14	(9)
Campanula rotundifolia					21	(15)	19	(13)
Chenopodium album					22	(16)		
Cirsium arvense	30	(20)						
Delphinium nuttallianum	26	(18)	17	(12)				
Draba nemorosa	13	(8)	13	(8)	10	(5)	11	(6)
Draba sp. (1)[1]	27	(19)			17	(12)	20	(14)
Epilobium angustifolium and *Epilobium ciliatum*[2]	22	(15)	18	(13)	8	(3)	7	(2)
Galeopis tetrahit	23	(16)						
Galium boreale	14	(9)	11	(6)	12	(7)	9	(4)
Geum sp. (2)[1]	10	(5)	15	(10)	14	(9)	16	(11)
Heuchera richardsonii			25	(18)				
Lepedium densiflorum	17	(12)	9	(4)	9	(4)	10	(5)
Linum silcatum	11	(6)	24	(17)	13	(8)	15	(10)
Malva rotundifolia	31	(21)	26	(19)	23	(17)	21	(15)
Potentilla sp. (1)[1]	18	(13)	19	(14)	18	(13)	12	(7)

Table 2.5. cont'd

Ranunculus cymbalaria and *Ranunculus pusillus*[2]	15	(10)	10	(E)	16	(11)	13	(8)
Solidago missouriensis	32	(22)			24	(18)		
Taraxacum officinale	33	(23)					22	(16)
X1			21	(15)				
X2			30	(20)				
<u>Monocotyledons</u>								
Agropyron sp. (4)[3]	2	(2)	5	(4)	1	(1)	1	(1)
Bouteloua gracilis	24	(8)	27	(8)	20	(6)		
Carex sp. (1)[1]	7	(5)	4	(3)	5	(3)	3	(3)
Cyperus schweinitzii	34	(11)						
Danthonia parryi	20	(6)	28	(9)				
Festuca rubra	28	(9)	20	(6)				
Helictrichon hookeri	19	(7)	22	(7)			17	(6)
Juncus bufonius, Juncus tenuis, and *Juncus torreyi*[2]	5	(4)	6	(5)	6	(4)	2	(2)
Koeleria macrantha	1	(1)	1	(1)	2	(2)	5	(4)
Muhlenbergia cuspidata	29	(10)						
Poa sp. (6)[4]	3	(3)	2	(2)	7	(5)	6	(5)
Stipa sp. (1)[1]			29	(10)				

[1] Number of unidentified species.
[2] Species grouped together in which identification separating each was not always possible.
[3] *Agropyron* species present in 1986 in each soil stratum included *Agropyron dasystachyum* var. *dasystachyum*, *Agropyron pectiniforme*, and *Agropyron smithii*. Also present in the upper soil stratum was *Agropyron repens*. Presence of species in each treatment was not determined due to the large number of emerged seedlings.
[4] *Poa* species present in 1986 in each soil stratum included *Poa compressa*, *Poa pratensis*, and *Poa sandbergii*. Also present in the upper soil stratum was *Poa cusickii*, *Poa nevadensis*, and *Poa puccinellia*. Presence of species in each treatment was not determined due to the large number of emerged seedlings.
[5] Ranking of species overall species.
[6] Ranking of species within dicotyledon and monocotyledon groups.

Table 2.8. Dicotyledon and monocotyledon species observed in the above-ground vegetation and the seed bank in 1985 and 1986 in both grazed and ungrazed treatments and upper (0-2.5 cm) and lower (2.5-5.0 cm) soil strata.

Species (common name)		Above-ground vegetation	Seed Bank 1985	Seed Bank 1986
<u>Dicotyledons</u>				
Forbs				
Achillea millefolium	(common yarrow)	+	-	+
Agastache foeniculum	(giant hyssop)	+	-	-
Agoseris glauca	(false dandelion)	+	-	-
Amaranthus retroflexus	(red-root pigweed)	-	+	+
Androsace septentrionalis	(fairy candelabra)	+	+	+
Anemone canadensis	(Canada anemone)	+	-	-
Anenome multifida	(cut-leaved anemone)	+	-	-
Anenome patens	(prairie crocus)	+	-	+
Antennaria parvifolia	(small-leaved everlasting)	+	+	+
Antennaria monocephala[1]	(pussy-toes)	+	-	-
Apocynum cannabinum[1]	(Indian-hemp)	+	-	-
Arabis holboellii var. *retrofracta*	(reflexed rock cress)	+	-	+
Arctium tomentosum	(woolly burdock)	+	-	-
Artemisia biennis[1]	(biennial sagewort)	+	-	-
Artemisia frigida	(pasture sagewort)	+	+	+
Artemisia ludoviciana var. *ludoviciana*	(prairie sagewort)	+	-	-
Aster ericoides subspp. *pansus*	(tufted white prairie aster)	+	+	+
Aster laevis	(smooth aster)	+	-	-
Astragalus alpinus	(alpine milk-vetch)	+	-	-
Astragalus bisulcatus	(two-grooved milk-vetch)	+	-	-
Astragalus crassicarpus	(ground plum)	+	-	-
Astragalus missouriensis	(Missouri milk-vetch)	+	-	-
Astragalus pectinatus	(narrow-leaved milk-vetch)	+	-	-
Balsamorhiza sagittata	(balsam-root)	+	-	-
Campanula rotundifolia	(harebell)	+	-	+
Carduus nutans	(nodding thistle)	+	-	-
Castilleja sp.	(Indian paintbrush)	+	-	-
Cerastium arvense	(field chickweed)	+	-	-
Chamaerhodes erecta	(bunge)	+	-	-
Chenopodium album	(goosefoot)	+	+	+
Cirsium arvense	(Canada thistle)	+	+	+
Cirsium undulatum	(wavy-leaved thistle)	+	-	-
Cirsium vulgare	(bull-thistle)	+	-	-
Commandra umbellata var. *pallida*	(bastard toad-flax)	+	-	-
Coryphantha vivipara	(ball cactus)	+	-	-
Cryptantha macounii	(clustered oreocarya)	+	-	-
Cynoglossum officinale	(hound's tongue)	+	-	-

Table 2.6.cont'd

		Above-ground vegetation	Seed Bank 1985	Seed Bank 1986
Delphinium bicolor	(low larkspur)	+	-	-
Delphinium nuttalianum	(larkspur)	-	+	+
Descurainia sophia	(flixweed)	+	-	-
Dodecatheon conjugens	(shooting star)	+	-	-
Draba nemorosa	(yellow whitlow-grass)	+	+	+
Draba sp. (2)[2]	(whitlow-grass)	-	+	+
Epilobium angustifolium	(fireweed)	-	+	+
Epilobium ciliatum	(northern willowherb)	-	+	+
Erigeron caespitosus	(tufted fleabane)	+	-	-
Erigeron glabellus var. *pubescens*	(smooth fleabane)	+	-	-
Eriogonum flavum	(yellow umbrella-plant)	+	-	-
Erysimum aesperum	(prairie rocket)	+	-	-
Erysimum cheiranthoides	(wormseed mustard)	+	-	-
Erysimum inconspicuum	(small-flowered rocket)	+	-	-
Gaillardia aristada	(gaillardia)	+	-	-
Galeopis tetrahit	(hemp nettle)	-	-	+
Galium boreale	(northern bedstraw)	+	+	+
Gaura coccinea	(scarlet butterfly-weed)	+	-	-
Geranium viscosissimum	(sticky purple geranium)	+	-	-
Geum sp. (2)[2]	(avens)	-	+	+
Geum triflorum	(old man's whiskers)	+	-	-
Glycyrrhiza lepidota	(wild licorice)	+	-	-
Grindelia squarrosa	(gumweed)	+	-	-
Gutierrezia sarothrae	(broomweed)	+	-	-
Haplopappus spinulosus	(spiny ironplant)	+	-	-
Hedysarum sulphurescens	(yellow hedysarum)	+	-	-
Helianthus sp.	(sunflower)	+	-	-
Heterotheca villosa	(golden aster)	+	-	-
Heuchera richardsonii	(alumroot)	+	-	+
Hymenoxys richardsonii	(Colorado rubber-plant)	+	-	-
Lappula occidentalis	(bluebur)	+	-	-
Lepidium densiflorum	(common peppergrass)	+	+	+
Lesquerella arenosa var. *arenosa*	(bladder-pod)	+	-	-
Liatris punctata	(dotted blazing star)	+	-	-
Linum lewisii	(wild blue flax)	+	-	-
Linum rigidum	(yellow flax)	+	-	-
Linum sulcatum	(grooved yellow flax)	-	-	+
Lithospermum ruderale	(woolly gromwell)	+	-	-
Lomatium macrocarpum	(long-fruited parsley)	+	-	-
Lupinus argenteus[1]	(silvery-lupine)	+	-	-
Lupinus sericeus	(perennial lupine)	+	-	-
Lygodesmia juncea[1]	(skeleton-weed)	+	-	-
Malva rotundifolia	(round leaved mallow)	-	+	+
Medicago sativa[1]	(alfalfa)	+	-	-
Mentha arvensis	(wild mint)	+	-	-
Monarda fistulosa var. *menthifolia*	(wild bergamot)	+	-	-
Opuntia polyacantha	(prickly-pear)	+	-	-
Orthocarpus luteus	(owl's-clover)	+	-	-
Oxytropis sericea	(early-yellow loco weed)	+	-	-
Paronychia sessiliflora	(low whitlow-wort)	+	-	-
Penstemon albidus	(white beard-tongue)	+	-	-

Table 2.6. cont'd

		Above-ground vegetation	Seed Bank 1985	Seed Bank 1986
Penstemon nitidus	(smooth blue beard-tongue)	+	-	-
Petalostemon candidum	(white prairie clover)	+	-	-
Petalostemon purpureum	(purple prairie clover)	+	-	-
Phlox hoodii	(moss phlox)	+	-	-
Plantago patagonica var. *patagonica*	(Pursh's plantain)	+	-	-
Potentilla anserina	(silverweed)	+	-	-
Potentilla arguta[1]	(white cinquefoil)	+	-	-
Potentilla hippiana	(woolly cinquifoil)	+	-	-
Potentilla sp. (2)[2]	(cinquefoil)	-	+	+
Psoralea esculenta	(Indian breadroot)	+	-	-
Ranunculus cymbalaria	(seaside buttercup)	-	+	+
Ranunculus pusillus	(buttercup)	-	+	+
Ratibida columnifera	(prairie coneflower)	+	-	-
Rudbeckia hirta	(black-eyed susan)	+	-	-
Selaginella densa	(little club moss)	+	-	-
Senecio canus	(prairie groundsel)	+	-	-
Solidago missouriensis	(low goldenrod)	+	-	+
Sphaeralcea coccinea	(scarlet mallow)	+	-	-
Taraxicum officinale	(common dandelion)	+	+	+
Thermopsis rhombifolia	(golden bean)	+	-	-
Thlaspi arvense	(pennycress)	+	-	-
Tragopogon dubius	(goat's-beard)	+	-	-
Vicia americana	(wild vetch)	+	-	-
Unknown X1		-	-	+
Unknown X2		-	-	+
Shrubs				
Amelanchier alnifolia	(saskatoon)	+	-	-
Arctostaphylos uva-ursi	(kinnikinnick)	+	-	-
Artemisia cana	(sagebrush)	+	+	+
Crataegus rotundifolia	(roundleaved hawthorne)	+	-	-
Elaeagnus commutata[1]	(silver-berry)	+	-	-
Juniperus horizontalis	(creeping juniper)	+	-	-
Populus tremuloides[1]	(aspen popular)	+	-	-
Potentilla fruticosa	(shrubby cinquifoil)	+	-	-
Rosa arkansana	(prairie rose)	+	-	-
Salix sp.[1]	(willow)	+	-	-
Symphoricarpos albus	(western snowberry)	+	-	-
<u>Monocotyledons</u>				
Agropyron dasystachyum var. *dasystachyum*	(northern wheat grass)	+	+	+
Agropyron pectiniforme	(crested wheat grass)	+	+	+
Agropyron repens	(quack grass)	-	+	-
Agropyron smithii	(western wheat grass)	+	+	+
Agropyron trachycaulum var. *trachycaulum*	(slender wheat grass)	+	-	-
Agropyron trachycaulum var. *unilaterale*	(awned wheat grass)	+	-	-
Agrostis scabra	(hair grass)	+	-	-
Allium cernuum	(nodding onion)	+	-	-

Table 2.6.cont'd

		Above-ground vegetation	Seed Bank 1985	Seed Bank 1986
Allium textile	(prairie onion)	+	-	-
Bouteloua gracilis	(blue grama)	+	+	+
Bromus inermis	(awnless brome)	+	-	-
Bromus mollis		+	-	-
Calamagrostis montanensis	(plains reed grass)	+	-	-
Calamovilfa longifolia	(sand grass)	+	-	-
Carex filifolia	(thread-leaved sedge)	+	-	-
Carex retrorsa[1]	(turned sedge)	+	-	-
Carex sp. (1)[2]	(sedge)	-	-	+
Carex stenophylla subspp. *eleocharis*		+	-	-
Cyperus schweinitzii	(sand nut-grass)	-	-	+
Danthonia parryi	(Parry oat grass)	+	-	+
Festuca rubra	(red fescue)	+	-	+
Festuca scabrella	(rough fescue)	+	-	-
Helictotrichon hookeri	(Hooker's oat grass)	+	+	+
Juncus balticus	(wire rush)	+	-	-
Juncus bufonius	(toad rush)	-	+	+
Juncus tenuis	(slender rush)	-	+	+
Juncus torreyi	(Torrey's rush)	-	+	+
Koeleria macrantha	(june grass)	+	-	+
Muhlenbergia cuspidata	(plains muhly)	+	+	+
Oryzopsis hymenoides	(Indian rice grass)	+	-	-
Phleum pratense	(timothy)	+	-	-
Poa compressa	(Canada bluegrass)	-	+	+
Poa cusickii	(early blue grass)	-	-	+
Poa nevadensis	(blue grass)	-	-	+
Poa pratensis	(Kentucky bluegrass)	+	+	+
Poa puccinella	(blue grass)	-	-	+
Poa sandbergii	(Sandberg bluegrass)	+	+	+
Schizachyrium scoparium subsp. *scoparium*	(little bluestem)	+	-	-
Sisyrinchium montanum	(blue-eyed grass)	+	-	-
Stipa comata	(needle and thread)	+	-	-
Stipa curtiseta	(western porcupine grass)	+	-	-
Stipa sp. (1)[2]	(needlegrass)	-	-	+
Stipa viridula	(green needle grass)	+	-	-
Zigadenus elegans	(white camas)	+	-	-
Zigadenus venenosus	(death camas)	+	-	-

[1]Recorded by Willms (unpublished data, 1986)
[2] Number of unidentifiable species.

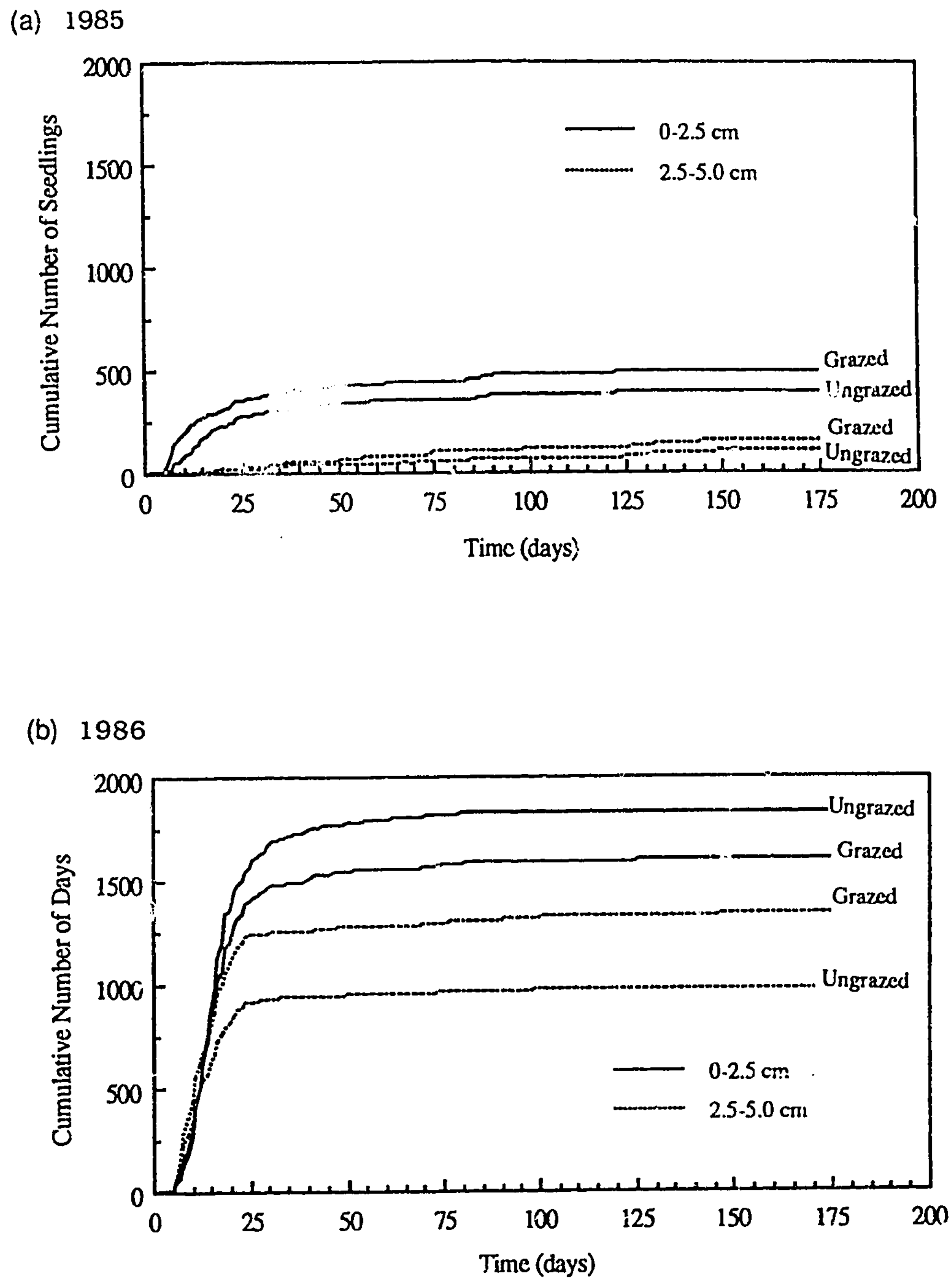

Figure 2.1. The cumulative number of seedlings emerged over 175 days in (a) 1985 and (b) 1986 in grazed and ungrazed treatments within the upper (0-2.5 cm) and lower (2.5-5.0 cm) soil strata.

