The effect of fire on Yellowstone ecosystem seed banks

by David Lee Clark

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science in Biological Sciences
Montana State University
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Abstract:
This paper describes the seed banks of fourteen habitat types which span the full spectrum of environments found in the Greater Yellowstone ecosystem, from dry grasslands, through forested zones, to alpine tundra. Seed bank characteristics are also described across two secondary seres in which lodgepole pine was dominant, and for two mid-seral stages of a sere in which whitebark pine was co-dominant.

The effects of wildfire on the seed banks were measured. The effect of three specific temperatures (50,100, and 150°C) on germination of seed bank taxa was measured in the laboratory.

Seed bank compositio was determined by identifying and enumerating germinants from soil cores collected at three distinct sites in each habitat type. The effect of fire was estimated by comparing samples from adjacent burned and unburned portions of each site. Three successive germination trial periods were used to insure germination of most seeds.

Undisturbed seed bank densities averaged about 4000 seeds/m2, with fewer (less than 1000 seeds/m2) occurring in dry grasslands and dense coniferous forests, and more appearing in aspen groves (7000 seeds/nr) and seasonally wet meadows (14000 seeds/m2). Seed bank species richness averaged about 35 taxa/habitat type, with fewer species (10-20) in dry grasslands and dense forests. Fire reduced seed bank density and species richness in nonforested habitat types by approximately 20% and 15%, respectively. In forests, seed bank density and species richness were reduced by approximately 80% and 65%, respectively.

The density and diversity of soil seed banks parallel the aboveground density and richness. They are low where resources are limited by climate or competition. Seed bank density declines with stand age in the seres investigated, while species richness and correspondence with the aboveground vegetation remain more nearly constant across each sere.

The effect of fire on seed banks of nonforested plant communities is relatively minor. The seed banks of forests are more heavily impacted by fire, and especially in the dense coniferous forests, where undisturbed seed banks are initially depauperate. On such sites, the contribution of buried seeds to postfire revegetation may be limited.

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TABLE OF CONTENTS

TABLE OF CONTENTS--Continued

LIST OF TABLES

LIST OF TABLES--Continued

LIST OF FIGURES

ABSTRACT

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INTRODUCTION

The fires that occurred during 1988 in the Greater Yellowstone area provided a unique opportunity to investigate the effect of disturbance across an entire landscape. Extreme drought and high winds combined to create conditions under which all plant communities in the path of a fire were flammable, and a great variety of them burned, creating a mosaic of burned and unburned treatments across the full spectrum of indigenous vegetation.

Approximately 536,500 ha of forested and 32,400 ha of nonforested land were burned at varying levels of intensity by the 8 major and 241 minor fires which occurred (GYCC 1989).

Postfire data indicated that soil heating was high enough to cause complete combustion of litter and humus in only a very small percentage of this area, where fuel loads were abnormally high or intense firestorms occurred. As a result, the effect of soil heating on buried seeds and vegetative reproductive structures was felt to be relatively small over the vast majority of the region (Shovic 1988).

Current USDI National Park Service and USDA Forest Service policies generally preclude postfire reseeding in wilderness-designated areas, although exceptions do occur. The rationale for these policies is based on the realization that, because fire is an integral process in natural ecosystems, the landscape changes which result from fire are basic to the maintenance of those natural systems (Leopold et al. 1963, Houston 1971, Mutch 1977). The preservation of genotypic integrity and the

desire to minimize the introduction of noxious weeds are further reasons for these policies. Even the introduction of annuals for temporary soil stabilization may upset natural successional trajectories, while mechanical seeding methods (eg., furrowing and tilling) cause soil disturbance which is probably detrimental to those vegetative propagules that survived the fire (Ratzlaff 1990).

The adaptations to fire exhibited by many plant species (Stickney 1986) and the multi-aged mosaic of communities which characterize the Yellowstone landscape provide tangible evidence of the capability of natural processes to bring about postfire recovery. This study was done to measure the potential contribution of the soil seed bank to such recovery. Determining the actual importance of surviving seeds is left to later work.

Objectives

This study had four major objectives:

1. To compare the undisturbed soil seed banks across a wide spectrum of major northern Rocky Mountain plant communities in terms of composition and density.

2. To determine how seed bank composition and density change with increasing stand age in three forest seres.

3. To estimate the effect of fire on these seed banks, and thus on their potential contribution to postfire revegetation in each community.

4. To estimate the effect of specific temperatures on seed germination, and thus to refine the interpretation of fire effects.

Literature Review

Concepts

The soil seed bank is comprised of all viable seeds found in the litter, on the soil surface, or below the soil surface. These dormant seeds generally occur in numbers which are far greater than those of plants which contribute vegetative cover to a community (Harper 1977). The seed bank has both a horizontal and a vertical distribution, derived from the initial dispersal of seeds and their subsequent movement through the soil. The seed bank also has a temporal distribution. It contains both transient and persistent seeds (ie., seeds germinating within one year of dispersal, and seeds which remain in the soil for long periods), and thus seed bank composition may change seasonally, annually, or over a period of many years (Simpson et al. 1989).

The spatial arrangement of seeds is clustered. The aggregation of parent plants and relatively short seed dispersal distances of many species, the entrapment of seeds in soil depressions, and the caching of seeds by animals are but a few of the mechanisms which would lead to such concentrations. Bigwood and Inouye (1988) described the spatial patterns of seeds in a fallow field, and concluded that there was probably no scale at which seeds were not clustered, although the aggregation was highly irregular and the pattern was not far from random. Also, the dispersion of seeds tended to become more random with depth. This seems reasonable, since the spatial patterns of parent plants change with time. Weather and animal activity may also disperse seed aggregations.

Studies of a wide variety of plant communities have shown a consistent and precipitous decline in viable seed densities as depth of burial increased, with few or no viable seeds remaining at depths greater than 10 cm (Kellman 1970, Moore and Wein 1977, Pratt et al. 1984, Kramer and Johnson 1987, Morin and Payette 1988). In an exceptional case, viable seeds were found in English meadow soils at depths of 25 to 30 cm (Chippinpdale and Milton 1934).

