AN ABSTRACT OF THE THESIS OF

Mary P. Maret for the degree of Master of Science in Botany and Plant Pathology presented on December 17, 1996. Title: Effects of Fire on Seedling Establishment in Upland Prairies of the Willamette Valley, Oregon

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Prior to European settlement, native prairie dominated the landscape of the Willamette Valley. Today, due to urbanization, agriculture, and the cessation of burning, only isolated remnants of these grasslands still exist. In response to conservation concerns, there has been a move to restore the remaining prairies in the Willamette Valley, and prescribed burning and sowing native seed are often top candidates for grassland restoration. However, the effects of burning on native seedling establishment and the spread of weedy exotics are largely unknown.

In this study, I investigated how prescribed burning affects native and exotic species seedling establishment on three upland prairie vegetation types in the Willamette Valley. The general approach was to sow a known number of seeds from several native and exotic grassland species into experimentally manipulated plots, designed to separate the effects of litter removal from the other effects of burning, and to monitor seedling densities. Germinability and dormancy characteristics of the sowed seeds were also addressed. An additional study focused on the fire temperatures at soil surface in three grassland vegetation types and two burn sizes.

Burning increased the establishment of most or all of the sown native species in the two low quality, exotic grass sites. Exotic seedling establishment also tended to increase, but did not differ significantly from unburned plots for most species tested. On

the higher quality, native bunchgrass site, burning did not significantly improve native species establishment, but did significantly increase the establishment of short-lived exotic species over those in unburned plots.

The germination and dormancy characteristics of the native and exotic species tested indicate that grasses, both native and exotic, are more likely than forbs to be non-dormant in the autumn following dispersal. Forbs, especially native forbs tend to require cold-stratification for maximum germinability.

During grassland fire, temperatures at soil surface were relatively cool. Fire temperature intensity was highest in the higher quality native bunchgrass vegetation. These burns reached higher temperatures significantly closer to the soil surface than the plot burns in lower quality sites dominated by annual or perennial exotic grasses. Average temperatures in a two hectare broadcast burn and in replicated 2m × 2.5m plot burns in an annual exotic grassland were very similar.

Prescribed burning can be an excellent tool for the restoration of low-quality upland prairies when combined with sowing native seeds in the fall. However, on high-quality prairie, prescribed burning may be a poor restoration choice for promoting native seedlings, as burning promoted weedy species without enhancing native seedling establishment.

Effects of Fire on Seedling Establishment

in Upland Prairies in the Willamette Valley, Oregon

by

Mary P. Maret

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Mary P. Maret, Author

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CHAPTER 1

INTRODUCTION

RATIONALE

Prior to European settlement, Oregon's Willamette Valley was dominated by prairies and open oak savannas (Smith 1949; Habeck 1961; Johannessen et al. 1971; Towle 1982). Although the Willamette Valley's climate and soils are amenable to forest growth (Franklin and Dyrness 1989), grasslands were maintained through annual fires set by the native Kalyapuya ("people of the tall grass"). Fires were set during late summer to increase the growth of food plants and to aid in hunting (Boyd 1986). The frequent burning effectively arrested the encroachment of woody plants, promoting an open grassland and oak savanna landscape, which supported an abundant variety of native plants (Towle 1982; Boyd 1986). With European settlement, the burning of the native prairies was suppressed and most of the valley was gradually developed for agricultural or urban uses. Woody species and exotic weeds have since invaded many of the remaining natural areas (Habeck 1961; Towle 1982).

Today, only isolated remnants of the Willamette Valley grasslands still exist. These remaining grasslands are highly fragmented and in critical need of conservation and restoration (Towle 1982). The Nature Conservancy (1983) lists Willamette Valley grasslands as one of the most endangered habitats in Oregon. Furthermore, many rare

and protected plant species depend upon the integrity of the remaining native grassland communities (Wilson et al. 1995).

In response to these conservation concerns, there has been a move to restore native Willamette Valley grassland communities. Two key objectives in the restoration of grassland habitats are the promotion of native species and the control of exotic weedy species. Although prescribed burning is often a top candidate for grassland habitat management, the widespread invasion of exotic weeds has significantly altered these grasslands, creating challenges for land managers. Many of the exotic species now present may tolerate or even be stimulated by fire and the reintroduction of grassland fires could actually create conditions which would promote the spread of weedy plants. Therefore, in order to evaluate prescribed burning as a restoration tool, it is important to be able to predict the response of both the desired natives and the weedy exotics present on the site.

Prescribed burning potentially alters plant population dynamics through two main mechanisms: 1) by affecting the net growth or tissue death of established plants; and 2) by changing the rates of establishment of new individuals from seed. In this thesis, I examined how fire alters seedling establishment of common native and exotic plants in the Willamette Valley upland prairies.

OBJECTIVES

The primary objective of the study described in Chapter 2 was to determine

effects of prescribed fire on seedling establishment on western Oregon upland prairies,

using an experimental design to separate the effects of litter removal from the other

effects of burning involved in the seedling establishment response. The second objective

was to determine how seedling dynamics, as determined by three seedling censuses, are

affected by burning and litter effects over the course of the growing season. The third

objective was to evaluate the usefulness of prescribed fire as a restoration tool in

promoting a native plant community through changes in seedling establishment. The

general approach was to sow a known number of seeds from several native and exotic

grassland species into experimentally manipulated plots, and to monitor seedling

densities in three censuses between December and May.

The field experiments were conducted on three representative vegetation types of

upland prairie: annual exotic grass, perennial exotic grass, and native bunchgrass. The

Annual Exotic Grass site was dominated by several exotic annual grasses including

Taeniatherum caput-medusae Nevski, *Cynosurus echinatus* L., *Bromus mollis* L., and

Avena fatua L. The Perennial Exotic Grass site was dominated by the exotic

rhizomatous grass, *Arrhenatherum elatius* L. and the Native Bunchgrass site was

dominated by *Festuca idahoensis* Elmer var. *roemeri* Pavlick and *Elymus glaucus*

Buckl., with a component of several exotic annual grasses.

Many prairie sites in the Willamette Valley, including the Annual Exotic Grass

and Perennial Exotic Grass sites of this study, do not contain enough mature native

plants to provide an adequate source of native seed to respond to manipulations, such as prescribed fire, through increased native seedling establishment. Sowing seed is a common way of reintroducing native plants into such sites, and one of the factors affecting sowing success is the germination characteristics of the seeds employed. It is also important to understand the germination characteristics of the weedy species present on site in order to control the dominance and spread of these plants. Chapter 3 investigates seed germinability and dormancy characteristics of fourteen species common to upland prairies in the Willamette Valley. Specific objectives of this study were to describe the extent of dormancy for each species, to determine germination response to after-ripening, cold-stratification, and fluctuating temperatures, and to compare dormancy characteristics between grasses and forbs, and native and exotic species. Dormancy was tested by sowing seeds onto moistened filter paper in Petrie dishes and measuring the proportion of germinated seeds. Seeds of species that exhibited dormancy in initial tests were retested for dormancy following treatments of additional storage time (after-ripening), cold-stratification, and exposure to alternating temperatures.

The effectiveness of prescribed fire in meeting management goals may also depend on the fire intensity achieved during the burn (McKell et al. 1962). In particular, post-fire seedbed characteristics may differ between burns depending on the fire temperatures generated near the soil surface. Small plots used for research may not burn intensely enough at the soil surface to adequately represent the seedbed characteristics of a larger-scale burn. Also, burn intensities may vary between grassland vegetation types,

potentially altering seedling response. Chapter 4 describes the maximum temperatures measured during small plot burns in three grassland vegetation types (annual exotic grass, perennial exotic grass, and native bunchgrass), as well as temperatures in a large management-style broadcast burn. Specific objectives of this study were to gain basic information on soil surface fire temperatures in Willamette Valley upland prairies, to determine if there were significant temperature differences between prescribed burns in three vegetation types and, to evaluate the effectiveness of using small, replicated research burns to represent the fire temperatures of a larger management-style burn. Fire temperatures were measured by vertically inserting small cards, each with a series of paint strips of known melting temperatures, into the soil prior to burning. After burning, the melting points of each paint was measured relative to the soil surface.

Chapter 5 provides a synthesis of recommendations for managing and restoring upland prairies in the Willamette Valley. These recommendations are based on the results of the three major research topics: 1) fire effects on seedling establishment, 2) seed dormancy characteristics of common upland prairie plants, and 3) maximum fire temperatures near the soil surface.

CHAPTER 2

EFFECTS OF PRESCRIBED BURNING ON
GRASSLAND SEEDLING ESTABLISHMENT

ABSTRACT

Prescribed burning has been proposed for restoring upland prairies in the Willamette Valley, Oregon. Fire removes plant litter, often creating favorable microsites for seedling establishment, but other burn effects, independent of litter removal, may also affect establishment rates. Seedling response to burning may also be influenced by the type of prairie vegetation. Four experimental treatments (burn, clip and rake, burn with litter added, and unmanipulated) were applied to 2m × 2.5m plots to determine how burning, through litter removal and non-litter burn effects, influences seedling emergence and survival. Seeds of common exotic and native prairie species were sowed into experimental plots. The experiment was replicated on three sites representing three common types of prairie vegetation: Annual Exotic Grass, Perennial Exotic Grass, and Native Bunchgrass. Emerged seedlings were censused in the winter, early spring, and late spring following sowing. In both the Annual Exotic Grass and the Perennial Exotic Grass sites, burning significantly improved the seedling establishment of all or most sowed native species. Exotic seedling establishment on burned plots also tended to increase, but did not differ significantly from unburned plots for most species tested. Litter removal was a significant component of the burn effect for seedling establishment on both the Annual and Perennial Exotic Grass sites, but was most important on the

Perennial Exotic Grass site, probably due to this site's thicker litter layer. On the Native

Bunchgrass site, burning did not significantly improve native species establishment, but

did significantly increase the seedling establishment of short-lived exotic species over

those in unburned plots. Seedling establishment on this site was mostly unaffected by

litter removal or non-litter burn effects.

INTRODUCTION AND LITERATURE REVIEW

Rationale

Prior to European settlement, Oregon's Willamette Valley was dominated by

prairies and open oak savannas (Smith 1949; Habeck 1961; Johannessen et al. 1971;

Towle 1982). Although the Willamette Valley's climate and soils are amenable to forest

growth (Franklin and Dyrness 1989), grasslands were maintained through annual fires

set by the native Kalyapuya ("people of the tall grass"). Fires were set during late

summer to increase the growth of food plants and to aid in hunting (Boyd 1986). The

frequent burning effectively arrested the encroachment of woody plants, promoting an

open grassland and oak savanna landscape, which supported an abundant variety of

native plants (Towle 1982; Boyd 1986). With European settlement, the burning of the

native prairies was suppressed and most of the valley was gradually developed for

agricultural or urban uses. Woody species and exotic weeds have since invaded many of

the remaining natural areas (Habeck 1961; Towle 1982).

Today, only isolated remnants of the Willamette valley grasslands still exist. These remaining grasslands are highly fragmented and in critical need of conservation and restoration (Towle 1982). The Nature Conservancy (1983) lists Willamette Valley grasslands as one of the most endangered habitats in Oregon. Furthermore, many rare and protected plant species depend upon the integrity of the remaining native grassland communities (Wilson et al. 1995).

In response to these conservation concerns, there has been a move to restore native Willamette Valley grassland communities. Two key objectives in the restoration of grassland habitats are the promotion of native species and the control of the exotic weedy species. Although prescribed burning is often a top candidate for grassland habitat management, the widespread invasion of exotic weeds has significantly altered these grasslands, creating challenges for land managers. Many of the exotic species now present may tolerate or even be stimulated by fire. The reintroduction of grassland fires could actually create conditions which would promote the spread of exotic weedy plants. Therefore, in order to evaluate prescribed burning as a restoration tool, it is important to be able to predict the response of both the desired natives and the weedy exotics present on the site.

Prescribed burning potentially alters plant populations dynamics through two main mechanisms: 1) by affecting the net growth or tissue death of established plants and; 2) by changing the rate at which new individuals establish from seed. The scope of this review pertains to how prescribed fire may alter seedling germination and establishment in a grassland system. It is a progressive discussion beginning with

generalities about seed germination and seedling establishment, leading to how prescribed fire specifically changes the seedling environment, with special emphasis on the effects of herbaceous litter, which is removed during prescribed fire.

Seedling Germination

The period between seed germination and seedling establishment is often the most hazardous stage in a plant's life cycle (Potvin 1993). Seedlings are much more vulnerable to mortality than either seeds or established plants. Although seeds are susceptible to mortality from predation, microbial disease, and senescence (Clark 1996), they are usually far more resistant to environmental stresses than seedlings of the same species (Mayer and Poljakoff-Mayber 1989). A germinated seed (i.e., seedling) is vulnerable to mortality from harsh climatic conditions, herbivory, trampling, disease, and interference from neighboring plants. Young seedlings also have fewer defenses to unfavorable conditions than established plants, due to their smaller size and less mature systems. Yet, despite high risk of seedling mortality, the recruitment of new individuals through seedlings is crucial for the long term success of many terrestrial plant populations (Weaver and Mueller 1942).

A seed becomes a seedling when the radicle has emerged from the seedcoat (Mayer and Poljakoff-Mayber 1989). Seedling success depends upon many biotic and abiotic factors (Laude 1956; Grime et al. 1981; Gross 1984; Cheplick and Quinn 1987; Hamrick and Lee 1987; Fowler 1988). Because many of these factors vary by season in temperate regions, the timing of germination is important to seedling success (Masuda

and Washitani 1990). Seedlings may avoid unfavorable seasonal conditions, such as drought, desiccation, extreme temperatures, and frost heaving by germinating in response to seasonal cues. Temperature is probably the most important control of germination timing in mesic temperate areas (Went et al. 1962; Baskin and Baskin 1988; Masuda and Washitani 1990; Pons 1991a; Olff et al. 1994). Seeds must also have adequate water availability and aeration to germinate (Mayer and Poljackoff-Mayber 1989).

Although some seeds germinate as soon as moisture, temperature, and aeration levels are adequate (Grime et al. 1981), complete germination at first opportunity may not be optimum for plant population success. Mechanisms that delay germination until additional conditions are met may improve the probability for seedling establishment.

Fatal germination occurs when a germinated seed dies due to conditions that do not support seedling growth and establishment. Many species avoid fatal germination, in response to transient, "unseasonal" weather changes, by incorporating cold-stratification and/or after-ripening requirements. Cold-stratification occurs when imbibed seeds are exposed for a given period of time to cold temperatures. This requirement essentially limits germination prior to the winter season. Once stratified, many species will germinate under a broad range of conditions (Bostock 1978; Pons and Van Tooren 1988; Van Tooren and Pons 1988). The need for after-ripening, i.e., the complex biochemical changes within an aging seed (Baskin and Baskin 1985), also prevents early germination by inhibiting germination until the seed has aged sufficiently. As the seed ages, the range of conditions adequate for germination increases (Baskin and

Baskin 1985; Goodwin et al. 1995). Besides "enforced delays", germination requirements for some seeds change with the seasons, correlating with favorable seasons for seedling establishment (Baskin and Baskin 1985; Fenner 1987; Baskin and Baskin 1989; Masuda and Washitani 1990; Pons 1991a; Olff et al. 1994).

In addition to time, seedling success also depends upon spatial conditions. Openings in dense vegetation, such as in mesic grasslands, are important for seedlings. Most seedlings cannot survive under a dense grassland canopy, apparently due to overwhelming competition for resources (Fenner 1978; Grime et al. 1981; Gross and Werner 1982; Gross 1984; Winn 1985; McConnaughay and Bazzaz 1987; Peart 1989; Pons 1989; Reader 1991; Thompson and Baster 1992; Potvin 1993). The size of the gap may be crucial as it not only affects resource availability but also the microclimate. Thus suitable gaps in the vegetation are important for the successful recruitment of new individuals. By delaying seed germination until there is an appropriate size gap in the vegetation, new plants will experience decreased competition with neighbors, and thus improve the chances of survival (Grubb 1977; Gross and Werner 1982; Fenner 1985; Aguilera and Lauenroth 1993). Distinctive environmental conditions found in vegetation gaps, such as increased light quantity and quality, elevated diurnal temperature and humidity fluctuations, and increased nitrate levels may be cues for germination (Bostock 1978; Pons 1991a).

Gaps not only have more light reaching the soil surface than in leaf-shaded areas, but the quality of light also differs. Decreased red/far red light ratios as found beneath a leaf canopy may be detected by the seed's photoreceptor phytochrome, thus enabling the

seed to detect the presence of surrounding vegetation and/or litter cover. In grasslands, a low red/far red light ratio often inhibits germination (King 1975; Fenner 1978; Silvertown 1980; Pons and Van Tooren 1988; Van Tooren and Pons 1988; Pons 1991b; Pons 1992; Derigbus et al. 1994), though some species, particularly those with large seeds or of the family Poaceae are able to germinate in dark, shaded conditions (Grime et al. 1981).

Vegetation gaps also have increased diurnal temperature and humidity fluctuations. Some seeds, especially those with hard seedcoats, may require temperature and/or humidity fluctuations to stimulate germination (Steinbauer and Grigsby 1957; Bostock 1978; Fenner 1978; Grime et al. 1981; Rice 1985). On the other hand, these fluctuations combined with high light levels will inhibit germination of some species, probably as an adaptation to remain dormant in highly desiccating situations (Grime et al. 1981; Van Tooren and Pons 1988).

Seeds may also detect vegetation gaps by higher levels of available soil nitrogen in openings as compared with highly competitive areas. Higher nitrate levels have been found to increase seed germination, especially in combination with other gap clues (Steinbauer and Grigsby 1957; Bostock 1978; Pons 1989).

For certain species from some fire-prone ecosystems, germination has been stimulated by exposing seeds to certain factors unique to fire or post-fire conditions. High temperatures (Went et al. 1952; Keeley et al. 1985; Keeley 1987), smoke (Dixon et al. 1995), leachate from charred wood (Keeley et al. 1985; Keeley 1987; Thanos and Rundel 1995), and nitrogen additions (Thanos and Rundel 1995) by themselves or in

combination, have been shown to stimulate germination of certain chaparral species. However, species with direct dependence on fire cues for germination are uncommon (Cushwa et al. 1968). No grassland species appear to be stimulated by conditions unique to fire, such as short periods of high heat or ash additions (Old 1969; Lloyd 1971; Hulbert 1988). Changes in grassland seed germination following fire is generally attributed to the removal of litter and decreased competition from perennial species (Went et al. 1952) rather than to the direct effects of the fire itself.

Seedling Establishment

Seedling establishment is a process of seedling persistence and growth. The point at which a seedling has become established is usually defined by the researcher according to the objectives of the study (Fenner 1985). Although it is generally understood that a seedling should be completely autotrophic (not reliant on seed reserves) before considered established, seedling establishment in field studies often includes a standard for potential continued seedling growth and survival (Gross and Werner 1982; Ries and Svejcar 1991).

Seedling establishment is directly related to the presence of microsites with the specific requirements that permit germination, seedling growth, and seedling survival (Harper 1977). Both fire and the presence of herbaceous litter alter the seedling microenvironment, and thus affect seedling establishment and population dynamics in plant communities.

Effects of Fire on Seedling Establishment

Fire is a common and important component in the development and maintenance of most grassland communities in North America (Vogl 1974), often creating favorable microsites for seedling establishment (Wright 1974). Grassland fire removes above-ground vegetation, creating areas of bare mineral soil conducive to seedling establishment by temporarily reducing competition from living neighbors (Went et al. 1952; Cheplick and Quinn 1988), such as many woody invaders (Adams et al. 1982) and other species that cannot survive periodic fire (Ewing and Engle 1988; Grilz and Romo 1994).

Ash deposition and charred vegetation in the post-fire seedbed also alter the seedling environment. Ash and charred vegetation may add nutrients directly to the soil or stimulate nutrient cycling by soil microorganisms (review by Raison 1979). Although complete ashing removes all nitrogen, ash may contain a variety of minerals (Kellman et al. 1985). Incompletely combusted plant material leaches considerable amounts of nitrogen to the soil (Thanos and Rundel 1995). Ash also darkens the color of the soil surface, thus increasing solar absorption and indirectly heating the soil. However, ash deposition in grasslands is relatively light, often is insufficient to cover the soil (Raison 1979), and may be present only a short period of time. Lloyd (1971) and Cheplick and Quinn (1988) found no evidence of a grassland seedling growth response to ash, and grass production in tallgrass prairie has not been shown to be significantly influenced by ash additions (Old 1969; Lloyd 1971; Hulbert 1988).

Grassland fire often increases soil fertility, usually through increased nitrogen availability (Old 1969; Hulbert 1988; Blank et al. 1994; Brewer and Platt 1994; Ojima et al. 1994). Although nitrogen is volatilized during the burning process, heat transforms organic nitrogen into ammonium, a form more available for plant growth and microbial nitrification (Debano et al. 1979; Dunn et al. 1979). Although nutrient cycling in the soil could also be altered by temporary soil heating from flames (Raison 1979), grassland fires tend to heat only a very thin (<1cm) layer of soil near the surface (see review in Fire Temperature chapter). Due to the low heat transfer to soil, the influence of heat directly on the soil chemistry is probably negligible (Heyward 1938; Norton and McGarity 1965), and any increase in soil fertility is more likely due to differences in the post-fire environment, such as warmer soils, than to the direct effects of fire.

The most important post-fire changes in grassland microsites have been attributed to the removal of dead plant material, collectively called plant litter (Old 1969, Rice and Parenti 1978, Hulbert 1988). Fire is probably the most important abiotic agent of litter destruction (Facelli and Pickett 1991a). In the absence of fire (or other litter removing processes), grassland litter decomposes slowly, accumulating a dense thatch on the soil surface, which affects seedling microsites through a variety of mechanisms.

Effects of Plant Litter on the Seedling Environment

In a mediterranean-type climate, grasses and forbs senesce during summer months, the above-ground stems and leaves dying back each year. New growth from underground organs or seeds commences with fall rains and continues until the dry

summer months when soil moisture becomes inadequate for continued growth. Litter from dead herbaceous material does not decompose as fast as it is accumulated, allowing a thatch to increase each year. The presence of plant litter changes the microenvironment in many ways and thus can have important effects on seedling germination and survival (review by Facelli and Pickett 1991).

A litter layer reduces light quantity (Evans and Young 1970; Goldberg and Werner 1983) and quality (Knapp and Seastedt 1986; Vasquez-Yanes et al. 1990) at the soil surface, altering the microclimate for seeds and seedlings (Rice 1985). Inadequate light below the litter layer can be fatal, particularly in small-seeded species which lack the reserves of larger seeds (Gross 1984). Satisfactory light to maintain sufficient photosynthetic rates are important for seedlings to grow and establish. Also, overshaded environments can alter seedling development and affect morphological and physiological aspects of the plant, such as root to shoot ratios (Peterson and Facelli 1992) or leaf thickness and stomatal density (Knapp and Seastedt 1986; Ballere et al. 1988). Shaded dicot seedlings also often form elongated hypocotyls (Barrett 1931; Peterson and Facelli 1992). This greater resource expenditure may weaken seedlings (Hamrick and Lee 1987; Peterson and Facelli 1992) and small seeded species may not have enough resource reserves to penetrate a thick litter layer (Gross 1984; Fenner 1985). Furthermore, etiolated seedlings are more vulnerable to mechanical damage (Barrett 1931; Clark and Clark 1989) and desiccation (Hamrick and Lee 1987) than compact, more robust seedlings.

Plant litter also moderates temperatures at the soil surface (Evans and Young 1970; Willms et al. 1993). This temperature is modified in two major ways: litter intercepts solar radiation, keeping soil cooler during spring and summer months (Hulbert 1969; Old 1969), and it also reduces air movement, thus insulating the soil from freezing (MacKinney 1929) and diurnal temperature fluctuations (Evans and Young 1970).

The presence of plant litter affects the movement of water between the soil and the atmosphere, generally increasing soil moisture (review by Facelli and Pickett 1991a). The high water-holding capacity of grassland litter promotes increased microsite humidity and inhibits excessive drying at the soil surface (Evans and Young 1970; Goldberg and Werner 1983). A litter layer may also help conserve soil moisture by reducing soil temperature and air movement and thus evaporation (Willms et al. 1993). In regions where water is limiting, a litter layer often reduces the danger of seedling desiccation (Evans and Young 1970; Gross 1984; Fowler 1986; Hamrick and Lee 1987; Cheplick and Quinn 1987; Keeley 1992). However, moisture conservation by litter may matter little when water is either unavailable for conservation, or abundant water for growth makes conservation irrelevant (Willms et al. 1993), or during periods of cloudy weather (Evans and Young 1970).

Litter accumulation may create a physical barrier for seeds reaching the soil and to seedling emergence. Seeds filtering through a litter layer may be impeded, or fail to reach the soil, leading to delayed or unsuccessful germination (Fowler 1986; Hamrick and Lee 1987). Matted litter may also be a physical obstruction for seedlings, increasing

mortality, when they are unable to penetrate this type of barrier (Bergelson 1990 a, 1990b).

Plant litter may also affect the seedling environment chemically. The decomposition of herbaceous litter may directly release both nutrients and allelopathic substances into the soil. Allelopathic substances can be leached in rainwater passing through litter (Rice 1979) although there is no evidence of litter allelopathy in grassland field tests (Old 1969; Hulbert 1988; Rice and Parenti 1978). Large amounts of nutrients are also present in decaying grassland litter (Old 1969). The physical changes produced by litter can affect nutrient availability by influencing the abundance and activity of nutrient cycling organisms in the soil and in the litter (Knapp and Seastedt 1986).

The presence of litter may affect the vulnerability of seeds and seedlings to predators and pathogens. The humid, moist conditions below a litter layer can promote fungal and bacterial pathogens (Fowler 1988; Facelli and Pickett 1991). Litter may increase the abundance of seed and seedling predators by providing habitat (Facelli 1994) thus reducing seedling establishment (Reader and Beisner 1991; Facelli 1994). On the other hand, seeds and seedlings may be less apparent to predators under litter, improving the chance of seedling establishment (Clark et al. 1991; Reader 1993).