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III. POTENTIAL SEED YIELD, SPECIES COMPOSITION AND ABUNDANCE OF SEED RAIN, AND THEIR RESEMBLANCE TO THE SEED BANK UNDER SHORT DURATION GRAZING AND REST IN A TRANSITIONAL MIXED PRAIRIE/FESCUE GRASSLAND IN ALBERTA

INTRODUCTION

The annual potential gain of dispersed seed to the soil is dependent on plant abundance and seed production (Howe and Chancellor, 1983). Seed yield in North American grasslands varies from as low as 720 seeds m^{-2} in a xeric grassland to as high as 118,000 seeds m^{-2} in a mesic grassland (Brown, 1943). Seed yield is generally less on grazed grasslands than on ungrazed grasslands even with rest-rotation grazing systems (Eckert and Spenser, 1987).

Seed rain is the composition and abundance of dispersing plant propagules arriving on a surface (Foster Huennecke and Graham, 1987), forming a potential source of colonists for recruitment to a habitat or for plant regeneration after disturbance (Harper 1977; Rabinowitz and Rapp, 1980). In a tallgrass prairie, seed rain was 19,726 seeds m^{-2} or 125 seeds per trap over a 26 week period (Rabinowitz and Rapp, 1980). Estimates of seed rain from other habitats such as forests range from 106 seeds m^{-2} to 653 seeds m^{-2} (Wagner, 1965; Ryvarden, 1971: cited from Rabinowitz and Rapp, 1980). Species richness varies from 12 species (Wagner, 1965) to 57 species (Ryvarden, 1971: cited from Rabinowitz and Rapp, 1980). Of 30 species captured on tallgrass prairie, 21 contributed less than 50 seeds each to seed rain while 9 contributed to over 90% of the seed rain (Rabinowitz and Rapp, 1980).

Seeds are generally spatially dispersed in an uneven pattern (Harper, 1977). For a single grassland species, seed may be dispersed in a random pattern in space or spatially clumped whereas for the whole plant population seed is usually quite clumped (Rabinowitz and Rapp, 1980). Seed rain in a tallgrass prairie is temporally bimodal, representing levels of seed production of grassland species (Rabinowitz and Rapp, 1980). Peaks occur in early summer and autumn and are largely represented by *Gramineae* and *Compositae* species, respectively.

Rabinowitz and Rapp (1980) found most species present in seed rain were present in the seed bank, while the majority of species present in the seed bank were not present in the seed rain. They suggest species present in the soil but absent from the seed rain likely represent past successional stages in the grassland, or have a pulsed input and respond when conditions are favorable for germination.

The absence of seed of some species in the seed rain is likely due to trap design which does not ensure equal representation of all species in the community as observed by Foster Huenneke and Graham (1987). Awned grass species have greatest capture rates while smooth round seeds bounce off traps. Seed capture is also reduced as the season progresses due to capture of seed by leaves of tussock grasses and increasing height of seed fall (Rabinowitz and Rapp, 1980). In contrast, Werner (1975) considered sticky traps effective and unbiased for measuring seed rain in grasslands (Werner, 1975). The use of sticky traps may be best adapted for use in grasslands with plants of low stature (Rabinowitz and Rapp, 1980)

It was hypothesized that the abundance and composition of seed rain would significantly differ for grazed and ungrazed treatments. The main objectives of this study were to determine potential seed yield, species composition and abundance of seed rain, and their resemblance to the seed bank under short duration grazing in a transitional mixed prairie/fescue grassland compared with an ungrazed treatment. The efficiency of seed capture and the implications of this data for the seed bank and potential succession were considered.

MATERIALS AND METHODS

Site Description

The study site was northwest of Fort Macleod, Alberta on the edge of the Porcupine Hills (49^{0} 47' N Lat, 113^{0} 39' W). The area is transitional between the mixed prairie and the rough fescue grassland associations with *Koeleria macrantha, Agropyron dasystachyum* var. *dasystachyum, Stipa curtiseta* and forbs such as *Artemisia frigida* common elements of the flora (Moss and Campbell, 1947; Moss, 1983).

Soils are predominantly Orthic Black Chernozems (Agriculture Canada, 1977). Topography is gently undulating to very severely sloped. Rock outcrops and exposed till are evident. The area has a continental prairie climate with dry summers and cold winters. Annual precipitation averages 450 mm and from 1982 to 1986 was 408, 322, 367, 423, and 435 mm, respectively (Dormaar et al., 1989). Growing season precipitation from 1982 to 1986 was 193, 77, 160, 247, and 280 mm, respectively (Shipwheel Grasslands, 1987). Chinook winds are frequent with average wind velocities of 50 km h^{-1} but occasionally as high as 100 km h^{-1} causing extreme temperature changes (Agriculture Canada, 1977). High summer temperatures, low precipitation, and strong winds result in high potential evapotranspiration and often a moisture deficit, while low winter temperatures, little snowfall, and strong winds combine to provide a harsh winter climate for vegetation.

Grazing Treatment

Since 1982, the 960 hectare study area has been managed under short duration grazing as pertaining to the Savory Grazing Method (Holistic Resource Management). Seventeen permanent fields radiate from a central cell where water and handling facilities are located (Figure I.1, Appendix I). Stocking rate from 1982 to 1986 averaged 277 cow/calf pairs per grazing season with 235 and 250 cow/calf pairs, respectively, in 1985 and 1986 (Mary Holtman, personal communication, 1986), which is approximately twice that recommended under continuous grazing (Wroe et al., 1988).

Cattle grazed from early May to as late as November in some years. Grazing regime is dependent on plant growth and varies each year with movement timed to prevent overgrazing. In general, three rotations are interspersed with two rests. Grazing periods in early spring average 2.5 days in each field, extending to 4 to 5 days by the third rotation. Rest increases from 40 to 60 days as the season progresses to facilitate recovery of forage after grazing. Grazing occurred from May 6 to October 30 in 1985 and from April 29 to

November 13 in 1986 (Mary Holtman, personal communication, 1986).

Seed Yield

Five fields, in which a 10 by 30 m exclosure was erected in each, were randomly selected for another study in 1982 by Dormaar et al. (1989). Within each of the five exclosures five randomly fixed, 1 m^2 quadrats were established in 1986. Concurrently, quadrats were also randomly selected from a marked unfenced 10 by 30 m grazed area adjacent to and generally upwind of the exclosure. Weekly records were kept of the number of plants and culms, and monocotyledon and dicotyledon species producing seed within each quadrat from May 11 to September 13. Forty random samples of mature inflorescences of each species were harvested, at the time when it appeared seed was mostly mature, to determine potential seed production. Only mature seed was counted. The seasonal pattern of flowering and seed production for each species in the quadrats was monitored throughout the season. Botanical names are from Moss (1983) with some common names adapted from Looman (1982) and Vance et al. (1984).

Seed Rain

In each of the five fields, five 6 m transects were randomly located inside each exclosure and in the abstract grazed 10 by 30 m area adjacent to the exclosure. Four traps were placed along each transect at 1.5 m intervals. Sticky seed traps consisting of a petri dish (nine cm in diameter) mounted on a wooden rod (Werner, 1975) were driven into the ground to a height of 2.5 cm above ground level. Filter paper, covered with "Tacky-toes", a non-drying sticky gel substance, was placed in the petri dishes. Seeds falling on the surface were captured and constituted seed rain. Traps were monitored weekly from May 11 to September 13, 1986 with the exception of approximately two weeks during grazing of each replicate of the grazed treatment. Filter paper were collected and replaced weekly. Samples were stored at 5 ^{o}C in a refrigerator until the seeds were removed. Seeds were counted, separated into monocotyledon and dicotyledon species, and identified using comparisons of harvested seed and keys from Martin and Barkely (1961) and Musil (1963). Botanical names are from Moss (1983) with some common names adapted from Looman (1982) and Vance et al. (1984).

Statistical Analyses

An estimate of seed yield for each treatment was determined by multiplying mean seed production for each species times the mean number of plants and/or culms per m^2 in each quadrat producing seed averaged per field (replicates). Seed yield was determined for descriptive purposes only.

Seed rain data were analyzed using a split-plot model for total, dicotyledon, and monocotyledon seed. Data from the ungrazed treatment were balanced with the grazed treatment prior to analyses by ignoring data collected during the grazing period in each replicate of the grazing treatment. All parameters were analyzed with an SPSS.X analysis of variance program. Data were tested for homogeneity of variance using the Bartlett-Box test. Lack of homogeneity of data resulted in transformation of all data using the natural log. Upon comparison of transformed data with raw data, tests of significant were similar enough to present untransformed data as the results (Dr. R. Hardin, personal communication, 1989). Analysis were performed at the 0.05% level of significance.

RESULTS

Seed Yield

Mean total seed yields in grazed and ungrazed treatments were 59,512 seeds m^{-2} and 37,979 seeds m^{-2}, respectively. Dicotyledon seed yield in the grazed treatment was more than twice as great as in the ungrazed treatment (Table 3.1a). This was largely a result of *Antennaria parvifolia*, *Artemisia frigida*, *Draba nemorosa*, and *Solidago missouriensis* each having a large seed yield. *Artemisia frigida* had the highest rate of seed production per unit area in both treatments representing nearly 30% of the total dicotyledon seed yield in each.

Monocotyledon seed yield was greater in the grazed treatment than the ungrazed treatment with seed of *Koeleria macrantha* representing

87% of the total monocotyledon seed yield in each treatment (Table 3.1b). *Agropyron dasystachyum* var. *dasystachyum* seed yield was similar between treatments while *Festuca scabrella* seed yield was nearly three times as great in the ungrazed treatment as in the grazed treatment. Monocotyledon seed yield was greater than dicotyledon seed yield in each treatment (Table 3.1b). These differences were more extreme in the ungrazed treatment.

Species present in each treatment differed slightly with more dicotyledon species present in the grazed treatment (Table 3.1a and b). Slightly more than half of all species had greater seed yield in the grazed treatment than the ungrazed treatment due to greater plant abundance. Variability between fields (replicates) is presented in Table III.1 (Appendix III).

Seed Rain Composition and Abundance

Numbers of seed captured for total, monocotyledon and dicotyledon species did not differ significantly between treatments (Table 3.2). Total seeds captured per trap over 18 weeks corresponded to a seed rain of 6025 seeds m^{-2} in the grazed treatment and 5993 seeds m^{-2} in the ungrazed treatment (Tables 3.3a and b). Seed rain per field (replicate) and treatment is presented in Table III.3 (Appendix III).

Of the 30 species captured in the grazed treatment 20 were dicotyledons and 10 were monocotyledons (Table 3.3a). Twenty-five species were captured in the ungrazed treatment, 15 dicotyledons and 10 monocotyledons (Table 3.3b). All species captured in the seed rain in the ungrazed treatment were present in the grazed treatment. However, five dicotyledons were present in the grazed treatment which were absent from the ungrazed treatment. Four of the five species had lower seed yields or were absent from the vegetation of the ungrazed treatment in comparison to the grazed treament (Table 3.1a and b).

Seed of monocotyledon species was far more abundant in the seed rain than seed of dicotyledon species, representing 73% and 79% of the seed captured in grazed and ungrazed treatments, respectively. Seed of *Koeleria macrantha* was most abundant in the seed rain of both treatments (Table 3.3a and b). The most abundant dicotyledon species in the ungrazed treatment were *Lepidium densiflorum* and *Senecio canus* while *Antennaria parvifolia* and *Draba nemorosa* were most abundant in the grazed treatment.

Patterns of Seed Rain

Total seed rain in the grazed treatment appeared in five distinctive small peaks throughout June to September (Figure 3.1). Few seeds were captured in May. Monocotyledon species, especially *Koeleria macrantha*, and to a lesser extent, *Agropyron dasystachyum* var. *dasystachyum*, produced the peaks beginning in late June (Table 3.3a). The greatest seed rain of monocotyledon seed occurred in the week ending August 2. Dicotyledon seed showed one small, distinct peak from June 7 to 14 produced by *Draba nemerosa*, *Antennaria parvifolia*, and *Senecio canus*.

Total seed rain in the ungrazed treatment appeared in several small peaks with a larger peak in the week ending August 2 (Figure 3.1b). Monocotyledon species producing these peaks were mainly *Koeleria macrantha* and *Agropyron dasystachyum* var. *dasytachyum* (Table 3.3b). Dicotyledon seed rain was similar to the grazed treatment but with *Lepidium densiflorum* and *Draba nemerosa* comprising the small peak in early June. *Senecio canus* dispersed abundantly in late August producing the fall peak. Patterns of flowering and dispersal of these and other species observed in the seed rain are presented in Figures 3.2 and 3.3. The seed rain patterns of the most abundant species in the seed rain, *Koeleria macrantha* and *Agropyron dasystachyum* var. *dasytachyum*, are presented in Figure III.1 (Appendix III).

Differences in seed rain across fields were significant for all comparisons (Table 3.2). Field variability was also apparent from various field interactions.

Comparison of Seed Rain, Seed Bank, and Seed Yield

In the seed bank in 1986 there were 2004 and 1940 seeds m^{-2} in the grazed and ungrazed treatments, repectively (Chapter 2). This is approximately one-third of the 6025 and 5993 seeds m^{-2} observed in the seed rain. Capture of seeds was low compared to the estimates of seed yield, 59, 512 and 37, 978 seeds m^{-2} in grazed and ungrazed treatments, respectively.

In the grazed treatment, *Koeleria macrantha* and *Agropyron* sp. were most abundant in both the seed rain and the seed bank (Table 3.4), and had the greatest seed yields (Table 3.1b). *Koeleria macrantha* represented over half of the seed rain but only 20% of the seed in the soil. *Agropyron* sp. represented 26% of the total seed in the soil but only 10% of the total seed in the rain. *Artemisia frigida* and *Androsace septentrionalis* were more abundant in the seed bank than the seed rain even though these species, especially *Artemisia frigida*, were observed producing great amounts of seed per unit area (Table 3.1a). Dicotyledon species having the greatest seed yield in the grazed treatment were present in the seed rain (Tables 3.1a and 3.4).

In the ungrazed treatment *Koeleria macrantha* and *Agropyron* sp. were most abundant in both the seed rain and the seed bank, as well as being the most productive species per unit area (Table 3.4 and 3.1b). *Koeleria macrantha* represented over half the seed rain but only a quarter of the seed bank (Table 3.4). *Agropyron* sp. composition was similar in both seed bank and seed rain. *Poa* sp. were third most abundant in the seed bank while fourth in the seed rain. *Carex* sp., the fourth most abundant in the seed bank, had few seeds captured in the seed rain even though plants were observed producing seed (Table 3.1b). Ranking of *Artemisia frigida* in the seed bank and seed rain was similar (Table 3.4). In contrast, *Androsace septentrionalis* was present only in the seed bank. Dicotyledon species having the greatest seed yield in the ungrazed treatment were not all present in the seed rain (Table 3.1a and 3.4). *Lepidium densiflorum* was fairly abundant in the seed rain in the ungrazed treatment even though it was not observed producing seed in this treatment (Table 3.1a).