The dormancy period of seeds is extremely variable among species. While the seeds of willows (Salix spp.) remain viable for only a few days, the seeds of some legumes (Fabaceae spp.) may retain viability for up to 200 years (Wareing and Phillips 1984). Factors which contribute to dormancy in seeds may include inherent traits of the species, such as incomplete embryo development prior to dispersal, the presence of a biochemical inhibitor, the nature of the seed coat, and specific photoperiod and temperature requirements for germination (Harper 1977). Environmental factors which interact to contribute to dormancy include soil moisture content, soil oxygen and carbon dioxide concentrations, light requirements resulting from burial, and the degree of scarification received by the seed coat (Harper 1977). Persistent species have adopted and adapted to various combinations of dormancy factors to provide each with the capability of temporal dispersion in a changeable environment.

Donelan and Thompson (1980) concluded that, with very few exceptions, only early and mid-successional species are capable of producing persistent seeds. They suggest that persistent seeds, due to their high cost and low return in stressful or stable environments,

should be favored in environments characterized by relatively low stress and recurrent disturbance.

The persistent seed component of the seed bank, which may contain species which are otherwise no longer present in the community, represents a partial record of the vegetational and environmental history of a site (van der Valk and Davis 1979). Following disturbance, persistent seeds may also profoundly affect the future of the site. Egler (1954) suggested that the viable propagules remaining on site may be a more important factor in defining the course of secondary succession than the dispersal of seeds from other sites.

Seed Banks of Undisturbed Communities

While the seed banks of northern Rocky Mountain grasslands have received little attention, the seed bank characteristics of other grasslands are better known. The nearest grassland communities for which seed bank data is available are a mid-grass prairie in central Saskatchewan (Archibold 1980), a mixed-grass prairie in western North Dakota (Iverson 1981), and a semiarid prairie in north-central Colorado (Coffin and Lauenroth 1989). General findings of these studies include: a) the majority of seeds were those of annual and biennial forbs; b) only moderate (25-60%) correspondence between species contributing plant cover and species of the seed bank; and c) low seed bank densities at the coolest and driest locations (446-1667 seeds/m^2 in Saskatchewan, 122-2748 seeds/m^2 in Colorado), and high seed bank densities at the location with more moderate growing-season conditions (3865-7740 seeds/m^2 in North Dakota). Studies of more distant grassland seed banks conducted by Major and Pyott (1966), Thompson and Grime (1979), Donelan

and Thompson (1980), Rabinowitz (1981), Roberts (1981), Graham and Hutchings (1988), and Abrams (1988) support these findings.

No shrubland seed banks of the northern Rocky Mountain region had been sampled prior to the present study. Hassan and West (1986) have, however, investigated a sagebrush (Artemisia tridentata) seed bank in central Utah. They found a very low seed density in this semi-desert community (92 seeds/m^2 maximum). A significant rank correlation between percent cover and viable seed density was reported, suggesting good correspondence of aboveground and seed bank taxa.

The seed banks of coniferous forests have been investigated at many locations, including two studies conducted in the northern Rocky Mountains. Kramer and Johnson (1986) investigated the Douglas fir/ninebark (Pseudotsuga menziesii/Physocarpus malvaceus), grand fir/ Rocky Mountain maple (Abies grandis/Acer glabrum), and grand fir/blue huckleberry (Abies grandis/Vaccinium globulare) habitat types in central Idaho, and Morgan and Neuenschwander (1987) investigated a red cedar/Queen's cup beadlily (Thuja plicata/Clintonia uniflora) habitat type in northern Idaho. Other studies in coniferous forests have been conducted by Olmsted and Curtis (1947), Quick (1956), Livingston and Allessio (1968), Kellman (1970, 1974), Johnson (1975), Strickler and Edgerton (1976), Moore and Wein (1977), Whipple (1978), Archibold (1978), Granström (1981), Pratt et al. (1982), Conn et al. (1984), Morin and Payette (1987), and Fyles (1989). General findings of these studies include: a) low (20-30%) correspondence of species contributing plant cover and species in the seed bank, with large numbers of early to mid-seral annual, biennial and perennial forb seeds, and few shrub and

tree seeds; and b) very low to moderate seed bank densities (a median of about 600 seeds/m^2). The ponderosa pine (Pinus ponderosa)-dominated community sampled by Pratt et al. (1982) was a notable exception. This relatively open forest contained very high seed bank densities (about 14000 seeds/m^2), and had better (55%) correspondence between cover-contributing and seed bank species.

The seed banks of alpine tundra communities were sampled by Archibold (1984) and Morin and Payette (1987). Studies of arctic tundra seed banks have been conducted by Leck (1980), McGraw (1980), Freedman et al. (1982), Fox (1983), Gartner et al. (1983), Roach (1983) and Archibold (1984). General findings of these studies include: a) good correspondence between cover-contributing and seed bank species, the vast majority of seeds being those of perennial forbs, graminoids, or shrubs present in the vegetation; and b) seed densities ranging from 0-21,859 seeds/m^2. The frigid conditions of tundra sites may confound the transient/persistent seed dormancy classification, since otherwise transient seeds may remain viable for prolonged periods at the low soil temperatures which prevail (McGraw and Vavrek 1989). Although low seed production is typical of tundra vegetation (Savile 1972, Bell and Bliss 1980), moderately high seed bank densities resulting from low turnover of seeds would seem a reasonable expectation in tundra communities. The large seed banks reported by McGraw (1980), Fox (1983), and Archibold (1984) seem to support this premise.

Effect of Fire on Seed Banks

There are two major sources of propagules that initate the postfire vegetational recovery of a site. These may be termed the offsite colonizers, whose seeds are carried from other locations by animals, wind, and water, and the survivors. The survivors include vegetative propagules (rhizomes, corms, caudices, and bulbs) which resprout, and residual colonizers, the seeds of which survived in either the crowns of trees or within the soil seed bank (Stickney 1986).

Seeds are generally able to tolerate considerable exposure to heat. Sampson (1944) found that grass seeds survived temperatures of 82°C to 116°C for 5 minutes. He also determined that the seeds of most chaparral species survived temperatures of 115°C to 127°C for 5 minutes, and that species with particularly hard or thick seed coats tolerated temperatures of 150°C.