Summary

With all of the combined positive and negative affects of post-burn seedbeds and litter removal, the net effects of fire on seedling germination and establishment in the Willamette Valley upland prairies is largely unknown. This is especially true because

nearly all grassland research in North America has focused on midwestern tallgrass

prairie or on arid rangelands. However, there are several patterns of litter removal and

non-litter burn effects that can be expected for upland prairies of western Oregon. Non-

litter burn effects change the favorability of seedling microsites primarily by decreasing

canopy cover and competition from living neighbors. Ash depositions and changes due

to direct heating of soil surface are probably of little importance, due to their transient

nature and the lack of an ash effect found on other grassland systems. Litter removal

during burning improves seedling microsites by increasing light penetration and

temperature fluctuations, and by reducing fungal and bacterial pathogens and physical

barriers to seeds and seedlings. Moisture conservation is probably irrelevant to western

Oregon grassland seedlings, as there is abundant precipitation during the majority of the

growing season, especially during the time of most germination and establishment.

Objectives

Three main objectives were addressed in this study. The primary objective was

to determine effects of prescribed fire on the establishment of seedling establishment on

western Oregon upland prairies, using an experimental design to separate the effects of

litter removal from the other effects of burning involved in the seedling establishment

response. A second objective was to determine how seedling dynamics, as determined

by three seedling censuses, are affected by burning and litter effects over the course of

the growing season. A third objective was to evaluate the usefulness of prescribed fire

as a restoration tool in promoting a native plant community through changes in seedling establishment.

METHODS

Study Sites

Experimental plots were established at three study sites in the Willamette Valley, Oregon. Two of the three study sites were located on Carson Prairie of Oregon State University's Dunn Research Forest. One of the Carson Prairie sites (Native Bunchgrass Site) was dominated by native bunchgrasses, *Festuca idahoensis* Elmer var. *roemeri* Pavlick and *Elymus glaucus* Buckl., with a component of several exotic annual grasses. The other Carson Prairie site (Annual Exotic Grass Site) was dominated by several exotic annual grasses including *Taeniatherum caput-medusae* Nevski, *Cynosurus echinatus* L., *Bromus mollis* L., and *Avena fatua* L. Carson Prairie is a south facing upland prairie, 20 km north of Corvallis, Oregon, in the foothills of the Coast Range. The elevation is approximately 240m above mean sea level. Soils are Witzel very cobbly loam.

A third study site (Exotic Perennial Grass Site) was located on Amazon Dike No. 2 Management Unit at Fern Ridge Reservoir. This site, managed by the Army Corps of Engineers, is 12 km west of Eugene, Oregon. The site is dominated by an exotic perennial grass, *Arrhenatherum elatius* L., although there is also a suppressed understory of other forbs and graminoids, including scattered patches of the desired bunchgrass,

Festuca rubra L. The elevation is approximately 375m above mean sea level, with a flat aspect. Soils are Salkum silty clay loam.

The climate of the Willamette Valley is characterized by mild, wet winters, and moderate, dry summers. The average annual precipitation in Corvallis, Oregon is 137 cm. Average maximum January temperature is 11°C and maximum average July temperature is 31°C (Oregon Climate Service, Hyslop Farm, 1961-1990). The average annual precipitation for Eugene, Oregon is 121 cm. Average maximum January temperature is 8°C and maximum temperature in July is 28°C (Oregon Climate Service, Eugene Airport, 1961-1990).

Study Species

Key grassland species were chosen on each of the three study sites to examine the relationship between prescribed burning and litter removal on seedling survival and establishment (Table 2.1). Common names are listed in the appendix. Key species were selected to characterize the native and exotic community of grasses and forbs common (or desired) within each study site. Mature seeds (or fruits, such as achenes and caryopses) of the key species were collected from each study site, but outside of experimental treatment blocks, the summer of 1995, as they became available. Native seeds were not available in adequate quantities from the Exotic Perennial Grass Site and

Table 2.1. Description of study species for three sites.

Annual Exotic Grass Site

Species	Native to Oregon?	Growth form	Life-span
Centaurea cyanus L.	no	forb	annual
Dactylis glomerata L.	no	grass	perennial
Daucus carota L.	no	forb	biennial
Elymus glaucus Buckl.	yes	grass	perennial
Eriophyllum lanatum (Pursh) Forbes	yes	forb	perennial
Festuca idahoensis Elmer var. *roemeri* Pavlick	yes	grass	perennial
Madia elegans Don ex Lindl.	yes	forb	annual
Taeniatherum caput-medusae Nevski.	no	grass	annual

Perennial Exotic Grass Site

Species	Native to Oregon?	Growth form	Life-span
Arrhenatherum elatius L.	no	grass	perennial
Elymus glaucus Buckl.	yes	grass	perennial
Eriophyllum lanatum (Pursh) Forbes	yes	forb	perennial
Festuca rubra L.[1]	yes	grass	perennial
Hypochaeris radicata L.	no	forb	perennial
Plantago lanceolata L.	no	forb	perennial
Potentilla gracilis Dougl.	yes	forb	perennial

Native Bunchgrass Site

Species	Native to Oregon?	Growth form	Life-span
Chrysanthemum leucanthemum L.	no	forb	perennial
Dactylis glomerata L.	no	grass	perennial
Daucus carota L.	no	forb	biennial
Elymus glaucus Buckl.	yes	grass	perennial
Eriophyllum lanatum (Pursh) Forbes	yes	forb	perennial
Festuca idahoensis Elmer var. *roemeri* Pavlick	yes	grass	perennial
Madia gracilis (Smith) Keck	yes	forb	annual
Taeniatherum caput-medusae Nevski.	no	grass	annual

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[1] *Festuca rubra* has recently been re-defined by taxonomists as an introduced cultivar and not a true native species. Nonetheless, *Festuca rubra* closely resembles the native fescue (*F. idahoensis* var. *roemeri*) and is often found in association with native prairie plants.

were collected from other local sources. A detailed description of seed collection, storage and processing can be found in Chapter 3.

Experimental Design

The effects of prescribed burning and litter removal on seedling establishment were examined using a randomized complete block design with four treatments: burned (B); clipped and raked to remove litter (-L); burned with litter added (B+L); and unburned plots with natural litter layer intact (NM).

The experimental design was planned to test four main hypothesis (Table 2.2). The effect of prescribed burning (H_1) was tested by comparing seedling numbers in treatments B and NM. The numbers of seedlings in -L and NM were also compared to test the effect of litter removal (H_2). Seedling numbers in treatments -L and B, as well as in NM and B+L, were compared to test the importance of litter removal as a burn effect (H_3). If litter removal is a sufficient explanation for the burn effect on seedling establishment, then seedling densities should be the same in -L as in B, as well as the same in B+L as in NM. The burn effect, independent of litter removal (H_4), was tested by comparing seedling numbers in B and B+L. If non-litter burn effects are a sufficient explanation for the burn effect on seedling establishment, then seedling densities should be the same in B as in B+L. In cases where there is a significant burn effect (H_1), but the burn effect can not be sufficiently explained by either litter removal or cumulative non-litter burn effects (H_3, H_4), it is assumed that both litter and non-litter effects serve as partial explanations of the burn effect.

Table 2.2. Description of study hypotheses, tests, and predictions. Tests and predictions are based on the comparisons seedling densities of key species under four treatment types: B = burned, -L = clipped and raked to remove litter, B+L = burned with litter added, and NM = no manipulation. The symbols, ≠ and = , in the prediction column refer to a significant and non-significant statistical difference, respectively.

Hypotheses	Seedling Densities	
	Test	Prediction
H_1: Burning affects the seedbed in a way that changes seedling establishment.	B vs. NM	B ≠ NM
H_2: Litter removal affects the seedbed in a way that changes seedling establishment.	-L vs. NM	-L ≠ NM
H_3: Litter removal is a sufficient explanation of the burning effect.	B vs. NM	B ≠ NM
	-L vs. NM	-L ≠ NM
	B vs. -L	B = -L
	B+L vs. NM	B+L = NM
H_4: Cumulative non-litter burn effects are a sufficient explanation of the burning effect.	B vs. NM	B ≠ NM
	B vs. -L	B ≠ -L
	B vs. B+L	B = B+L

Each of the four treatments was randomly assigned to one of four 2m × 2.5m meter plots within each of eight blocks. All 2 m × 2.5 m plots were experimentally manipulated in late September, 1995. Plot burning for treatments B and B+L was accomplished by wetting narrow (25cm) mowed aisles within the plot perimeter and igniting dead plant material with a fusee. The resulting fires were comparable to a larger grassland burn with regard to temperature, speed, and flame height (See Chapter 4). Litter, in treatment -L plots, was removed by hand after vegetation was clipped to stubble. The removed litter was spread over the burned B+L treatment plot within each block. The added litter was covered and secured with a light bird netting until the litter

layer had stabilized (December 1995). Treatment plot NM was not experimentally manipulated.

Ten 5cm × 5cm subplots were set up within the center of each 2m × 2.5m plot. Subplots were arranged in a grid with subplots about 5 cm apart. The eight test species were assigned randomly to subplots. One hundred seeds of each species were sown by hand, one species per subplot, in late September/early October of 1995. The two remaining subplots were controls and were not sown with seeds, in order to account for any seedling emergence from seeds naturally present on the plots. All seeds were sown on the soil surface, under the litter layer, if present. High densities of sown seeds were used in the experiment to ensure that seeds were present in similar densities within each experimental subplot.

Monitoring Seedling Densities

Seedlings were censused three times during the growing season: mid-December 1995; mid-March 1996; and mid-May 1996. Seedlings were censused by counting all seedlings of each species sowed within each subplot. Seedlings of each test species were also identified and counted by species within the two unsown subplots of each plot. Seedlings that survived to the last census, in May, were considered established, as seedling densities changed little between the March and May census.

Data Analysis

Seedling response to treatments

The number of seedlings of species (or category of species) that were present per 100 sown seeds (SN_i) in a subplot, was calculated for each of the eight species using the following equation:

$$SN_i = N_{si} - N_{ci}$$

where N_{si} is the number of seedlings of species i present in the subplot where seeds of species i were sown, and N_{ci} is the mean number of seedlings of species i that were present in the two unsown subplots within each plot. The term N_{ci} was included in the equation to allow for possible variation between plots in the number of seedlings of species i that emerged from seeds naturally present on the site. Seedling categories included native and exotic species

The change between censuses in the number of seedlings of species i in subplots where seeds of species i were sown (CN_i) was calculated for each of the eight species, for both of the intervals between censuses, with the following equation:

$$CN_i = SN_{ib} - SN_{ia}$$

where SN_{ib} is the adjusted number of seedlings of species i that were present in the later census (from the first equation), and SN_{ia} is the adjusted number of seedlings of species i that were present in the earlier census, in subplots where seeds of species i were sown (from the first equation).

Statistical Analysis

Mean seedling numbers were calculated from SN_i and CN_i values for the eight

plots per treatment. Treatment effects were assessed statistically by analysis of variance

(ANOVA) for a randomized block design (Ramsey and Schafer 1994), using the

statistical software Statgraphics 5.0. Treatment means were compared by Fisher's

protected least significant difference (LSD) procedure at P=0.05, as recommended by

Ramsey and Schafer (1994) for planned comparisons.

Where necessary, the data were transformed to meet the assumptions of analysis

of variance (natural log and square-root transformations). For ease of interpretation,

means reported in the tables and figures were calculated on the basis of untransformed

data.

RESULTS

Treatment Effects on Seedling Establishment

Annual Exotic Grass Site

Treatment B effects

By the May census, five of the eight species tested had significantly higher

seedling densities in treatment B than in treatment NM (H_1) (Table 2.3). These five

species included all four of the native species tested. *Festuca idahoensis*, *Elymus*

glaucus, *Madia gracilis*, and *Eriophyllum lanatum* had between 230% to 450% higher

Table 2.3. Annual Exotic Grass site: Average seedling numbers in three censuses of subplots sown with 100 seeds in four treatment types, the F-ratio and the probability (p-value) of a more extreme F-ratio. Treatments include: B = burned, -L = clipped and raked to remove litter, B+L = burned with litter added, and NM = no manipulation. All means shown are for untransformed data. Transformations were applied as necessary before analysis of variance (LOG = natural log transformation, and SQRT = square-root transformation). Treatments sharing superscripts were statistically indistinguishable (α=0.05).

Table 2.3

May 1996

Species	Treatment				F-ratio	p-value
	B	-L	B+L	NM		
Elymus glaucus	22.5a	13.5ab	11.4b	5.8b	4.27	0.017
Eriophyllum lanatum	17.0a	7.8b	8.0b	3.1b	8.22	0.001
Festuca idahoensis	31.8a	15.0b	10.5b	9.6b	4.87	0.010
Madia elegans	36.0a	31.1a	10.4b	10.5b	8.54	<0.001
Total native species (LOG)	107.3a	67.4b	40.3c	29.0c	20.55	<0.001
Centaurea cyanus	36.9a	17.8b	18.8b	4.6c	14.68	<0.001
Dactylis glomerata	2.4	5.1	2.4	2.3	0.66	0.589
Daucus carota	20.5	13.3	8.9	13.3	2.59	0.080
Taeniatherum caput-medusae	24.8	25.7	12.1	9.0	1.52	0.238
Total exotic species	84.6a	61.9ab	42.2bc	29.1c	8.98	<0.001

March 1996

Species	Treatment				F-ratio	p-value
	B	-L	B+L	NM		
Elymus glaucus (LOG)	18.3a	14.4a	10.3ab	6.3b	3.84	0.025
Eriophyllum lanatum (SQRT)	18.6a	8.6b	8.5b	2.6c	10.17	<0.001
Festuca idahoensis	26.5a	14.4b	7.1b	6.6b	9.35	<0.001
Madia elegans	35.0a	36.9a	11.9b	11.2b	11.80	<0.001
Total native species (LOG)	98.4a	74.3a	37.8b	26.7c	31.91	<0.001
Centaurea cyanus	31.4a	19.9b	14.8b	4.4c	12.42	<0.001
Dactylis glomerata	4.1	8.6	4.4	4.8	1.46	0.253
Daucus carota	11.1	9.8	6.2	8.1	1.37	0.278
Taeniatherum caput-medusae	25.8a	31.1a	10.2b	6.4b	5.82	0.005
Total exotic species	72.3a	69.4a	35.6b	23.6b	14.41	<0.001

December 1995

Species	Treatment				F-ratio	p-value
	B	-L	B+L	NM		
Elymus glaucus	26.0	23.3	29.1	19.1	0.89	0.465
Eriophyllum lanatum (LOG)	2.8a	1.0b	2.0ab	0.5b	3.62	0.030
Festuca idahoensis	24.3	17.6	11.5	14.0	1.90	0.161
Madia elegans	36.0	42.6	45.6	27.7	3.10	0.050
Total native species	89.2	84.5	82.5	61.4	2.40	0.097
Centaurea cyanus	31.0	34.3	43.4	27.1	2.97	0.057
Dactylis glomerata	3.0	9.5	2.3	8.8	1.91	0.159
Daucus carota	12.0a	15.0a	6.1b	14.4a	7.66	0.001
Taeniatherum caput-medusae	36.1	42.0	41.0	29.5	2.30	0.107
Total exotic species	82.1	100.8	87.3	79.7	1.67	0.203

seedling densities in treatment B than in treatment NM. The largest difference between treatments B and NM occurred with the exotic forb, *Centaurea cyanus*, which averaged over 700% more seedlings in treatment B.

Seedling densities of the remaining species tested (all exotics) did not differ significantly between treatments B and NM. However, every species tested had higher seedling densities in treatment B than in treatment NM (Table 2.4).

The native species as a group had significantly higher (370%) seedling densities in treatment B than in treatment NM. Likewise, even though only *Centaurea cyanus* had a significant treatment B effect, the exotic species as a group also had significantly higher (290%) collective seedling densities in treatment B than in treatment NM.

Treatment -L effects

Seedling densities of two of the eight species tested, *Madia elegans*, and *Centaurea cyanus* were significantly higher in treatment -L than in treatment NM (H_2) (Table 2.3). *Madia elegans*, a native annual forb, averaged 196% more seedlings in treatments -L than in NM, while seedling densities of *Centaurea cyanus*, an exotic annual forb, averaged 287% higher in treatment-L than in NM. Although seedling densities of the other six species tested did not significantly differ between these two treatments, all eight species had higher average seedling densities in treatment -L than in treatment NM (Table 2.4).

As a group, the native species had significantly greater seedling numbers in treatment -L than in treatment NM. However, this effect was largely due to the

Table 2.4. Summary of planned comparisons of seedling establishment (May census results) and hypothesis tests in three study sites. Treatments include: B = burned, -L = clipped and raked to remove litter, B+L = burned with litter added, and NM = no manipulation. The symbols > and < represent higher and lower, respectively, seedling density averages in the treatment to the left in the top of the column. Double symbols represent statistically significant differences (α = 0.5). A dash (—) means that the comparison was not planned in the absence of statistically significant differences in the first two columns. The hypotheses are described in Table 2.2. Results supporting hypotheses are represented with a "**yes**" while unsupported hypotheses are represented with a "no".

Annual Exotic Grass Site

Species	Planned Comparisons					Supports Hypothesis?			
	B v. NM	-L v. NM	B v. -L	B+L v. NM	B v. B+L	H_1	H_2	H_3	H_4
Elymus glaucus	>>	>	>	>	>>	**yes**	no	no	no
Eriophyllum lanatum	>>	>	>>	>	>>	**yes**	no	no	no
Festuca idahoensis	>>	>	>>	>	>>	**yes**	no	no	no
Madia elegans	>>	>>	>	<	>>	**yes**	**yes**	**yes**	no
Total native species	>>	>>	>>	>	>>	**yes**	**yes**	no	no
Centaurea cyanus	>>	>>	>>	>>	>>	**yes**	**yes**	no	no
Dactylis glomerata	>	>	—	—	—	no	no	no	no
Daucus carota	>	>	—	—	—	no	no	no	no
Taenitherum caput-medusae	>	>	—	—	—	no	no	no	no
Total exotic species	>>	>>	>	>	>>	**yes**	**yes**	**yes**	**no**

Table 2.4, continued.

Perennial Exotic Grass Site

Species	Planned Comparisons					Supports Hypothesis?			
	B v. NM	-L v. NM	B v. -L	B+L v. NM	B v. B+L	H_1	H_2	H_3	H_4
Elymus glaucus	>>	>>	>	<	>>	**yes**	**yes**	**yes**	no
Eriophyllum lanatum	>	<	—	—	—	no	no	no	no
Festuca rubra	>>	>>	<	<	>>	**yes**	**yes**	**yes**	no
Potentilla gracilis	>>	>>	<	>	>>	**yes**	**yes**	**yes**	no
Total natives	>>	>>	>	<	>>	**yes**	**yes**	**yes**	no
Arrhenatherum elatius	<	<	—	—	—	no	no	no	no
Hypochaeris radicata	>>	>>	>	>	>	**yes**	**yes**	**yes**	**yes**
Plantago lanceolata	>	>	—	—	—	no	no	no	no
Total exotics	>>	>	>	>>	>	**yes**	no	no	no

Native Bunchgrass Site

Species	Planned Comparisons					Supports Hypothesis?			
	B v. NM	-L v. NM	B v. -L	B+L v. NM	B v. B+L	H_1	H_2	H_3	H_4
Elymus glaucus	>	>	—	—	—	no	no	no	no
Eriophyllum lanatum	>	<	—	—	—	no	no	no	no
Festuca idahoensis	>	>	—	—	—	no	no	no	no
Madia gracilis	<	>	—	—	—	no	no	no	no
Total natives	>	>	—	—	—	no	no	no	no
Chrysanthemum leucanthemum	>	<	—	—	—	no	no	no	no
Dactylis glomerata	>	>	—	—	—	no	no	no	no
Daucus carota	>>	>	>	<	>>	**yes**	no	no	no
Taeniatherum caput-medusae	>>	>	>>	<	>>	**yes**	no	no	no
Total exotics	>>	>	>	<	>>	**yes**	no	no	no

substantial contribution of *Madia elegans* (Table 2.3). The exotic species also had

significantly higher seedling densities in treatment -L. But, like the natives, this

difference can be attributed to one species, *Centaurea cyanus* (Table 2.3).

<u>Litter removal as a burn effect</u>

Litter removal was at least a partial explanation for the observed burn (treatment

B) effect on seedling densities of *Elymus glaucus, Festuca idahoensis, Madia elegans,*

Eriophyllum lanatum, and *Centaurea cyanus.* I could not evaluate the role of litter

removal by burning on the seedling densities of *Dactylis glomerata, Daucus carota,* or

Taeniatherum caput-medusae, because neither burning (treatment B) nor litter removal

(treatment -L) had a significant effect relative to unmanipulated plots (treatment NM).

The seedling response of the native forb, *Madia elegans,* to treatment B appeared

to be caused entirely by litter removal (H_3) (Table 2.4). *Madia* seedling densities in

treatments where litter had been removed (B and -L) were significantly higher than

where the litter remained intact (NM). There was also no significant difference between

seedling densities in treatments with similar litter presence (B+L and NM) or absence (B

and -L) even though one treatment in each pair had been burned.

Litter removal was an important component of the treatment B effect on the

establishment of the native grass, *Elymus glaucus,* but the treatment B effect is not

completely explained by litter removal. Seedling densities where litter had been

removed (treatments B and -L) or was present (B+L and NM) were not significantly

different from each other, indicating that litter removal was a significant component of

the burn effect. However, seedling densities in treatment B, but *not* treatment -L, were significantly higher than seedling densities in treatment NM, suggesting that litter removal alone cannot account for the entire burn effect. In addition, although there were no significant differences between treatments B+L and NM, the average *Elymus* seedling density in treatment B+L was nearly twice that of treatment NM (Table 2.3). This difference also suggests that litter removal may only be a part of the entire burn effect.

Litter removal was a partial but limited explanation for the significant treatment B effect on the exotic forb, *Centaurea cyanus*. Although both treatments where litter had been removed (B and -L) had significantly higher seedling densities than unmanipulated plots (treatment NM), seedling densities in treatment B were significantly higher than those in treatment -L. Also, seedling densities treatment B+L were significantly higher than those in treatment NM, even though the two treatments had similar litter levels. These results suggest that litter removal is an important component of a portion of the burn (treatment B) effect, but other, non-litter factors contributed to the overall burn effect.

The native grass, *Festuca idahoensis,* and the native forb, *Eriophyllum lanatum*, responded similarly to treatments. For these two species, the relationship between burning (treatment B) and litter removal was unclear. Only treatment B had significantly different (higher) seedling densities from unmanipulated plots (treatment NM) (Table 2.3).

For the native species as a group, litter removal was a partial but incomplete explanation for the seedling response of the treatment B effects. Even though both

treatments where litter had been removed (B and -L) had significantly higher seedling densities than unmanipulated plots (treatment NM), native seedling densities in treatment B were significantly higher than those in treatment -L, indicating that litter removal cannot account for the entire treatment B effect. In addition, there was no significant difference between treatments B+L and NM, indicating that burning without the effect of litter removal does not significantly promote native seedlings.

For the exotic species as a group, the seedling response to treatment B appeared to depend on the removal of litter. (Even though certain exotic species could not be evaluated individually, all four exotic species were included in the group analysis.) There was no significant difference between seedling densities in treatments with similar litter presence (B+L and NM) or absence (B and -L) even though one treatment in each pair had been burned, and both treatments B and -L significantly promoted seedling densities over treatment NM. These results show that litter removal is sufficient to explain the effects of burning on seedling establishment.

Non-litter burn effects

All individuals or groups (native or exotic) of species with significant treatment B effects had significantly higher seedling densities in treatment B than in treatment B+L (Table 2.3), indicating that non-litter burn effects were not a sufficient explanation of burning effects on seedling establishment (H_4). However, in the cases where litter removal was a partial or incomplete explanation of the treatment B effects on seedling

densities, intuitively, the remaining "unexplained" treatment B effect can be attributed to burn effects that are independent of litter removal.

Exotic Perennial Grass Site

<u>Treatment B effects</u>

Four of the seven species tested had significantly higher seedling densities in the May census in treatment B than in treatment NM in the May census (H_1). Of these four, three were native species, and one was an exotic species. The natives, *Potentilla gracilis*, *Festuca rubra* and *Elymus glaucus* averaged between 220% and 350% higher seedling densities in treatment B than in treatment NM. The exotic forb, *Hypochaeris radicata*, averaged 575% higher seedling densities in treatment B than in treatment NM.

Seedling densities of the remaining species tested did not differ significantly between treatments B and NM. However, seedling densities of the native forb, *Eriophyllum lanatum*, and the exotic forb, *Plantago lanceolata*, averaged higher in treatment B than in treatment NM (Table 2.5). In fact, only one of the eight species tested (the exotic grass, *Arrhenatherum elatius*) had lower average seedling densities in treatment B than in treatment NM (Table 2.4).

Collectively, the native species had significantly higher seedling densities in treatment B than in NM. The exotic species also had significantly higher collective seedling densities in treatment B than in treatment NM, but this difference was largely due to the substantial contribution of *Hypochaeris radicata* (Table 2.5).

Table 2.5. Perennial Exotic Grass site: Average seedling numbers in three censuses of subplots sown with 100 seeds in four treatment types, the F-ratio and the probability (p-value) of a more extreme F-ratio. Treatments include: B = burned, -L = clipped and raked to remove litter, B+L = burned with litter added, and NM = no manipulation. All means shown are for untransformed data. Transformations were applied as necessary before analysis of variance (LOG = natural log transformation, and SQRT = square-root transformation). Treatments sharing superscripts were statistically indistinguishable (α=0.05).