In both treatments some species of the seed rain were not present in the seed bank while others present in the seed bank were not present in the seed rain (Table 3.4). In both cases, seed rain resembled the seed bank more than the seed bank resembled the seed rain. Even though numerous species were observed producing seed (Table 3.1), many were not found in either the seed rain or seed bank. The most common seeds captured in the seed bank, seed rain, and observed in the flowering communities were species from the *Compositae*, *Cruciferae*, and *Gramineae* families. Seed of *Festuca scabrella* was not found in the seed bank, was found only sparingly in the seed rain, and was moderately abundant in the above-ground vegetation, especially in the ungrazed treatment. Although seed yield varied with grazing treatment, seed rain and seed bank were not influenced by treatment.

DISCUSSION

Seed Yield

Seed yield varies with the number of mature plants producing seed. The greater abundance of total seed per unit area in the grazed treatment than in the ungrazed treatment was partially related to the greater plant abundance of most species in the former treatment. These results appear to reflect the effects of continued heavy grazing, where changes in vegetation occur with movement towards a community having greater species diversity favoring less desirable species, such as unpalatable plants and grasses too short to be grazed. Dicotyledon species such as *Artemisia frigida* were especially abundant, as well as *Koeleria macrantha*, an increaser grass, which is quite resistent to grazing. Many of these species are opportunistic weedy species which are productive and high seed yielding. Plant stress from grazing in this treatment was not a major influence on seed production in 1986 due to favorable moisture conditions. If moisture and forage had been limited, seed yields in the grazed treatments would likely have been very low, or at least lower than those observed in 1986.

In the exclosure, with rest, natural plant succession proceeds towards the climax vegetation with increased vigor and abundance of the more desirable productive plants such as *Festuca scabrella* and *Agropyron dasystachyum* var. *dasystachyum*. The result of this though may be to reduce seed production due to stress from high plant density of monocotyledon species, which has been observed by Whisenant (1988), or from enhanced vegetative propagation. Some species, such as *Festuca scabrella*, benefited from protection from grazing resulting in higher seed yields than in the ungrazed treatment. This is likely due to increased plant vigor, and size (Johnston and MacDonald, 1967), and plant numbers. Seed yield of *Festuca scabrella* in the grazed treatment was lower due to reduced plant numbers following heavy grazing. Plants may also remain vegetative making them less accessable to the grazing animal (Johnston and MacDonald, 1967).

Seed Rain

It was initially assumed that a high intensity short duration grazing system would substantially reduce seed rain considering the physical effects of trampling and grazing on vegetation and the high level of bare ground that was observed. However, if seed yield is an indication of seed rain then the latter should have been substantially greater in the grazed treatment than in the ungrazed treatment. Lack of significant differences between treatments in seed rain is likely related to the presence of *Koeleria macrantha*, abundant in the vegetation of each treatment. The abundance of seed of this species in the seed rain likely overshadows the seed rain of other species.

Seed rain in the ungrazed treatment may have been underestimated due to closing of the vegetation as the season progressed resulting in seed loss due to capture in leaves of tussock grasses, as observed by Rabinowitz and Rapp (1980). This would have occurred to a greater extent in the ungrazed treatment since grazing and trampling prevented closure of gaps in the vegetation of the grazed treatment.

Species richness in the seed rain in each treatment was low compared to the types of species observed producing seed in each, but similar to seed rain found in a tallgrass prairie by Rabinowitz and Rapp (1980). The presence or absence of a species in the seed rain is likely related to the amount of seed produced per unit area of that species. A certain level of seed yield, species dependent, may be necessary before a species is observed in the seed rain. The dispersal distance of each species is likely a factor also influencing seed capture.

The absence of certain species in the seed rain, while related in part to their abundance and seed production, may have also been related to the efficiency of capture by the traps. Although Werner

(1985) considered traps effective and unbiased for seed capture, observation of captured seed in this study indicates small, light weight seeds are most easily captured by these traps. This observation was also reported by Foster Huenneke and Graham (1987). Capture of large seeds, such as *Stipa* sp. which were moderately abundant in the seed rain, was likely enhanced by the presence of awns. Foster Huenneke and Graham (1987) found unawned *Festuca* sp. captured with intermediate efficiency, in comparison to other awned, elongated seeds. However, relatively few seeds of *Festuca scabrella* were observed in this study, even when seed production was observed in the ungrazed treatment. Dicotyledon species well represented in the seed rain were from the *Compositeae* family, with capture likely enhanced by the pappus, and the small seed size, and from the *Crucifereae* family whose seeds are minutely small and round. In contrast, Foster Huenneke and Graham (1987) found poor capture of round seeds as they tended to bounce off traps. Traps used in this study were so sticky small rodents were unable to free themselves upon contact suggesting seed loss in the manner observed by Foster Huenneke and Graham (1987) was unlikely.

Rate of capture is decreased by increased vertical drop (Foster Huenneke and Graham, 1987); however, in grasslands such as in this study, with plants fairly low in stature and frequent wind, capture of seed was not likely influenced greatly by vertical drop. Some species, such as *Carex* sp., may not be observed in traps because of their low stature and other plants impeding movement of their seed. Spatial distribution may also influence types of seeds in the seed rain with species with small localized populations away from the trap vicinity not observed in the seed rain. Werner (1975) observed that capture from tall flowering weeds was restricted to a lateral distance of 1.5 m from the parent plants. Seed predation may also result in underestimation of seed rain in both treatments as small rodents were observed eating the seed. This however, likely accounted for little seed loss due to the stickiness of the traps.

The abundance of *Koeleria macrantha* in the vegetation resulted in its dominating the seed rain in both treatments. Patterns of seed rain over time are determined largely by the identity of species dispersing

(Rabinowitz and Rapp, 1980) so it was not surprising that the individual patterns of seed rain of *Koeleria macrantha* and *Agropryon* sp. were near duplicates of the total seed rain since these species were most abundant on the site. Patterns in the ungrazed treatment with one large peak, represented largely by graminoid species, were similar to those observed by Rabinotwitz and Rapp (1980).

Comparison of Seed Rain, Seed Bank, and Seed Yield

Comparison of seed rain to seed density in the soil indicates a reduction in the numbers of seed becoming incorporated into the soil; this was also observed by Rabinowitz and Rapp (1980). This reduction of seed numbers does not indicate the annual mortality of new seeds (Rabinowitz and Rapp, 1980). Instead, this likely reflects the lack of persistence of some seed in the soil, its ability to germinate or become incorporated into the soil. The discrepancy in numbers between seed yield and seed rain may be related in part to seed being retained by the plant and not dispersed (Harper, 1977). Some correlation in species composition between seed rain and the seed bank within treatments would be expected for abundant species producing vast amounts of seed, such as *Koeleria macrantha.* The presence of species in the soil not observed in the seed rain likely indicates remnants of past vegetations or erratic reproduction (Rabinowitz and Rapp, 1980).

Measuring seed rain is useful in determining species with the greatest seed yield since their seed is most likely to be captured. Seed rain may also help predict the future direction of the seed bank, at least over the short-term, since species composition of the seed bank is related to seed present in the above-ground vegetation at some point in time. Comparing the composition of the seed rain with the seed bank over the long-term may help predict the persistence of seed of certain species in the soil and recognize factors influencing seed burial and persistence. With knowledge of seed persistence in the soil of various grassland species, long-term projections of seed bank composition may be possible. Differences in species composition between the seed bank, seed rain, and the flowering community will always be present though due to the constantly changing vegetation and the persistence of seeds in the soil from past successional stages.

It is interesting to note that species noticeably absent, or present in very small amounts in the seed bank (e.g. *Festuca scabrella* and *Helictotrichon hookeri*, respectively) were also present in small numbers in the seed rain, even with abundant seed produced. Perhaps seed characteristics and morphology which limit seed incorporation or persistence in the soil (e.g. large seeds accentuated with awns) are also the factors influencing seed capture in the traps.

In this study neither grazing or the lack of grazing influenced species composition or seed density of the seed rain. With continued deterioration of the grassland and increased abundance of weedy dicotyledon species, similarities between the flowering community, seed rain, and seed bank, should improve as seed of these species is generally more persistent in the soil. As range condition improves in the ungrazed treatment and the climax stage is approached, seed rain and composition of the seed bank will likely be less similar. It has been observed that as succession proceeds, there are fewer seeds found in the soil relating to the successional stage (Numata et al, 1964). It is apparent, from the species observed producing seed and the absence of their seed in the seed rain and soil, that the seed bank will never fully represent all species in the vegetation.

CONCLUSIONS

Numbers of seeds captured did not differ significantly between treatments but seed yield was greater in the grazed treatment. Species composition of the seed rain was similar between treatments due to *Koeleria macrantha* which dominated the seed rain in both treatments. In contrast, the presence of *Festuca scabrella* seed in the ungrazed treatment did not ensure its representation in the seed rain. Although seed yield was great in both treatments and many species were observed producing seed, very few seeds were actually captured in the seed rain. Many species in the seed rain are present in the seed bank, although the majority of species in the seed bank are not present in the seed rain with the exception of the most common species in each.

Table 3.1a. Mean seed yield (seeds m^{-2}) of dicotyledon species in grazed and ungrazed treatments.

	Grazed	Ungrazed
Achillea millefolium	-	125
Agoseris glauca	7	22
Androsace septentrionalis	234	99
Anenome patens	48	27
Antennaria parvifolia	5513	852
Arabis holboellii var. *retrofracta*	53	-
Artemisia frigida	6307	2803
Aster ericoides subspp.*pansus*	196	255
Campanula rotundifolia	9	-
Cerastium arvense	218	217
Cryptantha macounii	95	73
Descurainia sophia	193	96
Draba nemorosa	4237	304
Erigeron caespitosus	900	-
Erigeron flavum	212	-
Erysimum aesperum	552	966
Erysimum cheiranthoides	750	454
Galium boreale	310	911
Gaillardia aristada	26	5
Gaura coccinea	5	4
Gutierrezia sarothrae	27	99
Heterotheca villosa	91	173
Heuchera richardsonii	123	92
Hymenoxys richardsonii	444	430
Lappula occidentalis	18	-
Lepidium densiflorum	50	-
Lesquerella arenosa var. *arenosa*	56	90
Liatrus punctata	152	151
Linum lewesii	61	10
Linum rigidum	47	-
Lomatium macrocarpum	69	58
Lupinus argenteus	6	-
Orthocarpus luteus	-	731
Petalostemon purpureum	52	80
Senecio canus	96	154
Solidago missouriensis	1173	135
Sphaeralcea coccinea	75	17
Thermopsis rhombifolia	13	17
Total	22,417	9,452

Table 3.1b. Mean seed yield (seeds m^{-2}) of monocotyledon species in grazed and ungrazed treatments.

	Grazed	Ungrazed
Agropyron dasystachyum var. *dasystachyum*	2093	1956
Agropryon trachycaulum var. *trachycaulum*	272	-
Allium cernuum	7	17
Allium textile	5	19
Bouteloua gracilis	51	30
Calamovilfa longifolia	11	40
Calamagrostis montanensis	42	19
Carex sp.	111	28
Festuca scabrella	113	405
Helictotrichon hookeri	52	186
Koeleria macrantha	32,396	24,704
Muhlenbergia richardsonii	37	34
Poa pratensis	1193	620
Stipa comata	711	392
Stipa curtiseta	6	-
Schizachyrium scoparium var. *scoparium*	2	-
Zygadenus venenosus	67	-
Total	37,095	28,526

Table 3.2 Significant effects (P<0.05) from transformed data for dicotyledon (D), monocotyledon (M), and total (T) seed rain.

Parameters[1]		Degrees of Freedom	D	M	T
	T	1	NS	NS	NS
error	FT	4			
	W	17	*	*	*
error	FW	68			
	TW	17	NS	NS	NS
error	FTW	68			
	F	4	*	*	*
	FT	4	*	*	*
	FTW	68	*	*	*
error	S(F,T,W)	719			

[1]Parameters T=treatment (grazed and ungrazed); W=week (May 7 to September 13 1986); F=field (fields 1 through 5); S=samples

Table 3.3a. Mean seed rain (seeds m^{-2}) for each species recorded weekly and arranged in order of first date of capture in the grazed treatment in 1986.

	May[1]	June				July				Aug.					Sept.		
	31	7	14	21	28	5	12	19	26	2	9	16	23	30	6	13	TOTAL
Lesquerella arensosa var. *arenosa*	4			13			6			20	3	2			6		54
Agropyron dasystachyum var. *dasystachyum*		16	30		80	9	30	80	99	130	30	52	22	11	5	20	614
Draba nemorosa		30	173	20	25	6			2	11	2			6			275
Antennaria parvifolia		44	138	133	16			2									333
Carex sp. (1)[2]		2	3					5		11							21
Compositae (2)[2]		3	25														28
Festuca scabrella		3	8	3	3				5	3							25
Koeleria macrantha		31	61	33	300	264	586	283	612	345	80	89	245	75	35	20	3059
Senecio canus			122	27													149
Lepidium densiflorum			2	80	53	11	8	2	5	16				5			182
Unknown Dicotyledon (1)[2]			3		2	8		2									15
Stipa curtiseta							2										2
Stipa comata			2		8	2		3									15
Stipa sp.[3]			2	16	6	2	11	3	3	11	5	2	2	8	2	3	76
Erigeron sp. (1)[2]			5		204			2	2	5		42					260
Agropyron sp. (1)[2]				8						2							10
Androsace septentrionalis[4]				2			5										7
Anenome patens[4]				2							11	13					26
Arabis holboellii var. *retrofracta*				8													8
Erysimum sp.[3]				3		5	3			3	5						19
Erysimum aesperum					17	5				3	2		2			13	42
Poa pratensis					118			138	5	11	80	41	31	11			435
Gaillardia aristida						2											2
Poa sp. (1)[2]						5	2	2	132				13				154
Helictotrichon hookeri							3	3					3				9
Erysimum cheiranthoides							50	13	3				16	19		3	104
Thlaspi arvense[4]								2									2
Artemisia frigida										3			25			19	47
Heterotheca villosa										8		13		2		13	36
Solidago missouriensis[4]																5	5

Table 3.3a. cont'd

Liatris punctata												5	6				11
TOTAL	4	129	549	373	832	319	706	540	868	582	218	259	352	150	48	96	6025

[1] Seeds were not captured prior to May 31.
[2] Number of unidentifiable species. Unknown *Agropyron* and *Poa* sp. are different from those already identified.
[3] *Erysimum* and *Stipa* sp. represent the previously identified species of each in which seed was not positively identified.
[4] Species present in the grazed treatment but absent from the ungrazed treatment.

Table 3.3b. Mean seed rain (seeds m^{-2}) for each species recorded weekly and arranged in order of first date of capture in the ungrazed treatment in 1986.

	May[1]		June				July			August				September			
	31	7	14	21	28	5	12	19	26	2	9	16	23	30	6	13	TOTAL
Antennaria parvifolia		2	58	49	2	13								3			127
Compositae (1)[2]		3	11	2										2			18
Draba nemorosa		16	33	11	68	5	3	2	6								144
Helictotrichon hookeri		8				27	9	2	3			2	5	2	2		60
Koeleria macrantha		6	33	27	46	177	312	275	414	1135	213	121	251	223	11	11	3255
Lepidium densiflorum		3	35	33	60	47	138	42	74	31	5				2	8	478
Agropyron dasystachyum var. *dasystachyum*			23	45	143	16	72	68	137	152	100	80	50	53	3	2	944
Agropyron sp. (1)[2]			3	9	35	2					2	5	5	5			66
Festuca scabrella				9	2	13	6	5	6				8				49
Stipa comata				2	11		2	5	5	23	5		13	6	2		74
Carex sp. (1)[2]					2		2										4
Compositae (1)[2]					5								2			2	9
Senecio canus					41									138			179
Poa sp. (1)[2]						14	53	3	46	16	42	9	3	36		3	225
Unknown Dicotyledon (1)[2]							6										6
Poa pratensis							38					17					55
Stipa sp.[3]							2	6	6	2							16
Erysimun aesperum									13	17	9	6	11	6		3	65
Erysimum cheiranthoides									3	3			5	3			14
Erigeron sp. (1)[2]									27	8				5			40
Lesquerella arenosa var. arnenosa									8	3		8	6	5			30
Gaillardia aristida																	
Heterotheca villosa												2	2	3		2	9
Liatris punctata												2	6	3		6	17
Stipa curtiseta												2		2			4
Artemisia frigida													28	63	14		105
TOTAL	0	38	196	187	415	314	643	402	748	1394	378	254	395	558	34	37	5993

[1] Seeds were not captured prior to May 31.
[2] Number of unidentifiable species. Unknown *Agropyron* and *Poa* sp. are different from those already identified.
[3] *Stipa* sp. represent the previously identified species in which seed was not positively identified.