Fire may also enhance germination in some taxa. Temperatures of 115°C to 130°C usually increased the rate of germination in chaparral species (Sampson 1944). Ehrenreich and Aikman (1963) and Grant et al. (1963) reported a higher percentage of germination in seeds from burned grassland sites than in seeds from adjacent unburned sites. Seed coat characteristics, such as unusual thickness and hardness, or the presence of a water-impermeable coating, may require alteration by heat treatment for germination to occur. Fire may promote germination of seeds through alteration of the seedbed environment. Germination cues may result from increased solar heating of blackened soils, chemicals leached from charred wood, release from inhibiting compounds, and increased light and stratification due to the combustion of litter and duff layers (Parker

and Kelly 1989). Many of these factors, as well as the reduction of competition from formerly present plants and the increased availability of mineral nutrients (Sharrow and Wright 1979), may also enhance seedling survival and development.

The frequency of fire may drastically affect seed bank composition and renewal. If the intervals between fires are too long, seed longevity may be exceeded, and if intervals are too short, perennial plants may not have time to produce seed (Zedler et al. 1983, Fox and Fox 1986). The relative dominance of sprouting and nonsprouting species in the postfire vegetation is thus influenced by fire frequency (Gill 1975, Gill and Groves 1981). The implications of fire frequency to secondary succession must therefore be considered by managers considering modification of fire frequencies.

The seasonal timing of fire affects germination and seedling establishment in terms of seedbed environment (Parker 1987), predation (Bond et al. 1984), and dispersal of offsite colonizers. Fires which occur in different seasons will have different impacts on the seasonally transient component of the seed bank.

Clearly, the effect of fire on seed banks is not simply a question of how many seeds are destroyed. The variables which interact before, during, and after a fire to produce the final effect are many, and our understanding of them in most plant communities is very incomplete.

While one expects buried seeds of grasslands to be little affected by fire, seeds very near the soil surface are likely to be destroyed. Soil surface temperatures of grassland fires may range from 83°C to 682°C, depending on the amount of fine fuel accumulation and the wind

conditions during the fire, although temperatures in excess of 66°C generally last for less than 6 minutes (Stinson and Wright 1969). Temperature increases below the soil surface were negligible at depths of 0.6 cm (Heyward 1938) and 1.0 cm (Norton and McGarity 1965).

Few studies of the effect of fire on grassland seed banks test our hypothesis. In one tall-grass prairie community in northeastern Kansas, seed bank densities decreased by 16% in a 4-year burn interval, and by 50% in an annual burn interval (Abrams 1988). Both decreases were primarily attributable to losses incurred by only one species, Kentucky bluegrass (Poa pratensis).

Buried seeds are more likely to be affected by heat in shrubland fires than in grassland fires. The range of soil surface temperatures in California chaparral fires (260°C to 685°C) are similar to those given for grassland fires. The duration of heat exposure is longer, however; temperatures exceeding 100°C may last for 15 minutes (DeBano et al. 1977). Below the surface, temperatures range from 90°C to 195°C at a depth of 2.5 cm, and the maximum temperature at a depth of 5 cm for all fire intensities is about 50°C.

Consistent with our expectation, fire caused an immediate 55% reduction in total seed bank density in a sagebrush shrubland (Hassan and West 1986). Only a few species of grasses exhibited significant postfire decreases. Cheatgrass brome (Bromus tectorum) seed density was immediately reduced as a result of the fire, although one year later the density of this species in the seed bank was nearly twice as high in the burned treatment as in the control.

The potential for depletion of seed bank reserves as the result of fire is probably even higher in coniferous forests, particularly where large fuel loads have accumulated. Fires in coniferous forests may result in extremely high soil surface temperatures. Bentley and Fenner (1958) estimated that where heavy accumulations of logs and deep slash occur, surface temperatures may reach 1005°C. While burning Douglas fir slash, Neal et al. (1965) reported temperatures of 432°C at a soil depth of 0.6 cm, 182°C at 2.5 cm, 83°C at 7.6 cm, and 62°C at 12.5 cm. These temperatures probably represent a worst-case scenario, and soil temperatures reached during the burning of coniferous forests undoubtedly range between those cited for shrublands and those cited here.

Two previous studies have indicated that serious declines in seed bank density do not always occur, however. In a spring burn of a mixed white spruce/paper birch/quaking aspen (Picea glauca/Betula papyrifera/Populus tremuloides) forest in northern Saskatchewan, seed densities were highest on moderately burned (ground fire) plots, and virtually identical on the unburned and most intensely burned (crown fire) plots (Archibold 1978). Autumn broadcast burning of clear-cuts did not cause a difference between shrub seedlings on 2-year-old burns and shrub vegetation on undisturbed plots, although red-stem ceanothus (Ceanothus sanquineus) seedling cover was substantially greater on the burned plots (Morgan and Neuenschwander 1987). While no other previous studies have investigated the effect of fire on coniferous forest seed banks, many authors discuss the implications of burning on their study areas.

The effect of fire on cottongrass (Eriophorum vaginatum) tussock tundra communities was investigated by Wein and Bliss (1973) in northern Alaska. The contribution of the seed bank to postfire recovery was minor, due to high seedling mortality. Resprouting was the primary source of postfire vegetation, and no offsite colonizers were recorded. Brief (30 to 150 seconds) exposures to artificial heat treatments of 100°C, 200°C, and 300°C indicated that cottongrass seeds within the burned peat profile would not have survived the fire.

Two previous studies have included the application of artifical heat treatments to seed bank samples. Strickler and Edgerton (1976) compared germination from samples subjected to prestratification heat treatments at 60°C, 80°C, and 100°C to controls. Although the 60°C and 80°C treatment samples produced more seedlings than the control samples, and the 100°C treatment samples produced the fewest seedlings, treatment means were not significantly different. Pratt et al. (1984) compared samples subjected to 75°C and 100°C heat treatments, both before and after stratification, to controls. The maximum number of seedlings occurred in the 75°C prestratification treatment. Poststratification heat treatments significantly inhibited overall germination. The germination response of individual species to heat treatments ranged from inhibition to stimulation.