Table 2.5

May

Species	Treatment				F-ratio	p-value
	B	-L	B+L	NM		
Elymus glaucus	39.9a	31.1a	5.3b	8.9b	18.76	<0.001
Eriophyllum lanatum	10.9a	5.0a	4.8a	6.0a	1.03	0.400
Festuca rubra	64.8a	65.6a	12.6b	19.1b	17.79	<0.001
Potentilla gracilis	14.6a	15.0a	6.5b	4.5b	5.04	<0.009
Total native species	130.1a	116.8a	38.5b	29.1b	25.72	<0.001
Arrhenatherum elatius	7.1a	5.3a	22.2b	9.4a	3.38	0.037
Hypochaeris radicata (LOG)	23.0a	12.8a	6.6ab	3.4b	5.13	0.008
Plantago lanceolata (SQRT)	29.0	20.3	15.9	10.3	2.95	0.057
Total exotic species	59.1a	38.3ab	44.7a	23.1b	4.37	0.015

March

Species	Treatment				F-ratio	p-value
	B	-L	B+L	NM		
Elymus glaucus	37.0a	34.9a	8.5b	10.5b	14.61	<0.001
Eriophyllum lanatum	12.5	5.0	7.0	5.6	1.18	0.340
Festuca rubra	54.0a	47.9a	7.8b	20.3b	25.24	<0.001
Potentilla gracilis	9.8	10.5	6.1	2.9	1.73	<0.193
Total native species	113.3a	98.3a	29.4b	39.3b	18.83	<0.001
Arrhenatherum elatius	7.3a	8.9a	22.8b	10.3a	3.50	<0.034
Hypochaeris radicata	19.4a	14.3a	3.9b	3.2b	9.79	<0.001
Plantago lanceolata	23.1a	15.2	11.0b	6.1b	4.60	<0.013
Total exotic species	49.8a	38.4a	37.7a	19.6b	5.24	0.007

December

Species	Treatment				F-ratio	p-value
	B	-L	B+L	NM		
Elymus glaucus	38.8a	32.8ab	11.8c	27.3b	9.92	<0.001
Eriophyllum lanatum (LOG)	8.8a	0.4b	2.8b	0.5b	6.29	0.003
Festuca rubra	48.3	51.5	28.4	39.8	1.99	0.146
Potentilla gracilis	0.0	0.0	0.0	0.0	—	—
Total native species	95.8a	84.6ab	42.9c	67.5b	8.48	<0.001
Arrhenatherum elatius	9.2a	9.8ab	28.8c	22.5bc	4.81	0.011
Hypochaeris radicata (LOG)	20.3a	11.1a	0.3b	1.5b	12.02	<0.001
Plantago lanceolata (SQRT)	7.8a	4.4ab	1.8bc	1.0c	7.47	0.001
Total exotic species	37.2	25.3	30.8	24.9	5.24	0.344

<u>Treatment -L effects</u>

Seedling densities of four of the seven species tested were significantly higher in treatment -L than in treatment NM (H$_2$). Three of these four species, *Potentilla gracilis*, *Festuca rubra*, and *Elymus glaucus*, were native species and averaged between 230% and 350% higher seedling densities in treatment -L than in treatment NM. Of the three exotic species tested, only *Hypochaeris radicata* had significantly higher (275%) seedling densities in treatment -L than in NM.

Seedling densities of the remaining species tested did not differ significantly between treatments -L and NM. However, the exotic forb, *Plantago lanceolata*, averaged approximately 100% higher seedling densities in treatment -L than in treatment NM (Table 2.5). Both the native forb, *Eriophyllum lanatum*, and the exotic grass, *Arrhenatherum elatius,* had lower average seedling densities in treatment -L than in treatment NM.

As a group, the native species had significantly higher seedling densities in treatment -L than NM. On the other hand, seedling densities of the exotic species as a group had no significant difference between treatments -L and NM.

<u>Litter removal as a burn effect</u>

Litter removal was a sufficient explanation of the burn (treatment B) effect on seedling densities of *Elymus glaucus, Festuca rubra, Hypochaeris radicata, and Potentilla gracilis* (H$_3$). I could not evaluate the role of litter removal by burning on the

seedling densities of *Arrhenatherum elatius*, *Eriophyllum lanatum* or *Plantago lanceolata* because neither burning (treatment B) nor litter removal (treatment -L) had a significant effect relative to unmanipulated plots (treatment NM) for these individual species.

The seedling response of the natives, *Festuca rubra*, *Elymus glaucus*, *Potentilla gracilis*, native species as a group, and the exotic, *Hypochaeris radicata*, to treatment B appeared to be dependent on the removal of litter (H_3). Seedling densities in treatments where litter had been removed (B and -L) were significantly higher than where the litter had remained intact (NM). There was also no significant difference between seedling densities in treatments with similar litter presence (B+L and NM) or absence (B and -L) even though one treatment in each pair had been burned. The relationship between litter removal and treatment B for the exotic forb, *Hypochaeris radicata*, was somewhat weaker than those of the three native species. Although there was no significant difference between *Hypochaeris* seedling densities in treatments B and -L, they were 80% higher in treatment B than in treatment -L, suggesting that there may be additional non-litter burn effects.

For the collective exotic species, litter removal was a partial explanation of the treatment B effect. (Even though certain exotic species could not be evaluated individually, all three exotic species were included in the group analysis.) Seedling densities did not differ significantly between treatments B , and -L. However, of these two treatments, only treatment B had significantly more seedlings than treatment NM, indicating that litter removal, by itelf, is not a sufficient explanation of the burn effect.

Non-litter burn effects

Only one of the seven species tested, the exotic forb *Hypochaeris radicata*, was significantly affected by treatment B effects which were independent of litter removal (H_4). Although litter removal was an important component of the treatment B effect (see "Litter Removal as a Burn Effect" section), non-litter burn effects were also evident. There was no significant difference between *Hypochaeris* seedling densities in treatments B and B+L, indicating that non-litter burn effects made a significant contribution to the treatment B effect.

When evaluated as groups, non-litter burn effects were more important for the exotic species than for the native species. Exotic seedling densities in treatments B and B+L were not significantly different, and both were significantly higher than those of treatment NM. These results indicate that burn effects which were independent of litter removal were a significant component of the treatment B effect on the collective exotic species. In contrast, there was no evidence of a non-litter removal treatment B effect for the native species as a group. Besides having significantly higher seedling densities in treatment B than in treatment B+L, litter removal was a sufficient explanation of the overall burn effect (see "Litter Removal as a Burn Effect" section).

Native Bunchgrass Site

Treatment B effects

In contrast to the other sites, only two of the eight Native Bunchgrass site species tested had significantly higher seedling densities in treatment B than in treatment NM by the May census (H_1) (Table 2.4). These two species, *Taeniatherum caput-medusae* and *Daucus carota* (both exotics) had 262% and 99%, respectively, more seedlings per subplot in treatment B than in treatment NM. Seedling densities of the remaining species did not differ significantly between treatments B and NM.

Although not significant, three of the four native species, *Elymus glaucus*, *Festuca idahoensis* and *Eriophyllum lanatum*, averaged between 30% and 130% higher seedling densities in treatment B than in treatment NM. The fourth native species, *Madia gracilis*, averaged 67% fewer seedlings in treatment B than in treatment NM. The other two exotic species tested, *Dactylis glomerata* and *Chrysanthemum leucanthemum* had similar average seedling densities in treatments B and NM (Table 2.6).

For the native species as a group, there was no significant difference in native seedling densities in treatment B than in treatment NM. However, there were, on average, 22% more native seedlings in treatment B. On the other hand, for the exotic species as a group, there were significantly more exotic seedlings in treatment B than in treatment NM.

Table 2.6. Native Bunchgrass site: Average seedling numbers in three censuses of subplots sown with 100 seeds in four treatment types, the F-ratio and the probability (p-value) of a more extreme F-ratio. Treatments include: B = burned, -L = clipped and raked to remove litter, B+L = burned with litter added, and NM = no manipulation. All means shown are for untransformed data. Transformations were applied as necessary before analysis of variance (LOG = natural log transformation). Treatments sharing superscripts were statistically indistinguishable (α=0.05).

Table 2.6

May

Species	B	-L	B+L	NM	F-ratio	p-value
Elymus glaucus	17.0	20.1	6.1	13.1	2.47	0.090
Eriophyllum lanatum	22.9	9.7	12.5	9.9	0.64	0.598
Festuca idahoensis	20.7	12.0	3.5	11.1	2.82	0.064
Madia gracilis	18.3a	45.3b	23.4a	30.6ab	3.13	0.048
Total native species	78.8a	87.0a	45.4b	64.7ab	3.09	0.049
Chrysanthemum leucanthemum	26.8	23.6	8.0	26.5	1.41	0.269
Dactylis glomerata	3.8	7.2	3.8	2.8	0.84	0.487
Daucus carota	23.9a	18.4ab	8.5b	12.0b	4.07	0.020
Taeniatherum caput-medusae	49.6a	22.8b	6.5c	13.7bc	17.85	<0.001
Total exotic species	104.1a	71.9ab	26.8c	54.9bc	7.01	0.002

March

Species	B	-L	B+L	NM	F-ratio	p-value
Elymus glaucus	17.4a	15.0a	2.9b	11.8a	4.67	0.012
Eriophyllum lanatum	20.9	13.3	11.4	11.4	0.80	0.506
Festuca idahoensis	20.3a	13.7a	2.5b	6.0b	9.93	<0.001
Madia gracilis	19.8a	53.1c	28.4ab	40.9bc	5.16	0.008
Total native species	78.3ab	95.0a	45.1c	63.3bc	3.98	0.022
Chrysanthemum leucanthemum	21.5a	22.9a	4.1b	24.7a	3.40	0.037
Dactylis glomerata	3.8a	10.3b	2.3a	3.4a	3.43	0.037
Daucus carota	15.8a	12.0ab	4.6c	7.8bc	8.84	<0.001
Taeniatherum caput-medusae	38.7a	26.9b	5.1c	14.2c	18.49	<0.001
Total exotic species	79.7a	72.0ab	15.9c	50.1b	10.97	<0.001

December

Species	B	-L	B+L	NM	F-ratio	p-value
Elymus glaucus	18.6	27.6	21.3	37.8	3.02	0.053
Eriophyllum lanatum (LOG)	4.5	1.6	0.6	0.2	1.78	0.182
Festuca idahoensis	20.1	17.0	12.3	21.8	0.76	0.530
Madia gracilis	17.8a	60.0b	70.0b	65.8b	11.85	<0.001
Total native species	61.0a	106.2b	104.1b	125.5b	7.42	0.001
Chrysanthemum leucanthemum	19.0	26.8	28.3	29.2	0.41	0.749
Dactylis glomerata	4.7	12.0	7.4	5.4	1.01	0.409
Daucus carota	12.8a	12.3a	1.8b	12.5a	13.03	<0.001
Taeniatherum caput-medusae	44.8a	42.4a	38.6ab	23.9a	3.36	0.038
Total exotic species	81.3	93.6	61.3	85.7	1.58	0.224

Treatment -L effects

No species tested had significantly different seedling densities between treatments -L and NM (H_2). However, for six of the eight species, average seedling densities in treatment -L were higher than those in treatment NM (Table 2.4).

For the native species as a group, seedling densities were not significantly different between treatments -L and NM. However, average native seedling densities were 34% higher in treatment -L than in treatment NM. Likewise, seedling densities of the exotic species as a group did not differ significantly between treatments -L and NM, but on average there were 31% more exotic seedlings in treatment -L than in treatment NM.

Litter removal as a burn effect

Although litter removal by itself (treatment -L) was not sufficient to cause significant differences in seedling establishment between treated and unmanipulated plots (treatment NM) (H_3), litter removal was at least a partial explanation for the observed burn (treatment B) effect on *Daucus carota* and *Taeniatherum caput-medusae* seedling densities. I could not evaluate the role of litter removal by burning on the seedling densities for *Chrysanthemum leucanthemum*, *Dactylis glomerata*, *Elymus glaucus*, *Eriophyllum lanatum*, *Festuca idahoensis*, or *Madia gracilis* because neither burning (treatment B) nor litter removal (treatment -L) had a significant effect relative to unmanipulated plots (treatment NM).

For the exotic forb, *Daucus carota*, litter removal was an important but not complete explanation of the significant treatment B effects on *Daucus* seedling densities. Seedling densities in treatments where litter had been removed (B and -L) or was present (B+L and NM) were not significantly different from each other, indicating that litter removal was a significant component of the burn (treatment B) effect. However, seedling densities in treatment B, but *not* in treatment -L, were significantly higher than seedling densities in treatment NM, suggesting that litter removal alone cannot account for the entire treatment B effect.

For *Taeniatherum caput-medusae*, the relationship between burning (treatment B) and litter removal was unclear. Only treatment B had significantly different (higher) seedling densities from unmanipulated plots (treatment NM). Litter removal by itself was not sufficient to cause significant differences in seedling establishment between treated and unmanipulated plots.

Although litter removal could not be evaluated for three of the four individual exotic species, when the exotic species were evaluated collectively, litter removal was an important component of the significant treatment B effect. There was no significant difference between seedling densities in treatments with similar litter presence (B+L and NM) or absence (B and -L) even though one treatment in each pair had been burned. However, the exotic seedling densities in treatment B, but *not* in treatment -L, were significantly higher than seedling densities in treatment NM. This result suggests that litter removal can only be a partial explanation of the treatment B effect.

I could not evaluate the role of litter removal by burning on the native seedling densities as a group because neither burning (treatment B) nor manual litter removal (treatment -L) had a significant effect relative to unmanipulated plots (treatment NM).

Non-litter burn effects

No species or group (native or exotic) of species was significantly affected *primarily* by a burn effect that was independent of litter removal (H_4). Individuals or groups of species with treatment B effects had significantly higher seedling densities in treatment B than in treatment B+L (Table 2.4), indicating that a non-litter burn effect was not a sufficient explanation of the treatment B effect. However, in the cases where litter removal was a partial or incomplete explanation of the treatment B effects on seedling densities, the remaining "unexplained" treatment B effects can be attributed to "other" burn effects that are independent of litter removal.

Seedling Population Dynamics

Annual Exotic Grass Site

Centaurea cyanus

Most seedling emergence for *Centaurea cyanus* occurred in the fall prior to the December census (Figure 2.1). Initial (December) average seedling densities were similar for each treatment (Figure 2.1). The significant treatment effects on seedling
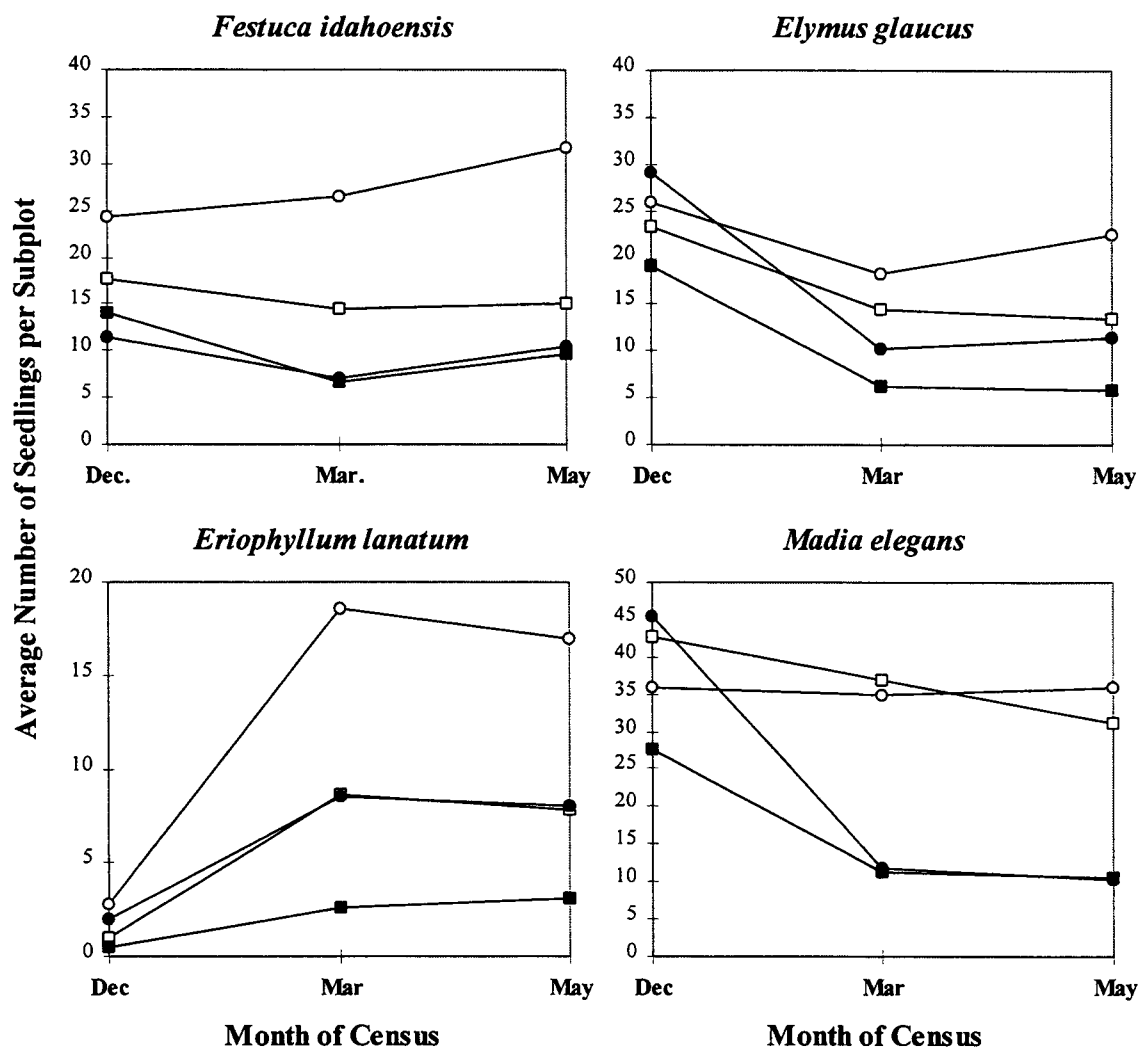
Figure 2.1. Annual Exotic Grass Site, native species. Changes in the average number of seedlings present (#seedlings/subplot) in four treatments between censuses. Three censuses were conducted over the growing season: December 1995, March 1996 and May 1996. Each subplot had been planted with 100 seeds of the respective species. The four treatments included: O = burned, □ = clipped and raked to remove litter, ● = burned with litter added, ■ = no manipulation.

establishment were partially due to significantly greater decreases in seedling densities during the winter interval in treatments -L, B+L and NM than in treatment B.

Dactylis glomerata

Although very few *Dactylis glomerata* seedlings were counted in any census, the majority of *Dactylis* seedling emergence appeared to have occurred by the time of the December census (Figure 2.1). *Dactylis glomerata*'s seedling populations dynamics were not significantly affected by treatments (Tables 2.3, 2.7).

Daucus carota

Most *Daucus carota* seedlings emergence appeared to occur both in the fall and during the spring interval (Figure 2.1). Treatment effects were evident during the winter interval, with significantly less seedling density decrease in treatments B and B+L than in treatment NM (Table 2.7).

Elymus glaucus

The majority of *Elymus glaucus* seedling emergence appeared to have occurred by the time of the December census (Figure 2.2). During the winter interval, seeding densities decreased in every treatment. Although these winter decreases did not differ significantly among treatments, the greater decreases in the treatments with litter (NM and B+L) (Figure 2.2) contributed to the significant treatment differences in seedling establishment.

Table 2.7. Annual Exotic Grass Site: Average change in seedling counts during two intervals in subplots sown with 100 seeds in four treatment types, the F-ratio and the probability (p-value) of a more extreme F-ratio. Treatments include: B = burned, -L = clipped and raked to remove litter, B+L = burned with litter added, and NM = no manipulation. All means shown are for untransformed data. Transformations were applied as necessary before analysis of variance (LOG = natural log transformation). Treatments sharing superscripts were statistically indistinguishable (α=0.05).

Winter Interval

Species	Treatment B	-L	B+L	NM	F-ratio	p-value
Centaurea cyanus	0.4a	-14.3b	-23.1b	-22.7b	8.73	<0.001
Dactylis glomerata	1.1	-.9	2.1	-4.0	1.00	0.414
Daucus carota	-0.9ab	-5.2bc	0.2a	-6.3c	3.21	0.044
Elymus glaucus	-7.8	-8.9	-18.9	-12.9	1.94	0.154
Eriophyllum lanatum (LOG)	15.8a	7.6ab	6.5bc	2.1c	4.43	0.015
Festuca idahoensis	2.2	-3.3	-4.4	-7.4	1.99	0.147
Madia elegans	-1.0a	-5.6ab	-27.9c	-16.6bc	5.81	0.005
Taeniatherum caput-medusae	-10.3a	-10.9a	-30.8b	-23.1ab	3.49	0.034

Spring Interval

Species	Treatment B	-L	B+L	NM	F-ratio	p-value
Centaurea cyanus	5.5	-2.2	3.9	0.3	5.71	0.005
Dactylis glomerata	-1.7	-3.5	-2.0	-2.5	0.30	0.825
Daucus carota	9.4	3.5	2.7	5.2	2.04	0.139
Elymus glaucus	4.3	-0.9	1.1	-0.5	0.89	0.461
Eriophyllum lanatum	-1.6	-0.8	-0.5	0.5	0.71	0.558
Festuca idahoensis	5.3	0.6	3.4	3.0	0.48	0.699
Madia elegans	1.0	-5.8	-1.6	-0.7	2.03	0.141
Taeniatherum caput-medusae	-0.1	-6.7	2.3	1.8	1.70	0.198

Figure 2.2. Annual Exotic Grass Site, exotic species. Changes in the average number of seedlings present (#seedlings/subplot) in four treatments between censuses. Three censuses were conducted over the growing season: December 1995, March 1996 and May 1996. Each subplot had been planted with 100 seeds of the respective species. The four treatments included: O = burned, □ = clipped and raked to remove litter, ● = burned with litter added, ■ = no manipulation.

Eriophyllum lanatum

Although few *Eriophyllum* seedlings had emerged by the December census, there were significantly more December seedlings counted in burned (treatment B) than in unburned (-L and NM) plots (Table 2.3). Most *Eriophyllum lanatum* seedling emergence occurred during the winter interval (Figure 2.2). There were significantly greater winter increases in treatments without litter (B and -L) than in unmanipulated plots. These emergence differences contributed to the significant treatment effects observed in the May census.

Festuca idahoensis

The bulk of *Festuca idahoensis* seedling emergence appeared to be in the fall, although some new seedlings emerged in each census (Figure 2.2). Although there were no significant differences in either December census seedling densities or in winter or spring seedling density changes between censuses, there was a consistent trend which led to the significant treatment effects on *Festuca*'s seedling establishment: Seedling counts in burned (treatment B) plots had the highest December seedling counts, and continued to have the highest average seedling density increases of all treatments during the winter and spring intervals (Tables 2.3, 2.7).

Madia elegans

Most seedling emergence for *Madia elegans* occurred in the fall, and December seedling densities were very similar among treatments (Figure 2.2). The significant treatment effects on seedling establishment were due to higher seedling density decreases during the winter interval in treatments with litter (NM and B+L) (Figure 2.2). There was very little change during the spring interval, with average changes in seedling numbers within treatments ranging from -6 to 1 seedlings.

Taeniatherum caput-medusae

Most *Taeniatherum caput-medusae* seedlings appeared to have emerged by the time of the December census and these seedling densities were very similar among treatments (Figure 2.1). The significant treatment effects on March seedling densities were due to higher seedling density decreases during the winter interval in treatments with litter (NM and B+L). During the spring interval, there were no significant treatment effects on seedling density change, but small average increases in plots with litter (B+L and NM) and small decreases in plots without litter (B and -L) neutralized any significant treatment effects on seedling establishment.

Perennial Exotic Grass Site

Arrhenatherum elatius

Most or all of *Arrhenatherum elatius*'s seedling emergence appeared to have occurred in the fall prior to the December census (Figure 2.3). Treatment effects were first detected in the December census as there was significantly fewer *Arrhenatherum* seedlings counted in burned plots (treatment B) than in plots where litter was present (NM and B+L). Plots where litter had been clipped and raked (treatment -L) also had very low average December seedling counts as compared to those in treatment NM (Figure 2.3, Table 2.4), but variability was high enough that this difference was not significant. This initial treatment effect on seedling densities was transient. Although there were no significant differences among treatments, the winter seedling count decreases in unmanipulated plots averaged more than six to twelve times greater than the decreases in treatments without litter (B and -L) (Table 2.8), dissolving the significant treatment differences in seedling densities. Seedling densities changed very little during the spring interval.