Table 3.4. Ranking of species in the seed bank in 1986 in grazed and ungrazed treatments in 5 cm of soil determined by the Dominance Hierarchy Curve.

Species	Rank in Seed Bank		Rank in Seed Rain	
	Grazed	Ungrazed	Grazed	Ungrazed
Dicotyledons				
Achillea millefolium	36	-	-	-
Amaranthus retroflexus	26	-	-	
Androsace septentrionalis	5	7	21	-
Anemone patens	23	24	14	-
Antennaria parvifolia	8	14	4	7
Arabis holboellii var. *retrofracta*	14	9	20	-
Artemisia cana	18	18	-	-
Artemisia frigida	4	6	11	8
Aster ericoides subssp. *pansus*	13	16	-	-
Campanula rotundifolia	27	26	-	-
Chenopodium album	28	-	-	-
Cirsium arvense	33	-	-	-
Compositae (2)[1]	-	-	13	15
Delphinium nuttallianum	29	19	-	-
Unknown Dicotyledon (1)[1]	-	-	17	-
Draba nemorosa	10	13	5	6
Draba sp. (1)[1]	19	27	-	-
Epilobium angustifolium and *Epilobium ciliatum*[2]	24	8	-	-
Erigeron sp. (1)[1]	-	-	6	14
Erysimum aesperum and *Erysimum cheiranthoides*	-	-	10	13
Galeopis tetrahit	15	-	-	-
Galium boreale	11	11	-	-
Gaillardia aristada	-	-	23.5	-
Geum sp. (2)[1]	9	17	-	-
Heuchera richardsonii	-	28	-	-
Heterotheca villosa	-	-	12	17
Lepidium densiflorum	12	10	7	3
Lesquerella arenosa var. *arenosa*	-	-		10
Liatris punctata	-	-	18	16
Linum silcatum	25	20	-	-
Malva rotundifolia	17	25	-	-

Table 3.4. cont'd

Potentilla sp. (1)[1]	16	15	-	-
Ranunculus cymbalaria and *Ranunculus pusillus*[2]	30	12	-	-
Senecio canus	-	-	8	5
Solidago missouriensis	-	-	22	-
Taraxacum officinale	34	29	-	-
Thlaspi arvense	-	-	23.5	-
Unknown 1	-	23	-	-
Unknown 2	-	33	-	-
Monocotyledons				
Agropyron sp. (4)[3]	1	2	2	2
Bouteloua gracilis	21	30	-	-
Carex sp. (1)[1]	7	4	16	18
Cyperus schweinitzii	35	-	-	-
Danthonia parryi	22	31	-	-
Festuca rubra	31	21	-	-
Festuca scabrella	-	-	15	12
Helictrichon hookeri	20	22	19	11
Juncus bufonius, *Juncus tenuis*, and *Juncus torreyi*[2]	6	5	-	-
Koeleria macrantha	2	1	1	1
Muhlenbergia cuspidata	32	-	-	-
Poa sp. (6)[4]	3	3	3	4
Stipa sp.[5]	-	32	9	9

[1] Number of unidentified species.

[2] Species grouped together in which identification separating each was not always possible.

[3] *Agropyron* species present in 1986 included *Agropyron dasystachyum* var.*dasystachyum*, *Agropyron pectiniforme*, *Agropyron smithii*, and *Agropyron repens*. Presence of species in each treatment was not determined due to the large number of emerged seedlings. Species present in the seed rain in both treatments included *Agropyron dasystachyum* var.*dasystachyum*, and an unidentified *Agropyron* sp.

[4] *Poa* species present in 1986 included *Poa compressa*, *Poa pratensis*, *Poa sandbergii*, *Poa cusickii*, *Poa nevadensis*, and *Poa puccinella*. Presence of species in each treatment was not determined due to the large number of emerged seedlings. Species present in the seed rain in both treatments included *Poa pratensis* and an unidentified *Poa* sp.

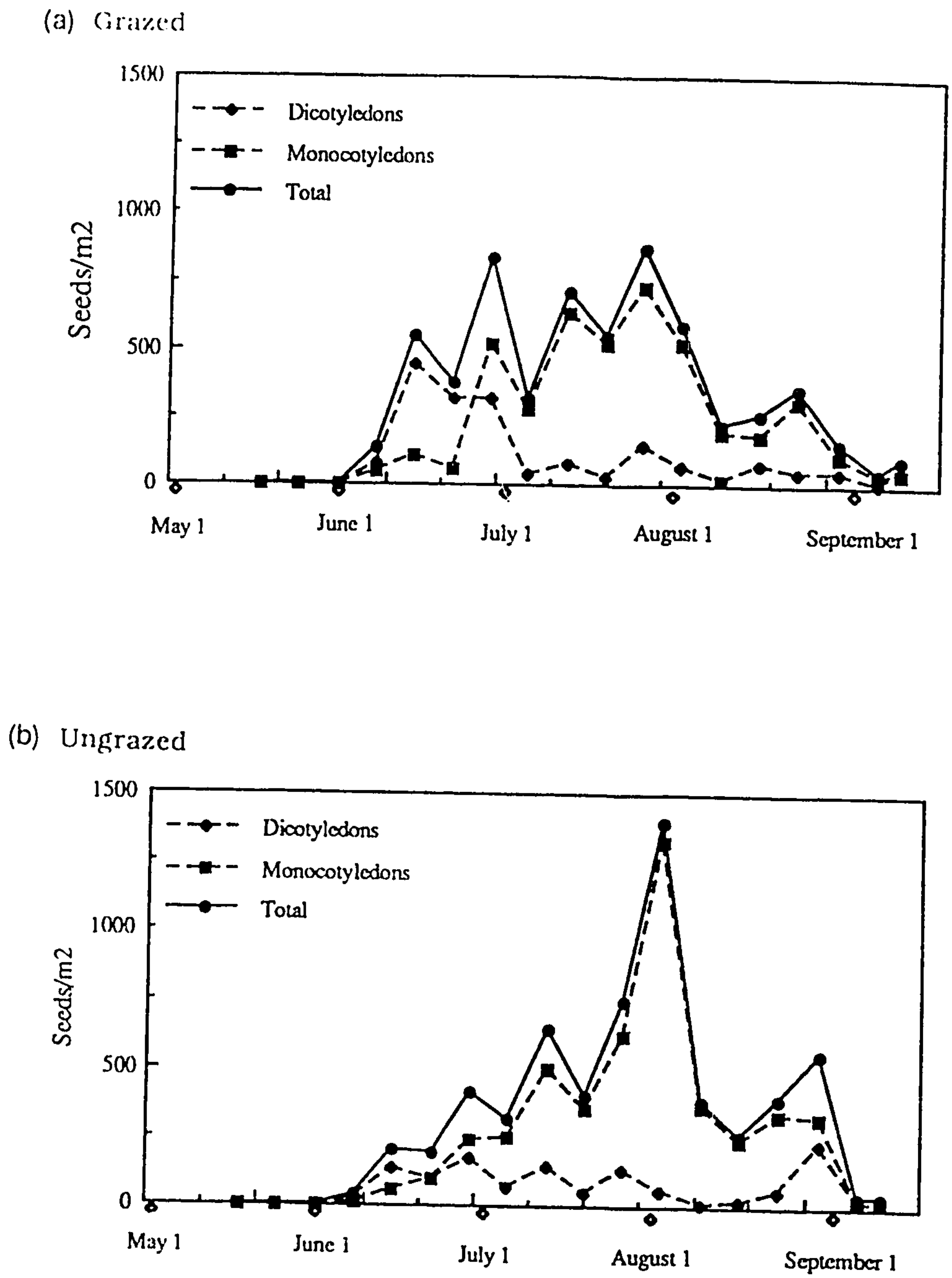

Figure 3.1. Dicotyledon, monocotyledon, and total seeds m^{-2} estimated from seed rain in (a) grazed and (b) ungrazed treatments in 1986.

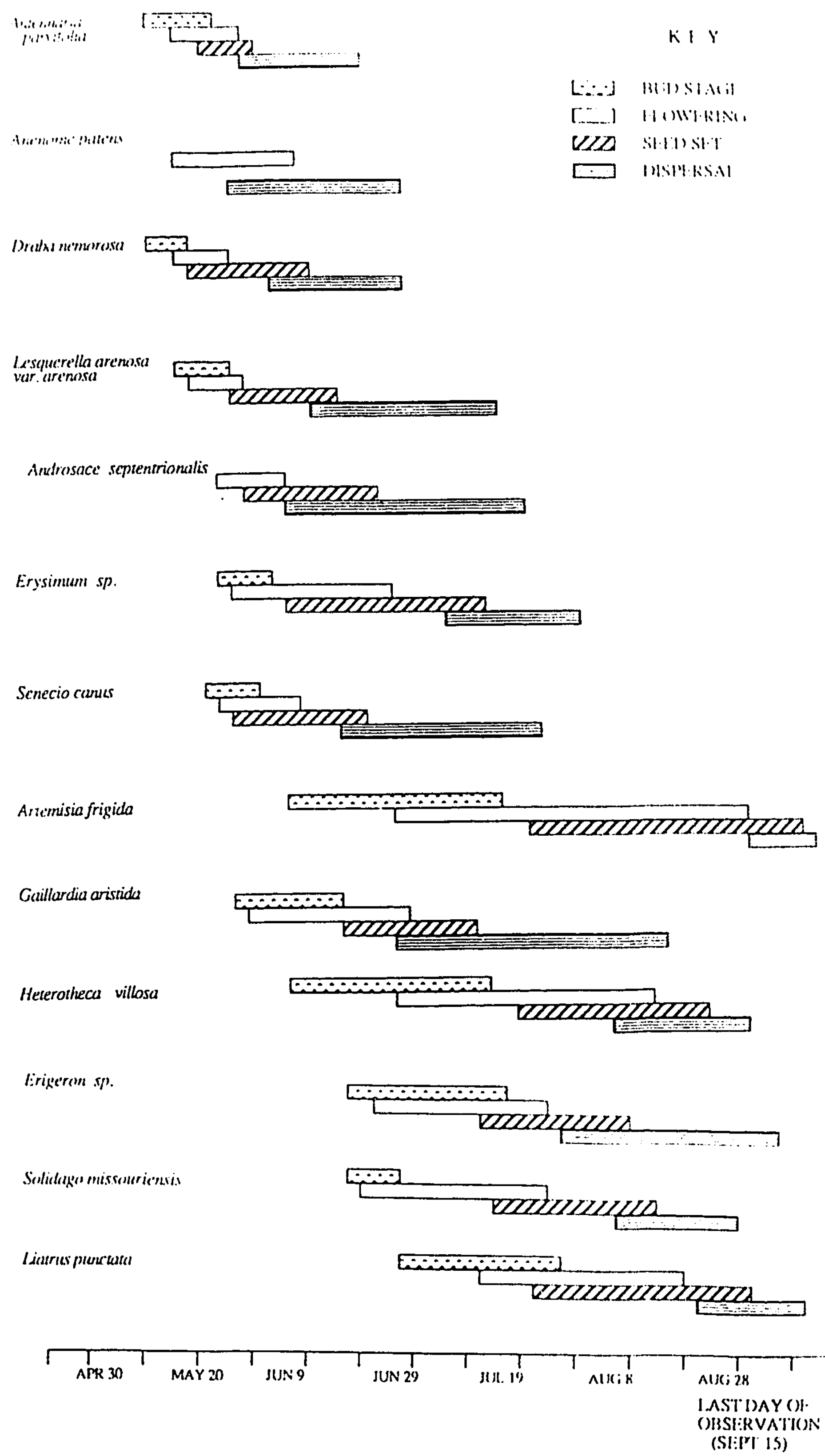

Figure 3.2. Flowering and dispersal patterns of some dicotyledon species in the seed rain based on visual observation.

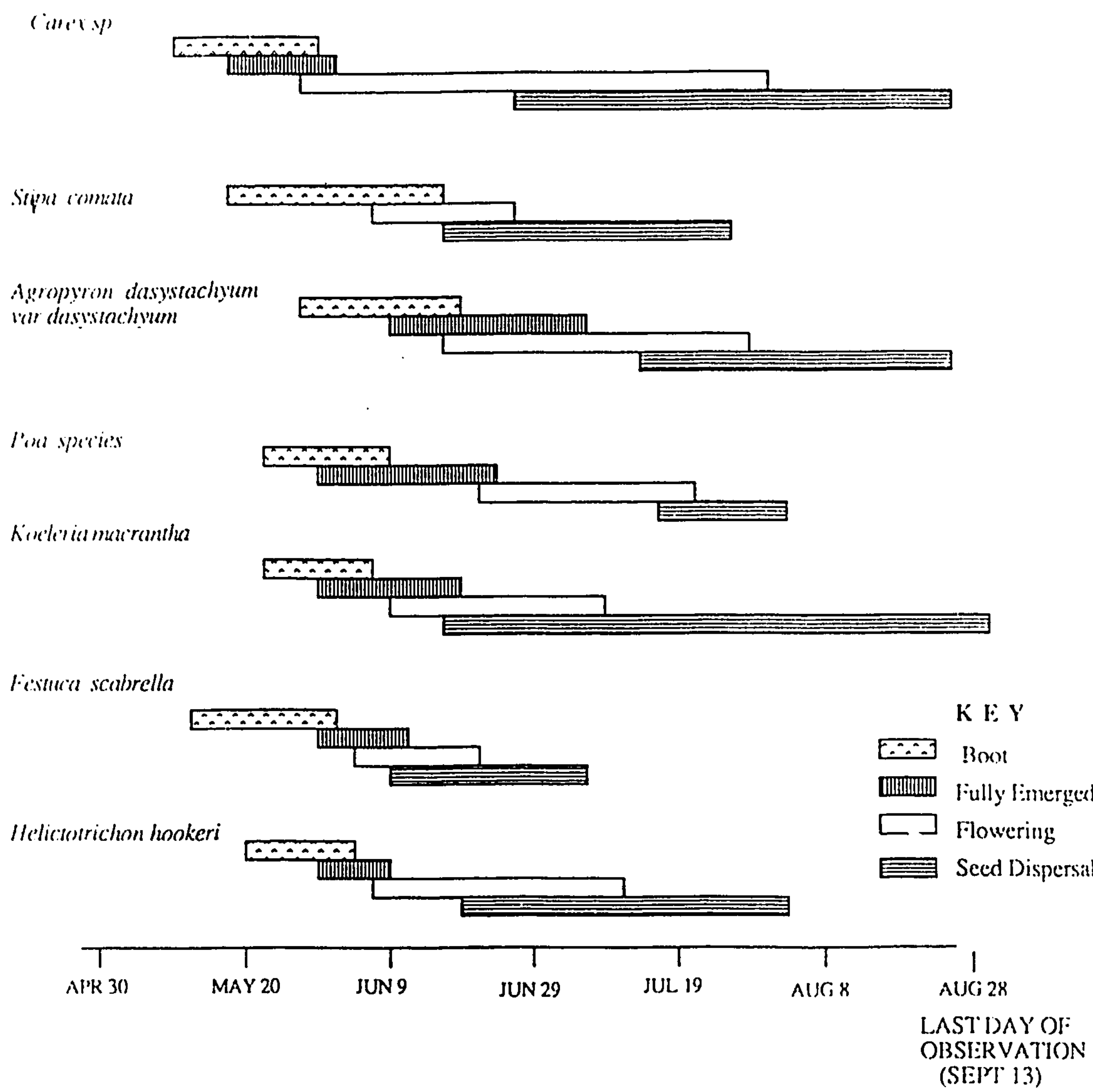

Figure 3.3. Flowering and dispersal patterns of some monocotyledon species in the seed rain based on visual observation.

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IV. GENERAL DISCUSSION AND CONCLUSIONS

Proponents of short duration grazing systems suggest that seed production and natural seed in the soil will provide plants for revegetation, resulting in an upward trend in succession (Kingsberry, personal communication, 1987; Savory, 1988). Theories related to the role of the seed bank in natural grasslands imply that the seed bank provides a reserve of dormant plants that may replenish the mature vegetation when losses occur (Major and Pyott, 1966; Rabinowitz, 1981).

Many grasslands are poorly managed resulting in greater species diversity with an increased number of undesirable species present. Grazing on this study site over five years, compounded by drought, decreased the abundance of desirable perennial grass species in favor of increaser grasses and forbs, many of which were unpalatable (Dormaar et al, 1989). Mortality of some species, such as *Festuca scabrella*, was high, while large gaps existed between plants and bare ground was common. Revegetation of this grassland by palatable grass species is necessary to increase forage productivity and grassland condition. If the seed bank has a functional significance in grasslands such as these, its role and importance is likely related to the type of seed bank (Thompson and Grime, 1979), the mortality rate of seeds in the soil, the vegetation type (Thompson, 1987), and the type and severity of disturbance (Moore and Wein, 1977).