Seed Banks of Successional Series

The seed bank characteristics of a secondary successional series were first studied by Oosting and Humphreys (1940) in an old field/pine/oak-hickory series in the Piedmont region of North Carolina. In this region, weeds and grasses dominate abandoned fields for approximately

the first 10 years, pines are dominant for the next 100 years, and stands of co-dominant oak and hickory ultimately occupy the former fields. The sites investigated ranged in age from 0 to 200+ years since abandonment. Seed bank density declined irregularly with stand age; a maximum density of 13,181 seeds/m^2 was recorded in a field abandoned for one year, while 1,180 seeds/m^2 were obtained from an oak-hickory stand. The number of species occurring in the seed bank, however, remained relatively constant with time. Seed banks were composed of species represented in the aboveground vegetation of each seral stage, as well as species which persisted from previous stages but were no longer present in the vegetation. Many of the species occurring aboveground in the forested stages were rare or absent in the seed bank. This was especially true for woody taxa.

Livingston and Allessio (1968) investigated the seed banks of an oldfield successional sere in Massachusetts. Sampled sites ranged from a field abandoned for one year to an 80-year-old pine stand with a hardwood understory. Seed bank density exhibited a slight tendency to decline with stand age; a maximum of 5,016 seeds/m^2 in a 25-year-old pine stand and a minimum of 1,249 seeds/m^2 in a 36-year-old pine stand were recorded. No trend was apparent in the number of species occurring in stands of different ages. Although a slight majority of seed bank species were also present as aboveground vegetation, many seeds were of species common in younger stages of the sere, but no longer present aboveground. The seeds of shrubs and trees were rare.

In England, Donelan and Thompson (1980) studied the seed banks of a sere ranging from quarried grassland through shrubland to mature oak

woodland. The quarry site had been abandoned for 15 years, while the oak woodland site was at least 200 years old. Seed banks declined irregularly in both density and number of species. Correspondence of seed bank species and the aboveground vegetation was poor; several species common in the vegetation were absent or rare in the seed bank, and among woody taxa, only the seeds of birch were found. A lack of persistent seeds from previous age classes is a notable contrast to the earlier studies in America. The authors attribute this finding to the largely hypothetical nature of the successional series.

In northern Sweden, Granström (1982) studied the seed banks of coniferous forest stands ranging in age from 16 to 169 years. No decline in seed bank density with stand age was found, with a maximum of 758 seeds/m^2 in the 169-year-old stand, and a minimum of 239 seeds/m^2 in a 29-year-old stand. The number of seed bank species decreased slightly in older stands. Good correspondence of cover-contributing and seed bank species was reported throughout the sere. The author suggests that the differences from previous studies are due to the historically low frequency of disturbance of the study area. The relatively high degree of human manipulation in these stands, ie., select-cutting and thinning, may also contribute to these findings.

In an investigation of seed bank changes resulting from clearing and cultivation of forests in Alaska, Conn et al. (1984) sampled the seed banks of cleared, but uncultivated forest, as well as mature spruce forest. These stands should represent the initial and final stages of secondary succession. Seed bank density in the cleared stands averaged 5,313 seeds/m^2, and density in the mature forest stands averaged 672

seeds/m^2. The number of species in both cases was very low. Half of the seed bank species present in the mature forest were native colonizers which did not occur in the aboveground vegetation. The seed bank of the cleared forest was primarily composed of native colonizers.

Houle and Phillips (1988) studied the seed banks of a primary successional series occurring in the soil-filled depressions of granite outcrops in Georgia. A winter annual characterizes the inital stage of this sere, followed by other annual forbs and lichens, mosses and perennial forbs, and ultimately shrubs, vines and trees. As stand age increased, seed bank densities changed very little, and the number of species in the seed bank increased. Good correspondence between cover-contributing and seed bank species was found. The later stages of this sere, during which an overstory canopy develops, were not sampled. The constancy of these seed bank characteristics throughout the sere is therefore unknown.

Methodology

The probable clustered spatial pattern of seeds necessitates careful consideration of the manner in which seed-containing soil samples are collected. The fact that many studies of seed banks have included samples that were both too few in number and too large in volume has been noted by Major and Pyott (1966), Whipple (1978), and Bigwood and Inouye (1988). The sample size should be as large as feasible and the volume of each sample should be small in order to maximize precision. Subsampling of multiple cores which have been collected at randomly dispersed locations may be the most practical

technique available for obtaining reasonably accurate density estimates of seed banks (Bigwood and Inouye 1988).

There are two basic methods of estimating seed bank densities from soil samples. Seeds may be extracted and counted directly, or they may be germinated and the seedlings counted. A combination of both techniques may be used if greater precision is desired (Olmsted and Curtis 1947, Johnson 1975, Conn et al. 1984, Kramer and Johnson 1987).

Seed extraction involves passing soil samples through a series of sieves in order to separate size fractions, and then removing, identifying, and counting seeds from each fraction (Olmsted and Curtis 1947). Viability of seeds may be determined by using tetrazolium chloride to stain the embryo (Malone 1967), flotation (Malone 1967, Roberts and Ricketts 1979), or petri dish germination tests (Conn et al. 1984).

The seedling emergence method generally requires the use of a greenhouse or growth chamber in order to maintain conditions favorable for germination. This method may be expected to yield underestimates of seed density, since optimal germination conditions for all species are probably never achieved. Graber and Thompson (1978) extended germination trials over 2.5 years in order to provide a variety of photoperiod and temperature stimuli, and thus increase the number of dormant seeds enumerated. The seedling emergence method is most applicable to studies at or above the community level, since seed extraction from large numbers of samples is extremely tedious (Simpson et al. 1989).