Elymus glaucus

The majority of *Elymus glaucus* seedlings appeared to have emerged by the time of the December census (Figure 2.4). Treatment effects were first evident by the December census, as significantly more seedlings were counted in treatment B than in treatments NM or B+L. December seedling densities in treatment -L, were in between,
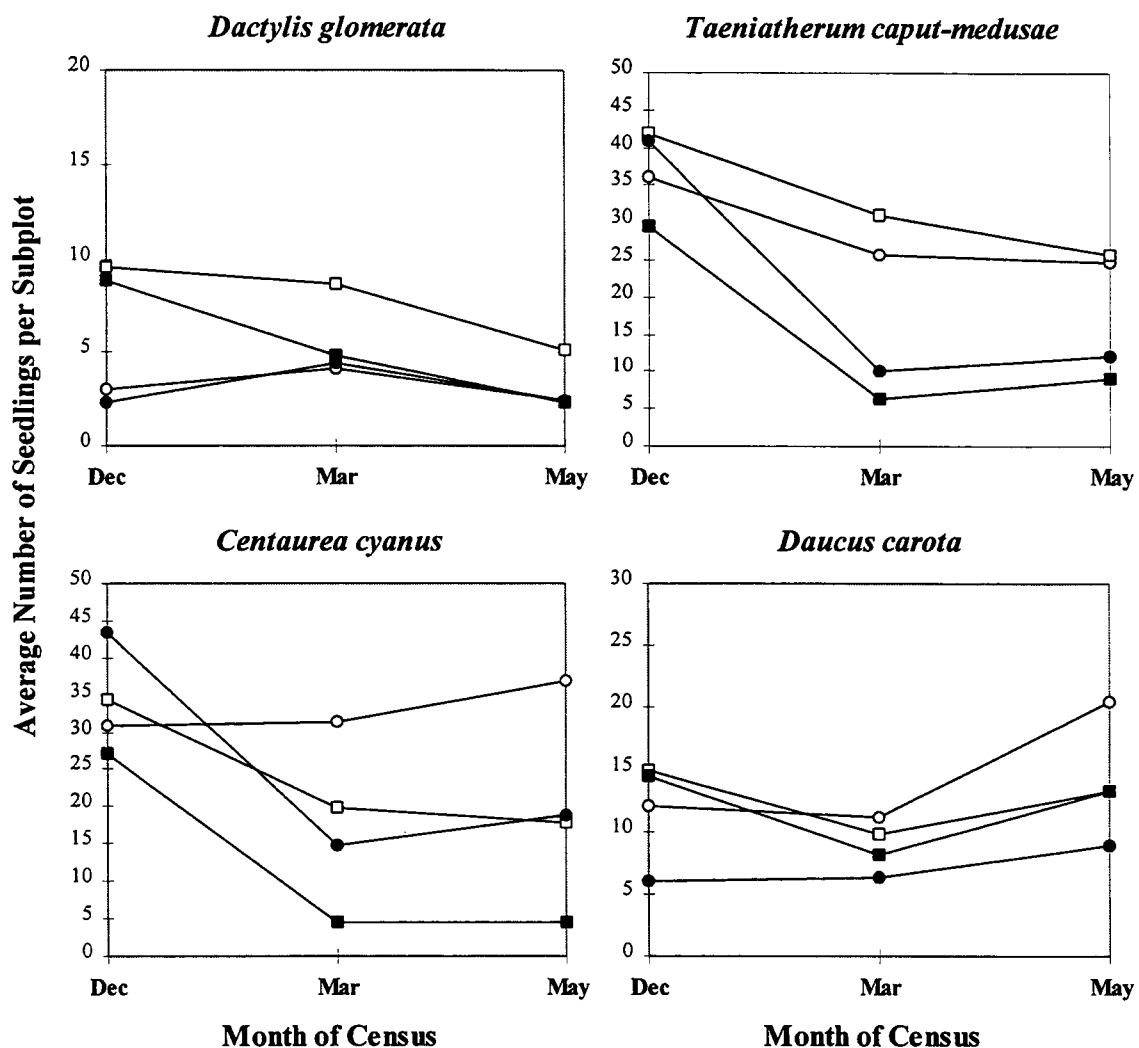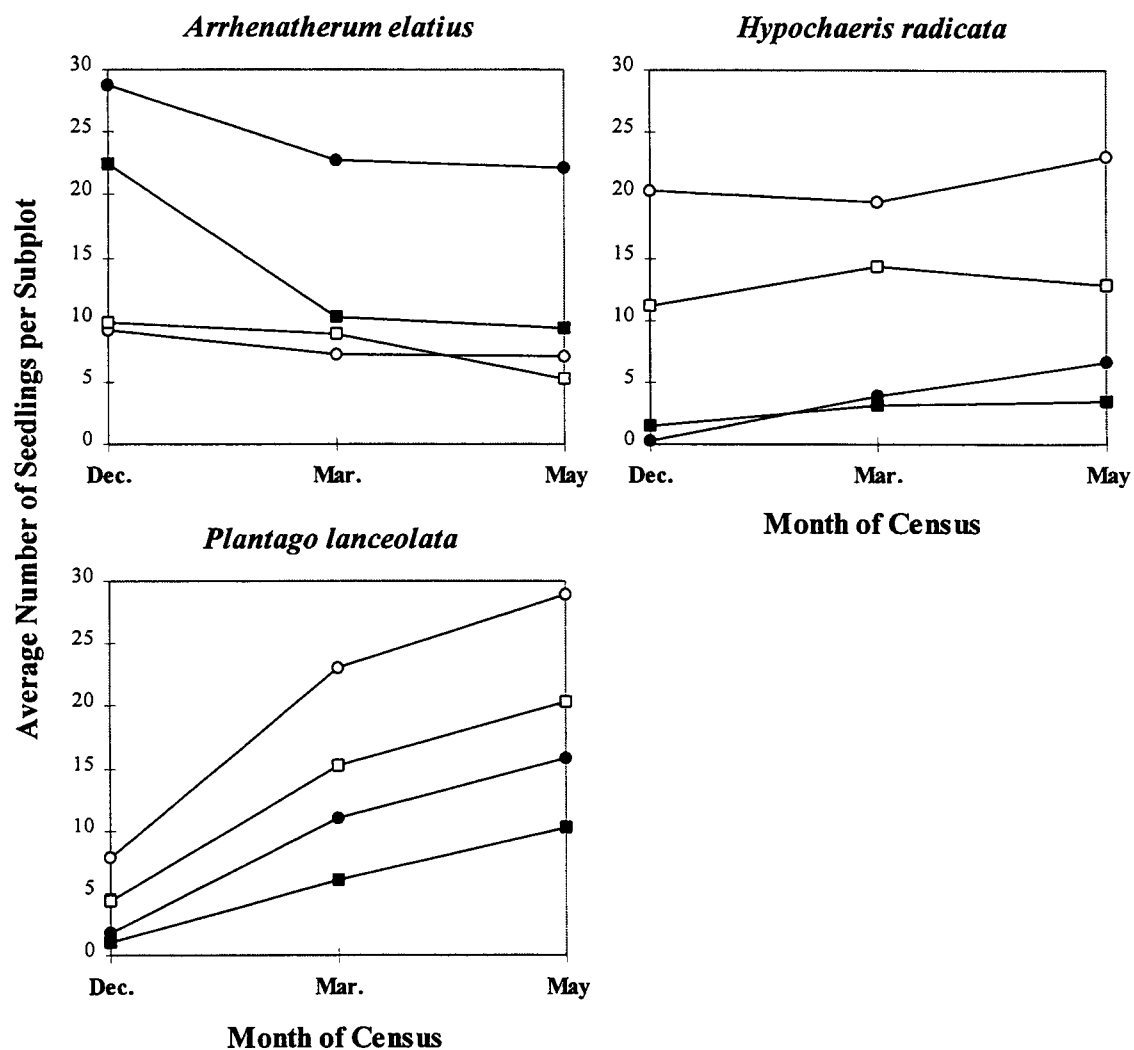
Figure 2.3. Perennial Exotic Grass Site, exotic species. Changes in the average number of seedlings present (#seedlings/subplot) in four treatments between censuses. Three censuses were conducted over the growing season: December 1995, March 1996 and May 1996. Each subplot had been planted with 100 seeds of the respective species. The four treatments included: O = burned, □ = clipped and raked to remove litter, ● = burned with litter added, ■ = no manipulation.

Table 2.8. Perennial Exotic Grass site: Average change in seedling counts during two intervals in subplots sown with 100 seeds in four treatment types, the F-ratio and the probability (p-value) of a more extreme F-ratio. Treatments include: B = burned, -L = clipped and raked to remove litter, B+L = burned with litter added, and NM = no manipulation. All means shown are for untransformed data. Transformations were applied as necessary before analysis of variance (LOG = natural log transformation). Treatments sharing superscripts were statistically indistinguishable (α=0.05).

Winter Interval

Species	Treatment B	-L	B+L	NM	F-ratio	p-value
Arrhenatherum elatius (LOG)	-1.9	-0.9	-5.9	-12.3	2.054	0.137
Elymus glaucus	-1.8a	2.1a	-3.3a	-16.8b	4.135	0.019
Eriophyllum lanatum	4.3	4.6	4.3	5.1	0.02	0.987
Festuca rubra	5.8a	-3.6a	-20.6b	-19.5b	6.484	0.003
Hypochaeris radicata (LOG)	-0.9	3.1	3.6	1.8	1.537	0.234
Plantago lanceolata (LOG)	15.4	10.9	9.3	5.1	0.452	0.719
Potentilla gracilis	9.8	10.5	6.1	2.6	1.86	0.193

Spring Interval

Species	Treatment B	-L	B+L	NM	F-ratio	p-value
Arrhenatherum elatius	-0.2	-3.6	-0.6	-0.8	0.68	0.573
Elymus glaucus	2.9	-3.8	-3.3	-1.6	0.83	0.492
Eriophyllum lanatum	-2.1	0.0	-2.1	0.4	1.27	0.310
Festuca rubra	10.8	17.8	4.9	-1.1	2.94	0.057
Hypochaeris radicata	3.6	-1.5	2.8	0.3	1.52	0.239
Plantago lanceolata	5.9	5.0	4.8	4.1	0.09	0.965
Potentilla gracilis	4.9	4.5	0.4	1.9	2.46	0.091

Figure 2.4. Perennial Exotic Grass Site, native species. Changes in the average number of seedlings present (#seedlings/subplot) in four treatments between censuses. Three censuses were conducted over the growing season: December 1995, March 1996 and May 1996. Each subplot had been planted with 100 seeds of the respective species. The four treatments included: O = burned, □ = clipped and raked to remove litter, ● = burned with litter added, ■ = no manipulation.

but not significantly different from either B or NM. Average changes during the winter interval were generally small (-3.3 to 2.1 seedlings), except for those in treatment NM, which averaged a 16.8 seedling decrease per subplot, significantly more seedling loss than in any other treatment. Seedling densities changed very little during the spring interval.

Eriophyllum lanatum

Few seedlings of *Eriophyllum lanatum* had emerged by the time of the December census, averaging between 0.2 and 4.9 seedlings per subplot. Nonetheless, December seedling densities were significantly higher on burned (treatment B) plots than in the other treatments. Seedling densities increased during the winter interval, with no significant differences in increase among treatments. There was very little change during the spring interval in any treatment. Although treatments had little effect on seedling density changes after the December census, the initial "headstart" in treatment B was largely maintained the remainder of the growing season (Figure 2.4). However, there was enough variability among treatments, that this difference was not significant in either the March or the May census.

Festuca rubra

The bulk of seedling emergence for *Festuca rubra* occurred prior to the December census, although some new seedlings emerged each census (Figure 2.4).

December seedling densities in treatments -L and B were higher but not significantly different from those in treatments NM and B+L. During the winter interval, there were significantly greater decreases in seedling densities in treatments with litter (B+L and NM) than in treatments without litter (B and -L) (Table 2.8). Seedling densities generally increased during the spring interval, and although there were no significant differences, the greatest increases occurred in treatments B and -L.

Hypochaeris radicata

Seedling emergence of *Hypochaeris radicata* appeared to occur primarily in the fall (Figure 2.3). December seedling densities were significantly higher in treatments without litter (B and -L) than in treatments with litter (B+L and NM). Average changes during the winter and spring intervals were relatively small (-1.5 to 3.6 seedlings) and uniform among treatments.

Plantago lanceolata

Seedlings of *Plantago lanceolata* emerged throughout the fall, winter and spring (Figure 2.3). By the time of the initial (December) census, there were significantly higher *Plantago* seedling densities in plots without litter (treatments B and -L) than in unmanipulated plots (NM). During the winter and spring intervals, there were no significant differences in seedling density increase among treatments. Nonetheless, seedling density increases were consistently highest in treatment B, followed by those in

treatment -L, and then B+L, with the smallest average increases in treatment NM (Table 2.8).

Potentilla gracilis

Most or all *Potentilla gracilis* seedling emergence appeared to have occurred after December, as no *Potentilla* seedlings were counted in the December census. The significant differences in seedling establishment were due to a diverging pattern of higher seedling count increases were higher in treatments without litter (B and -L), and lower increases in treatments with litter (B+L and NM) during both winter and spring intervals (Figure 2.4).

Native Bunchgrass Site

Chrysanthemum leucanthemum

Most *Chrysanthemum leucanthemum* seedling emergence had occurred by the December census (Figure 2.5). There were no significant differences in initial (December) seedling densities in planned comparisons. Changes in seedling densities were very small (-4.5 to 5.3 seedlings), except for the high (-24.1 seedlings) winter decreases in treatment B+L. However, in planned comparisons, there were no significant treatments effects on *Chrysanthemum* seedling population dynamics.
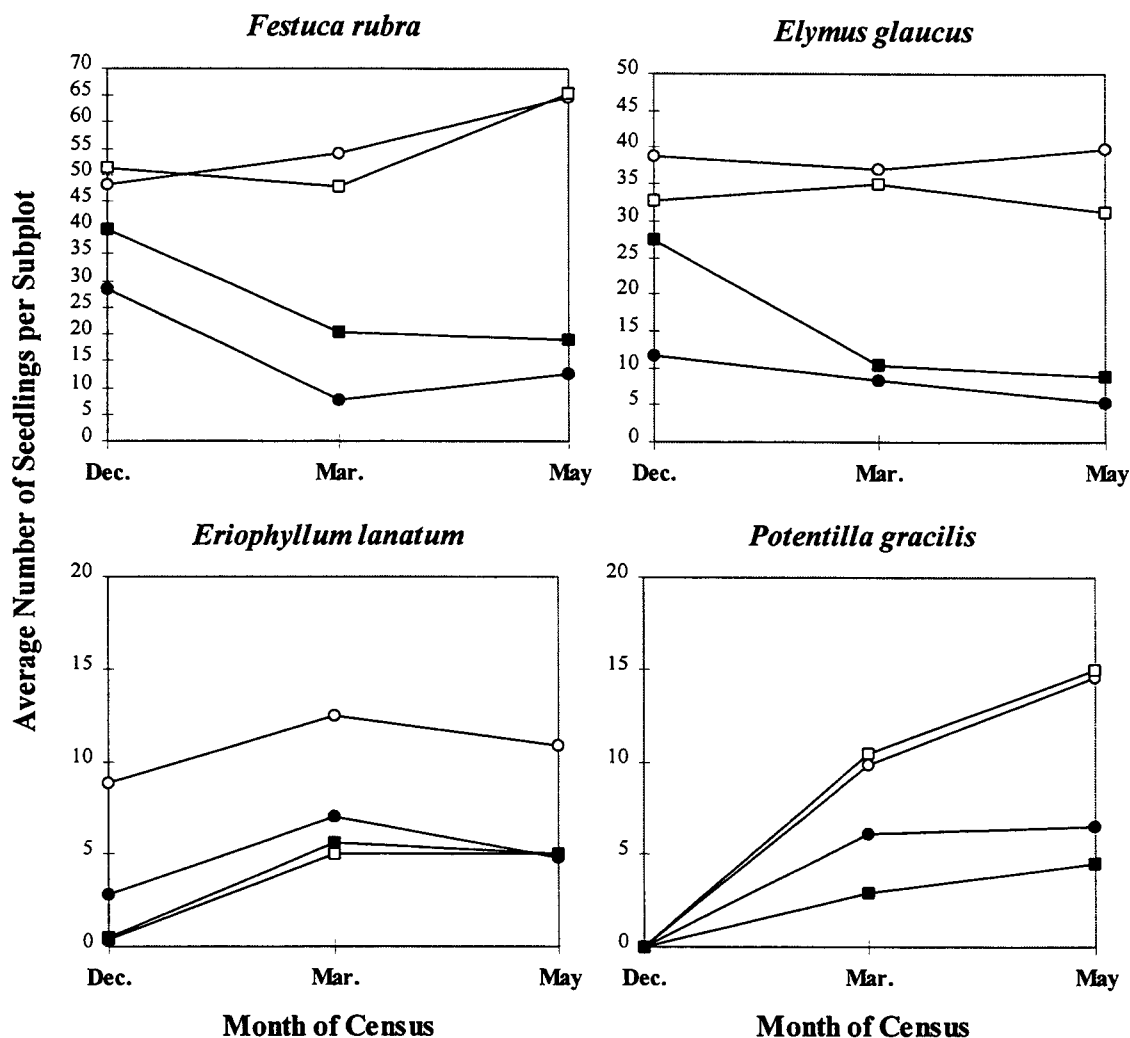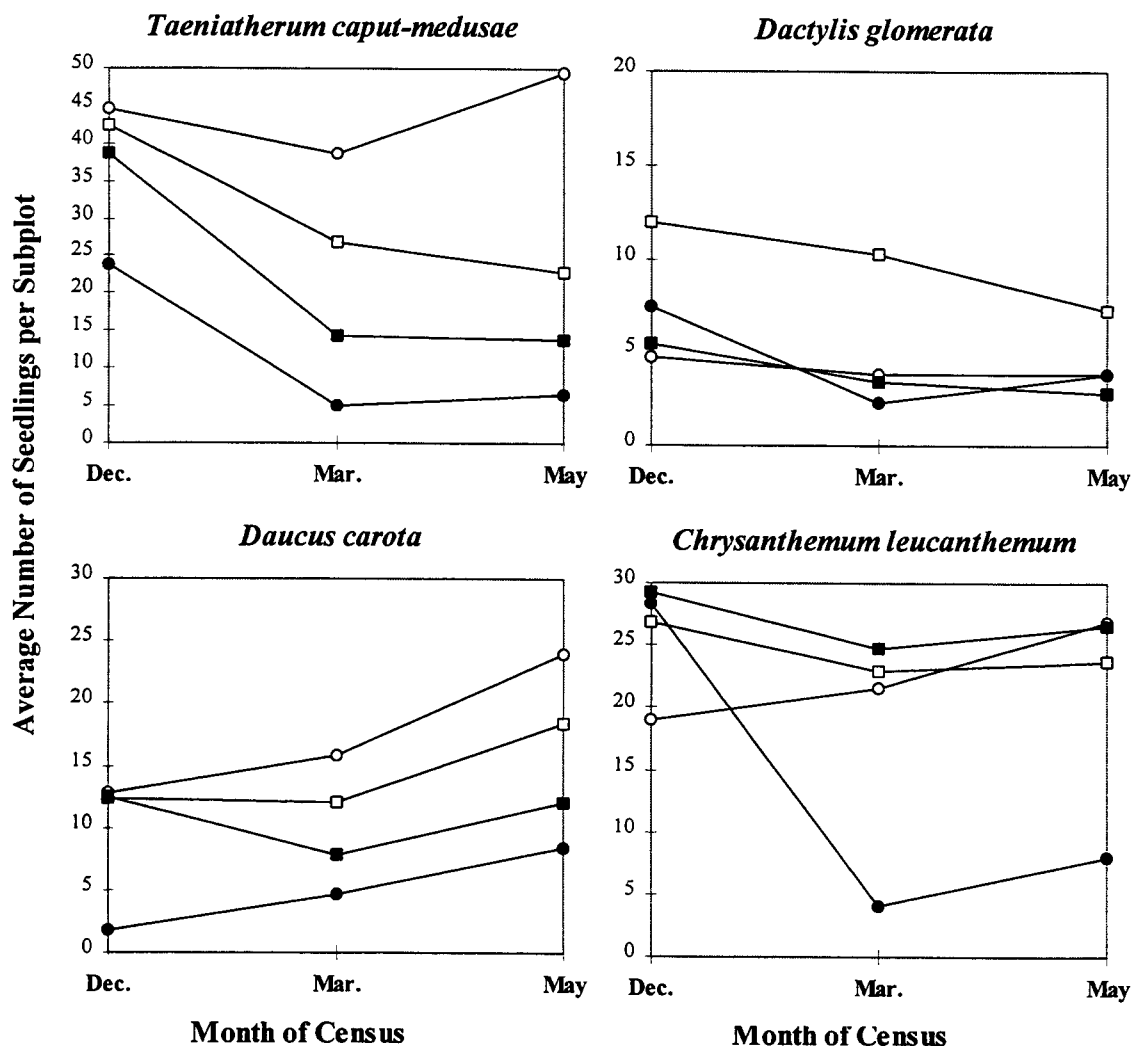
Figure 2.5. Native Bunchgrass Site, exotic species. Changes in the average number of seedlings present (#seedlings/subplot) in four treatments between censuses. Three censuses were conducted over the growing season: December 1995, March 1996 and May 1996. Each subplot had been planted with 100 seeds of the respective species. The four treatments included: O = burned, □ = clipped and raked to remove litter, ● = burned with litter added, ■ = no manipulation.

Dactylis glomerata

The majority of *Dactylis* seedling emergence appeared to have occurred by the time of the December census (Figure 2.5). Although there were no significant differences among treatments, the highest average seedling densities occurred in treatment -L. During the winter, there was little change in average seedling densities (-4.7 and -1.1 seedlings), but by the March census, the treatment difference suggested by the December data had become statistically significant (Table 2.6). This effect was transient, however because small changes in seedling densities in the spring dissolved any treatment differences on final seedling establishment.

Daucus carota

Daucus carota emerged throughout the fall, winter and spring, but the highest seedling increases occurred during the fall and spring (Figure 2.5). There were no significant treatment differences in initial (December) seedling counts in planned comparisons. During the winter interval, seedling densities in burned plots (treatment B and B+L) tended to increase, while those on unmanipulated plots (treatment NM) tended to decrease (Figure 2.5), contributing to the significant treatment effects on March seedling densities. These significant treatment effects were maintained to the May census (Table 2.4), as the spring interval increases were relatively uniform across treatments (Figure 2.5).

Elymus glaucus

The majority of *Elymus glaucus* seedling emergence appeared to have occurred by the time of the December census (Figure 2.6). Although there were no significant differences in initial (December) seedling densities, there were approximately twice as many seedlings counted in unburned (treatment NM) than in burned (treatment B) plots (Table 2.6). Significant treatment effects were first evident during the winter interval, as seedling density decreases were significantly smaller in treatment without litter (B and - L) than in unmanipulated (NM) plots (Table 2.9). However, these winter differences were not enough to produce significant treatment differences in March seedling densities. During the spring interval, there was little change (-0.4 to 5.1 seedlings) in average seedling densities.

Eriophyllum lanatum

Very few seedlings were counted in the initial (December) census, and there were no significant differences among treatments. The majority of *Eriophyllum lanatum* seedling emergence appeared to have occurred during the winter interval (Figure 2.6). No significant treatment effects were found in any census, or in the changes between censuses. Seedling densities in treatment B, however, had the highest average increases in seedling densities between censuses (Figure 2.6).
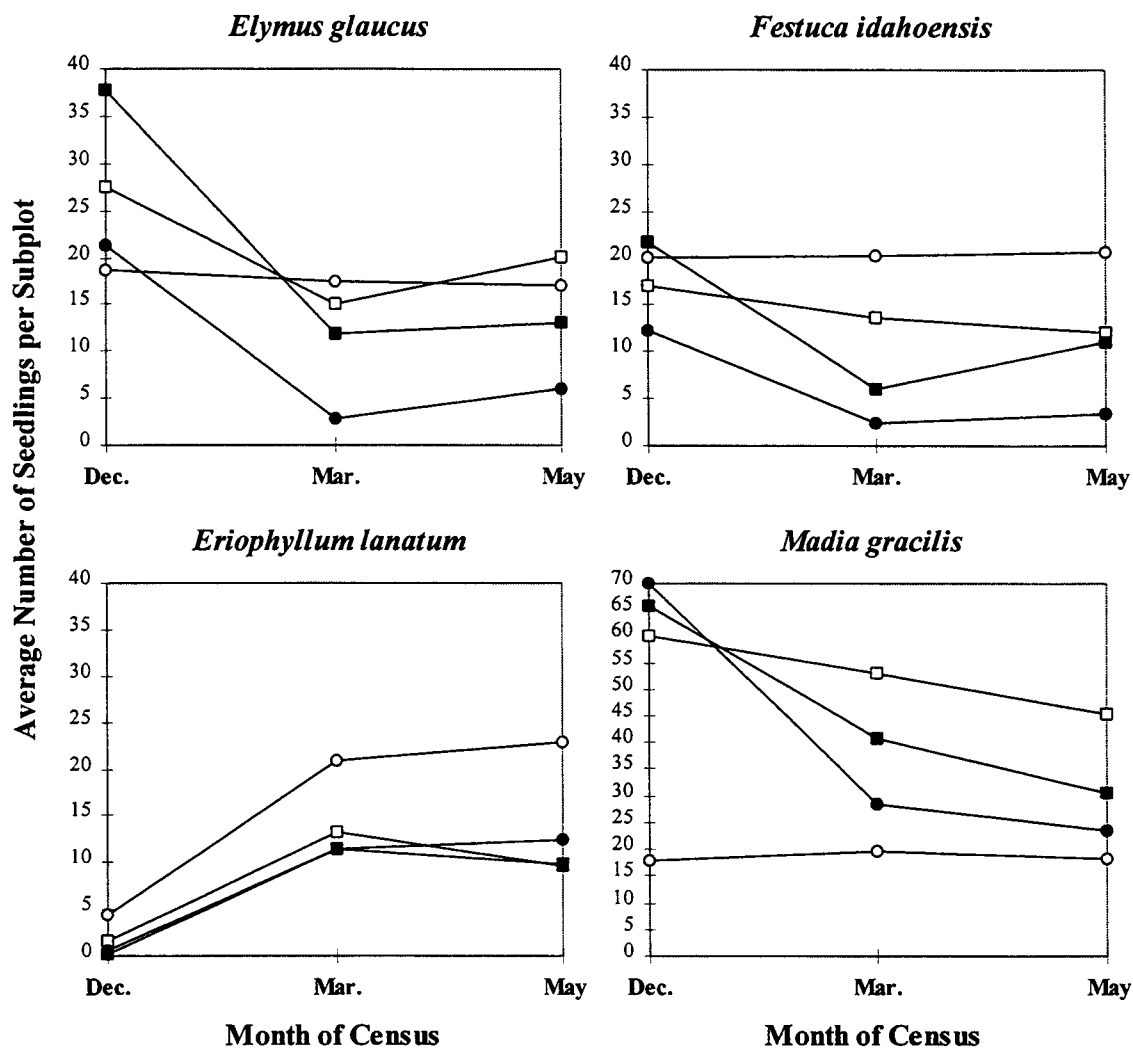
Figure 2.6. Native Bunchgrass Site, native species. Changes in the average number of seedlings present (#seedlings/subplot) in four treatments between censuses. Three censuses were conducted over the growing season: December 1995, March 1996 and May 1996. Each subplot had been planted with 100 seeds of the respective species. The four treatments included: O = burned, □ = clipped and raked to remove litter, ● = burned with litter added, ■ = no manipulation.

Table 2.9. Native Bunchgrass site: Average change in seedling counts during two intervals in subplots sown with 100 seeds in four treatment types, the F-ratio and the probability (p-value) of a more extreme F-ratio. Treatments include: B = burned, -L = clipped and raked to remove litter, B+L = burned with litter added, and NM = no manipulation. All means shown are for untransformed data. Transformations were applied as necessary before analysis of variance (LOG = natural log transformation). Treatments sharing superscripts were statistically indistinguishable (α=0.05).