Differences in seed density and species composition observed in this study between years are related largely to seed persistence in the soil and subsequently may determine the type and role of the seed bank. Grime (1979) suggested each species has its own type of seed bank, both in terms of the longevity patterns of the buried seeds and their germination responses at different times of the year. In this study it was shown that the seed bank in 1985 was comprised largely of unpalatable species, many of which were absent from the above-ground vegetation. Low seed density was likely a result of depletion of seed in the soil over time due to sequential years of low moisture availability limiting seed production. High temperatures at this time may have also attributed to depletion of seed in the soil (Schafer and

Chilote, 1970). The remaining seed in the soil likely represented the persistent seed bank in which most species were represented by only a small number of seeds. These characteristics of the seed bank may indicate the role of this persistent seed bank in revegetation is minor as there likely are insufficient numbers of seeds for successful germination and emergence in this perennial grassland. Success of seedling emergence is often low, with death the fate of many new seedlings (Darwin, 1859). The presence of dicotyledon species in the seed bank which were absent from the above-ground vegetation indicates the role of this seed bank is also related to primary stages of succession. This is supported by Numata et al. (1964), who found the numbers of seeds and species in seed banks of Japanese meadows declined as succession proceeded. The usefulness of this type of seed bank in grasslands is likely confined to revegetation from catastrophic or man-made disturbance or fire and is desirable from a soil conservation perspective in which seedling presence rather than species composition is more important.

Long-lived perennials often have more temporary seed banks (Weaver and Cavers, 1979) since a considerable percentage of buried seeds die each year due to poor seed persistence (Roberts, 1970). The large increase in seed density in the seed bank in 1986 and dominance by perennial grass species, especially *Koeleria macrantha*, implies the majority of seed in the soil is present only temporarily until either germination or death. The production of large numbers of seed, as observed here in 1986, may be advantageous in enhancing seed density in the soil, making up for years in which seed production has been unsuccessful (Cavers, 1983). These large flushes of seed production are important since soil seed density in comparison to seed yield in the vegetation indicates very little seed is actually incorporated into the soil, even if only temporarily. The larger the numbers of seeds present in a habitat, the greater the chances are that a few will survive in the soil (Staniforth and Cavers, 1977). Production of large numbers of seed may enable many potentially desirable microsites to be filled, allowing some seed to become successfully established in the year of seed production. Newly arrived seed to the soil is more likely to produce new seedlings than is old seed (Naylor,

1972) providing the environment is ideal for successful germination and emergence.

The presence in 1986 of more monocotyledon seeds in the soil than dicotyledon seeds in 1986 suggests recruitment from the transient seed bank may be more desirable in terms of species composition than if recruitment is from the persistant seed bank observed in 1985. Emergence patterns in this study indicate monocotyledon species germinate more rapidly from the soil than dicotyledon seeds which, if true, may also be favorable in plant recruitment. The importance of the transient seed bank is likely short-term since studies indicate high seed mortality over time. Transient seed banks have been noted as responsible for recovery from plant mortality and seasonally-predictable damage (Thompson and Grime, 1979). Unfortunately, seed of many species most desirable for the revegetation of perennial grasslands have high rates of mortality which may influence the direction of revegetation.

The role of the seed bank in a perennial grassland may be determined by the mortality rate of the perennial species. Mortality rates of perennial species are generally low with life-spans of 10 to 40 years common (Rabotnov, 1969). Thompson (1987) indicated the presence of a seed bank is important for species with high mortality rates under high intensity disturbance. The significance of the seed bank is likely diminished with proper management of grasslands which encourage more perennial species. With improved range condition and increased abundance of perennial grasses, the importance of the seed bank likely diminishes further. Species which possess more than one mechanism for survival, such as vegetative propagation and perennial root sytems, are also not as dependent on the seed bank. , On a grassland similar to this study site, Archibold (1981) found few seeds of perennial grass species, with vegetative propagation the most important mechanism for regeneration.

In contrast, poorly managed grasslands with high mortality rates of perennial species may be more dependent on the seed bank for revegetation than those grasslands in good condition. Moore and Wein (1977) suggested that the type and severity of disturbance is important in determining the role of the seed bank. There is no doubt that recovery of prairie glacial marshes after drawdown, a very destructive natural process, is dependent on the seed bank. Yet, it is not clear if grazing and trampling are enough of a disturbance on grasslands for the seed bank to have a major role in revegetation. It is likely the role of the seed bank is more important in grasslands in poor condition, yet, those factors which have resulted in deteriorated grasslands may also cause the seed bank to become depleted.

Recommended grazing systems vary in intensity, frequency, and seasonal timing of grazing, with each claiming to provide a unique means of favorably modifying range condition. With each system there are different levels of success at different times and places. Holistic Resource Managment (Savory Grazing Method) has many claims for the health of the environment. Savory (1988) suggested that periodic high animal impact promotes successional progress due to the herd effect while low animal impact neither advances nor reverses succession as much as rest. Most closely related to this study, and the role of the seed bank, are claims that the herd effect increases "seed planting", provides a good seed bed by chipping crusted soil, increases infiltration of water, facilitates germination of seed, lays litter, promotes plant decay, and protects bare soil by trampling down old plant material (Savory, 1979; Savory and Parsons, 1980; Savory 1988).

Savory (1988) reported enhanced plant succession, from the herd effect, resulting in thousands of new perennial plants sprouting in low and unpredictable rainfall environments. Howell (1976, 1978) also reported that short duration grazing resulted in a return and increase of rare grasses. Many of these species and individual plants are assumed to emanate from the seed bank although this was not clearly proven in these reports of favorable succession. Kingsberry (personal communication, 1987), in discussing short duration grazing, suggested that concerns regarding plant reproduction are unnecessary as natural seed in the soil will provide plants for future generations. Tainton (1985) observed rest within grazing regimes allows for improved plant vigor and seed production resulting in seedling establishment. They considered rest an important aspect of management where grassland reclamation and improvement are long-term goals.

In this study, the role of the herd effect in "planting seed" or burying seed in the soil appears minimal since seed density and species composition were similar in both treatments. If the herd effect influences seedling emergence and successful plant establishment in the grazed treatment as indicated by Savory (1988), species composition of the seed bank in 1985 indicates potential succession would be unfavorable as the majority of species present were early successional, weedy, unpalatable species. Seed of *Artemisia frigida* was especially abundant in the soil. The most desirable species, such as *Festuca scabrella*, were absent from the seed bank in this study. Other researchers have also found claims for favorable succession are unlikely. Heitschmidt and Walker (1983) found little evidence to suggest hoof action was important for enhanced seedling emergence, and suggested physical animal impact much above "normal" is likely to deter rather than accelerate plant succession by reducing plant cover. Tainton (1985) noted that the intensity of hoof action needed to disturb the soil crust enough to improve water infiltration and effectively bury seed is likely to destroy the seedlings which do develop. As well, deeply buried seeds likely have little functional significance because they must be brought closer to the soil surface to germinate, exposing them to conditions which stimulate activity within the seed. Disturbance in grasslands is likely not great enough to bring these seeds to the soil surface. Instead, they will become persistent residents of the soil remaining dormant for a long time (Roberts and Feast, 1970). Naeth et al. (1990a and b) showed overstocking reduced infiltration and compacted soil in fescue and mixed prairie grassland.

The observed deterioration in range condition under this short duration system (Dormaar et al., 1989) does not support the theory that intermittent rest, allowing species to produce seed for immediate germination or for incorportation into the seed bank for use at a later date, will result in an upward trend of succession. Instead, the seed bank may be partially responsible for the deterioration in range condition, assuming recruitment is from the seed bank, since most seed present in the persistent seed bank in 1985 is from unfavorable species. Grazing systems of mixed swards which promote favorable succession through rest, seed production and seed banks, tend to ignore the fact that undesirable species are also able to set seed during rest and can become potential individuals in the vegetation. This is also likely since often undesirable species produce more seed which has a longer seed-bed life. In contrast, in 1986, the seed bank would have provided more desirable species in terms of succession and range condition, but lack of these species in the seed bank in the previous year suggests their persistence is not long term, and therefore, the seed of these species would not likely contribute to the vegetation in the following season.

Total rainfall in the growing season and rainfall in relation to grazing are considered a major influence on sward dynamics (Walker et al., 1986). In this study, in 1986, it appeared rainfall also influenced the dynamics of the seed bank by enhancing seed yield, resulting in increased abundance of monocotyledon seed in the soil and in the seed rain. Since individual species respond differently to weather and grazing (Olson et al., 1985) it is difficult to manage a mixed sward for enhanced seed production and species composition of seed in the soil. Mixed swards may respond to the application of management activated at critical times, coinciding with certain rainfall characteristics, with the effects on the most desirable forage species recognized. Thus, in years of improved moisture conditions, and enhancement of monocotyledon seed production and seed in the soil, there may be some favorable succession from these species in gaps created from long-term disturbances such as drought. It should not be assumed though that seed production or presence of seed in the soil will ensure establishment of new individuals since it is well recognized that favorable microsites for successful emergence are few and seedling mortality is high. In this study it was observed that seed production of a specific species, *Festuca scabrella*, would not ensure the presence of seed in the soil even in the same year of seed production. It may be argued that when considering the low mortality of many perennial species in grasslands, just one seedling surviving out of many may be significant in providing an individual for future generations of that species (Rabotnov, 1969). In considering the changes involved in the grassland studied here, it is likely more than just one seedling is needed to fill the many large gaps in the vegetation produced by overgrazing. Management objectives and principles encouraging vegetative propagation, rather than seed production of perennial grasses should be a priority in grassland management.

There are a large number of questions which remain unanswered because of the lack of data in the literature regarding seed banks. Fortunately, data regarding species composition and seed density is becoming more common. The dynamics of seed banks and factors influencing these need to be addressed, so that specific recommendations concerning grassland management can be made with consideration to the role of the seed banks in natural grasslands. While some ecologists have put strong emphasis on seedling mortality (Cavers, 1983), it is becoming more apparent that differences among plants in patterns of mortality after germination may be trivial and that seed mortality is more important to vegetation dynamics (Hickman, 1979). Understanding the effect of variables, such as weather, which influence the seed bank (Johnston and MacDonald, 1967), may enable management to be directed towards developing a combination of grazing and rest encouraging seed production and vegetative reproduction. It is unlikely the seed bank can be managed enough in mixed swards in natural grasslands to comprise seeds of favorable species that can lead to improved range condition through management. At present, grasslands should not be managed without consideration for the effects of high intensity grazing on desirable grass species. Similarily, one should not assume seed production or the seed bank assures revegetation by desirable species.

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APPENDIX I. STUDY SITE DESCRIPTION

Site Selection

The study area, Shipwheel Ranch, is located approximately 16 km northwest of Fort McLeod and on the edge of the Porcupine Hills (49^o 47'N, 113^o 39'W). The legal land description is sections 30, 31, and 32, township 9, and range 27, west of the 4th meridian. The site encompasses 960 hectares and is divided into 17 permanent fields of which 15 merge at the centre cell where water and handling facilities are located (Figure I.1). Access to all fields is possible at the centre cell.

Five of the 17 fields (2, 5, 8, 12, and 15) were randomly chosen as research sites in 1982 (Dormaar et al., 1989). In each of these fields a permanent 10 by 30 m exclosure was erected in sites vegetationally similar. The areas of fields 2, 5, 8, 12, and 15 are 52, 33, 39, 53, and 74 hectares, respectively.

History and Utilization

The study site was purchased by Blake and Mary Holtman in 1979. Land ownership changed at least three times prior to the Holtman's aquisition. The most recent use prior to their purchase was summer range for as many as 1000 yearlings. Range condition was fair at the time of purchase. The effects of land tillage can still be seen in at least three areas which are the lowest forage producing (Mary Holtman, personal communication, 1987). These areas are found in fields 2 through 7 and 12 through 15. Some of the homesteading likely occurred between 1907 and 1911, and in the 1930's (Mary Holtman, personal communication, 1987).

The study site has been used for intensive beef cattle production since 1979 by the Holtman's. The first three years were spent managing a "high intensity short duration grazing system" after which the Holtman's have concentrated on applying the Savory Grazing Method principles (Holistic Resouce Management) shifting towards what they feel is a more holistic approach of management. A high intensity short duration grazing system is not holistic management as it does not incorporate a time element in the grazing scheme (Mary Holtman, personal communication, 1987).

Simplified, the grazing regime is rotational depending on plant growth and varies each year. Movement of cattle is timed to prevent heavy use of forage during periods of rapid growth, and to allow recovery after grazing (Dormaar et al., 1988). In general, the first grazing period averages 2.5 days followed by 40 days of rest. As the season progresses the time spent in each paddock increases, as well as the rest period. By rotation three average grazing time is 4.5 days. Overall, three grazing rotations occur with two rest periods interspersed throughout the growing season. Grazing occurred from May 3 to October 6 1984, from May 6 to October 30 1985, and from April 29 to November 13 1986 (Mary Holtman, personal communication, 1986).

Cattle numbers since 1982 have averaged 272 cow/calf pairs per grazing season. During 1985 and 1986, cow/calf pairs were 235 and 250, respectively. This stocking rate is about two to three times that recommended under continuous grazing for this area (Wroe et al., 1988).

Physiology, Relief, and Drainage

The study site is situated in the Third Prairie Steepe physiographic region (Agriculture Canada, 1977). The topography is gently undulating with some gently hummocky land to severely sloped areas. Elevation varies from 900 to 1150 meters. Glacial deposits can be found as well as small areas of exposed bedrock and eroded sites. Drainage is mainly by the Oldman River.

Soils

Soils of the entire site are classified mainly into the Metisko and Parsons soil series with soils at the very northern end of the study site dominantly Orthic Dark Brown Chernozems from the Metisko soil series (Agriculture Canada, 1977). Associated with these soils are the Orthic Dark Brown Chernozems from the Scollard series. These soils are found on very gentle sloping land with slopes ranging from 0.5 to

5.0%. Many of these soils have developed on sandy skeletal material. Exposed till is evident.

The east and southeastern soils of the ranch, in which fields 8, 12, and 15 are found, are dominantly Rego Black Chernozems of the Parsons series. These are also associated with the Calcareous Dark Brown Chernozems (Poltener) and the Orthic Black Chernozems (Beazer). The topography is undulating and inclined with slopes between 2 and 15%. Soils have developed on fine-loamy morainal material.

Fields 2 and 5 are found mostly on Rego Black Chernozems and to a much smaller extent associated with the Rego Black Chernozems from the Beazer soil series. The topography varies from gentle to very steep slopes of 5 to 45%. These soils have developed over fine-loamy morainal veneer and blanket over bedrock. Rock outcrops are evident.

The agricultural capacity of these soils is restricted mostly to grazing. There is a poor capacity for irrigated agriculture (Agriculture Canada, 1977).

Climate

The area has a continental prairie climate which is characterized by warm summers and cold winters (Agriculture Canada, 1977). Mean summer temperature is approximately 15 °C with July being the warmest month. Mean winter temperature is -8 °C with January being the coldest month. The frost free period and the growing season average 90 days and 180 days, respectively.

The area is characterized by low precipitation. Annual precipitation is 350 to 400 mm. Average annual precipitation from 1979 to 1986 was 450 mm (Dormaar et al., 1989) and precipitation for the growing season was 198 mm, respectively (Mary Holtman, personal communication, 1987). Approximately 70% of the total precipitation falls in the growing season, especially in June (Agriculture Canada, 1977).

Prevailing winds are from the west to northwest with strongest winds from the south. Chinook winds cause extreme changes in temperature. High summer temperatures, low precipitation, and strong winds often result in high potential evapotranspiration and a moisture deficit while low winter temperature, little snowfall, and strong winds combine to provide a harsh winter climate for the vegetation.

Vegetation

The study site is a transition zone between the mixed prairie and fescue grasslands with the former at lower elevations and the latter on upper slopes. The vegetation type is characterized by *Stipa curtiseta/Agropyron* species (Wroe et al., 1979). The original grasslands were once dominated by *Stipa curtiseta* associated with varying amounts of other midgrasses such as *Festuca scabrella*, *Agropyron dasystachyum* var. *dasystachyum*, *Agropyron smithii*, and *Koeleria macrantha*. *Bouteloua gracilis* was found on sandy soils (Wroe *et al.* 1979). With prolonged overgrazing, these grasslands are now dominated by low growing species such as *Koeleria macrantha*, *Bouteloua gracilis*, *Artemisia* sp., *Carex* sp., *Selaginella densa* and *Phlox hoodii*. Invaders such as *Taraxicum officinale*, *Lepidium densiflorum*, *Grindelia squarrosa* and other annuals are now abundant. In 1981, 70% of the grass was in fair to poor condition with a recommended stocking rate of 0.8 AUM ha^{-1} (R. Wroe, personal communication, 1987).