METHODS

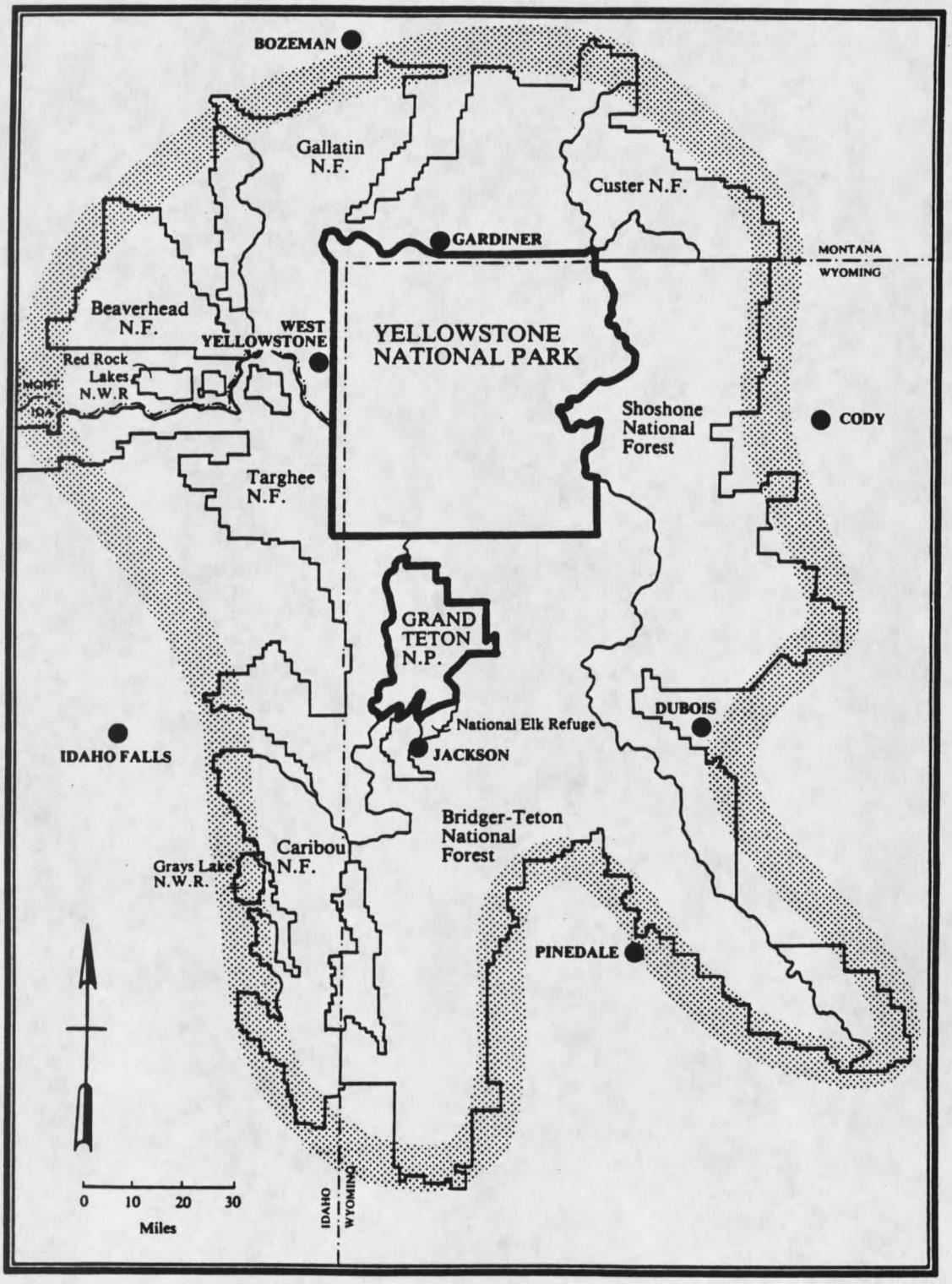
Study Area

Yellowstone National Park (YNP) is located in the northwestern corner of Wyoming. It occupies the central portion of a large mountainous region astride the Continental Divide, which has been collectively termed the Greater Yellowstone ecosystem (Figure 1). This 4.8 million ha ecosystem is comprised of mostly public land, and also includes Grand Teton National Park, two national wildlife refuges, and portions of seven national forests in Wyoming, Montana, and Idaho. The lower elevations of valleys dissecting the region are for the most part privately owned (GYCC 1987).

The geology of the ecosystem is complex. Mountain ranges in the area were formed by the late Cretaceous-early Tertiary thrust faulting of sedimentary layers, the volcanic extrusion of andesite and basalt during the Eocene, and another major uplift and faulting episode during the Pliocene. The quaternary eruptions of the Yellowstone caldera blanketed much of YNP with rhyolitic tuff, and later, with rhyolite flows. The uplands of the region experienced at least three distinct periods of glaciation. The most recent of these (the Pinedale Glaciation) ended about 8500 years ago (Keefer 1971).

Elevations within the region range from 1300 m (4265 ft) in the lower valleys to more than 3660 m (12,000 ft) on some mountain peaks.

Figure 1. The Greater Yellowstone Ecosystem (GYCC 1987).



Forest soils are alfisols and inceptisols, and are generally rocky and shallow. Mollisols derived from glacial till are common in the higher valleys and upland meadows. The soils of lowlands are mollisols, inceptisols, and entisols. They are generally derived from alluvium and are typically well drained, although soils derived from loessial deposits overlying alluvium are not uncommon. Lowlands may have localized alkaline areas (Montagne et al. 1982).

General characteristics of the climate include long, cold winters and short, cool summers. The northern and eastern portions of the region have a cool, dry continental climate regime. The western and southern portions, which contain the first mountain masses encountered by storm systems crossing the Snake River Plains, receive significantly more moisture (Steele et al. 1983). Annual precipitation extremes range from 254 mm (10 in) at Gardiner, Montana to over 2000 mm (78 in) along the Continental Divide in the southwest corner of YNP (Dirks 1974).

Approximately 80 percent of the ecosystem is forested. Grassland and sagebrush communities are interspersed throughout the forests, however, and occur extensively in the lower river valleys.