Winter Interval

Species	Treatment				F-ratio	p-value
	B	-L	B+L	NM		
Chrysanthemum leucanthemum	2.5a	-3.9a	-24.1b	-4.5a	4.17	0.018
Dactylis glomerata	-1.1	-1.7	-4.7	-1.3	0.73	0.543
Daucus carota	2.9	-0.3	2.9	-4.7	2.99	0.054
Elymus glaucus	-1.3a	-12.6ab	-18.4bc	-26.0c	5.31	0.007
Eriophyllum lanatum	16.4	11.6	10.8	11.2	0.29	0.831
Festuca idahoensis (LOG)	0.1	-3.3	-9.8	-15.8	1.51	0.241
Madia gracilis (LOG)	2.0a	-6.9a	-41.6b	-31.6ab	4.14	0.023
Taeniatherum caput-medusae	-4.6a	-14.6ab	-21.0b	-22.4b	3.60	0.037

Spring Interval

Species	Treatment				F-ratio	p-value
	B	-L	B+L	NM		
Chrysanthemum leucanthemum	5.3	0.7	3.9	1.8	0.35	0.791
Dactylis glomerata	0.7	-3.2	1.8	-1.1	2.32	0.105
Daucus carota	8.2	6.4	3.9	4.2	0.62	0.608
Elymus glaucus	-0.4	5.1	3.2	1.4	1.01	0.410
Eriophyllum lanatum	1.9	-3.6	1.1	-1.4	1.11	0.367
Festuca idahoensis (LOG)	0.4	-1.7	1.0	5.1	0.99	0.418
Madia gracilis	-1.5	-7.8	-5.0	-3.6	0.50	0.689
Taeniatherum caput-medusae	9.5a	-6.0c	1.5b	-0.1bc	7.02	0.002

Festuca idahoensis

The bulk of seedling emergence for *Festuca idahoensis* appeared to be in the fall (Figure 2.6), and there were no significant differences in initial (December) seedling counts among treatments. During the winter interval, although seedling density changes were not significant, average seedling densities in the treatments without litter (-L and B) changed little (0.1 to -3.3 seedlings), while those in treatments with litter (B+L and NM) had higher decreases (-9.8 to -15.8). These winter changes contributed to the significant treatment effects on March seedling densities (Table 2.6). This effect was transient, however, as seedling densities tended to increase during the spring, dissolving any overall significant treatment effects on seedling establishment (May census).

Madia gracilis

The majority of *Madia gracilis* seedlings appeared to have emerged by the time of the December census and initial (December) *Madia* seedling densities were significantly lower in treatment B than in other treatments. During the winter interval, average seedling densities decreased in all treatments (Figure 2.6, Table 2.6). Although these winter decreases appeared to be split, with smaller decreases in treatments B and -L than in treatments B+L and NM (Figure 2.6), the differences between those in treatments B, -L and NM were not significant (Table 2.9). *Madia* seedling densities continued to decrease during the spring interval, but these average decreases were small (-1.5 to -7.8 seedlings) and did not differ significantly among treatments.

Taeniatherum caput-medusae

The majority of *Taeniatherum caput-medusae* seedling emergence appeared to occur by the time of the December census and there were no initial (December) significant differences in seedling densities among treatments (Figure 2.5, Table 2.6). During the winter interval, seedling densities decreased across all treatments, with significantly greater decreases in treatments with litter (B+L and NM) than in treatment B. Winter seedling decreases in treatment -L were in-between but not significantly different from those of treatments B or NM. There was very little average change in seedling densities during the spring interval (-6 to 1.5 seedlings), except in treatment B, which had significantly greater increases (9.5 seedlings) than any other treatment (Table 2.9).

DISCUSSION

How Prescribed Burning Affected Seedling Establishment

The recruitment of new individuals through seedlings is only successful when there is a favorable microenvironment for seed germination, seedling emergence and seedling survival (Harper 1977). Prescribed burning often improves seedbed microsites and seedling growing conditions by removing plant litter, or through the other non-litter microsite changes that accompany burning (Hulbert 1988).

Seedbed changes accompanying prescribed burning may affect seedling densities through new seedling emergence and/or seedling mortality. Although seedling emergence and mortality were not measured directly in this study, these processes were surmised by comparing changes in seedling densities between censuses. Seedling

density increases and decreases were interpreted as new seedling emergence and seedling mortality, respectively. It is possible (and presumable) that some seedlings emerged and died before they were counted. However, it was assumed that the three censuses (in December, March and May) were sufficient to account for most seedlings, and thus these data would provide an adequate interpretation of seedling population dynamics.

Annual Exotic Grass Site

Prescribed burning on the Annual Exotic Grass site created favorable microsites for seedling establishment primarily through litter removal, although litter removal was seldom a complete explanation of the overall burn effect. Both litter removal and non-litter burn effects were, however, important explanations of the burning effects on seedling population dyanamics for many species sown into the Annual Exotic Grass site. The favorable microsites created by litter removal and non-litter burn effects were primarily ones which promoted winter seedling survival and secondarily promoted seedling emergence.

Both of the native grasses, *Elymus glaucus* and *Festuca idahoensis*, established significantly better in burned plots than in unmanipulated plots. The mechanism of litter removal was a partial explanation of the burn effect on *Elymus* seedling establishment. *Elymus* establishment patterns were largely determined by differential winter mortality and litter removal. Burning or hand-clearing tended to improve average winter *Elymus* seedling survival, contributing to the significantly increased seedling establishment in burned plots. The mechanisms behind the burn effect on *Festuca*'s seedling establishment were less clear. While average *Festuca* seedling emergences and winter survival tended to be promoted in the burned plots, the role of litter removal and non-litter burn effects were not distinct.

Of the two exotic grasses, only seedling populations of *Taeniatherum caput-medusae* responded to treatments. *Dactylis glomerata* had relatively low overall seedling emergence (Figure 2.1) and did not appear to respond to experimental manipulations. For *Taeniatherum*, although the majority of its emergence was not significantly affected by treatments, burning, primarily through litter removal, significantly improved its winter seedling survival over unmanipulated plots. These effects led to significantly greater March seedling densities in burned hand-cleared plots over the treatments with litter. Despite these trends, changes during the spring interval dissolved any overall burn effect on seedling establishment.

Taeniatherum caput-medusae was the only species tested in the Annual Exotic Grass site whose significant burn effects on March seedling densities did not persist to the May census, but this process was most likely an artifact of seedling competition, rather than of treatment effects. Seedlings, especially fast growing species, compete for resources (Ross and Harper 1972; Fenner 1978) and severe crowding of these highly competitive winter annual species may have led to mortality in dense stands. Seeds were planted in much higher densities than would occur naturally in the field, and a large proportion of *Taeniatherum* seedlings had emerged in the fall. During the winter, *Taeniatherum* rapidly puts down deep root systems (Harris and Wilson 1970). Rapid above-ground growth and flowering commenced between the March and May census (personal observation) and this rapid growth in crowded conditions probably contributed to greater net mortality in the high-density populations (Figure 2.1). If competition was indeed a factor for *Taeniatherum* establishment, as it appeared to be, the March results would be more indicative of seedling establishment patterns under natural conditions. Therefore, *Taeniatherum* seedlings establishment would be expected to increase on burned seedbeds due the improved winter survival associated with litter removal.

Like the native grasses, both native forbs, *Eriophyllum lanatum* and *Madia elegans*, established significantly better in burned plots than in unmanipulated plots.

Burning affected *Eriophyllum*'s seedling establishment patterns primarily by promoting winter seedling emergence, while *Madia* seedlings responded to burning through improved winter survival. For *Eriophyllum*, the relative roles of litter removal and non-litter burn effects on overall seedling establishment were not clear (Table 2.4), but burning did promote *Eriophyllum*'s winter seedling emergence primarily through litter removal (Table 2.7). For *Madia*, litter removal was clearly a sufficient explanation behind the burn response. Burning, primarily through litter removal, significantly improved *Madia*'s winter seedling survival (Table 2.7), leading to significantly increased establishment on both burned and hand-cleared plots (Figure 2).

Of the two exotic forbs tested, only *Centaurea cyanus* established significantly better in burned plots than unmanipulated plots. *Centaurea*'s increased establishment in the burned plots was primarily due to increased winter survival. Litter removal and non-litter burn effects were of roughly equal importance in the burn effect on *Centaurea* establishment. Burning also significantly promoted the winter seedling survival of *Daucus carota*. Non-litter burn effects were strongly associated with this increased survival. This burn effect, however, was not powerful enough to significantly influence overall *Daucus* seedling establishment patterns.

Perennial Exotic Grass Site

Burning created favorable microsites for seedling establishment on the Perennial Exotic Grass site primarily through the removal of litter. Grass seedlings responded to treatments primarily through differential winter mortality, while the forb seedlings were more influenced by treatment effects on seedling emergence.

Burning significantly promoted the seedling establishment of both native grasses, *Festuca rubra* and *Elymus glaucus*, with litter removal a sufficient explanation of the burn effect. Litter removal increased *Festuca* and *Elymus* seedling establishment

primarily through decreased winter mortality and secondarily through increased seedling emergence. Winter seedling survival was most important for *Festuca rubra*'s establishment, as improved seedling establishment in burned and hand-cleared plots was primarily due to their lower winter mortality. Litter removal also tended to increase average spring *Festuca* emergence, further promoting seedling establishment in plots where litter had been removed. Winter seedling survival was also an important treatment effect for seedling populations of *Elymus glaucus*. However, unlike *Festuca*, non-litter burn effects, as well as those of litter removal, contributed to *Elymus* seedlings' winter survival (Table 2.8). Burning also significantly promoted *Elymus*' fall seedling emergence, but the magnitude of this treatment effect was relatively small, compared to those of winter mortality, and thus contributed less to seedling establishment patterns.

In contrast to the native grasses, burning did not significantly affect the seedling establishment of the exotic grass, *Arrhenatherum elatius*, although burning did have dramatic effects on *Arrhenatherum* seedling dynamics. The burned seedbed both inhibited seedling emergence and increased winter seedling survival. A relatively thick litter layer (as found in the unmanipulated and burned with litter added treatments) strongly promoted *Arrhenatherum*'s seedling emergence while litter removal was strongly associated with low seeding emergence (Figure 2.3). Both litter removal and non-litter burn effects increased winter seedling survival. Inter-seedling competition was not a likely factor in the high winter mortality of unmanipulated plots, because the burned with litter added treatment plots had high emergence as well as low winter mortality (Figure 2.3). This pattern of high seedling emergence combined with low mortality in the burned with litter added treatment was unique among all species tested and the mechanism behind this pattern was not clear.

While treatments affected the grasses in the Perennial Exotic Grass site mostly through changes in winter mortality, the forbs responded to treatments primarily through differential emergence patterns. Treatment effects on seedling emergence had the

greatest effect on the seedling establishment patterns of the native *Potentilla gracilis* and the exotic *Hypochaeris radicata*. *Hypochaeris* emerged mostly in the fall, with fall emergence significantly promoted in plots where litter had been removed, either by burning or by hand-clearing. There was also some evidence that non-litter burn effects may have promoted *Hypochaeris*'s spring emergence (Table 2.8). *Potentilla*'s emergence occured over the winter and spring, in diverging emergence patterns between low litter and high litter treatments (Figure 2.4). Like *Hypochaeris*, *Potentilla* emergence was promoted where litter had been removed, either by burning or hand-clearing. These results indicate that burning increased the seedling establishments of *Hypochaeris* and *Potentilla* primarily by removing the litter layer, which improved seedling emergence.

Although ultimately the seedling establishments of the native forb, *Eriophyllum lanatum* and the exotic forb, *Plantago lanceolata*, were not significantly affected by the burning or litter treatments, burning did change the seedling population dynamics for these forbs. The burned seedbed significantly promoted fall seedling emergence of both *Eriophyllum* and *Plantago*. Few *Eriophyllum* or *Plantago* seedlings had emerged by the December census, but these fall emergents occurred almost exclusively on the burned seedbeds for *Eriophyllum*, and on both burned and hand-cleared plots for *Plantago* (Table 2.5). These results indicate that for *Plantago*, burning promoted fall emergence through litter removal. The mechanism (litter removal, or non-litter burn effects) behind the burn effect for *Eriophyllum* was not clear. These initial "headstarts" for *Eriophyllum* and *Plantago* were largely maintained as higher average seedling establishment in these treatments (Figures 2.3 and 2.4), but a substantial amount of subsequent emergence in all treatment types obscured any significant differences in seedling establishment.

In general, few species were able to establish under the litter layer of the Perennial Exotic Grass Site and burning increased the seedling establishment of most species by removing the litter. Grime (1979) hypothesized that in productive grasslands,

a large-growing species, such as *Arrhenatherum elatius*, (the dominant species at the Perennial Exotic Grass site) can create and maintain a near-monoculture by producing a high density of litter. The litter acts as an "exclusion mechanism" by which seedling establishment and new growth of other species is obstructed. Meanwhile, the vegetative spread of the dominant species is not inhibited because its new shoots are robust and capable of penetrating a thick layer of litter (Grime 1979). These ideas are consistent with the observed patterns at the Perennial Exotic Grass site.

Native Bunchgrass Site

Prescribed burning did not create more favorable microsites for most species sown into the Native Bunchgrass site. Although nearly all species had higher average seedling establishment on burned plots, only one of the eight species tested was significantly increased above those in unmanipulated plots (Figure 2.4). Despite the lack of differences in seedling establishment, most species seedling dynamics were affected by burning and litter treatments. In general, the grasses were affected primarily by treatment differences in winter mortality, while the forbs were more likely to be affected by differential emergence patterns among treatments.

Although the seedling establishments of the native grasses, *Elymus glaucus* and *Festuca idahoensis*, ultimately were not significantly affected by burning or litter treatments, treatment effects were, in fact, significant factors in these species' seedling population dynamics. The main effect of treatments on the native grasses was through differential winter mortality, primarily through litter effects and secondarily through non-litter burn effects (Table 2.9). Most native grass seedling emergence was not significantly affected by the removal of litter or other microsite changes associated with burning, because the majority of seedling emergence for both *Elymus* and *Festuca* had occurred by the time of the December census with no significant differences among

treatments. However, during the winter interval, seedling mortality was least severe in treatments with litter removed (indicating a litter effect), followed by the burned with litter added treatment (indicating a non-litter burn effect). These treatment differences were significant for *Elymus*. For *Festuca*, winter seeding moralities did not differ significantly among treatments, but the patterns of winter mortality were important influences on the significant treatment differences between March seedling densities.

Similarly, the exotic grass, *Taeniatherum caput-medusae*, also responded to treatments primarily through differential winter seedling mortality, and the treatments did not significantly affect the majority of emergence which occurred in the fall. However, unlike the native grasses, *Taeniatherum* seedlings also responded to treatments through differential spring emergence, and these treatment effects ultimately led to significantly different establishment rates. The burned plots significantly promoted winter seedling survival and spring seedling emergence, but neither the litter nor the non-litter burn effects sufficiently explained either of these burn effects. However, decreased winter mortality was most associated with litter removal, while increased spring emergence was most associated with non-litter burn effects.

Competitive effects did not appear to be a prevailing factor for the seedling dynamics of *Taeniatherum* in the Native Bunchgrass site. If competition had been a factor contributing to mortality, we would expect higher seedling mortality in the treatments with the higher initial seedling densities, which did not occur in either the winter or the spring interval. In fact, during the winter interval, treatments with the highest *Taeniatherum* seedling densities also had the lowest mortalities. There was also no relationship between seedling densities and relative mortality during the spring interval (Figure 2.5).

The other exotic grass, *Dactylis glomerata*, did not respond to treatments like the other grasses sown into the Native Bunchgrass site. Relatively little *Dactylis* seedling emergence appeared throughout the study (although like the other grasses, most

seedlings had emerged by December) and *Dactylis* population dynamics were not significantly affected by prescribed burning (Tables 2.6 and 2.9).

The forb species were less likely to respond to burning than the grasses. Only seedling populations of the annual *Madia gracilis* and the biennial *Daucus carota* were significantly affected by burning. Seedlings of the perennial forbs, *Chrysanthemum leucanthemum* and *Eriophyllum lanatum*, did not appear to respond to the burned seedbed.

Burning affected the native *Madia gracilis* population dynamics primarily by inhibiting *Madia* seedling emergence. The roles of litter removal and non-litter burn effects are unclear in this response. Treatments may have also affected winter and spring *Madia* mortalities, but the observed significant differences in winter and spring seedling mortalities were probably due to severe inter-seedling competition between these fast-growing annual plants, rather than to treatment effects. Mortality from competition is suspected because the treatments with the highest December seedling densities (averaging between 60 and 70 seedlings per 25 cm^2) also had the highest winter mortalities (Figure 2.6). These competitive effects (or treatment differences) continued to result in higher mortalities where densities were highest in the spring (Figure 2.6), ultimately resulting in a lack of signficant treatment effects on *Madia* seedling establishment.

The cause of *Daucus carota*'s seeding dynamics in burned plots were more difficult to surmise because a fair amount of emergence took place between December and May (Figure 2.5), possibly masking the effects of mortality. Gross (1984) found plant litter and vegetative cover delayed *Daucus* emergence, and contributed to greater mortality, but did not significantly affect *Daucus*'s total emergence over the growing season. In the present study, mortality effects appeared to be dominant in the winter, where unmanipulated plots had greater mortality than in burned or hand-cleared plots.

In the spring interval, seedling emergence appeared the dominant factor, as treatments without litter had greater seedling emergence than those with litter.

Comparison and Overview of Three Sites

Litter removal was a significant component of the burn effect for the seedling establishment of many species of the Perennial Exotic Grass and Annual Exotic Grass Sites, while seedling establishment on the Native Bunchgrass Site was mostly unaffected by burning and litter manipulations.

Litter removal was the most important component of the overall burn effect for the Perennial Exotic Grass Site. For most sowed species, the native species in particular, burning effects on seedling establishment were sufficiently explained by litter removal. These results were not unexpected because, of the three sites, the Perennial Exotic Grass Site had the largest accumulations of litter, averaging about 4 cm in depth (personal observation). Thus litter on the Perennial Exotic Grass site was a more controlling component of the seedbed environment than on the other two sites. In tallgrass systems, where high levels of litter accumulate relatively quickly (Dix 1969), improved growing conditions following fire are also attributed to litter removal (Hulbert 1969; Old 1969; Rice and Parenti 1978; Knapp and Seastedt 1986; Hulbert 1988).

Although litter removal was most important where the litter level was highest, the degree of litter accumulation cannot entirely explain litter removal as a component of a burn effect. Both the Annual Exotic Grass Site and the Native Bunchgrass Site had

similar lighter litter loads (approximately 2 cm deep), but species response between these two sites differed dramatically. Most species of the Annual Exotic Grass Site were significantly influenced by litter removal as a burn effect, although litter removal was seldom a complete explanation of burn effects. In contrast, most species of the Native Bunchgrass Site did not respond significantly to either litter removal nor non-litter burn effects, even when these components were in "combination" (i.e. burned plots). Furthermore, litter removal was a minor, or even questionable component of the overall burn effect for the two species of the Native Bunchgrass Site that had a significant seedling establishment response to burning.

The results for the Annual Exotic Grass and Native Bunchgrass Site were unexpected. In general, undisturbed perennial grasslands are expected to inhibit colonization from seedlings more than in annual grasslands (Peart 1989). Competition from existing vegetation can severely limit the probability of seedling establishment (Potvin 1993) and a disturbance, such as fire, creates open conditions, temporarily freeing new seedlings from competition with perennial neighbors (e.g. Cheplick and Quinn 1988). Furthermore, the native bunchgrass community historically has persisted and potentially evolved under the influence of annual anthropogenic fire (Boyd 1986). For these reasons, I expected more seedlings with burning and hand clearing in the Native Bunchgrass site.

I expected that seedlings sown into burned plots in the Annual Exotic Grass site would respond to mainly to the removal of litter, rather than to non-litter burn effects, because of the lack of perennial plants on this site. Vegetation response to non-litter

burn effects, such as ash deposition or direct soil heating, are generally undetectable in grassland systems (Heyward 1938; Old 1969; Lloyd 1971; Cheplick and Quinn 1988; Hulbert 1988). Also, seedlings can not be affected by the burn response of mature perennial plants where mature perennials do not exist. Seedlings in annual grasslands, as opposed to perennial grasslands, will experience neighbors with similar phenologies and thus asymmetrical competition is much weaker than in perennial stands. Although annual grass seedlings are often superior competitors (Harris and Wilson 1970), seedling establishment of perennial species is more likely in annual grasslands than in perennial grasslands (Peart 1989).

The inability to remove litter through clipping and raking as thoroughly as through burning may have limited the capacity to discern litter effects from non-litter burn effects on the Annual Exotic Grass Site and Native Bunchgrass Site. Even very small amounts of litter can reduce the survival rates of grassland seedlings (Fowler 1988). Inevitably, a small amount of litter remained on hand-cleared sites, and the stubble was both higher and more common than those of burned sites (personal observation). Because there were intermediate amounts of litter present on the unmanipulated plots of these sites, there was a more gradual gradient of litter levels between burned, clipped and raked, and unmanipulated plots than in the Perennial Exotic Grass Site. This more gradual gradient may have blurred the comparison of burning and litter removal on these sites (e.g. Old 1969). Small differences between burned and hand-cleared plots may have been insignificant on the Perennial Exotic Grass Site, due to of the much greater contrast between "high litter" and "low litter" treatments.

It is possible that certain treatments may have affected the number of naturally dispersed seeds present on each plot, hence the results would not be based entirely on seedbed differences. If seeds were present in litter, then the clipped and raked treatment plots would have fewer seeds, and the burned with litter added treatments more seeds than the other treatments. This type of problem is unlikely for several reasons. First, by the time of the treatments (late September/early October), most dispersed seeds would have filtered through the litter to the soil surface. Secondly, sowing densities in subplots were much higher than the naturally occurring seeds. Finally, establishment from unsown subplots was accounted for to minimize the effect of plot-to-plot seedbank differences.

Prescribed Burning as a Restoration Tool

Annual Exotic Grass Site

Prescribed burning was an effective site treatment for improving the establishment of sowed native seed, although it also increased the establishment of annual exotic species. Sowing native seed into burned sites significantly promoted both the collective and the individual species seedling establishment of all four common native grassland plants tested. Although the burn treatment also enhanced the collective establishment of the common exotic species above unmanipulated levels, only *Centaurea cyanus*, as an individual species, had significantly more seedling establishment in the burned plots than in the unmanipulated plots. However, it is likely

that seedling competition in artificially high densities corrupted a significant

Taeniatherum caput-medusae increase in burned plots. Proportionally, burning

increased the success of sowed native seedlings more dramatically than those of the

exotic species, as compared to relatively equal establishment in the unmanipulated plots

(Table 2.3).

Unfortunately, under natural conditions, exotic species seed production in the

Annual Exotic Grass Sites would undoubtedly overwhelm the quantity of native seeds

that could be realistically collected and imported to the site. Thus, because burning

significantly increases collective exotic seedling establishment, prescribed burning could

create a greater weed problem. Burning could be most beneficial if exotic species seed

production was first reduced, such as by mowing prior to seed maturation.

The effectiveness of sowing native seed into unburned plots was limited in

establishing native seedling populations. Likewise, there was less exotic seedling

establishment in unmanipulated than in burned plots. As *Madia elegans* was the only

native species well-represented naturally on the site, seeds of other native species would

have to be imported for a restoration effort through prescribed burning. If sowing native

seed is not an option, leaving the site unburned would maintain exotic plants at lower

levels until a sowing project into the burn area could be implemented.

Perennial Exotic Grass Site

Prescribed burning was a very effective site treatment for improving the

establishment of sowed native seed. Burning also created more favorable microsites for

certain exotic species, but the establishment response for native species was generally much more dramatic than for the exotic species (Table 2.5).

Controlling the dominance of *Arrhenatherum elatius* is an important concern, as this rhizomatous grass dominates the site, making establishment of new plants a challenge. However, this species appears to propagate little from seed (Grime 1979; Tanphiphat and Appleby 1989; this chapter), so attempting to manipulate *Arrhenatherum* seedling establishment in mature stands, through site treatments is not a worthwhile endeavor. Fortunately, burning promoted the seedling establishment of other species, especially the natives, without increasing *Arrhenatherum* seedlings.

Native Bunchgrass Site

Prescribed burning was a poor site treatment on the Native Bunchgrass Site for promoting native species through seeding regeneration. Native seedling establishment in burned plots did not improve on burned seedbeds, but instead, burning actually encouraged short-lived weedy invaders. Establishment of perennial exotics, however, was unaffected by burning.

Because this site had a large component of mature native species (and thus a natural seed supply), a goal of prescribed burning would be to maintain or improve the existing native population, rather than to improve the seedbed for imported seed. Native seedling establishment was generally higher with burning, although not significantly so. Thus, a burn could be prescribed for another restoration purpose, such as for controlling shrub encroachment, without decreasing native seedling establishment.

Unfortunately, prescribed burning did promote the seedling establishment of

Taeniatherum caput-medusae and *Daucus carota*. Both of these species are short-lived

exotic pests, which rely exclusively on seeds for proliferation. Thus a prescribed burn

could degrade this site by shifting it towards a low-quality exotic annual grassland,

through an increase in weedy short-lived species.

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CHAPTER 3

SEED DORMANCY IN UPLAND PRAIRIE PLANTS
OF THE WILLAMETTE VALLEY

ABSTRACT

Seeds of fifteen herbaceous species common to Western Oregon upland prairies were tested for germination characteristics using a standardized procedure in laboratory tests. Measurements were conducted on four-month old seed and on samples subjected to additional after-ripening, cold-stratification, and fluctuating temperatures. Dormancy characteristics were compared between grasses and forbs, and native and exotic species. All five grasses tested showed little or no dormancy in initial tests with four-month old seed. In contrast, only two of the nine forbs tested were non-dormant in initial tests. All four of the native forbs tested contained a portion of dormant seeds and responded most dramatically to cold-stratification with a significant loss of dormancy. Seeds of exotic forbs had more variable response to treatments, and were more likely to be non-dormant at four months of age.

INTRODUCTION AND LITERATURE REVIEW

<u>Rationale</u>

Seed germination and seedling establishment are important for the regeneration and persistence of most terrestrial plant populations. Successful regeneration from seed

is often attributed to environmental characteristics which favor conditions for seedling

growth and establishment (Angevine and Chabot 1979; Mayer and Poljakoff-Mayber

1989). Mechanisms which delay germination can be interpreted as a strategy to avoid

conditions unfavorable for seedling growth, and to allow for seed dispersal and/or burial

before germination (Mayber and Poljakoff-Mayber 1989; Simpson 1990).