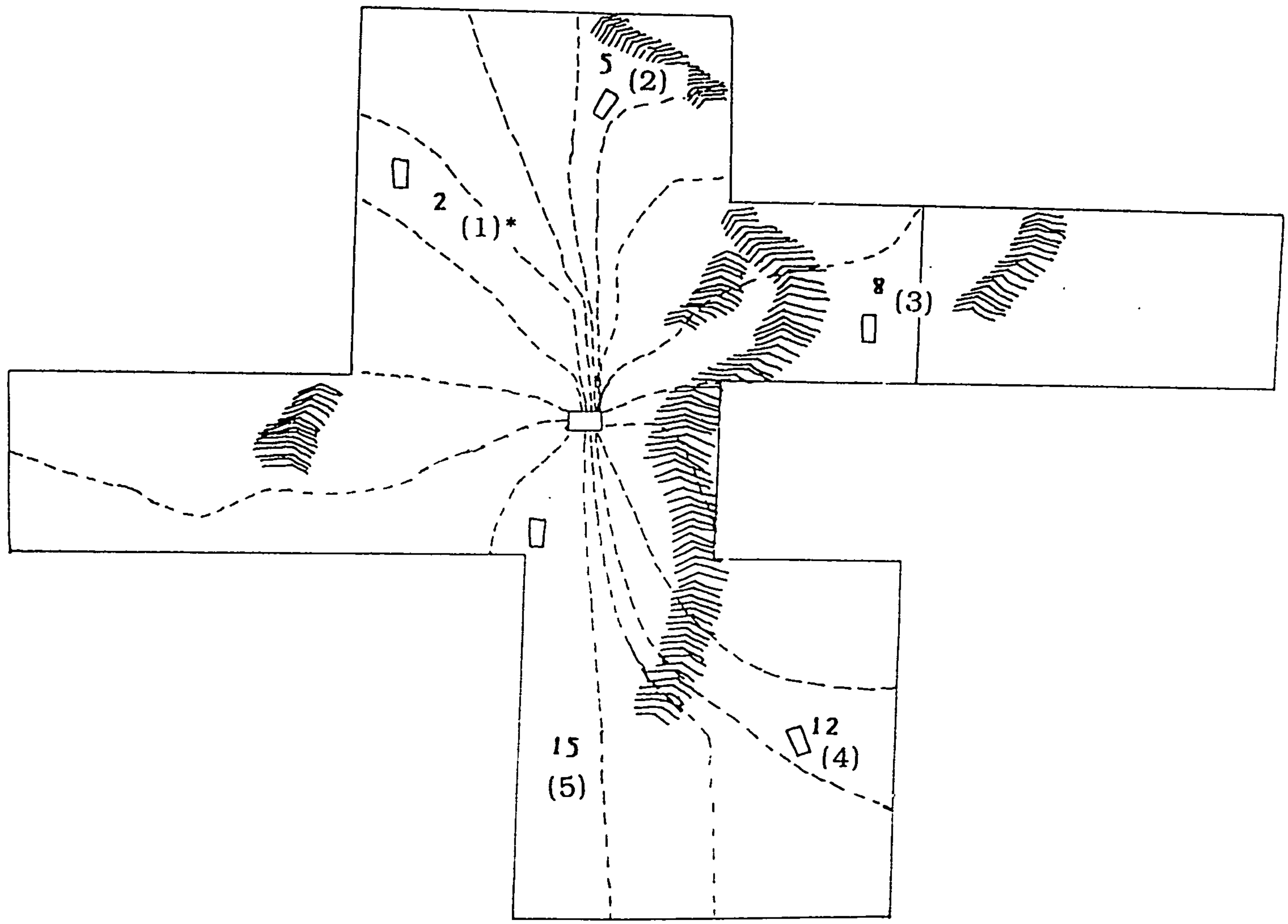

Figure I.1. Study site in the transitional mixed prairie/fescue grasslands in southern Alberta. (*Fields are numbered from 1 through 17. Fields 2, 5, 8, 12, and 15 represented the field replicates and were referred to as 1 through 5 for the purposes of this study).

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Appendix II. TABLES AND FIGURES RELATING TO THE SEED BANK IN MIXED PRAIRIE/ROUGH FESCUE GRASSLAND

Table II.1. Percentage composition[1] of dicotyledon and monocotyledon seed in the seed bank in grazed and ungrazed treatments in the upper (0-2.5 cm) and lower (2.5-5.0 cm) soil strata.

	1985		1986	
Treatment	Dicotyledon (%)	Monocotyldon (%)	Dicotyeldon (%)	Monocotyledon (%)
UPPER SOIL STRATUM				
Grazed	75.9	24.0	31.4	68.5
Ungrazed	77.6	22.4	22.3	77.7
LOWER SOIL STRATUM				
Grazed	66.5	33.0	31.2	68.8
Ungrazed	70.5	29.5	25.1	74.9
TREATMENT MEANS (%)				
Grazed	71.2	28.8	31.2	68.9
Ungrazed	74.2	26.0	23.7	76.3

[1] Percent composition determined from mean seed density in Table 2.1 (Chapter 2).

Table II.2. Significant effects (0.05%) from transformed data for seed density (seeds m^{-2}) and species number in the seed bank for dicotyledon (D), monocotyledon (M), and total (T) seed.

Parameters[1]		Degrees of freedom	Seed m^{-2}			Species Number		
			D	M	T	D	M	T
	Y	1	*	*	*	*	*	*
	F	4	NS	*	NS	NS	*	NS
error	YF	4						
	T	1	NS	*	NS	NS	*	NS
error	FT	4						
	L	1	*	*	*	*	*	*
error	FL	4						
	YT	1	NS	NS	NS	NS	NS	NS
error	YFT	4						
	YL	1	NS	*	*	NS	*	*
error	YFL	4						
	TL	1	*	NS	*	NS	NS	NS
error	FTL	4						
	YTL	4	NS	NS	NS	NS	NS	NS
error	YFTL	4						
	F	4	*	*	*	*	*	*
	YF	4	*	NS	*	NS	NS	*
	FT	4	*	NS	*	NS	NS	*
	YFT	4	*	*	*	*	NS	*
error	S(Y,F,T)	100						
	FL	4	NS	NS	NS	NS	NS	NS
	YFL	4	NS	NS	*	NS	NS	NS
	FTL	4	NS	NS	NS	NS	NS	NS
	YFTL	4	NS	NS	NS	*	NS	NS
	S(Y,F,T)	100	NS	NS	NS	NS	NS	NS
	YT+YFT	5	*	*	*	NS	*	*
	LS(Y,F,T)	100	NS	NS	NS	NS	NS	NS
error	LS(Y,F,T)	100						
	FT	4	NS	NS	NS	NS	NS	NS
	T	1	NS	NS	NS	NS	NS	NS
error	YT+YFT	5						

[1]Parameters consist of Y=year (1985 and 1986), T=treatment (grazed and ungrazed); L=soil stratum (0-2.5cm and 2.5-5.0 cm); F=fields; S=samples.

Table II.3. Mean seed density (seeds m^{-2}) in the seed bank in 1985 and 1986 for dicotyledon (D), monocotyledon (M), and total (T) seed in the five fields (replicates) in grazed and ungrazed treatments in the upper (0-2.5 cm) and lower (2.5-5.0 cm) soil strata.

	Seed m^{-2}					
	1985			1986		
	D	M	T	D	M	T
UPPER SOIL STRATUM						
Grazed						
1	424	69	493	597	2320	2917
2	660	21	681	660	632	1292
3	458	215	674	1035	2618	3653
4	556	319	875	764	535	1299
5	396	167	563	368	1375	1743
Ungrazed						
1	521	56	577	563	2410	2973
2	500	132	632	583	1472	2055
3	486	181	667	410	1472	1882
4	576	132	708	889	2007	2896
5	243	167	410	354	2402	2757
LOWER SOIL STRATUM						
Grazed						
1	90	35	125	882	2236	3118
2	195	83	278	396	264	660
3	49	35	84	535	2125	2660
4	174	83	257	660	486	1146
5	76	56	132	389	1208	1597
Ungrazed						
1	97	76	173	354	1507	1861
2	42	21	63	500	729	1229
3	208	14	222	250	826	1076
4	146	63	209	403	1000	1403
5	21	42	63	208	1056	1264

Within year seed density was significantly different for fields for all comparisons ($P<0.05$).

Table II.4. Percentage composition[1] of dicotyledons and monocotyledons in the seed bank in 1985 and 1986 in the five fields (replicates) in grazed and ungrazed treatments in the upper (0-2.5 cm) and lower (2.5-5.0 cm) soil strata.

	1985		1986	
Treatment	Dicotyledon (%)	Monocotyledon (%)	Dicotyledon (%)	Monocotylydon (%)
UPPER SOIL STRATUM				
Grazed				
1	86.0	14.0	20.5	79.5
2	96.9	3.1	51.1	48.9
3	68.0	31.9	28.3	71.7
4	63.5	36.5	58.8	41.2
5	70.3	29.7	21.1	78.9
Ungrazed				
1	90.5	9.7	18.9	81.1
2	79.2	20.9	28.4	71.6
3	72.9	27.1	21.8	78.2
4	81.4	18.6	30.7	69.3
5	59.3	41.7	12.8	87.1
LOWER SOIL STRATUM				
Grazed				
1	72.0	28.0	28.3	71.7
2	70.1	29.9	60.0	40.0
3	58.3	41.7	20.1	79.9
4	67.7	32.3	57.6	42.4
5	57.6	42.4	24.3	75.7
Ungrazed				
1	56.1	43.9	19.0	81.0
2	66.7	33.3	40.7	59.5
3	93.7	6.3	23.2	76.8
4	70.2	30.1	28.7	71.3
5	33.3	66.7	16.5	74.4

[1] Percent composition determined from seed density in Table II.4.

Table II.5. Mean seed density (seeds m^{-2}) in the seed bank in 1985 and 1986 in the five fields (replicates) shown for dicotyledon and monocotyledon species in the grazed (G) and ungrazed (Un) treatments in the upper (0-2.5 cm) and lower (2.5-5.0 cm) soil strata.

	Fields									
	1		2		3		4		5	
	G	Un	G	Un	G	Un	G	Un	G	Un
UPPER LAYER/1985										
Dicotyledons										
Annuals										
Amaranthus retroflexus	0	21	0	14	0	0	7	0	0	0
Androsace septentrionalis	195	236	111	56	42	201	56	21	14	28
Chenopodium album	0	0	7	7	0	0	0	0	0	0
Lepidium densiflorum	7	0	14	0	0	21	0	35	7	0
Malva rotundifolia	7	83	0	7	0	0	0	0	14	7
Perennial forbs										
Antennaria parvifolia	0	7	0	7	0	0	0	28	28	7
Artemisia cana	7	0	7	14	0	0	21	7	0	14
Artemisia frigida	118	49	437	319	285	222	375	368	160	76
Aster ericoides spp. *pansus*	0	0	0	0	7	0	7	14	70	0
Cirsium arvense	0	7	7	0	0	0	0	0	0	0
Draba nemerosa	0	0	0	0	0	0	0	0	7	0
Draba sp. (1)[1]	0	0	0	0	7	0	0	7	0	7
Epilobium angustifolium and *Epilobium ciliatum*[2]	14	28	42	42	104	28	56	69	28	42
Galium boreale	14	28	0	28	0	0	0	0	7	7
Geum sp. (2)[1]	0	28	7	7	0	0	21	21	14	35
Potentilla sp. (1)[1]	28	28	14	0	7	0	7	7	21	7
Ranunculus cymbalaria and *Ranunculus pusillus*[2]	21	7	0	0	0	0	7	0	21	0
Taraxacum officinale	7	0	0	0	0	0	0	0	0	0
Unidentified[3]	7	0	14	0	7	14	0	0	14	14
Subtotal	425	522	660	501	459	486	557	577	398	244

Table II.5. cont'd

	1		2		3		4		5	
	G	Un	G	Un	G	Un	G	Un	G	Un
Monocotyledons										
Agropyron sp. (3)[4]	14	14	0	14	0	0	132	69	0	7
Helictotrichon hookeri	0	7	0	0	7	0	7	0	7	14
Juncus bufonius, Juncus tenuis and *Juncus torreyi*	56	35	7	97	195	148	181	56	146	146
Muhlenbergia cuspidata	0	0	14	0	0	0	0	0	7	0
Poa sp. (3)[5]	0	0	0	21	14	35	0	0	7	0
Unidentified[13]	0	0	0	0	0	0	0	7	0	0
Subtotal	70	56	21	132	215	181	320	132	167	167
TOTAL	495	578	681	633	674	667	877	709	565	411

LOWER LAYER/1985

	G	Un	G	Un	G	Un	G	Un	G	Un
Dicotyledons										
Annual forbs										
Androsace septentrionalis	42	49	132	14	35	139	56	42	28	14
Chenopodium album	0	0	7	0	0	7	7	7	0	0
Lepidium densiflorum	0	0	7	7	0	14	0	14	0	0
Linum silcatum	0	0	0	0	0	14	0	0	0	0
Malva rotundifolia	7	14	14	0	7	0	7	0	0	0
Perennial forbs										
Antennaria parvifolia	7	0	0	0	0	0	0	0	0	0
Artemisa frigida	28	14	14	7	0	21	69	42	21	0
Draba nemerosa	0	0	0	0	0	0	21	0	0	0
Draba sp. (1)[1]	0	0	7	0	0	0	0	0	0	0
Epipobium angustifolium and *Epilobium ciliatum*[2]	0	7	0	7	0	7	7	21	7	0
Geum sp. (2)[1]	0	0	0	7	0	0	0	14	0	0
Potentilla sp. (1)[1]	0	14	7	0	0	0	7	7	0	7
Ranunculus cymbalaria and *Ranunculus pusillus*[2]	0	0	7	0	0	0	0	0	14	0
Unidentified[3]	7	0	0	0	7	7	0	0	7	0
Subtotal	91	98	195	42	49	209	174	147	77	21

Table II.5. cont'd

	1		2		3		4		5	
	G	Un	G	Un	G	Un	G	Un	G	Un
Monocotyledons										
Agropyron sp. (3)[4]	7	7	0	0	0	0	0	14	7	0
Boutelua gracilis	0	7	0	0	0	0	0	0	0	0
Helictotrichon hookeri	7	28	7	7	7	0	35	0	7	0
Juncus bufonius, Juncus tenuis and *Juncus torreyii*	14	28	76	14	14	14	49	42	42	42
Poa sp. (3)[5]	7	7	0	0	14	0	0	7	0	0
Subtotal	35	77	83	14	35	14	84	63	56	42
TOTAL	125	175	278	63	90	223	258	210	133	63
UPPER LAYER/1986										
Dicotyledons										
Annual forbs										
Amaranathus retroflexus	0	0	0	0	0	0	14	0	0	0
Androsace septentrionalis	118	49	83	139	243	104	160	111	90	49
Galeopis tetrahit	0	0	7	0	7	0	0	0	7	0
Lepidium densiflorum	14	14	21	90	0	14	14	14	14	7
Linum silcatum	0	0	69	0	28	0	7	14	35	0
Malva rotundifolia	0	0	0	7	0	0	7	0	0	0
Perennial forbs										
Achillea millefolium	0	0	0	0	0	0	7	0	0	0
Anemone patens	0	0	0	0	28	14	0	0	0	0
Antennaria parvifolia	14	35	28	14	229	7	14	7	0	21
Arabis holboelii var. *retrofracta*	70	243	21	14	104	0	21	7	7	28
Artemisa cana	0	0	0	0	56	56	7	0	0	0
Artemisa frigida	229	83	319	195	208	160	278	618	69	97
Aster ericoides spp. *pansus*	42	0	28	0	0	0	0	0	63	49
Cirsium arvense	0	0	0	0	0	0	0	0	7	0
Delphinium nuttallianum	0	35	7	0	7	0	0	0	0	0
Draba nemerosa	7	14	28	7	28	0	63	42	0	0