Habitat Type Selection

The habitat type (h.t.) system of environmental classification developed by Daubenmire (1952) groups land units according to their environmental qualities indicated by predicted ultimate plant species composition. Those units with similar environments, regardless of their current successional status, are classified as the same habitat type. The system thus provides a permanent method of land stratification based

on the premise that vegetational composition is an effective integrator of the climatic, edaphic, and zootic conditions which prevail on a site. While recognizing that each of these characteristics varies with location, it is assumed that their combined influence is equivalent on sites with comparable vegetation, and that similar disturbances will result in analogous responses at each site.

Habitat types investigated are designated in the standard format of series/type-phase, in which "series" is indicated by the dominant climax tree species (shrub or grass species in nonforested communities), "type" is indicated by the dominant or characteristic understory species, and "phase" provides a further refinement where needed (Pfister et al. 1977). The 14 habitat types selected for investigation in this study were chosen on the basis of their regional importance, their position along an altitudinal/moisture gradient, and the potential contribution of the results of this study to other research efforts.

All nonforested, Douglas fir, and aspen habitat/community types were sampled at 3 distinct replicate sites. Seral stages within each of 3 subalpine fir h.t.s were sampled at 3 distinct replicate sites, with two exceptions, as noted below. While these sites were not exact duplicates in terms of their aboveground and seed bank floristic composition and density, nor in terms of the intensity and duration of the fires which affected them, an estimate of inherent floristic variability was essential in discerning treatment effects at the community level of classification (Hurlbert 1984), and the presumed heterogeneity of the burn treatments was simply a reflection of reality at this level of classification.

Three habitat types were sampled in the Gallatin Valley as part of this study (Figure 2). All were remnant native plant communities. Although none were burned in 1988, their inclusion provided a better perspective of seed bank characteristics across the full spectrum of intact plant communities occurring in the Greater Yellowstone ecosystem.

Stipa comata/Bouteloua gracilis (Stco/Bogr)

The needle-and-thread/blue grama h.t. represents the low end of the altitudinal/moisture gradient. It occurs on well-drained valley floors and alluvial benches and fans. Soils are mildly alkaline and have a fine-loam texture (Mueggler and Stewart 1980). The elevations of sampled sites were 1320 m (4331 ft), 1345 m (4413 ft), and 1310 m (4298 ft).

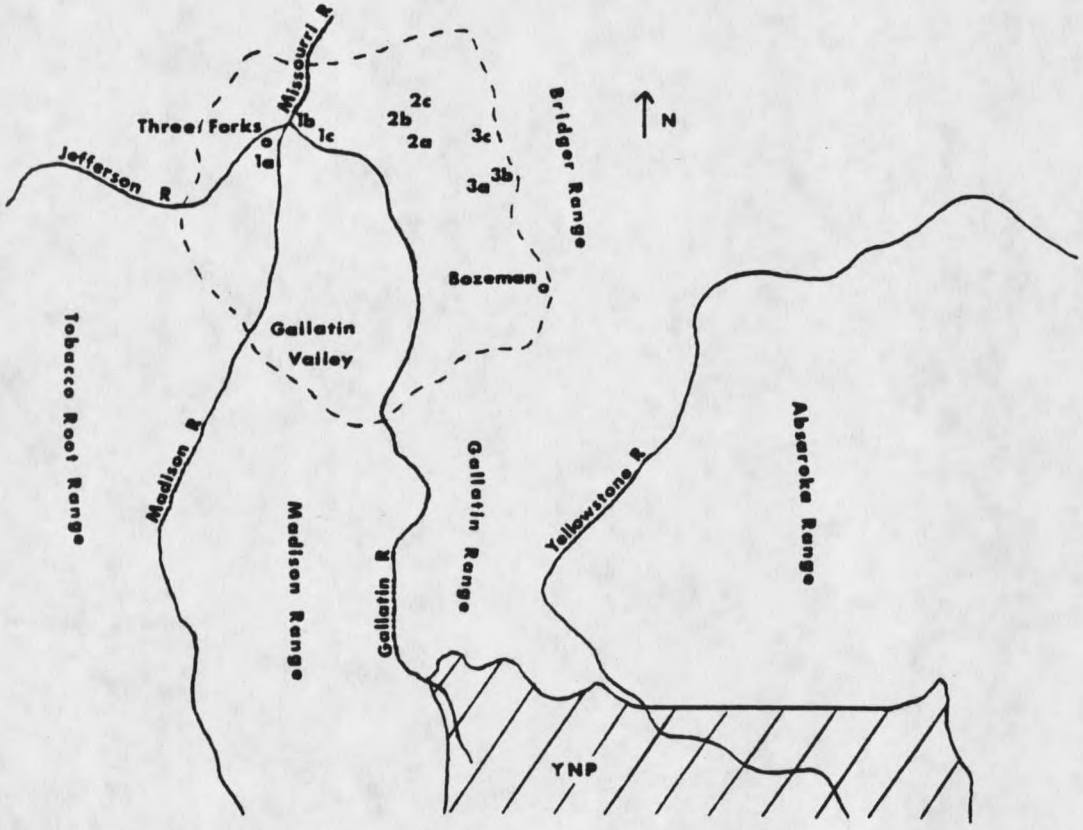
Agropyron spicatum/Poa sandbergii-Stipa comata (Agsp/Posa-Stco)

The bluebunch wheatgrass/Sandberg bluegrass-needle-and-thread h.t. is a moderately arid grassland and occurs on loamy soils of valley floors, benches and lower slopes (Mueggler and Stewart 1980). The elevations of sampled sites were 1410 m (4626 ft), 1380 m (4528 ft), and 1330 m (4364 ft).

Festuca idahoensis/Agropyron spicatum (Feid/Agsp)

The Idaho fescue/bluebunch wheatgrass h.t. is a mesic grassland very common in the region. It is generally found at the lower to middle elevations of mountain slopes (Mueggler and Stewart 1980). The elevations of sampled sites were 1440 m (4724 ft), 1420 m (4659 ft), and 1425 m (4675 ft).

Figure 2. Seed bank sampling sites in the Gallatin Valley, Montana.