The period between seed germination and seedling establishment is often the

most hazardous stage in a plant's life cycle (Mayber and Poljackoff-Mayber 1989;

Potvin 1993). Seedlings are much more vulnerable to mortality than either seeds or

established plants. Although seeds are susceptible to mortality from predation,

microbial disease, and senescence (Clark 1996), seeds are usually far more resistant to

environmental stresses than seedlings of the same species (Mayer and Poljakoff-Mayber

1989; Simpson 1990). A germinated seed (i.e., seedling) is vulnerable to mortality from

harsh climatic conditions, herbivory, trampling, disease and interference from

neighboring plants. Due to their small size and less mature systems, young seedlings

have fewer defenses to unfavorable conditions than established plants. Yet, despite high

risk of seedling mortality, the recruitment of new individuals through seedlings is

critical for the long term success of many terrestrial plant populations (e.g., Weaver and

Mueller 1942), and is determining for the achievement of restoration goals through

sowing seed.

As seeds are a means for propagation of the species, the timing of germination

may be expected to favor seedling survival. Seedling survival and growth is dependent

upon many environmental conditions which vary by season (Laude 1956; Grime et al.

1981; Masuda and Washitani 1990). All seeds must have adequate moisture, aeration, and an appropriate temperature range for germination to occur (Mayer and Poljakoff-Mayber 1989). Although the seasonal change in all three of these factors may influence germination timing, temperature is the most important controller of germination in mesic temperate areas (Went et al. 1952; Baskin and Baskin 1988; Masuda and Washitani 1990; Pons 1991; Probert 1992; Olff et al. 1994).

When a viable seed fails to germinate in conditions normally favorable for germination, it is considered dormant (Amen 1968; Mayer and Poljakoff-Mayber 1989; Simpson 1990). Seed dormancy is the temporary suspension of germination until additional conditions are met (Mayer and Poljakoff-Mayber 1989; Simpson 1990). Delaying germination for a period of time may be adaptive to allow seedlings to avoid temporary conditions that cannot support seedling growth, such as adverse weather conditions (Goodwin et al. 1995), inadequate light quantity or quality (King 1975; Fenner 1978; Van Tooren and Pons 1988; Pons 1991) or severe competition with other plants (Thompson et al. 1977; Pons 1989; Olff et al. 1994). It also allows the seed greater potential for dispersal by wind, water and organisms (Simpson 1990). A temporal dispersion of germination may also have population survival value, protecting the seed crop from eradication as a result of unfavorable environmental conditions which may follow germination (Simpson 1990).

On the other hand, the capacity for immediate germination is an important seed attribute in many situations. Precocious germination allows seedlings to procure resources earlier, have a longer growing season, and thus compete more effectively with

neighboring seedlings and established perennials (Young et al. 1969; Ross and Harper 1972). This strategy works especially well in mild climates and/or with seedlings adaptable to a wide range of environmental conditions.

Most species exhibiting seed dormancy have differing dormancy characteristics within the population (Mayer and Poljakoff-Mayber 1989; Simpson 1990; Murdock and Ellis 1992). Differing dormancy characteristics is believed to be an adaptation to environmental uncertainty, allowing additional opportunities in time for portions of a seed population to germinate and potentially survive into mature plants (Goodwin et al. 1995). The degree of dormancy within a species also may vary from year to year and from population to population (Laude 1956; Young et al. 1968; Doescher et al.1985; Goodwin et al. 1995).

After-ripening

The dormancy characteristics of many seeds decline with seed age due to complex biochemical changes within the seed. This loss of dormancy, known as after-ripening, causes initially dormant seeds to germinate under narrow, and then later, wider ranges of conditions (Baskin and Baskin 1985). In the western United States, the after-ripening requirements of many species allow a peak germinability during the fall rainy season (Laude 1956; Goodwin et al. 1995). Earlier germination, such as in response to a summer storm, may risk high seedling mortality from desiccation. After-ripening requirements that favor spring germination may also be adaptive when winter temperatures are too cool for seedling growth, or where winter seedling survival would be low. Some species do not reach peak germinability until after one or more years of

after-ripening (Laude 1956). This longer dormancy period is probably an adaptation to allow seed-burial (Simpson 1990).

Germination requirements may also change with the seasons, correlating peak germinability with favorable times for seedling establishment (Baskin and Baskin 1985; Fenner 1987; Baskin and Baskin 1989; Masuda and Washitani 1990; Pons 1991; Olff et al. 1994). For species with a pronounced seasonal change in dormancy, a longer residence time in the soil decreases the seasonal amplitude of variation in germinability (Baskin and Baskin 1985; Pons 1991).

Stratification

Cold-stratification is another common dormancy breaking mechanism. Stratification is the exposure of seeds to cool temperatures for a period of time. A stratification requirement essentially limits germination prior to the winter season. Once stratified, many species will germinate under a broad range of conditions (Bostock 1978; Pons and Van Tooren 1988; Van Tooren and Pons 1988; Pons 1991), often at low winter temperatures (Grime 1981).

Fluctuating Temperatures

Diurnal fluctuations in temperature may stimulate germination in some seeds (Steinbauer and Grigsby 1957; Bostock 1978; Fenner 1978; Grime et al. 1981; Rice 1985). The effectiveness of this stimulus varies according to amplitude of fluctuation and/or the presence of light (Bostock 1978; Grime et al. 1981). Ecologists have noted that many grassland seedlings establish most successfully in gaps in the litter and vegetation (Fenner 1978; Grime et al. 1981; Gross and Werner 1982; Gross 1984; Winn 1985; McConnaughay and Bazzaz 1987; Peart 1989; Pons 1989; Reader 1991;

Thompson and Baster 1992; Potvin 1993). The removal or lack of an insulating foliage or litter layer will result in larger diurnal temperature fluctuations (Thompson et al. 1977). Also, temperature fluctuations decrease with depth in the soil. Therefore, a temperature fluctuation requirement may prevent germination too deep in the soil, under dense litter, or in a closed canopy of plants (Thompson et al. 1977; Rice 1985). Because larger canopy gaps have greater temperature variability, a response to fluctuating temperatures may also be a mechanism to detect gaps of sufficient size in the vegetation (Thompson et al. 1977; Bostock 1978). In this way, seedlings can avoid competition with mature neighbors, and thus improve the chances of survival, by delaying seed germination until there is an appropriate sized gap in the vegetation (Grubb 1977; Gross and Werner 1982; Fenner 1985; Aguilera and Lauenroth 1993). On the other hand, these fluctuations combined with high light levels may inhibit germination of some species, probably as an adaptation to allow seedlings to avoid highly desiccating situations (Grime et al. 1981; Van Tooren and Pons 1988).

Importance of this Study for Restoration

The goal of many restoration projects is to promote a native plant community while controlling undesirable plants. Sowing seed is a common way of reintroducing native plants and one of the factors affecting sowing success is the germination characteristics of the seeds employed. An understanding of the germination characteristics of weedy species is also important for controlling the spread of these plants by seed.

Objectives

In the present study, seed dormancy characteristics were described for fourteen upland prairie species from the Willamette Valley. Specific objectives of this study were: 1) to describe the extent of dormancy for each species; 2) to determine germination response to after-ripening, cold-stratification, and fluctuating temperatures and; 3) to compare dormancy characteristics between grasses and forbs, and native and exotic species.

METHODS

Species

The species used in this experiment were chosen to represent a variety of native and exotic plants commonly found in upland prairies of the Willamette Valley. The list includes native and exotic grasses and forbs. Seeds of each species were collected by hand in the summer of 1995, as they became mature. Mature seeds were identified as those which could be easily removed from the parent plant by hand.

Most of the seeds were collected from two upland Willamette Valley prairies: Carson Prairie of Oregon State University's McDonald-Dunn Research Forest and Amazon-Dike No.2 Management Unit of the Army Corps of Engineers (near Fern Ridge Reservoir). Species collected from Carson Prairie included: *Centaurea cyanus* L., *Chrysanthemum leucanthemum* L., *Dactylis glomerata* L., *Daucus carota* L., *Hypochaeris radicata* L., *Madia elegans* Don ex Lindl., *Madia gracilis* (Smith) Keck, and *Taeniatherum caput-medusae* Nevski. The Amazon-Dike No.2 collections included: *Arrhenatherum elatius* L., *Hypochaeris radicata* L., *and Plantago lanceolata* L. *Potentilla gracilis* Dougl. was collected from Willow Creek Natural Area, of The Nature Conservancy. *Festuca rubra* L. was collected from a site, owned by the Army

Corps of Engineers, west of Green Oaks Road (near Fern Ridge Reservoir). *Elymus glaucus* Buckl. and *Eriophyllum lanatum* (Pursh) Forbes were collected from both Carson Prairie and an additional population: Baskett Butte National Wildlife Refuge (*E. glaucus*) and near the confluence of Amazon Creek and Fern Ridge Reservoir (*E. lanatum*). These populations were collected and stored separately.

Processing

Seeds were cleaned, sorted, and counted at the National Forage Seed Production Research Center (USDA-ARS) seed separation lab in Corvallis Oregon. The product of the processing was clean, filled seeds, in lots of one-hundred. In many cases the "seeds" included the entire fruit, such as achenes and caryopses.

Collected propagules were machine threshed with a Westrup LA-H thresher to detach and isolate the seeds from the other plant fragments. Repeated machine threshing was used to remove appendages from the seeds of *Elymus glaucus* (awns), *Taeniatherum caput-medusae* (awns) and *Hypochaeris radicata* (pappus). The removal of these appendages rendered these seeds better suited for accurate machine counting. In addition to machine threshing, seeds of *Arrhenatherum elatius* and *Dactylis glomerata* were processed with a hand-thresher to dislodge caryopses from the glumes, lemma, and palea. These caryopses separated easily and were better suited for machine counting than the entire propagule. *Centaurea cyanus* and *Chrysanthemum leucanthemum* seeds were picked from the collected inflorescence by hand to minimize seed loss in these smaller collections. *Daucus carota* seeds were also removed by hand due to the tendency of the barbed pericarps to cling together during machine processing.

In order to standardize seed weight during experimentation, unfilled and light seeds were removed with a Hoffman Oregon Seed Blower, with airflow settings held constant for each species. Plant debris remaining in the filled seed portion were

removed with sieve screens. Seeds of all species were machine-counted into lots of one-hundred and stored in stacked paper cups at room temperature ($\approx 20^{\circ}$C).

Germination Testing

Seed germinability was tested within the four treatments following identical procedures. For each species (or population of a species) seeds were sown into Petrie dishes (90mm diameter × 15mm deep) fitted with one sheet of filter paper. There were one-hundred seeds per dish and five dishes for every treatment tested. The filter paper was moistened with distilled water and seeds were kept moist. Germination was defined as the emergence of the radical or cotyledon from the seed coat or pericarp. Germinated seeds were counted and removed regularly until all seeds had germinated or until no new germination had occurred for at least four days. Ungerminated seeds were then counted and discarded. Tetrazolium tests for viability were not performed because many species had such small seeds or tiny embryos that the results would have been unreliable.

An initial test was performed in November 1995 to measure the germinability of four-month old seed. Seed dispersal of the test species occurs during the summer months when summer rainfall in the Willamette Valley is usually insufficient for successful seedling establishment. Therefore, the capacity for immediate germination was not tested. All seeds were after-ripened about four months, until autumn moisture conditions would be more favorable for natural germination in the field. Plates of seeds were then placed in a greenhouse where they were exposed daily to ambient light and 14 hours of fluorescent lights. Greenhouse temperatures were maintained at approximately 20°C during the day and 15°C at night. If germination was high (>80%) for a species, no further treatments were tested, and the seeds were considered non-dormant.

All species with less than 80% observed germination in the initial tests were subjected to three more treatments in February 1996: additional dry storage (after-ripening); cold stratification; and exposure to alternating temperatures, in an attempt to facilitate germination. All seeds employed in these additional treatments had been held in dry storage, as described above, for approximately seven months. Thus the seeds used in these additional tests had after-ripened for an additional four months.

Seeds were stratified by placing plates of moistened seeds in a dark chiller for six weeks at 5°C. Following chilling, the seeds were placed in the greenhouse (as in the initial tests). Another set of moistened seeds was exposed to alternating temperatures in an incubator programmed for 8 hours of 25°C (light) and 16 hours 15°C (dark) per day. A third set of seeds were germinated in the greenhouse (as in initial tests) as a control to separate the effects of additional after-ripening from those of stratification and fluctuating temperatures.

Data Analysis

Effects of after-ripening, stratification, and alternating temperatures were assessed by comparing mean germination proportions for each species. The number of germinants in "untreated" four-month and seven-month old seed was compared to evaluate the effect of after-ripening. The effect of cold stratification was evaluated by comparing germinant numbers in chilled and unchilled seven-month old seed. Germinant numbers of seeds exposed to alternating temperatures and seven-month old seed germinated in the greenhouse were compared to evaluate the importance of fluctuating temperatures in breaking dormancy.

Differences among germination treatment means for each species were assessed by analysis of variance (ANOVA), using the Statgraphics 5.0 statistical package (Ramsey and Schafer 1994). A Petrie-plate of 100 seeds was the experimental unit,

with five replications (dishes) per species per treatment. Means were compared by Fisher's protected least significant difference (LSD) procedure at P=0.05.

RESULTS AND DISCUSSION

Initial Tests - Grasses

Grime et al. (1981) noted that the Poaceae were the most likely among several large families (Asteraceae, Fabaceae, Cyperaceae, and Apiaceae) to be non-dormant upon maturity. In the present study, seeds of all five of the grass species tested (*Arrhenatherum elatius*; *Dactylis glomerata*; *Elymus glaucus*; *Festuca rubra*; and *Taeniatherum*) were non-dormant in initial tests (Table 3.1).

The lack of fall dormancy found in *Arrhenatherum elatius* is consistent with this species' phenology, as this perennial exotic grass germinates entirely in the fall, exhausting the seed supply until the following summer (Grime 1981; personal observation). Tanphiphat and Appleby (1989) also found *Arrhenatherum* to be non-dormant at maturity and to germinate under a wide range of conditions.

Festuca rubra in the United Kingdom, like *Arrhenatherum*, has been found to be a fall-germinant, with no persistent seed bank (Grime 1981). Olff et al. (1994) found this species to lack dormancy and to germinate rapidly, even at low temperatures.

Studies of European populations of *Dactylis glomerata* have found very little dormancy, especially from those populations from lower-latitudes (such as in Oregon) (Juntilla 1977; Probert et al. 1985).

Taeniatherum caput-medusae's lack of dormancy was typical of annual grasses, which often have a high potential for early and rapid germination (Grime et al. 1981). Although strains of *T. caput-medusae* from the western United States have a range of

Table 3.1. Proportion of seeds germinated in response to treatments. Different letters within rows indicate significant differences (Fisher's protected LSD, α=0.05) among treatments. All seeds were held in dry storage for 7-8 months except for those used in the Initial Test. Treatments included: 3-4 months of dry storage (Initial Test); 7-8 months of dry storage (After-ripen); moistened seeds exposed to 5 weeks of diurnal alternating temperatures of 15°/25°C (Alt. Temps); moistened seeds exposed to five weeks of 5°C (Cold Strat.). Species with greater than 80% germination in the initial test were considered non-dormant and no further tests were conducted. The two populations of *Eriophyllum lanatum* (C.P.=Carson Prairie, F.R.=Fern Ridge Reservoir) had nearly identical germination in the initial test (two-sample t-test, p-value=.8718), and thus were combined for the remainder of the study.

	Treatments & age of seed (months)					
	Initial Test 3-4	After-ripen (7-8)	Alt. Temps (7-8)	Cold Strat. (7-8).	Summary of ANOVA F-ratio	p-value
Grasses, Native						
Elymus glaucus (B.B.)	93.8	—	—	—	—	—
Elymus glaucus (C.P.)	82.8	—	—	—	—	—
*Festuca rubra**	98.5	—	—	—	—	—
Grasses, Exotic						
Arrhenatherum elatius	80.4	—	—	—	—	—
Dactylis glomerata	96.8	—	—	—	—	—
Taeniatherum caput-medusae	97.7	—	—	—	—	—
Forbs, Native						
Eriophyllum lanatum (C.P.)	4.9a	8.0a	11.6a	45.4b	26.45	0.0000
Eriophyllum lanatum (F.R.)	5.1a	↑	↑	↑	↑	↑
Madia elegans	63.2b	36.2a	70.2b	86.4c	15.37	0.0001
Madia gracilis	71.4b	27.8a	64.4b	99.2c	27.37	0.0000
Potentilla gracilis	5.0a	25.8c	13.4b	86.6d	273.39	0.0000
Forbs, Exotic						
Centaurea cyanus	73.0	72.0	67.2	80.2	1.88	0.1730
Chrysanthemum leucanthemum	99.4	—	—	—	—	—
Daucus carota	42.0a	82.2c	79.2c	56.2b	39.02	0.0000
Hypochaeris radicata	99.1	—	—	—	—	—
Plantago lanceolata	25.0a	29.6a	61.6b	82.8c	93.34	0.0000

* *Festuca rubra* had recently been re-defined by taxonomists as an introduced cultivar and not a true native species. Nonetheless, *Festuca rubra* closely resembles the native fescue (*F. idahoensis* var. *roemeri*) and is often found in association with native prairie plants.

dormancy characteristics, only strains from the harshest climates are dormant in the fall (Young et al. 1969).

In this study, the seed collections from both populations of *Elymus glaucus* were non-dormant (>80% germination), but there was significant variation between populations (p-value= .0038, two-sample t-test). Seeds of the Baskett Butte (B.B.) population had significantly higher germinability, averaging 94%, than those of the Carson Prairie (C.P.) population, which averaged 83% (Table 3.1).

It is possible that the removal of outer coverings or the awns during seed processing may have influenced germination in some of the grasses tested. Probert et al. (1985a) found that the removal of outer coverings (glumes, lemma, palea) of *Dactylis glomerata* stimulated germination of dormant seeds, although not as effectively as exposing intact seeds to light or alternating temperatures. The presence of awns on *Taeniatherum* has also been reported to delay germination in dormant seed from east of the Cascade Mountains (Nelson and Wilson 1969). However, the seeds used in the above studies were collected from harsher climates, where winter dormancy could be a survival mechanism. In the relatively warm winter rainfall climate of the Willamette Valley, the advantage of over-winter growth would probably outweigh any risks of winter mortality and therefore an awn-induced dormancy seems unlikely in four-month old seed.

Initial Tests - Forbs

The forbs were more likely than the grasses to have a significant portion of dormant seed within the species' seed collection. All four of the native forbs examined failed to attain a final germination percentage of 80% in initial tests (Table 3.1). In fact, two native forbs, *Eriophyllum lanatum* and *Potentilla gracilis*, had over 90%

ungerminated seed. *Madia elegans* and *M. gracilis* both had a much larger proportion of non-dormant seed, averaging between 50% and 75% (Table 3.1).

Of the exotic forbs, two of the five, *Hypochaeris radicata* and *Chrysanthemum leucanthemum* germinated almost completely (>99%) in initial tests (Table 3.1). Similar results for *C. leucanthemum* were obtained by Baskin and Baskin (1988) who reported that this species germinated over a wide range of temperatures at maturity. Also, Olff et al. (1994) reported that *H. radicata* was undormant and had rapid germination, even at low temperatures.

A third forb, the exotic annual *Centaurea cyanus*, may also have been fully germinable at four-months. Although only 76% of the *C. cyanus* seeds germinated in initial tests, its germinability was not significantly improved with stratification, exposure to alternating temperatures, or additional after-ripening (see below). As the viability of these seeds was not tested, it is possible that all or a portion of the ungerminated seeds were not viable.

The other two exotic forbs examined, *Daucus carota* and *Plantago lanceolata*, had a large portion (>50%) of dormant seeds in initial tests. Both of these species have been reported to have some dormant seeds in the fall (Baskin and Baskin 1988 for *D. carota*; Pons 1991a for *P. lanceolata*).

Most of the collections of seeds from species tested were either non-dormant or contained a majority of non-dormant seeds. Non-dormant seeds will germinate as soon as fall rains bring adequate moisture. These observations are consistent with the patterns of seedling emergence with seeds of these species sown in a field study (see Chapter 2). This capacity for autumn germination allows prairie seedlings to escape early competition by growing when established perennials are senescent. However, these fall germinants may be vulnerable to high mortality if winter conditions are harsh (Silvertown 1981). Temperatures in winter may also be too cool for seedling growth.

However, subsequent spring germination could also lead to mortality or inadequate growth due to a closed canopy (Olff et al. 1994).

The seven species with substantial dormancy were tested with additional after-ripening, stratification, and/or exposure to alternating temperatures.

After-ripening

An additional four month period of dry storage significantly increased the germinability of the forbs, *Daucus carota* and *Potentilla gracilis* (Table 3.1). Two forbs, *Madia elegans* and *M. gracilis*, decreased germinability with after-ripening. *Eriophyllum lanatum*, *Centaurea cyanus*, and *Plantago lanceolata* were unaffected by additional after-ripening. (The two populations of *Eriophyllum lanatum* had nearly identical initial germination rates (5%) in initial tests (p-value= .8718, two-sample t-test), and thus were combined for testing for effects of after-ripening, cold-stratification, and fluctuating temperatures.)

The exotic biennial forb, *Daucus carota*, nearly doubled its germinability to 82% with four months of additional after-ripening. Other studies have indicated that *Daucus carota* had two germination peaks, one in the fall and another in the spring (Baskin and Baskin 1988; Pons 1991a) that are based on seasonal dormancy cycles, but not necessarily after-ripening. It is possible that the "after-ripening effect" found in this species (and possibly also *Potentilla*) is an artifact of cyclical dormancy.

The other species which became less dormant with after-ripening was *Potentilla gracilis*, a native perennial forb. Although after-ripening increased *P. gracilis* germinability from 5.0% to 25.8%, a large portion of the seeds remained dormant.

Interestingly, two native annual forbs, *Madia elegans* and *Madia gracilis*, decreased in germinability with after-ripening (Table 1). Both of these native annual forbs had relatively high germination in initial tests (63.2% and 71.4%, respectively)

with four-month old seed, yet seven-month old seed (tested in February) had 43% fewer *Madia elegans* germinants and 61% fewer germinants of *Madia gracilis*. These results indicate that these two species became more dormant with an additional four months dry-storage at room temperature.

This pattern is similar to a dormancy cycle, described by Baskin and Baskin (1985) for some winter annuals. Baskin and Baskin (1985) noted that portions of some annual species' seed crops, which could not germinate in the fall due to inappropriate conditions for germination (such as lack of adequate light, moisture, or temperature), will enter a secondary dormancy. As these seeds enter secondary dormancy, they lose the ability to germinate at higher temperatures, but are still able to germinate at relatively low temperatures. As the *Madia* species seeds in the present study were held in dry storage until mid-winter, a portion of the seed may have entered a secondary conditional dormancy and thus could not germinate in the relatively warm conditions of the greenhouse. However, these seeds appeared to be released from any conditional dormancy during exposures to cooler temperatures in the chiller (see below).

Stratification

All four native forbs and one exotic forb responded dramatically to cold-stratificaton. In particular, the forbs, *Madia elegans*, *Madia gracilis*, *Potentilla gracilis*, and *Plantago lanceolata* had over 80% total germination with chilling, significantly more loss of dormancy than non-chilled seeds of the same age (Table 3.1).

Chilled *Eriophyllum lanatum* seeds had 45.4% germination, a significant loss of dormancy relative to the low (<10%) germinability in unchilled seeds. Yet, even when stratified, *Eriophyllum* still had a large portion of dormant (or possibly non-viable) seeds. *Potentilla gracilis* was another native forb whose germinability was greatly

improved following stratification. The total germination of chilled *Potentilla* seeds increased from 26% without chilling to 86.6% with stratification.

Although, the native annual forbs, *Madia elegans* and *Madia gracilis*, had become significantly more dormant with after-ripening (Table 3.1), stratified seeds of the same age were completely (or nearly completely) non-dormant. Stratified *Madia elegans* and *M. gracilis* averaged 86.4% and 99.2% total germination, respectively. Both of these *Madia* species had germinated completely during chilling at 5°C, indicating these species' ability to germinate at low winter temperatures. These results suggest that *Madia elegans* and *M. gracilis* may enter a secondary dormancy, during which time germination may only occur at low temperatures (Baskin and Baskin 1985).

Plantago lanceolata was the only exotic forb (of three with dormancy) which had significantly higher total germination with stratification than unchilled seed. The total germination of chilled *Plantago* seeds averaged 82.8% (from less than 30%), a considerable loss of dormancy. These results are consistent with those of Pons and Van Tooren (1988) who reported increased *Plantago lanceolata* germination following stratification.

Contrary to the results found by Baskin and Baskin (1988) and Grime et al. (1981), chilling did not increase the total germination of the exotic biennial *Daucus carota*. In the present study, stratification actually significantly decreased total *Daucus* germination, averaging 56% in chilled relative to 82% germination of unchilled seeds of the same age.

Alternating Temperatures

Exposing seeds to alternating temperatures (15/25°C) was the least effective method tested for breaking seed dormancy of most species. However, seeds of three forb species, *Madia elegans*, *Madia gracilis*, and *Plantago lanceolata*, had significantly

greater total germination in an incubuator with alternating temperatures than those of the same age germinated in the less variable conditions of the greenhouse (Table 3.1). However, these effects were significantly less than those of cold-stratification (Table 3.1).

A major limitation of this treatment was the variability (20/25°C) of temperatures in the greenhouse. Thompson et al. (1977) found that germination response to diurnal temperature fluctuation in a variety of species may be stimulated by a fluctuations ranging from 1 to 10°C. A comparison of seeds exposed to alternating 15/25°C with seeds germinated at a *constant* temperature would have been a more conclusive test.

Comparisons of Growth Forms

All of the five grasses showed little or no dormancy of four-month old seed. This indicates that most germination for these grasses would occur with the commencement of fall rains. On the other hand, the forbs as a group were much more likely to be dormant in the fall. Only two of the nine forbs tested were non-dormant in initial tests and both of these species were exotic species. All but one of the other forbs required additional treatments to break dormancy of a portion of their seeds. *Centaurea cyanus*, an exotic, consistently had high but incomplete germinability, which did not significantly change with treatments.