Table II.5. cont'd

	1		2		3		4		5	
	G	Un	G	Un	G	Un	G	Un	G	Un
Draba sp. (1)[1]	0	0	0	0	0	0	0	0	14	0
Epilobium sp. (2)[2]	7	0	7	7	14	7	0	14	0	7
Galium boreale	49	14	28	49	14	35	0	7	7	28
Geum sp. (2)[1]	21	0	0	7	35	7	90	35	35	7
Heuchera acauler	0	0	0	0	0	0	0	0	0	14
Potentilla sp. (1)[1]	0	7	7	7	28	0	21	7	7	14
Ranunculus cymbalaria and *Ranunculus pusillus*[2]	21	56	0	49	0	0	56	14	14	21
Solidago missouriensis	0	0	0	0	0	0	7	0	0	0
Taraxacum officinale	7	0	0	0	0	0	0	0	0	0
Unidentified X1	0	14	0	0	0	7	0	0	0	7
Unidentified X2	0	0	0	0	0	0	0	0	0	7
Unidentified[3]	0	0	7	0	0	0	0	0	0	0
Subtotal	599	564	660	585	1036	411	765	890	369	356
<u>Monocotyledons</u>										
Agropyron sp. (4)[4]	674	215	243	208	507	278	28	97	104	201
Bouteloua gracilis	0	0	0	0	0	0	0	0	21	0
Carex sp. (1)[1]	97	264	28	215	285	90	49	187	167	354
Cyperus schweinitzii	7	0	0	0	0	0	0	0	0	0
Danthonia parryi	0	0	0	28	42	7	0	0	0	0
Festuca rubra	0	0	0	0	14	7	0	0	0	0
Helictotrichon hookeri	14	14	0	0	0	0	14	0	21	7
Juncus bufonius, *Juncus tenuis* and *Junus torreyi* [2]	222	424	49	118	181	76	63	174	285	187
Koeleria macrantha	854	1069	118	368	1313	708	167	1278	444	1167
Muhlenbergia cuspidata	0	0	0	0	7	0	7	0	0	0
Poa sp. (6)[5]	451	410	187	528	271	306	208	264	333	486
Stipa sp. (1)[1]	0	0	0	7	0	0	0	7	0	0
Unidentified	0	14	7	0	0	0	0	0	0	0
Subtotal	2319	2410	632	1472	2620	1471	536	2007	1375	2402
TOTAL	2918	2974	1292	2057	3656	1882	1211	2897	1744	2759

Table II.5. cont'd

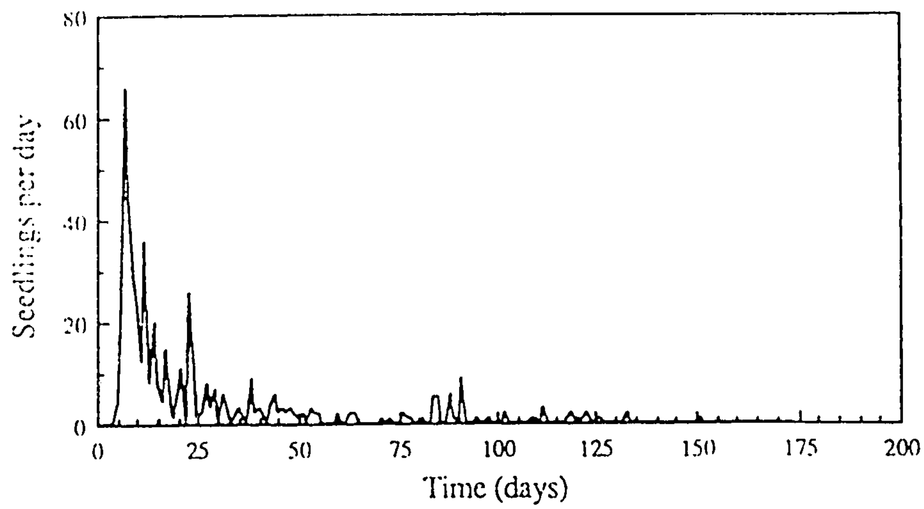
	1		2		3		4		5	
	G	Un	G	Un	G	Un	G	Un	G	Un
LOWER LAYER/1986										
Dicotyledons										
Annual forbs										
Androsace septentrionalis	174	153	49	229	271	21	153	153	104	28
Chenopodum album	0	0	14	0	0	0	0	0	0	0
Lepidium densiflorum	111	42	28	14	35	0	56	28	35	7
Linum silcatum	0	0	56	0	14	0	42	28	7	0
Malva rotundifolia	0	0	0	0	0	0	0	0	14	7
Perennial forbs										
Antennaria parvifolia	0	0	14	7	35	0	14	0	7	0
Artemisa cana	0	0	0	7	21	0	21	0	0	0
Artemisia frigida	208	0	167	83	35	146	97	69	49	0
Aster ericoides spp. *pansus*	83	0	0	7	0	21	21	0	7	7
Campanula rotundifolia	0	0	0	0	0	0	0	7	14	0
Draba nemerosa	63	0	7	0	14	0	97	42	7	35
Draba sp. (1)[1]	21	0	7	0	14	0	0	7	0	0
Epilobium angustifolium and *Epilobium ciliatum*[2]	97	63	42	83	21	63	132	42	63	83
Galium boreale	70	56	0	35	14	0	0	0	21	21
Geum sp. (2)[1]	7	0	7	7	35	0	21	14	42	0
Potentilla sp. (1)[1]	14	21	0	14	14	0	7	7	7	7
Ranunculus cymbalria and *Ranunculus pusillus*[2]	35	21	0	7	0	0	0	0	14	14
Solidago missouriensis	0	0	7	0	0	0	0	0	0	0
Taraxacum officinale	0	0	0	7	0	0	0	0	0	0
Unidentified[3]	0	0	0	0	14	0	0	7	0	0
Subtotal	882	355	398	500	537	251	661	404	391	209
Monocotyledons										
Agropyron sp. (3)[4]	1201	875	215	299	1278	743	326	535	681	472
Bouteloa gracilis	21	0	0	0	0	0	0	0	0	0
Carex sp. (1)[1]	195	222	0	132	250	35	14	139	83	63
Helictotrichon hookeri	0	7	0	0	0	0	0	0	0	7

Table II.5. cont'd

Juncus bufonius, *Juncus tenuis* and *Jun s torreyi* [2]	174	167	14	125	125	0	21	125	167	292
Koeleria macrantha	514	125	0	90	361	0	21	139	174	111
Poa sp. (3)[5]	132	111	35	83	111	49	104	63	104	111
Subtotal	2237	1507	264	729	2125	825	486	1001	1209	1056
TOTAL	3119	1862	662	1229	2662	1078	1147	1405	1600	1265

[1] Number of unidentified species.
[2] Species grouped together in which identification separating each was not always possible.
[3] *Agropyron* species present in 1985 in both soil strata included *Agropyron dasystachyum* var. *dasystachyum*, *Agropyron pectiniforme*, and *Agropyron smithii*. Also present in 1986 in the upper soil stratum was *Agropyron repens*. Presence of each species in each treatment was not determined due to the large number of emerged seedlings.
[4] *Poa* species present in 1985 in both soil strata included *Poa compressa*, *Poa pratensis*, and *Poa sandbergii*. Also present in in 1986 in the upper soil stratum was *Poa cusickii*, *Poa nevadensis*, and *Poa puccinella*. Presence of each species in each treatment was not determined due to the large number of emerged seedlings.

Upper soil stratum



Lower soil stratum

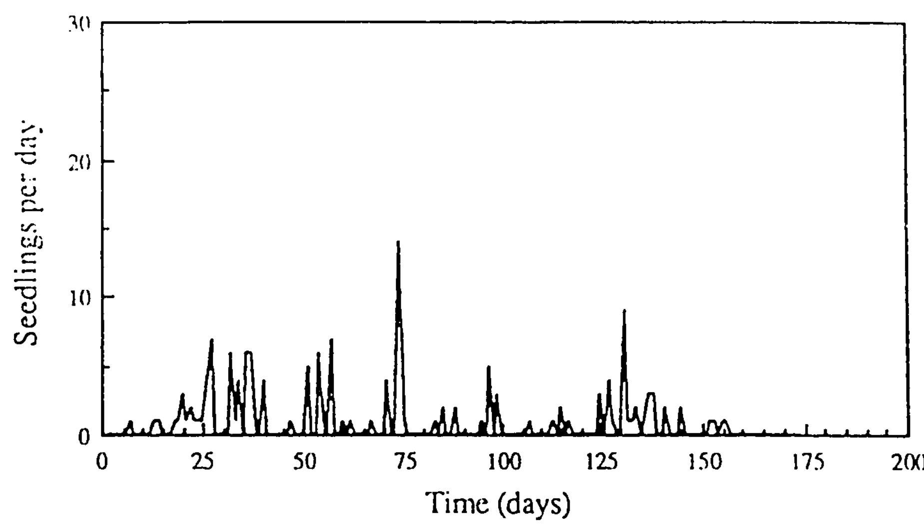


Figure II.1. Differences in emergence patterns between the upper (0-2.5 cm) and lower (2.5-5.0 cm) soil strata in 1985 shown for the grazed treatment as total numbers of seedlings emerged per day over 175 days.

APPENDIX III. TABLES AND FIGURES RELATING TO SEED YIELD AND SEED RAIN

Table III.1a. Mean seed yield (seed m^{-2}) of species in each field in the grazed treatment in 1986.

	Fields				
	1	2	3	4	5
Dicotyledons					
Agoseris glauca		27			9
Androsace septentrionalis	142	189	684	130	24
Anenome patens	60		85		94
Antennaria parvifolia	702	1544	23,213	1170	936
Arabis holboellii var. *retrofracta*			265		
Artemisia frigida	876	11,680	8760	7300	2920
Aster ericoides subspp. *pansus*	510		274	118	78
Campanula rotundifolia				22	22
Cerastium arvense	1054				37
Descurainia sophia		161		804	
Draba nemorosa	69	345	2346	17,733	690
Erigeron caespitosus	3537	771			191
Erigeron flavum			96		964
Erysimum aesperum	138	1932	276	414	
Erysimum cheiranthoides	179	2679			893
Galium boreale	1314	88			146
Gaillardia aristida	52				79
Gaura coccinea			18		8
Gutierrezia sarothrae	114				19
Heterotheca villosa	227	73	125	31	
Heuchera richardsonii	614				
Hymenoxys richardsonii	915	215	323		767
Lappula occidentalis				45	45
Lepidium densiflorum		25			223
Lesquerella arenosa var. *arenosa*		128		128	26
Liatrus punctata	181	95	17	310	155
Linum lewesii		187		119	
Linum rigidum			15		222
Lomatium macrocarpum					344
Lupinus sericeus	29				
Petalostemon purpureum	69	14	41		138

Table III. Ia. cont'd

Senecio canus	164	254		16	45
Solidago missouriensis	226		677	902	4061
Sphaeralcea coccinea		374			
Thermopsis rhombifolia	33	15	15	1	
Subtotal	11,205	21,156	36,965	29,243	13,518
<u>Monocotyledons</u>					
Agropyron dasystachyum var. *dasystachyum*	4202	4437	1020	184	622
Agropryon trachycaulum var. *trachycaulum*	1220	140			
Allium cernuum					36
Allium textile					24
Bouteloua gracilis	81	35	23	81	35
Calamagrostis montanensis	211				
Calamovilfa longifolia				18	37
Carex sp.	164	86	193	97	15
Festuca scabrella	16	146		243	162
Helictotrichon hookeri	76	184			
Koeleria macrantha	43,316	34,748	43,982	8092	31,844
Muhlenbergia richardsonii	48		110	24	5
Poa pratensis	310		5555	74	25
Stipa comata	144	90	682	1229	1408
Subtotal	49,788	39,866	51,565	10,042	34,213
TOTAL	60,993	61,022	88,530	39,285	47,731

Table III.1b. Mean seed yield (seed m^{-2}) of species in each field in the ungrazed treatment in 1986.

	Fields				
	1	2	3	4	5
Dicotyledons					
Achillea millefolium			626		
Agoseris glauca	66	36	9		
Androsace septentrionalis	47	71		378	
Anenome patens	51		17		68
Antennaria parvifolia	234	1357	140	2059	468
Artemisia frigida	584	6424	5256	584	1168
Aster ericoides subssp. pansus	78	118	862	39	180
Cerastium arvense	496				589
Cryptantha macounii		366			
Descurainia sofia				482	
Draba nemorosa		207		1311	
Erysimum aesperum	2070	1242	828	552	138
Erysimum cheiranthoides	482	1250		357	179
Gaura coccinea			10		10
Galium boreale	4234	292			29
Gaillardia aristada	26				
Gutierriezia sarothrae		475		19	
Heterotheca villosa	73	104	312		374
Huechera richardsonii				460	
Hymenoxys richardsonii		968	108	215	861
Lesquerella arenosa var. arenosa	64	384			
Liatrus punctata	181	26	301	34	215
Linum lewesii		17		17	17
Lomatium macrocarpum					292
Orthocarpus luteus				3655	
Petalostemon purpureum	276	83	14	28	
Senecio canus	25	349	16	33	349
Solidago missouriensis	677				
Sphaeralcea coccinea				58	29
Thermopsis rhombifolia	30	45	9		
Subtotal	9,694	13,814	8508	10,281	4966

Table III.Ib. cont'd

Monocotyledons					
Agropyron dasystachyum var. *dasystachyum*	755	4335	1122	663	2907
Allium cernuum	36	29	22		
Allium textile	40	24	16		16
Bouteloua gracilis	93	35		23	
Calamagrostis montanensis	97				
Calamovilfa longifolia	9			138	55
Carex sp.	54	6	37	30	15
Festuca scabrella	194	178	373	259	1021
Helictotrichon hookeri	756	140			32
Koeleria macrantha	19,040	55,216	9282	21,658	18,326
Muhlenbergia richardsonii	43	91			34
Poa pratensis		198	1786	347	768
Stipa comata	90	93	406	960	410
Stipa curtiseta	29				
Schizachyrium scoparium var. *scoparium*			11		
Zigadenus venenosus	13			320	
Subtotal	21,249	60,356	13,044	24,39	23,584
TOTAL	30,943	74,170	21,552	34,679	28,549

Table III.2 Mean seed production (+/- SE) of species per plant or culm averaged over 40 samples unless otherwise indicated.

Species	$\bar{X}$	+/-SE	Number of Samples
Dicotyledons			
Achillea millefolium	1044	53	22
Agoseris glauca	45	2	25
Androsace septentrionalis	118	14	40
Anenome patens	85	5	10
Antennaria parvifolia	234	18	40
Arabis holboellii var. *retrofracta*	147	10	40
Artemisia frigida	1460	116	2
Aster ericoides subspp. *pansus*	196	15	40
Campanula rotundifolia	110	5	40
Cerastium arvense	62	3	40
Cryptantha macounii	159	6	40
Descurainia sophia	804	115	16
Draba nemorosa	345	30	40
Erigeron caespitosus	478	27	40
Erigeron flavum	482	43	16
Erysimum aesperum	690	57	40
Erysimum cheiranthoides	893	411	40
Gaillardia aristada	131	9	18
Galium boreale	146	7	40
Gaura coccinea	13	3	7
Gutierrezia sarothrae	95	9	11
Heterotheca villosa	52	4	40
Heuchera richardsonii	767	62	40
Hymenoxys richardsonii	269	15	40
Lappula occidentalis	226	47	8
Lepidium densiflorum	124	10	16
Lesquera arenosa var. *arenosa*	64	5	40
Liatris punctata	43	6	40
Linum lewisii	85	7	40
Linum rigidum	74	7	40
Lomatium macrocarpum	86	5	40
Lupinus sericeus	48	5	16
Orthocarpus luteus	3655	860	5
Petalostemon purpereum	69	2	17
Senecio canus	41	2	30
Solidago missouriensis	1128	152	19
Sphaeralcea coccinea	144	7	40
Thermopsis rhombifolia	15	1	40
Monocotyledons			
Agropyron dasystachyum var. *dasystachyum*	51	2	40
Agropyron trachycaulum var. *trachycaulum*	50	2	40
Allium cernuum	36	2	40
Allium textile	40	3	40
Bouteloua gracilis	58	2	40

Table III. 2. cont'd

Calamagrostis montanensis	81	4	40
Calamovilfa longifolia	46	3	40
Carex sp.	4	6	40
Danthonia parryi	25	1	40
Festuca scabrella	81	3	40
Helictotrichon hookeri	54	2	40
Koeleria macrantha	238	45	40
Muhlenbergia cuspidata	24	1	40
Poa pratense	62	9	25
Schizachyrium scoparium var. *scoparium*	8	1	5
Stipa comata	16	1	22
Stipa curtiseta	6	1	21
Zygadenus venenosus	64	5	40

Table III.3. Mean seed rain (seeds m^{-2}) for each species, field, and treatment recorded weekly and arranged in order of first date of capture in 1986.