1a, 1b, 1c - Stco/Bogr sites
2a, 2b, 2c - Agsp/Posa-Stco sites
3a, 3b, 3c - Feid/Agsp sites

The remaining habitat types were sampled primarily within YNP, although a few sampling sites were located in the Gallatin and Shoshone National Forests (Figure 3). All sites had burned and unburned treatments, unless otherwise indicated.

Deschampsia caespitosa/Carex spp. (Deca/Carex)

The tufted hairgrass/sedge spp. h.t. is a moist meadow type found on deep, poorly drained soils in mountain valleys. It may also be found in swales of alpine tundra meadows. Standing water typically occurs on these sites early in the growing season, although the soil surface is usually dry by August (Mueggler and Stewart 1980). This h.t. represents the high end of the moisture gradient, and may be found near the high end of the altitudinal gradient as well. Vegetation is extremely dense in these meadows, and the mineral soil is covered by a mat of living and decaying rhizomes and stolons. The elevations of sampled sites were 1878 m (6160 ft), 2018 m (6620 ft), and 2390 m (7840 ft).

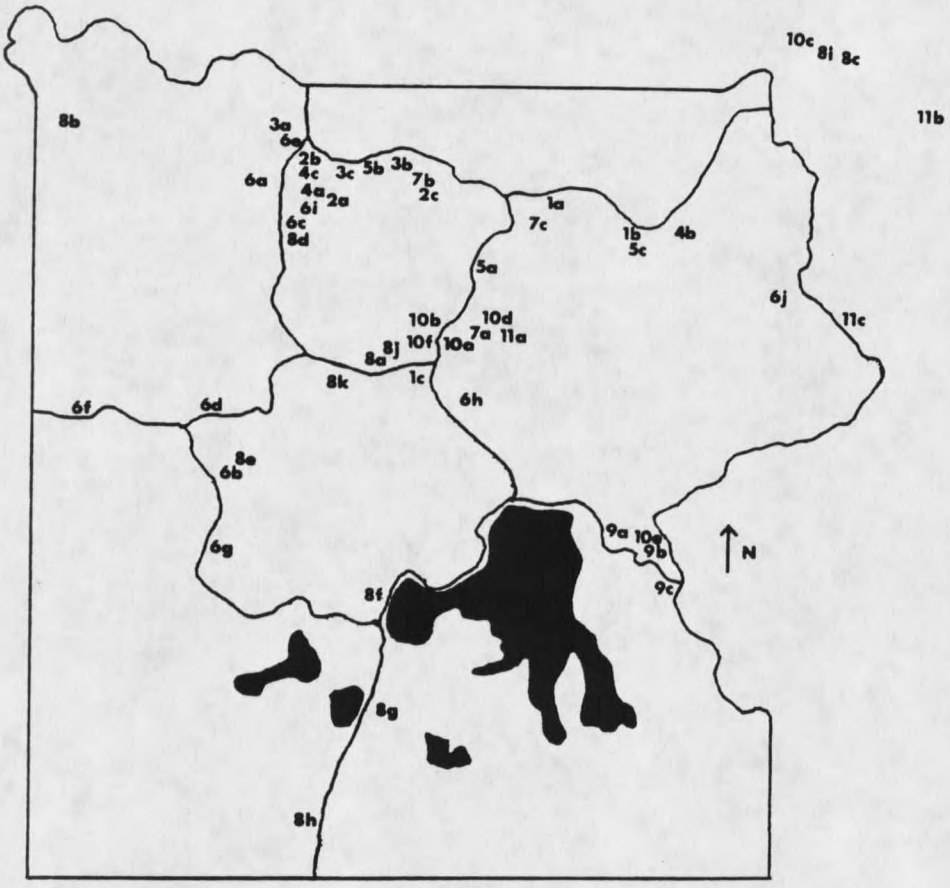
Pseudotsuga menziesii/Calamagrostis rubescens (Psme/Caru)

The Douglas fir/pinegrass h.t. is a major forested community of the region. It is found on dry mountain slopes and benches at moderate elevations (Steele, et al. 1983). Within YNP, the habitat type occurs only in a narrow region of relatively low elevation near the northern boundary. The elevations of sampled sites were 2048 m (6720 ft), 2097 m (6880 ft), and 2207 m (7240 ft).

Pseudotsuga menziesii/Symphoricarpos albus (Psme/Syal)

The Douglas fir/common snowberry h.t. is a common community of the region, particularly to the north of YNP. It occupies sites with soils

Figure 3. Seed bank sampling sites in and adjacent to Yellowstone National Park.



1a, 1b, 1c - Deca/Carex sites
2a, 2b, 2c - Psme/Caru sites
3a, 3b, 3c - Psme/Syal sites
4a, 4b, 4c - Potr/Caru sites
5a, 5b, 5c - Artr/Feid sites
6a - Abla/Caru LP0 site
6b, 6c, 6d - Abla/Caru LP1 sites
6e, 6f, 6g - Abla/Caru LP2 sites
6h, 6i, 6j - Abla/Caru LP3 sites
7a, 7b, 7c - Feid/Agca sites
8a, 8b - Abla/Vasc LP0 sites
8c, 8d, 8e - Abla/Vasc LP1 sites
8f, 8g, 8h - Abla/Vasc LP2 sites
8i, 8j, 8k - Abla/Vasc LP3 sites
9a, 9b, 9c - Abla/Vagl sites
10a, 10b, 10c - Abla/Vasc-Pial WB2 sites
10d, 10e, 10f - Abla/Vasc-Pial WB3 sites
11a, 11b, 11c - Feov/Poal sites

that are deeper and more moist than those of Psme/Caru sites (Steele et al. 1983). This habitat type also occurs only in the northern portion of YNP. The elevations of sampled sites were 2024 m (6640 ft), 2036 m (6680 ft), and 2304 m (7560 ft).

Populus tremuloides/Calamagrostis rubescens (Potr/Caru)

The aspen/pinegrass community type is a frequently encountered aspen grove association of the region. It occurs on moderate slopes and benches in moist soils of moderate depth (Mueggler 1988). This community sometimes occupies vast areas, but is more often found as localized clusters of clones. The term community type is used here in deference to the fact that the sites sampled may or may not be successional to one of the Douglas fir habitat types. Aspen communities are currently the subject of much research in YNP, although (and to some extent, because) they are a minor vegetation component locally. The elevations of sampled sites were 2073 m (6800 ft), 2103 m (6900 ft), and 2201 m (7220 ft).