Comparisons of Native and Exotic Species

There were no differences between the germination characteristics of native and exotic grasses, as all of the grasses tested were largely non-dormant in initial tests. There were, however, conspicuous differences between the native and exotic forbs. For

the native forbs, the most notable pattern was a dramatic loss of dormancy with cold-stratification, in every native forb tested. Seven months of after-ripening also significantly increased the germinability of *Potentilla gracilis*, while significantly decreasing the germinability of *Madia elegans* and *M. gracilis*. The exotic forbs were much more varied in their germinability and dormancy breaking requirements. Most of the exotic forbs did not require cold-stratification for optimal germinability. In fact, chilled seeds of one exotic forb, *Daucus carota*, had significantly more dormancy than untreated seeds of the same age. Only *Plantago lanceolata* significantly lost dormancy with cold-stratification. An additional four months of after-ripening significantly increased the germinability of *Daucus carota*. Two exotic forbs, *Hypochaeris radicata* and *Chrysanthemum leucanthemum*, exhibited no discernable dormancy in four-month old seed, and *Centaurea cyanus* had high initial germinability (76%) which did not improve with treatments (cold stratification, exposure to alternating temperatures, or additional after-ripening).

Implications for Restoration

Native seeds should be sown in the fall to take advantage of early germination and cold stratification. Early germinating seedlings often have a competitive advantage over later-germinating seedlings (Ross and Harper 1972) and are better able to compete with mature plants in the spring. Fall seeding also exposes seeds to a period of cold temperatures during the winter months, which is very important for the maximum germination of native forbs.

The potential for successful seed germination is a practical consideration for sowing restoration efforts. The poor germinability of filled *Eriophyllum lanatum* (<50% even with stratification) may make this species a poor candidate to grow from

seed. Alternative methods of introducing this plant, such as planting plugs, should be investigated, if the presence of this species is desired.

An understanding of germination characteristics of pest species is helpful for devising strategies for their control. The high germinability of many of the weedy species tested here would promote their regeneration, making them a problem in restoration projects. As many of these weedy species are mostly non-dormant the first autumn after dispersal, it is unlikely that they will form a large persistent soil seed bank. Site treatment efforts could be made to minimize the number of dispersed seed for new seedlings (such as mowing prior to seed maturation) as part of the restoration effort.

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CHAPTER 4

TEMPERATURES OF PRESCRIBED BURNS
IN WESTERN OREGON UPLAND PRAIRIES

ABSTRACT

Temperatures were measured in prescribed burns in three upland grassland vegetation types (Native Bunchgrass, Perennial Exotic Grass, and Annual Exotic Grass) and two burn sizes (2m × 2.5m plot burns, and a two hectare broadcast burn) in the Willamette Valley, Oregon. Constructed pyrometers recorded maximum temperatures between 1 cm below the soil surface and 3 cm above the soil. Plot burns in the Native Bunchgrass reached higher temperatures significantly closer to the soil surface than the plot burns in Annual Exotic Grass or Perennial Exotic Grass sites. Average temperatures in a two hectare broadcast burn and in replicated 2m × 2.5m plot burns in an annual exotic grassland were very similar. Average temperatures of the broadcast burn were about 79°C at the soil surface and about 211°C at 2cm above the soil surface, while average temperatures of the 2m × 2.5m plot burns were 69°C at soil surface and 197°C at 2 cm. These similar results show that the techniques used in burning small plots accurately reproduced the maximum temperatures of the broadcast burn.

INTRODUCTION AND LITERATURE REVIEW

<u>Rationale</u>

Ecologists are interested in the temperatures of grassland fires because fire temperature may have important effects on the vegetation and the microenvironment. The temperature at or near soil surface is of particular interest because of its potential

effects on dispersed seed survival and germination (Wright 1931; Bentley and Fenner 1958; McKell et al. 1962; Ewing and Engle 1988), survival and vigor of perennial plants (Wright 1971; Ewing and Engle 1988; Bidwell and Engle 1992), and soil microbiology and chemistry (Norton and McGarity; Hulbert 1988; Raison 1979; Ojima et al. 1994). In addition, differing species responses to fire temperature may impact competitive interactions, potentially altering population dynamics and community composition in the longer term (Bidwell and Engle 1992; Blankenspoor and Larson 1994; Grilz and Romo 1994).

Temperatures recorded during grass burning are variable and depend mainly on fuel distribution, moisture content, and prevailing weather conditions (Daubenmire 1968). Since the temperature at soil surface is ecologically important and the soil surface is a reasonably good reference point for comparing maximum fire temperatures between communities, this review will focus mainly on fire temperatures at or near the soil surface. I will review the reported maximum fire temperatures in grasslands, the relationship between soil surface temperatures and fire residence time, site factors affecting maximum fire temperatures, and the vertical distribution of temperatures during grassland fire. The intention of this review is to provide a context for temperatures we recorded in prescribed burns in an upland prairie in western Oregon.

Grassland Fire Temperatures

Temperatures measured at the soil surface during grass fires range from 38°C (Bentley and Fenner 1958) to 682°C (Stinson and Wright 1969). Fire temperatures of upland prairies in western Oregon have not been recorded, but several studies have measured fire temperatures in Willamette Valley wetland prairies, or in vegetation similar to upland prairie, but outside western Oregon. September burns in Willamette Valley wetland prairies have ranged between 38°C and 371°C at soil surface

(Pendergrass 1995). In central California, Bentley and Fenner (1958) reported maximum soil surface temperatures of 38°C to 121°C during a September burn in annual grasses. McKell et al. (1962) measured much higher maximum soil surface temperatures of 168°C to 593°C during an August burn in the same general type of vegetation. A bunchgrass fire in Japan yielded soil surface temperatures ranging from 86°C to 324°C (Ito and Iizumi 1969).

In the mixed and tallgrass prairies of North America, temperature ranges have generally been reported to be similar to those of McKell et al. (1962), ranging from 83°C to 682°C (Stinson and Wright 1969). However, mixed and tall grass prairie fires have been more commonly measured between 150°C and 480°C at soil surface (Stinson and Wright 1969; Rice and Parenti 1978; Engle et al. 1989; Engle et al. 1993).

In many other grassland burns, reported soil surface temperatures were relatively cool. Cheplick and Quinn (1988) recorded maximum soil surface fire temperatures of 85°C while burning grasslands in the New Jersey Pine Barrens. Australian native pasture burns yielded maximum soil surface temperatures ranging from 50°C to 78°C (Norton and McGarity 1965). In the long-leaf pine region of the southeastern US, where the primary fuel is dense grass, fire temperatures at soil surface reached between 65°C and 135°C (Heyward 1938). A hotter average soil surface temperature of 300°C was reported from a burn in a dry savanna-type grassland near New Guinea (Scotter 1970).

Relationship Between Maximum Temperatures and Duration of Heat

There is a strong positive correlation between soil surface temperatures and fire residence time (i.e. the length of time flames burn at one spot) in grassland fires (McKell et al. 1962; Smith and Sparling 1966a; Daubenmire 1968; Stinson and Wright 1969; Engle et al. 1989; Bidwell and Engle 1992). Fire residence time is increased where there is a heavy standing crop, large litter accumulations, or dense tussocks (Daubenmire

1968; Raison 1968). In a study in a mixed grassland in Texas, the cooler fires (those with soil surface temperatures of less than 260°C) maintained soil surface temperatures of at least 66°C for less than 2 minutes, while temperatures under the hottest fires remained above 66°C for up to 5.4 minutes (Stinson and Wright 1969). A slowly burning grass and brush understory in an open pine forest maintained higher temperatures for a longer period (Smith and Sparling1966). Scotter (1970) emphasized the predictability of this time-temperature relationship by basing his model of grassland fire soil temperatures on the duration of time the fire remains above 100°C. An exception to this trend usually occurs when fuel moisture is high enough to slow combustion and thus slow the spread of fire (Engle et al. 1993).

Burns may be prescribed to manipulate residence time, and thus soil surface temperatures, for management purposes by burning with or against the wind. A fire spreading against the wind is slower than when spreading with the wind, exposing the soil to higher temperatures for a longer period (Daubenmire 1968; Raison 1968). McKell et al. (1962) reported that slow-burning into a wind increased seed damage to an invasive annual grass.

It is well known that heat damage to seeds and other plant tissues is dependent on the duration of specific elevated temperatures (Daubenmire 1968). Time-temperature relationships have been used to quantify fire behavior and to explain the effects of fire on vegetation (Stinson and Wright 1969; Wright 1971; Hobbs and Gimmingham 1984). Because maximum soil surface temperatures are a reflection of fire residence time and temperature, they are useful surrogates for measures of the thermal environment of seeds, vegetative plant tissues, and soil.

Factors Affecting Fire Intensity

Temperatures of grassland burns depend mainly on fuel loads, moisture content, and prevailing weather conditions (Daubenmire 1968). One of the most influential factors affecting grassland fire intensity is the fuel load (Daubenmire 1968; Raison 1979). Grasslands with larger accumulations of herbaceous litter often generate higher burning temperatures for a longer period of time than those with less litter (Stinson and Wright 1969; Wright 1971; Ewing and Engle 1988), and through increased flammability, generally burn more completely (Bragg 1982). Stinson and Wright (1969) reported that in a series of burns in Texas, maximum soil surface temperatures (as well as residence time) increased proportionally with fuel load. Likewise, in tallgrass prairie, Engle et al. (1989) found fire intensity increased 400% from low fuel plots to high-fuel plots with more than twice the fuel load. On the other hand, Bentley and Fenner (1958) noted that unburned litter acted as an insulator. The highest soil surface temperatures occurred when the litter layer was very thin (<6mm). Incomplete burning of the litter accounted for lower temperatures at the soil surface in areas with deeper litter, where temperatures greater than 93°C occurred only in the upper part of the litter. Heyward (1938) also found that areas with thick, compact fuel at the soil surface did not burn completely, probably due to insufficient aeration in these fuels.

Fuel moisture levels also may influence maximum fire temperatures, especially at high levels. Higher moisture fuels may burn less completely and at lower temperatures than drier fuels. In two burns in tallgrass prairie, with roughly equal fuel loads, Engle et al. (1993) recorded a maximum soil surface temperature of 489°C when fuel moisture was 17%, but only 395°C with 76% fuel moisture. High fuel moisture can decrease fuel flammability, potentially increasing the amount of unburned litter (McKell et al.1962; Bragg 1982). In a British heathland fire, a mat of high moisture mosses did not ignite and insulated the soil surface from high temperatures (Hobbs and

Gimmingham 1984). However, differences when fuel moisture is low may not be significant to fire temperatures. Stinson and Wright (1969) found no moisture effect on fire temperature within a range of 12% to 22% on mixed Texas Prairie.

There are many other factors that may potentially affect grassland fire temperature, including ambient air temperature, wind speed, relative humidity, and slope. Fires can burn hotter in warmer ambient temperatures (Stinson and Wright 1969). Winds may elevate fire temperatures by increasing the oxygen supply (McKell et al. 1962; Daubenmire 1968; Wright 1971). High humidity may also lower fire temperatures by increasing fuel moisture (McKell et al. 1962; Daubenmire 1968; Engle et al. 1993), but may be inconsequential after ignition and spread (Smith and Sparling 1966; Stinson and Wright 1971). Finally, the area's topography can affect burn temperatures as fire burns uphill at a faster rate as the slope becomes steeper (Daubenmire 1968).

Vertical Distribution of Fire Temperatures in Grasslands

Soil heating below a grassland fire decreases rapidly with depth, with temperature increase negligible below 1 cm (Heyward 1938; Bentley and Fenner 1958; McKell et al. 1962; Scotter 1970; Wright 1973; Cheplick and Quinn 1988). Soil is a very good insulator because even the uppermost soil temperature cannot exceed $100^{\circ}C$ until all soil water has evaporated and dry soil does not conduct heat as well as moister soil (Scotter 1970). Heyward (1938) measured temperatures no higher than $80^{\circ}C$ between 3 mm and 6 mm below the soil surface, even under the highest fuel loads where flames reached 4 meters high. Thus grassland seeds, meristems, and vegetative organs below the soil surface are generally protected from damaging temperature increase, especially since most grassland fires heat the soil for a relatively short duration of time (Heyward 1938; Bentley and Fenner 1958; McKell et al. 1962; Scotter 1970; Cheplick

and Quinn 1988; but see Ewing and Engle 1988). In addition, this low heat transfer below the soil surface limits heat-related changes in soil fertility or microfauna. If the soil temperature attained is sufficiently high, soil organic matter can be destroyed and damage to soil biota can occur, causing a depletion of soil fertility. However, even during very intense grassland fires, the heat generated within the soil is usually insufficient to destroy organic matter (Norton and McGarity 1965).

Above the soil surface, temperatures vary, depending on the height and structure of the fuel, but they are usually much hotter than the temperatures at the soil surface (Smith and Sparling 1966; Raison 1979; Cheplick and Quinn 1988). Elevated temperatures associated with fire can damage seeds in the plant litter or on the stalk, elevated meristems, and photosynthetic tissues (Bentley and Fenner 1958; McKell et al. 1962; Wright 1971; Cheplick and Quinn 1988; Ewing and Engle 1988).

Objectives

In this study, we measured the maximum fire temperatures in three vegetation types of Willamette Valley upland prairies. Specific objectives of this study were: 1) to gain basic information on soil surface fire temperatures in Willamette Valley upland prairies; 2) to determine if there were significant temperature differences between prescribed burns in three vegetation types (native bunchgrass, annual exotic grass, or perennial exotic grass) and; 3) to evaluate the effectiveness of using small, replicated research burns to represent the fire temperatures of a larger management-style burn.

METHODS

Study Sites

Fire temperature data were collected from three vegetation types on two upland prairies in the Willamette Valley, Oregon. Two vegetation types, Native Bunchgrass and Annual Exotic Grass, were located on Carson Prairie, a south-facing upland prairie on the Oregon State University Dunn Research about 15 km north of Corvallis, Oregon. The elevation is ≈240m above mean sea level. The Native Bunchgrass site was dominated by the native bunchgrasses, *Festuca idahoensis* var. *oregana* Hack, *Elymus glaucus* Buckl., with a component of annual exotic grasses. The Annual Exotic Grass site was dominated by several annual exotic grasses including *Taeniatherum caput-medusae* Nevski, *Cynosures echinatus* L., *Bromus mollis* L., and *Avena fatua* L., as well as the forbs, *Daucus carota* L. and *Madia elegans* Don ex Lindl. The third vegetation type was located on the Amazon Dike No.2 unit of the US Army Corps of Engineers, Fern Ridge Reservoir, about 12 km west of Eugene, Oregon. This site is dominated by a perennial exotic grass, *Arrhenatherum elatius* L., although there is also a suppressed understory of other forbs and graminoids. The elevation is approximately 375m, with a flat aspect.

Fuel Load and Moisture Measurements

Fuel load was estimated by weighing litter and clipped standing herbaceous material from 0.5m × 0.5m quadrats within each vegetation type. Samples were taken from eight quadrats within the broadcast burn area of the Annual Exotic Grass site and from four quadrats in the Exotic Perennial Grass site. Due to time constraints, fuel weight data were not collected for the Native Bunchgrass site or the small plot burns of the Annual Exotic Grass site at the time of the experimental burns in September 1995.

Fuel weight data for these two sites was collected, however, in September 1996. Fuel load samples were dried at 70°C for 48 hours for measuring dry weight.

Moisture content in the fuel material was measured from small samples ($\approx$10-15 grams) of vegetation clipped from each site just prior to the first ignition. Six samples were taken within the broadcast burn of the Annual Exotic Grass site. Three samples each were taken from the Native Bunchgrass site and three from the Perennial Exotic Grass site. Fuel moisture samples were stored in airtight containers until returned to the laboratory for weighing and drying later in the day. Samples were weighed, dried for 48 hours at 70°C, and reweighed. Moisture content was calculated as a percentage of dry weight.

Fire Temperature Measurement

The maximum temperatures of the burns near soil surface were assessed with pyrometers (modified from Fenner and Bentley 1960). Each pyrometer consisted of 5cm x 7cm ceramic fiberboard with nine vertical strips of paint (Tempillaq by Tempil Division of Big Three Industries, Inc., South Plainsfield, NJ, USA) designed to melt at the following temperatures: 48, 69, 101, 139, 198, 274, 371, 500, and 649°C. A mica sheet, secured with two staples, covered the paint strips. Pyrometers were vertically inserted directly into the soil of areas to be burned and the soil was pushed around the pyrometer to eliminate air spaces. After the prescribed burn, the distance from the soil surface at which each paint melted was measured.

Experimental Design

The effect of vegetation type on burn temperatures near the soil surface was evaluated with a randomized complete block design. Eight blocks were established

within each vegetation type, with two burn plots (2m × 2.5m) per block. One pyrometer was inserted into the center of each small burn plot.

A two hectare broadcast burn within the Annual Exotic Grass was used to evaluate the effectiveness of using small plot burns to represent expected fire temperatures within a larger management-style burn. Although true replication could not be accomplished within a single broadcast burn, variability was recorded from six plots (6m × 6m) delineated within the larger burn area. Three pyrometers were installed into each plot within the broadcast burn.

Small Plot Burns

Small plot burning was accomplished by a wetting a narrow ($\approx$25 cm) mowed aisle within each plot and igniting the perimeter with a fusee. Wide buffers ($\approx$1.5m) had also been mowed and wetted around each block for safety. Small plot burns on the Native Bunchgrass site and the Annual Exotic Grass site were conducted concurrently on September 15, 1995. Burning began at 2:00pm and was completed by 3:00pm. Air temperature ranged from 30°C to 35°C with 36% to 46% relative humidity and only a slight breeze. The resulting fires were comparable to the larger broadcast burn with regard to speed, flame height, and ash characteristics (personal observation). Small plot burns on the Perennial Exotic Grass were conducted on September 19, 1995. Burning began at 11:00 am and was completed by 11:45 am. The air temperature was 23°C with 68% relative humidity and only a slight breeze. Each plot burned in 60±10 seconds with flame heights between 2 m and 4 m. These fire characteristics were comparable to those of a larger grassland fire.

Broadcast Burn

A two hectare broadcast burn area was established within the Annual Exotic Grass site of Carson Prairie. In preparation for the broadcast burn, a 2 m to 3 m foam (Firefoam 103B by Fire-Trol) firebreak was sprayed around the perimeter of the burn area. The area was burned on September 15, 1995. Fuels were ignited with drip torches. The upper slope was backburned prior to lighting the side slopes and lower slope of the burn area. The air temperature was 23°C with 63% relative humidity and only a slight breeze. Moisture content in fuel material averaged 30%. First ignition (backburning) began at 11:23 am and last flames were out by 11:40 am.

Data Analysis

The melting point distance from the soil surface for each block was calculated as the average of results from two subsamples. Pyrometers extended to 3 cm above the soil surface; when an indicator paint did not melt, it was arbitrarily given the value of 3.4 cm as the height of melting. Certain temperature paints did not melt in any plot, and were dropped from the analysis.

Average maximum temperatures (MT) for two distances (i) at and above the soil surface (0 cm and 2 cm) were also interpolated for each block from block average melting point distances with the following equation:

$$MT_i = T_{1i} + ((T_{1i} - T_{2i}) \div (MP_{2i} - MP_{1i}) \times (H_i - MP_{1i}))$$

where Hi is height of distance i from the soil surface, T_{1i} is the temperature of the indicator paint that melted immediately below distance i, MP_{1i} is the distance of its melting point from the soil surface, T_{2i}, is the temperature of the indicator paint that melted just above distance i, and MP_{2i} is the distance of its melting point from the soil surface.

Differences among treatment means were assessed statistically by analysis of variance (ANOVA), using the Statgraphics 5.0 statistical software. Means were compared by Fisher's protected least significant difference (LSD) procedure at P=0.05.

RESULTS AND DISCUSSION

Initial Fuel Conditions

The Perennial Exotic Grass site had the highest fuel loads of the three vegetation types, primarily due to the large contribution of decumbant litter (Table 4.1). Fuel loads of the Native Bunchgrass and Annual Exotic Grass sites were relatively similar to each other (Table 4.1). Fuel moisture levels were also very similar in all four burn types (Table 4.1). Although the fuel moisture content of the small plot burns in the Annual Exotic Grass site was not measured, it was presumably similar to that of the Native Bunchgrass Site, as both sites were burned simultaneously on the same south-facing slope. The somewhat higher fuel moistures of the broadcast burn in the Annual Exotic Grass site are not good indicators of the fuel moistures of the small plot burns on this site, as the larger burn was conducted several hours earlier in the day, when fuel moistures would be expected to be higher (McKell et al. 1969).

Table 4.1. Initial fuel moisture and dry weights for four types of prescribed burns. Fuel weight samples were collected and measured in two categories: standing vegetation, and decumbent herbaceous litter. Fuel moisture data were not collected at the time of the 2m × 2.5m plot burns in the Annual Exotic Grass site. * indicates that the fuel data were collected in September 1996, one year after the experimental burns were conducted. All other fuel data was collected at the time of burning in September 1995.

Vegetation Type (size of burn)	Moisture mean ± s.d.	Dry Weights (mean ± s.d.) (g/m²)		
		Standing	Litter	Total
Native Bunchgrass (2m×2.5m)	22 ± 8%	267 ± 76*	174 ± 39*	442 ± 86*
Perennial Exotic Grass (2m×2.5m)	21 ± 8%	271 ± 44	331 ± 44	602 ± 45
Annual Exotic Grass (2m×2.5m)	—	225 ± 83*	182 ± 73*	407 ± 153*
Annual Exotic Grass (2 hectare)	33 ± 16%	163 ± 45	155 ± 43	318 ± 61

Size of Burn

The broadcast burn and the small plot burns in Annual Exotic Grass showed remarkably similar maximum temperatures at all levels measured (Figure 4.1, Table 4.2). The broadcast burn did tend to reach "benchmark temperatures" (i.e. known temperatures from pyrometers) at slightly, but insignificantly, lower elevations within the measuring range (Table 4.2). The larger burn also had greater temperature variability than the small plot burns (Table 4.2).

The broadcast burn heated the soil to 48°C at an average soil depth of -5.9mm, about 1.5mm deeper, but not significantly different than that of the small plot burns. At the soil surface, the average maximum temperatures in the broadcast burn and the small plot burns were also very similar (Figure 4.1). In fact, the broadcast and small plot burns reached a maximum of 69°C at an average of slightly under (-0.03 cm) and over (0.03 cm), respectively, the soil surface. Above the soil surface, fire temperatures in the
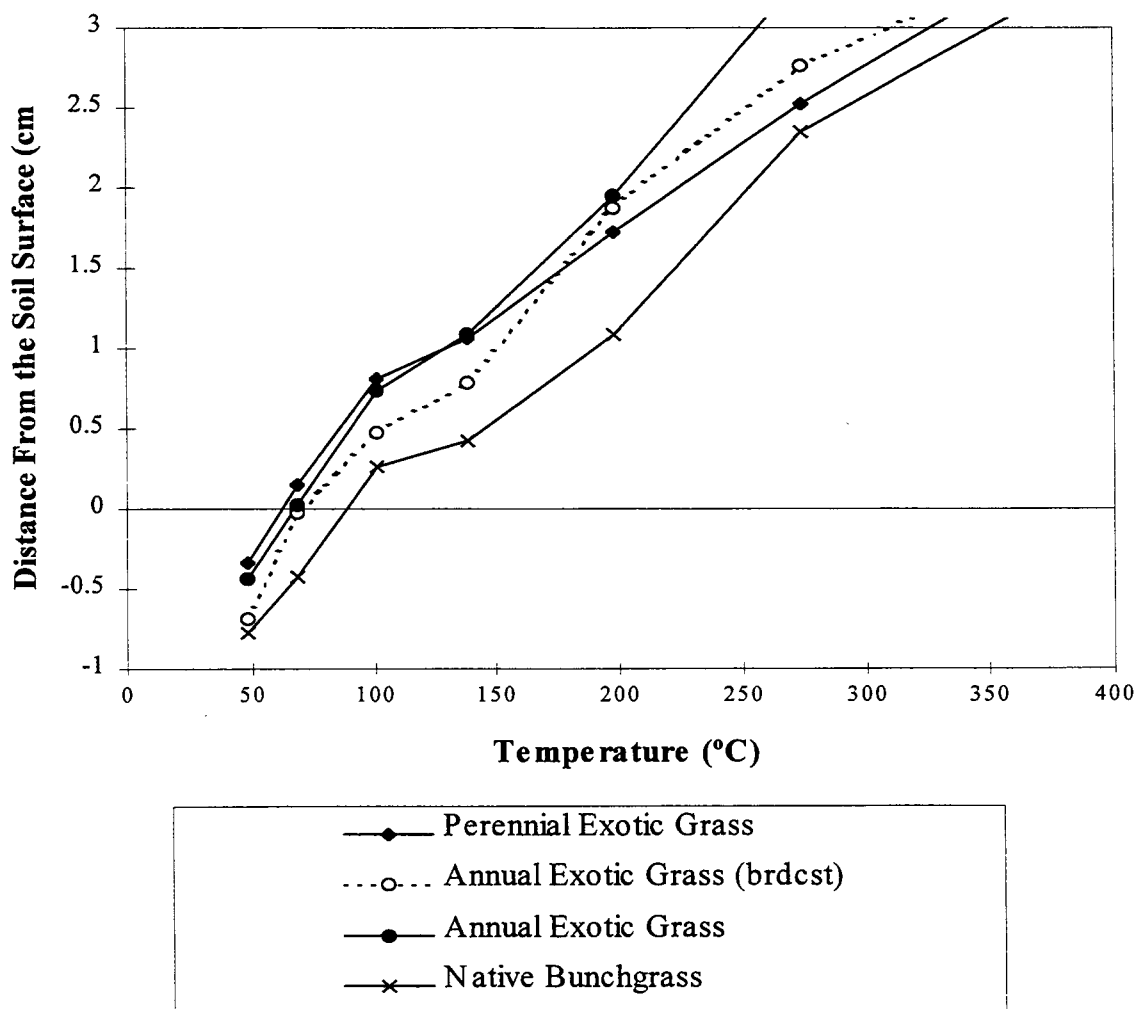
Figure 4.1. Maximum burn temperatures by distance (+ is above, - is below) from the soil surface in three vegetation types and two burn sizes. Temperatures were measured with pyrometers with temperature indicators of 38, 69, 101, 1139, 198, 274, 371, 500, and 649°C. The melting distance of each temperature indicator is an estimate of the maximum temperature reached at this elevation. Temperatures above 500°C or greater were not reached within the measuring range of 1 cm below to 3 cm above the soil surface in any vegetation type.