Grazed Treatment Field 1	May[1] 31	June 7	14	21	28	July 5	12	19	26	Aug. 2	9	16	23	September 30	6	13	TOTAL
Draba nemorosa	G		8							31	G			24			63
Anenome patens	R			8							R						8
Antennaria parvifolia	A			668	8						A						676
Koeleria macrantha	Z			79	126	951	2279	346	487	503	Z			189			4960
Lepidium densiflorum	E			401	212		16		8		E						637
Lesquerella arensosa var. *arenosa*	D			63							D						63
Stipa sp.[3]				16	8	8											32
Gaillardia aristada						8											8
Poa sp.(1)[2]						24			24								48
Agropyron dasystachyum var. *dasystachyum*							189	110	165							8	488
Androsace septentrionalis							24										24
Helictotrichon hookeri							8										8
Thlaspi arvense								8									8
Festuca s cabrella									24	16							40
Heterotheca villosa														8			8
Solidago missouriensis																24	24
TOTAL	-	0	8	1235	354	991	2516	464	708	550	-	0	0	237	0	32	7095

Table III. 3. cont'd

Ungrazed Treatment	May[1]		June				July				August				September		
Field 1	31	7	14	21	28	5	12	19	26	2	9	16	23	30	6	13	TOTAL
Koeleria macrantha			16	16	165	157	715	369	448	173		118	126	24			2327
Lepidium densiflorum			149	134	259		8	16	47	16						39	668
Antennaria parvifolia				197													197
Compositae (1)[2]				8													8
Agropyron dasystachyum var. *dasystachyum*					39		8	102	110	31		39	8	126		8	471
Draba nemorosa					8												8
Helictotrichon hookeri						141	31		8				16		8		204
Poa pratensis							189										189
Poa sp.(1)[2]							134							8			142
Stipa sp.[3]							8		8								16
Erysimum cheiranthoides									16	16							32
Erigeron sp. (1)[2]									16					8			24
Gaillardia aristida																	
Agropryon sp. (1)[2]												24	24	8			56
Lesquerella arenosa var. *arenosa*												8					8
Liatris punctata												8					8
Senecio canus														692			692
TOTAL	-	0	165	355	471	298	1093	487	653	236	-	197	174	866	8	47	5050

Table III. 3. cont'd

Grazed Treatment Field 2	May[1] 31	June 7	14	21	28	July 5	12	19	26	Aug. 2	9	16	23	30	Sept. 6	13	TOTAL
Koeleria macrantha		71	8	G	16	71	31	157	377	739	141	251	377		39	55	2333
Agropyron dasystachyum		63		R	322	16	8	79	141	369	63	63	63		16	24	1227
var. *dasystachyum*				A													
Carex sp. (1)[2]			16	Z				24		55							95
Antennaria parvifolia			8	E	16			8									32
Draba nemorosa			31	D	8				8	24	8						79
Lepidium densiflorum					55	16			16	79							166
Helictotrichon hookeri							8	16					16				40
Erigeron sp. (1)[2]								8	8	24		212					252
Stipa sp.[3]									16	24		8	8				56
Erysimum sp. (1)[2]										16	16						32
Lesquerella arenosa										24	16	8					48
var. *arenosa*																	
Eyrisimum aesperum										16	8		8				32
Heterotheca villosa											39	55					94
Liatris punctata												24	31				55
TOTAL	0	134	63	-	417	103	47	292	566	1370	291	621	503	0	55	79	4541

Table III. 3. con't

Ungrazed Treatment Field 2	May[1] 31	7	June 14	21	28	July 5	12	19	26	Aug. 2	9	16	23	30	Sept. 6	13	TOTAL
Koeleria macrantha			94		39	31	55	197	700	4897	809	283	228	731		39	8103
Agropyron dasystachyum var. *daystachyum*			31		16	16	16	102	212	707	362	102	47	31			1642
Antennaria parvifolia						63											63
Carex sp. (1)[2]					8		8										16
Draba nemorosa					31	24	16	8	16								95
Lepidium densiflorum					39	86	267	63	275	141	24						895
Helictotrichon hookeri						8	16	8	8								40
Festuca scabrella						31	24	24									79
Poa sp.(1)[2]									149	79	47		16	24			315
Stipa sp.[3]									24	31	8						63
Erigeron sp. (1)[2]									118	39							157
Erysimum aesperum									63	86	16	31		31		16	243
Lesquerella arenosa var. *arenosa*									39	16		31	31	24			141
Erysimum cheiranthoides													24	16			40
TOTAL	0	0	125	-	133	259	402	402	1604	5996	1266	447	346	857	0	55	11,892

Table III. 3. cont'd

Grazed Treatment
Field 3

	May[1] 31	June 7	14	21	28	July 5	12	19	26	Aug. 2	9	16	23	30	Sept. 6	13	TOTAL
Agropyron dasystachyum		16		G	47	31	63	86	244	118	55	197	16	39	G	55	967
var. *dasystachyum*				R													
Compositae (1)[2]		16		A											R		16
Senecio canus			613	Z											A		613
Draba nemerosa		141		E											Z		141
Erigeron sp. (1)[2]			24	D	1021										E		1045
Koeleria macrantha		16	16			865	330	519	1548	369	134	110	141	55	D	16	4119
Lepidium densiflorum			8				24	8						24			64
Antennaria parvifolia					31												31
Poa pratensis					590			692	24	55	393	204	157	55			2170
Lesquerella arenosa var. *arenosa*							31			79							110
Poa sp.(1)[2]							8	8	637					63			716
Stipa sp.[3]							16			31	24			8		16	95
Stipa viridula							8										8
Agropyron sp. (1)[2]										8							8
Gramineae																	0
Heterotheca villosa												8				63	71
Artemisia frigida														94			94
TOTAL	0	189	661	-	1689	896	480	1313	2453	660	606	519	314	338	-	150	10,268

Table III. 3. cont'd

Ungrazed Treatment Field 3	May[1] 31	7	June 14	21	28	5	July 12	19	26	2	August 9	16	23	September 30	6	13	TOTAL
Helictotrichon hookeri		24															24
Koeleria macrantha				8	47	165	47	291	542	181	16		142	110			1549
Poa sp.(1)[2]						71	134	16	79		149	31		149			629
Antennaria parvifolia				16													16
Festuca scabrella				24	8	31	8										71
Agropyron dasystachyum var. *dasystachyum*					39	8	47	8	220	24	63	63	55	71			598
Lepidium densiflorum						16											16
Stipa comata							8	24	16	24	16		8				96
Agropyron sp. (1)[2]									8					24			32
Erysimum aesperum											31						31
Poa pratensis												86					86
Stipa curtiseta												8		8			16
Heterotheca villosa												8	8				16
Compositae (1)[2]														8			8
TOTAL	0	24	-	48	94	291	244	339	865	229	275	196	213	370	-	0	3183

Table III. 3. cont'd

Grazed Treatment Field 4	May[1]		June				July				Aug.				Sept.		
	31	7	14	21	28	5	12	19	26	2	9	16	23	30	6	13	TOTAL
Antennaria parvifolia		181	676		24		G	G									881
Festuca scabrella		16	31	16	16		R	R									79
Koeleria macrantha		31	267	31	464	110	A	A	267	118	47	24	511	86	126		2082
Stipa comata			8		39	8	Z	Z									55
Stipa sp.[3]			8	24	24		E	E						31	8		95
Agropyron dasystachyum var. *dasystachyum*			118		8		D	D			31		31		8		196
Draba nemorosa			825	102	118	31								8			1084
Agropyron sp. (1)[2]				39													39
Androsace septentrionalis				8													8
Compositae (1)[2]				126													126
Erysimum aesperum					86	24											110
Artemisia frigida										16							16
Poa pratensis											8						8
Lesquerella arenosa var. *arenosa*															31		31
TOTAL	0	228	1933	346	779	173	-	-	267	134	86	24	542	125	173	0	4810

Table III. 3. cont'd

Ungrazed Treatment Field 4	May[1] 31	June 7	14	21	28	July 5	12	19	26	Aug. 2	9	16	23	September 30	6	13	TOTAL
Compositae (1)[2]		16	55														71
Draba nemorosa		79	165	55	236				16								551
Helictotrichon hookeri		16															16
Koeleria macrantha		31	39	31	189	322			141	275	94	71	589	79	47		1908
Agropyron sp. (1)[2]			16	47	118												181
Antennaria parvifolia			267	31	8												306
Lepidium densiflorum			16														16
Lesquerella arenosa var. *arenos*				55													55
Stipa comata				8	55				8	102	8		55	31	8		275
Agropyron dasystachyum var. *dasystachyum*					16	8			8				63	8			103
Festuca scabrella										31			39				70
Poa sp.(1)[2]											16	16					32
Artemisia frigida													141	86	47		274
Liatrus punctata													31	16			47
Agropyron sp.														16			16
TOTAL	0	142	558	227	622	330	-	-	173	408	118	87	918	236	102	0	3921

Table III. 3 .cont'd

Grazed Treatment Field 5	May[1] 31	7	June 14	21	28	5	July 12	19	26	2	Aug. 9	16	23	30	6	Sept. 13	TOTAL
Lesquerell arenosa var. *arenosa*	16									G							16
Antennaria parvifolia		39	8							R							47
Carex sp. (1)[2]		8								A							8
Draba nemorosa		8								Z							8
Koeleria macrantha		39	16	55	31	189	283	393	385	E	79	63	197	47	8	31	1816
Agropyron das ystachyum var. *dasystachyum*			31		24		79	47		D						16	197
Unknown Dicotyledon (1)[2]			16		8	39	8										71
Festuca scabrella			8														8
Arabis sp. (1)[2]				39													39
Erigeron sp.(1)[2]				16		24	16					8					64
Stipa sp.[3]				39			39	16									94
Senecio canus				134													134
Lepidium densiflorum						39									16	16	71
Erysimum cheiranthoides							252	63	16				79	94		16	520
Stipa comata								16									16
Compositae (1)[2]											55	63					118
Artemisia frigida													126				126
Erysimum aesperum													55				55
TOTAL	16	94	79	283	63	291	677	535	401	-	134	134	457	141	24	79	3388

Table III. 3. cont'd

Grazed Treatment Field 5	May[1] 31	7	14	June 21	28	5	July 12	19	26	2	August 9	16	23	September 30	6	13	TOTAL
Lepidium densiflorum	16		8	31		134	338	134	47								708
Antennaria parvifolia		8	24											16			48
Agropyron dasystachyum var. *dasystachyum*			86	228	605	47	291	126	134		79	197	79	31			1903
Koeleria macrantha			16	79	39	212	747	519	244		165	39	173	173	8	16	2430
Festuca scabrella				24													24
Draba nemorosa					63												63
Senecio canus					204												204
Stipa comata					8	8	8							8			32
Unknown Dicotyledon (1)[2]							31										31
Compositae (1)[2]					24							8		8		40	
Heterotheca villosa												8	8	16		8	40
Artemisia frigida														228	24		252
Erigeron sp. (1)[2]														16			16
Helictotrichon hookeri														39			39
Liatrus punctata																31	31
Poa sp.(1)[2]																16	16
TOTAL	16	8	134	362	943	401	1415	779	425	-	244	244	268	527	32	79	5840

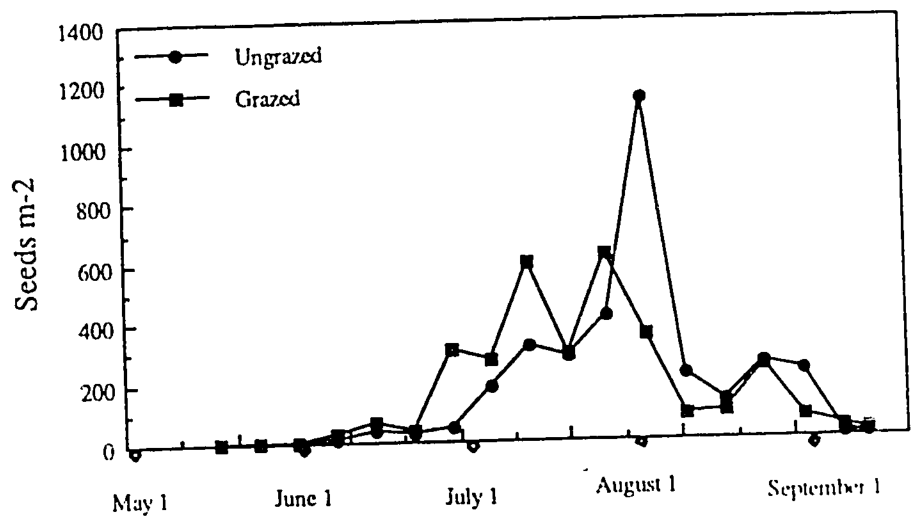
[1] Seeds were not captured prior to May 31.
[2] Number of unidentifiable species. Unknown *Agropyron* and *Poa* sp. are different from those already identified.
[3] *Erysimum* and *Stipa* sp. represent the previously identified species of each in which seed was not positively identified.
[4] Field 3 and 4 were each grazed the week of the 134th day.

Table III.4. Mean seed rain (seeds m^{-2}) recorded weekly for the ungrazed treatment in 1986 prior to balancing with grazed treatment shown in order of first date of capture prior to balancing with the grazed treatment.

	May[1] 31	7	June 14	21	28	5	July 12	19	26	2	Aug. 9	16	23	30	Sept. 6	13	TOTAL
Antennaria parvifolia		2	58	63	2	13								3			141
Compositae (1)[2]		3	11	2										2			18
Draba nemorosa		16	33	11	68	5	6	5	6								150
Helictotrichon hookeri		8	2			27	9	2	3			2	5	2	2		62
Koeleria macrantha		6	35	35	46	177	443	430	414	1152	287	121	251	223	11	11	3642
Lepidium densiflorum		3	35	33	60	47	138	42	74	31	5				2	8	478
Agropyron dasystachyum var. *dasystachyum*			25	49	143	16	74	68	137	248	100	80	50	53	3	2	1048
Agropyron sp. (1)[2]			3	9	35	2					2	5		5			66
Festuca scabrella				9	2	13	6	5	6				8				49
Stipa comata				2	11		3	5	5	25	5		13	6	2		77
Carex sp. (1)[2]					2		2										4
Compositae (1)[2]					5					35			2			2	44
Senecio canus					41									138			179
Poa sp. (1)[2]						14	53	3	46	16	42	9	3	36		3	225
Unknown Dicotyledon (1)[2]							6										6
Poa pratensis							38					17					55
Stipa sp.[3]							2		6	6	2						16
Erysimun aesperum									13	17	9	6	11	6		3	65
Erysimum cheiranthoides									3	3			5	3			14
Erigeron sp. (1)[1]									27	8				5			40
Lesquerella arenosa var. *arenosa*									8	3		8	6	5			30
Gaillardia aristida											3						3
Heterotheca villosa												2	2	3		2	9
Liatris punctata												2	6	3		6	17
Stipa curtiseta												2		2			4
Artemisia frigida													28	63	14		105
TOTAL	0	38	202	213	415	314	780	560	748	1544	455	254	395	558	34	37	6547[4]

[1] Seeds were not captured prior to May 31.
[2] Number of unidentifiable species. Unknown *Agropyron* and *Poa* sp. are different from those already identified.
[3] *Stipa* sp. represent the previously identified species of each in which seed was not positively identified.
[4] Monocotyledon, dicotyledon and total seed rain the ungrazed treatments prior to balancing with the grazed treatments was not significantly different($P>0.05$).

(a) *Koeleria macrantha*



(b) *Agropyron dasystachyum* var. *dasystachyum*

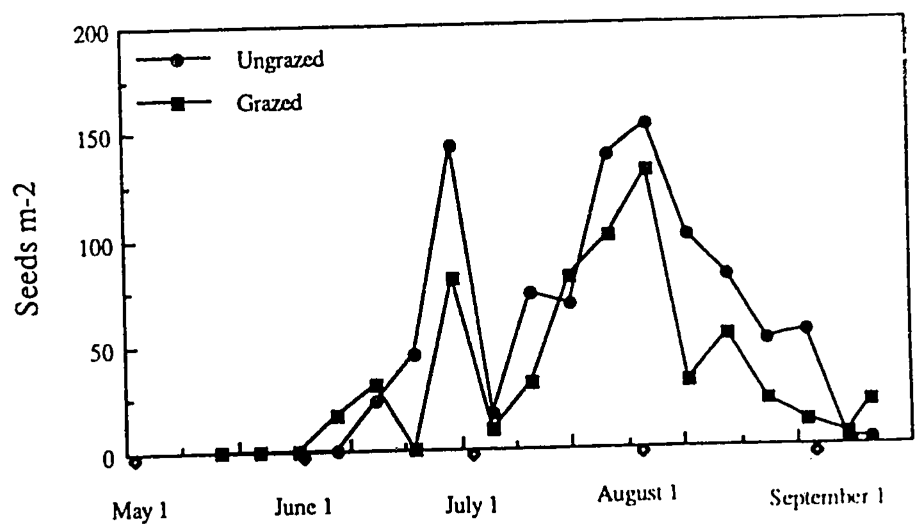


Figure III.1. Seed density estimated from seed rain of (a) *Koeleria macrantha* and (b) *Agropryon dasystachyum* var. *dasystachyum* shown per week in 1986.