Table 4.2. Average maximum burn temperatures as a relation to distance (+ is above and - is below) in three vegatation types and two burn sizes. Distances measured with pyrometers. Different letters within columns indicate significant differences (Fishers protected LSD, α=0.05). When a replicate did not reach the given temperature within the measuring range of of 1 cm below to 3 cm above the soil surface, it was arbritrarily given the value 3.4 cm. An * indicates that the average includes one or more of these 3.4 cm approximations. Temperatures above 500°C or greater were not reached within the measuring range of 1 cm below to 3 cm above the soil surface.

Vegetation Type (size of burn)		Distance from the soil surface (cm)						
		48°C	69°C	101°C	139°C	198°C	274°C	371°C
Native Bunchgrass (2m×2.5m)	mean	-0.78a	-0.41a	0.26a	0.42a	1.09a	2.35a	3.18*a
	s.d.	0.25	0.35	0.42	0.41	0.38	0.52	0.38
Perennial Exotic Grass (2m×2.5m)	mean	-0.33b	0.15b	0.82b	1.07b	1.72b	2.53a	3.40*a
	s.d.	0.44	0.31	0.50	0.48	0.51	0.51	0.00
Annual Exotic Grass (2m×2.5m)	mean	-0.44b	0.03b	0.74b	1.08b	1.95b	3.32*b	3.40*a
	s.d.	0.12	0.28	0.16	0.24	0.29	0.23	0.00
Annual Exotic Grass (hectare)	mean	-0.59ab	-0.03b	0.48ab	0.76ab	1.88b	2.75ab	3.39*a
	s.d.	0.51	0.34	0.44	0.49	0.49	0.61	0.00
Summary of ANOVA	F-ratio							
	p-value	0.0411	0.0046	0.0448	0.0154	0.0035	0.0117	0.1033

broadcast burn were somewhat hotter, reaching specific temperatures slightly, but not significantly, closer to the soil surface than those in the small plot burns (Table 4.2, Figure 4.1).

This similarity increases confidence that research results taken from replicated small plot burns will translate well into expected outcomes of larger management burns. Other research indicates that when grass is the primary fuel, relatively small plots adequately represented the fire temperatures of a larger burn. Heyward (1938), studying fires in grass beneath an open pine forest, found soil temperatures in a 16 hectare burn were no higher than those measured in 3m × 3m burns. In tallgrass prairie, Hulbert (1988) reported that the heat and fire speed of 2m × 2m burn plots were comparable to those of larger burns. Moreover, McKell et al. (1962) measured soil surface temperatures of up to 580°C on 9m × 9m burns in annual grass range, further indicating that small burn plots are adequate for estimating typical grassland fire temperatures. The higher variability in temperature found in our broadcast burn did indicate that the larger burn had more patchiness in burn intensity than in the small plot burns (Table 4.2).

Soil Surface Temperatures in Three Vegetation Types

The Native Bunchgrass site plots burned significantly hotter at soil surface than those in the Annual Exotic Grass or the Perennial Exotic Grass site (Table 4.3). By interpolation, the estimated average maximum temperature at soil surface was 66°C in Perennial Exotic Grass, 69°C in Annual Exotic Grass, and 93°C in Native Bunchgrass.

Table 4.3. Average maximum burn temperatures at the soil surface and at 2 cm above the soil surface for three vegetation types and two burn sizes. Temperatures at soil surface and two centimeters above the soil surface were interpolated from the melting points of temperature indicator paints. $\Delta°C/cm$ is the average rate of temperature increase between the soil surface and two centimeters above the soil surface. Different letters within columns indicate significant differences (Fishers protected LSD, $\alpha=0.05$).

Vegetation Type (size of burn)		Temperature (°C)		$\Delta°C/cm$
		0 cm	2 cm	
Native Bunchgrass (2m×2.5m)	mean ± s.d.	93 ± 20a	258 ± 37a	82 ± 13a
Perennial Exotic Grass (2m×2.5m)	mean ± s.d.	66 ± 29b	226 ± 48a	84 ± 23a
Annual Exotic Grass (2m×2.5m)	mean ± s.d.	69 ± 7b	197 ± 21a	64 ± 11a
Annual Exotic Grass (2 hectare)	mean ± s.d.	79 ± 20ab	211 ± 42a	66 ± 18a
Summary of ANOVA	F-ratio	3.86	3.03	2.30
	p-value	0.0270	0.0546	0.1103

These temperatures were relatively cool compared to soil surface temperatures measured in other grassland fires (e.g. McKell et al. 1962). These low temperatures coupled with a short residence times probably limited any heat-dependent changes of seeds at the soil surface. Even in a tallgrass prairie fire, where the typically high fuel levels will burn at considerably greater intensities fires than those of our study (Rice and Parenti 1978; Engle et al. 1989; Engle et al. 1993), the seedbank was much more affected by the species' ability to grow in the area's burning regime than any heat related seed death (Abrams 1988; Ewing and Engle 1988). Most seed injury requires high temperatures for two or more minutes, which is much longer than the fire residence times on our grasslands. For example, heating dispersed *Taeniatherum caput-medusae*

and *Bromus mollis* seeds to 160°C for two minutes did not decrease germinability (McKell et al. 1962). Cheplick and Quinn (1988) heated dispersed *Amphicarpum* seeds to 60°C for one minute, to synthesize typical burn conditions for this species, with no measurable decrease in germinability. Annual grass seeds tested by Wright (1931) germinated completely until heated to at least 95°C for a duration of five minutes.

Below Soil Surface Temperatures in Three Vegetation Types

Burn temperatures in all three grassland types decreased markedly below the soil surface (Figure 4.1). In fact, there was no measured temperature increase (>48°C), on average, below 1 cm beneath the soil surface in any vegetation type (Table 4.2). The Native Bunchgrass site had significantly higher soil temperatures at depth than the other vegetation types, reaching 48°C at an average depth of 7.8 mm below the soil surface, compared to 4.4mm and 3.3mm, respectively, below the soil surface in the Annual Exotic Grass and the Perennial Exotic Grass sites.

These results indicate that during the grassland fires, heat transfer to the soil is mild and limited to a thin layer near the surface. The low temperatures measured in the soil are consistent with soil temperature data described in other grassland fires (Bentley and Fenner 1958; McKell et al. 1962; Norton and McGarity 1965; Scotter 1970). The cool soil temperatures were most likely due to the low residence times typical of grassland fires. All of our small plot burns had a residence time of less than one minute (personal observation), which contributed to the uniformly low heat transfer to the soil.

Soil heating is greater where there are smoldering fuels, such in brush or forest fires

(Bentley and Fenner 1960; Raison 1968).

Since burning caused only small increases in soil temperatures, little or no direct

effect of heat on buried seed populations is expected (Norton and McGarity 1965;

Daubenmire 1968; Cheplick and Quinn 1988).

Above the Soil Surface Temperatures in Three Vegetation Types

Temperatures increased with distance above the soil surface to 3cm (Figure 4.1)

and undoubtedly continued to increase to some maximum temperature closer to flame

height (Heyward 1938; Bentley and Fenner 1958; McKell et al. 1962; Cheplick and

Quinn 1988). In the Annual Exotic Grass site, maximum fire temperatures rose

approximately $64^{\circ}C$ per centimeter, to an interpolated average of $197^{\circ}C$ at 2 cm.

Maximum burn temperatures in the Native Bunchgrass and Perennial Exotic Grass sites

increased at greater rates, each averaging an increase of $82^{\circ}C$ and $84^{\circ}C$, respectively, per

centimeter within 2 cm of the soil surface. The rate of temperature increase in the

Perennial Exotic Grass site may have been influenced by an uncombusted layer (≈ 1 to 2

cm thick) of moss which may have insulated the first centimeter above the soil surface.

Above 1 cm, maximum fire temperatures increased more rapidly (Figure 4.1).

In general, fires in the Native Bunchgrass site burned at higher temperatures

above the soil surface than in the Annual Exotic Grass or the Perennial Exotic Grass

sites. Burns in the Native Bunchgrass site attained all but the highest temperature

"benchmarks" (i.e. reaching a known temperature) significantly closer to the soil surface than burns in either of the other sites (Table 4.2).

At higher elevations from the soil surface, there were fewer differences between the Native Bunchgrass and other sites (Tables 4.2, 4.3). Native Bunchgrass burns reached 274°C (the highest temperature benchmark reached by burns in all three sites) significantly closer to the soil surface than the Annual Exotic Grass burns, and closer on average, but not significantly different, than those in Perennial Exotic Grass. However, the Native Bunchgrass site was also the only site to reach the burn temperature benchmark of 371°C within some of its blocks.

The Perennial Exotic Grass and the Annual Exotic Grass sites reached most temperature benchmarks at similar distances above the soil surface, especially those reached nearest the soil surface (Figure 4.1, Table 4.2). However, the burns in Perennial Exotic Grass reached 274°C, the highest temperature benchmark attained in both these sites, significantly closer to the soil surface than the Annual Exotic Grass burns.

Summary of the Three Vegetation Types

Of the three vegetation types, the Native Bunchgrass site burned at the highest temperatures at all heights near the soil surface (Table 4.3, Figure 4.1), reaching nearly all temperature benchmarks at significantly lower elevations than those of the Annual Exotic Grass site and the Perennial Exotic Grass site (Table 4.1). These higher burn temperatures of the Native Bunchgrass site may affect this plant community differently than would burns in the other two sites. The higher temperatures may lead to greater

plant injury or mortality in the bunchgrasses than in the rhizomatous grasses of the Perennial Exotic Grass site. Senescent bunchgrasses have elevated meristems, as opposed to those of rhizomatous species which are well-protected from heat underground. In a tallgrass prairie fire, bunchgrasses were damaged or killed while the rhizomatous species were unharmed (Ewing and Engle 1988). The Annual Exotic Grass site is also less vulnerable to direct plant injury from fire because nearly all seeds had dispersed by the burn time and thus were essentially protected from heat damage in our low intensity fires

Because both the Annual Grass site and the Native Bunchgrass site were located on Carson Prairie and were burned concurrently, the differences in burn temperatures should be due to differences in vegetation and fuels rather than abiotic factors. There was very little difference in fuel weights (Table 4.1) and since they were burned at the same time in the same vicinity, there was probably little difference in fuel moisture. Even if there were small differences in fuel moistures, when fuel moistures are low, any differences in moisture are unlikely to have a significant effect on fire temperatures in an actively burning plot (Smith and Sparling 1966; Stinson and Wright 1971). The most obvious biotic factor is the growth form difference between these two grass types. Bunchgrasses have a more compact growth form than annual grasses, with greater biomass near the soil surface. The bunchgrass growth form would allow a fire to burn for a longer period of time, and thus reach higher temperatures, in a bunchgrass system than in the less dense annual grasses (Wright 1971).

The Perennial Exotic Grass site was burned on a different day in a different location than the other two sites, so there are additional variables to consider when making comparisons. Weather conditions were somewhat different during the Perennial Exotic Grass site burns: the ambient air temperature was a little cooler and the relative humidity was somewhat higher than during the other burns. Both of these factors could have lowered burn temperatures on this site (Stinson and Wright 1971).

Many studies have supported the hypothesis that higher fuel loads in grasslands burn at higher maximum temperatures (Stinson and Wright 1969; Wright 1971; Ewing and Engle 1988; Engle et al. 1989), thus it is interesting that most temperature measurements in the Perennial Exotic Grass site, especially those nearest the soil surface, were not significantly different than those in the Annual Exotic Grass site, despite the Perennial Exotic Grass site having approximately 50% more total fuel (Table 4.1). These lower-than-expected temperatures near the soil surface temperatures were probably due to an insulating effect of an uncombusted moss layer found only on the Perennial Grass site. A damp moss layer would have considerable influence on moderating near soil temperatures (e.g. Hobbs and Gimmingham 1984). In a study of Australian grassland fire temperatures, the lack of relationship between fuel load and soil temperature was speculated to be due to a continuous lower stratum of spring-growing species in the high fuel plots, which may have shielded the soil from direct radiant heat transfer (Norton and McGarity 1965). Other researchers have also noted that an uncombusted litter layer is associated with lower soil temperatures (Heyward 1938; Bentley and Fenner 1968). The assumption of an insulating moss effect is consistent

with the rapid temperature increase that occurred above the moss layer (>1cm) on the

Perennial Exotic grass site (Figure 4.1).

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CHAPTER 5

MANAGEMENT RECOMMENDATIONS

INTRODUCTION

Prior to European settlement, native prairie dominated the landscape of the Willamette Valley. These prairies were maintained through annual fires set by the Kalyapuya Indians (Boyd 1986). With urbanization, agriculture and the cessation of fire, these once vast prairies have become isolated remnants, and are gradually being invaded by woody and exotic plants. Today, these prairies are considered among the rarest of Oregon's ecosystems.

In response to conservation concerns, there has been a move to restore the remaining prairies of the Willamette Valley. The purpose of this chapter is to provide recommendations for managing and restoring upland prairies in the Willamette Valley based on the results of the three major research topics: 1) fire effects on seedling establishment, 2) seed germinability and dormancy characteristics of common upland prairie plants, and 3) maximum temperatures of grassland fires near the soil surface.

SPECIES SELECTION FOR SEEDING MIXTURES

Sowings seeds is a common way of reintroducing native plants into degraded sites. Most seeds of species native to Willamette Valley upland prairie will need to be collected locally prior to sowing. These seeds, especially genetically compatible strains, are not generally available commercially. Seed collection is labor-intensive, and thus one criterion for species selection should be its establishment potential from seed in a degraded site.

Germinability

The potential for germination is a practical consideration for selecting species for sowing mixtures. Chapter 3 described a study of the germinability of filled seed for two native grasses and four native forbs commonly found on upland prairies in the Willamette Valley. The native grasses, *Elymus glaucus* L. and *Festuca rubra* L.[1], and the native forbs, *Madia elegans* Don ex Lindl., *Madia gracilis* (Smith) Keck, and *Potentilla gracilis* Dougl. had high proportions (>80%) of germinable seed. These five species are good candidates for use in a sowing mixture based on their high germinability.

On the other hand, filled seeds of the native forb, *Eriophyllum lanatum* (Pursh) Forbes, had low germinability (<50%) even following several treatments to stimulate germination (Chapter 3). Furthermore, collected seeds of *Eriophyllum lanatum* were of very low quality compared to those of the other native species, with less than 20% filled seed (personal observation). The poor germinability of filled seeds, combined with the overall low quality of collected seed makes *Eriophyllum lanatum* a poor candidate to be included in a sowing mixture. If the presence of this species is desired, alternative methods of introduction, such as planting plugs, should be investigated.

Festuca rubra vs. *Festuca idahoensis* var. *roemeri*

Festuca idahoensis Elmer var. *roemeri* Pavlick is the native fescue species of Willamette Valley upland prairies (B. Wilson, personal communication). Another common bunchgrass of upland prairies, *Festuca rubra* , has recently been identified by

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[1] *Festuca rubra* has recently been re-defined by taxonomists as an introduced cultivar and not a true native species. Nonetheless, *Festuca rubra* closely resembles the native fescue (*F. idahoensis* var. *roemeri*) and is often found in association with native prairie plants.

Oregon State University taxonomists as an introduced (exotic) cultivar (B. Wilson, personal communication). Nonetheless, *Festuca rubra* closely resembles the native fescue (*F. idahoensis*) and is often found in association with a native prairie community, including rare and endangered prairie species (personal observation).

Festuca idahoensis was not tested for germinability, due to lack of suitable seed, but seed collections of this species were of low quality (<20% filled seed) when compared to those of *Festuca rubra* (70-90% filled seed) (personal observation). Also, in field experiments with sowed seeds, the proportion of *F. rubra* establishment from seed was roughly double that of *F. idahoensis* (Chapter 2), suggesting that the "restoration potential" of *F. rubra* is considerably greater than that of the truly native *F. idahoensis*.

In sites where conserving the integrity of native *Festuca idahoensis* is not a concern, i.e., where no *F. idahoensis* exists on site or in the near vicinity, sowing *Festuca rubra* is the best choice for maximizing seedling establishment. However, on sites containing existing populations of *F. idahoensis* (or where it occurs in the near vicinity) efforts should be made to only include local collections of the native fescue (*F. idahoensis*) into the sowing mixture. This precaution will better protect these remaining native fescue populations from possible genetic contamination and/or competition with an introduced cultivar.

TIME OF SOWING

Native seeds should be sown in the autumn, just prior to fall rains, to take advantage of early germination and cold stratification. This recommendation is based on the results of a laboratory study (Chapter 3) and a field study (Chapter 2) concerning time of germination and dormancy characteristics of native seeds.

Laboratory results indicated the native grasses, *Elymus glaucus* and *Festuca rubra*, are non-dormant in the fall, and thus should germinate following the first fall rains (Chapter 3). Field data support this conclusion, as nearly all *Elymus* and *F .rubra* grass germination occurred in the fall (Chapter 2). Although the germinability of the native grass *Festuca idahoensis* was not tested in the lab, due to lack of suitable seed, field tests with sowed seeds of this species indicated that this native grass also germinates primarily in the fall (Chapter 2).

The native forbs were more likely to require a period of cold stratification for germination to occur. In particular, the perennial forbs, *Eriophyllum lanatum* and *Potentilla gracilis*, had very low germinability prior to being chilled, and the proportion of germinated seeds increased dramatically following six weeks of cold stratification (Chapter 3). Results of field study supported these conclusions, as most or all seedling emergence for *Eriophyllum* and *Potentilla* occurred after December (Chapter 2). The annual forbs, *Madia elegans* and *Madia gracilis*, also required chilling for maximum germinability, but nonetheless, the majority of seeds (63% and 71%, respectively) from these species were also non-dormant in the fall (Chapter 3).

Sowing native seed just prior to fall rains allows non-dormant seeds to germinate at first opportunity. Early germinating seedlings often have a competitive advantage over later-germinating seedlings (Ross and Harper 1972) and are better able to compete with mature plants in the spring. Fall sowing also exposes seeds to a period of cold temperatures during the winter months, which is very important for maximum germination of native forbs (Chapter 3).

CONTROL OF WEEDY SPECIES

Understanding the germination characteristics of pest species is useful to know for devising strategies for their control. Many species of weedy plants have high

germinability (Chapter 3) which would promote their regeneration, making them a problem in restoration projects. In particular, seeds of the grasses, *Arrhenatherum elatius* L., *Dactylis glomerata* L., and *Taeniatherum caput-medusae* Nevski., and the forbs *Centaurea cyanus* L., *Chrysanthemum leucanthemum* L., and *Hypochaeris radicata* L. were non-dormant in the first autumn after dispersal (Chapter 3), indicating that these species do not form a large persistent seed bank. For species such as these, site treatment efforts, such as mowing before seed maturation, could be made to control the spread of new seedlings as part of the restoration effort.

Unfortunately, prescribed burning cannot be expected to decrease the germinability of dispersed weed seeds present on the site. September burns in Willamette Valley upland prairies have relatively cool maximum fire temperatures at soil surface, combined with short residence times (Chapter 4), so that little or no heat-damage to seeds would be expected.

For the perennial exotic grasses, *Arrhenatherum elatius* and *Dactylis glomerata*, field study results indicate that, despite high germinability, these grasses proliferate little from seed (Chapter 2). Thus efforts to control these perennial grasses should be aimed toward reducing vegetative growth, rather than controlling spread from seeds.

PRESCRIBED BURNING AS A RESTORATION TOOL

Even when sown seeds are highly germinable, restoration through sowing will be unsuccessful if desired seedlings cannot emerge and survive the conditions into which they have been sowed. Prescribed burning, often a top candidate as a restoration tool in upland prairies, primarily due to its effectiveness in controlling woody species encroachment, may also have significant effects on both native and exotic seedling establishment. Chapter 2 examined the effectiveness of prescribed burning for improving native seedling establishment, while not encouraging a greater invasion of

exotic species, in three vegetation types: a low quality prairie dominated by annual exotic grasses (Annual Exotic Grass site); a low quality prairie dominated by *Arrhenatherum elatius* (Perennial Exotic Grass site); and a medium/high quality site dominated by native bunchgrasses (Native Bunchgrass site).

Annual Exotic Grass Site

Prescribed burning in September was an effective site treatment for improving the establishment of sowed native seed into an upland prairie dominated by annual exotic grasses, although burning also increased the establishment of short-lived weedy species. Sowing native seed into burned sites significantly promoted both the collective and the individual species seedling establishment of all four common native grassland plants tested (*Elymus glaucus*, *Eriophyllum lanatum*, *Festuca idahoensis*, and *Madia elegans*). Although the burn treatment also enhanced the collective establishment of the common exotic species above unmanipulated levels, only *Centaurea cyanus*, as an individual species, had significantly more seedling establishment in the burned plots than in the unmanipulated plots. However, it is likely that seedling competition in artificially high densities corrupted a significant *Taeniatherum caput-medusae* increase in burned plots. Burning increased the success of sowed native seedlings proportionally more than those of the exotic species, while on unburned plots, native and exotic species established at very similar rates.

Unfortunately, under natural conditions, exotic species seed production in the Annual Exotic Grass Sites would undoubtedly overwhelm the quantity of native seeds that could be realistically collected and imported to the site. Thus, because burning significantly increases collective exotic seedling establishment, prescribed burning could create a greater weed problem. Burning could be most beneficial if exotic species seed

production was first reduced before sowing, such as by mowing prior to seed maturation, and sowing native seeds into burned plots.

The effectiveness of sowing native seed into unburned plots was extremely limited in establishing native seedling populations, suggesting that sowing native seed into unburned annual grass prairie would be largely ineffective in promoting a native species community. Likewise, there was less exotic seedling establishment in unmanipulated than in burned plots. As *Madia elegans* was the only native species well-represented naturally on the site, seeds of other native species would have to be imported for a restoration effort through prescribed burning. If sowing native seed is not an option, leaving the site unburned would maintain exotic plants at lower levels until a sowing project into a burned area could be implemented.

Perennial Exotic Grass Site

Prescribed burning was a very effective site treatment for improving the establishment of sowed native seed into a prairie dominated by the exotic perennial grass, *Arrhenatherum elatius* (tall oatgrass). Burning also created significantly more favorable microsites for one certain exotic species tested, *Hypochaeris radicata*, but the establishment response for native species was generally much more dramatic than for the exotic species.

Like the Annual Exotic Grass site, sowing seeds into unburned plots in the Perennial Exotic Grass site was largely ineffective in establishing native seedlings. Few native seeds were able to become established in unburned vegetation, suggesting that there is little restoration potential in sowing seeds into unburned perennial exotic grass stands.

Controlling the dominance of *Arrhenatherum elatius* is an important concern, as this rhizomatous grass dominates the site, making establishment of new plants a

challenge. However, this species appears to propagate little from seed (Chapter 2), so attempting to manipulate *Arrhenatherum* seedling establishment in mature stands, through site treatments is not a worthwhile endeavor. Fortunately, burning promoted the seedling establishment of other species, especially the natives, without increasing *Arrhenatherum* seedlings.

Native Bunchgrass Site

Prescribed burning was a poor site treatment on a medium-high quality site dominated by native bunchgrasses for promoting native species through seedling establishment. Native seedling establishment in burned plots did not significantly improve on burned seedbeds, but instead, burning actually encouraged short-lived weedy exotics.

Because this site had a large component of mature native species (and thus a natural seed supply), a goal of prescribed burning on this site would be to maintain or improve the existing native population, rather than to improve the seedbed for imported seed. Average native seedling establishment was generally higher in burned than in unburned plots, although not significantly so. Thus, a burn could be prescribed for another restoration purpose, such as for controlling shrub encroachment, without decreasing native seedling establishment.

Unfortunately, prescribed burning did promote the seedling establishment of *Taeniatherum caput-medusae* and *Daucus carota*. Both of these species are short-lived exotic pests, which rely exclusively on seeds for proliferation. Therefore a prescribed burn could degrade this site by shifting it towards a low-quality exotic annual grassland, through an increase in weedy short-lived species.

Prescribed burning may pose additional threats to this higher quality native bunchgrass sites besides those of encouraging weedy invaders. The significantly higher

burn temperatures measured in the native bunchgrasses than in the degraded sites (Chapter 4) may have negative consequences on previously unburned mature bunchgrasses. The high burn temperatures associated with this site may lead to bunchgrass injury or mortality. Senescent bunchgrasses are more vulnerable to heat-related damage due to their elevated meristems, as opposed to those of rhizomatous species (such as *Arrhenatherum elatius*) which are well-protected from heat underground. For example, in a tallgrass prairie fire, bunchgrasses were damaged or killed while the rhizomatous species were unharmed (Ewing and Engle 1988). The Annual Exotic Grass site is also less vulnerable to direct plant injury from fire because nearly all seeds had dispersed by the time of burning and thus were essentially protected from heat damage in our low intensity fires. First year response of mature bunchgrasses to burning on this higher quality site show a tendency (although not significant) for the cover of burned bunchgrasses to decrease relative to their unburned counterparts (M. Maret, unpublished data). However, such short term data on cover response is not conclusive and longer term monitoring is necessary to detect true trends (i.e. Wilson and Clark 1996). In the meantime, if fall burning on higher quality upland prairie is desired, the prescription should be written for fires to be conducted on cooler, more humid days, to limit fire intensity (Chapter 4) and potential bunchgrass injury. On low quality prairie, especially those dominated by perennial weeds, intense fires are desired, to maximize potential damage to unwanted plants.

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APPENDIX

APPENDIX

COMMON NAMES OF SPECIES MENTIONED IN THESIS

<u>Species</u>	<u>Common name</u>
Arrhenatherum elatius L.	Tall oatgrass
Avena fatua L.	Wild oats
Bromus mollis L.	Soft cheat, soft chess
Centaurea cyanus L.	Bachelor buttons
Chrysanthemum leucanthemum L.	Ox-eye daisy
Cynosurus echinatus L.	Dogtail grass
Dactylis glomerata L.	Orchardgrass
Daucus carota L.	Queen Anne's lace, wild carrot
Elymus glaucus Buckl.	Western rye-grass
Eriophyllum lanatum (Pursh) Forbes	Common woolly sunflower
Festuca idahoensis Elmer var. *roemeri* Pavlick	Roemer's Idaho fescue
Festuca rubra L.	Red fescue
Hypochaeris radicata L.	Hairy cat's ears
Madia elegans Don ex Lindl.	Showy tarweed
Madia gracilis (Smith) Keck	Spreading tarweed
Plantago lanceolata L.	English plantain
Potentilla gracilis Dougl.	Slender cinquefoil
Taeniatherum caput-medusae Nevski.	Medusahead grass