Artemisia tridentata/Festuca idahoensis (Artr/Feid)

The big sagebrush/Idaho fescue h.t. is a mesic shrubland common on moderate mountain slopes in YNP and throughout the region (Mueggler and Stewart 1980). The elevations of sampled sites were 2024 m (6640 ft), 2109 m (6920 ft), and 2438 m (8000 ft).

Abies lasiocarpa/Calamagrostis rubescens (Abla/Caru)

The subalpine fir/pinegrass h.t. is commmon both within and to the north of YNP, and is a major community to the south. It occurs on well

drained, gentle to moderate slopes (Steele et al. 1983). Seral stands of this h.t. are generally dominated by lodgepole pine (Pinus contorta).

Seral stages, or, if one prefers, age-dependent overstory cover types, are readily recognized in lodgepole pine-dominated communities. Romme and Despain (1989) have described the post disturbance sequence which occurs in YNP: Following a stand-replacing fire (or other disturbance), there is a period of about 50 years prior to lodgepole pine canopy closure which they have termed the LP0 cover type. During the subsequent period of approximately 100 years, the site is characterized by a closed canopy of short, even aged, and usually dense lodgepole pine; this has been designated as the LP1 cover type. Over the next period of approximately 150 years, competition and attrition reduce the density of lodgepole pine, although the canopy remains closed and the trees grow taller. Engelmann spruce (Picea engelmannii) and subalpine fir seedlings and saplings appear in the understory. They have termed this mature lodgepole pine stage the LP2 cover type. The final period, 300+ years post fire, is characterized by a ragged canopy of mature lodgepole pine interspersed with spruce and fir, and has been designated the LP3 cover type. The LP3 type generally contains a large fuel load of downed dead trees, as well as considerable ladder fuels (trees of intermediate height which bridge the gap between the forest floor and the canopy) and thus readily accepts a stand-replacing fire, so that a subalpine fir-dominated community is rarely attained.

The seed bank composition of each of these seral stages was investigated by sampling 3 sites located within LP1, LP2, and LP3

communities. Only 1 site repesenting the Abla/Caru LPO type was located and sampled. The sites sampled ranged in elevation from 2067 m (6780 ft) to 2377 m (7800 ft).

Festuca idahoensis/Agropyron caninum (Feid/Agca)

The Idaho fescue/bearded wheatgrass h.t. is a mesic grassland found on relatively high and usually gentle mountain slopes. It is common in YNP and throughout the region (Mueggler and Stewart 1980). The elevations of sampled sites were 2121 m (6960 ft), 2262 m (7420 ft), and 2646 m (8680 ft).

Abies lasiocarpa/Vaccinium scoparium (Abla/Vasc)

The subalpine fir/grouse whortleberry h.t. is perhaps the most abundant community in the region. It typically occurs on well-drained soils of moderate slopes, ridges, and benches at relatively high elevations, although it may be found in areas of cool air drainage at lower elevations (Pfister et al. 1977). This h.t. occurs in vast stands on rhyolitic soils within YNP. The seed bank composition of the LP1, LP2, and LP3 seral stages of the Abla/Vasc h.t. was sampled at 3 sites each. Only 2 sites representing the LPO stage were located and sampled. The sites sampled ranged in elevation from 2231 m (7320 ft) to 2487 m (8160 ft).

Abies lasiocarpa/Vaccinium globulare (Abla/Vagl)

The subalpine fir/blue huckleberry h.t. is a very common community regionally, although it is generally restricted to the eastern and southern portions of YNP, where it occurs most often on andesitic soils (Despain 1990). It is commonly found on northern and eastern aspects at

moderate elevations (Steele et al. 1983), although the sites which I sampled had relatively high elevations and southern aspects. An attempt to locate paired burned and unburned treatments was made, but in this case it was not possible due to safety considerations. High winds, falling snags, smouldering duff, and steep slopes combined to make burned locations very hazardous. Unburned samples were collected from 3 sites representing the LP3 seral stage. The elevations of sampled sites were 2438 m (8000 ft), 2451 m (8040 ft), and 2682 m (8800 ft).

Abies lasiocarpa/Vaccinium scoparium-Pinus albicaulis (Abla/Vasc-Pial)

The subalpine fir/grouse whortleberry-whitebark pine h.t. is common at high elevations regionally and within YNP. At climax, it is occupied by codominant whitebark pine and subalpine fir, Engelmann spruce, and lodgepole pine (Steele et al. 1983). Seral stages preceding subalpine fir co-dominated stands have been described by Despain (1990). Succession parallels the series described for lodgepole pine-dominated stands, although the intervals of stages may be prolonged due to the harsh conditions and short growing seasons of this habitat type. The seed bank composition of the WB2 and WB3 seral stages within the Abla/Vasc-Pial h.t. was sampled at 3 sites each, although only 2 sites within each seral stage received burn treatments. The sites sampled ranged in elevation from 2560 m (8400 ft) to 2877 m (9440 ft).

Festuca ovina/Poa alpina (Feov/Poal)

Three alpine tundra sites were sampled. Although not classified in the literature, I call them sheep fescue/alpine bluegrass community types, because both of these species were well represented at each site.

There was, however, variation in the presence of other species. All 3 sites occurred on high alpine ridges. I was able to locate only 2 sites which had received a burn treatment. The elevations of sampled sites were 2865 m (9400 ft), 2987 m (9800 ft), and 2999 m (9840 ft).

Sampling Site Selection

The selection of sampling sites within habitat types and seral stages of habitat types was greatly facilitated by the use of habitat type and overstory cover type maps created during the mid-1980's by Despain et al. (unpubl.). These were photocopied and preliminary fire perimeters from aerial observations were added to them. I was thus able to select accessible sites within the appropriate plant communities which were likely to have adjacent burned and unburned treatments.

Upon reaching a potential sampling site, species composition and stand structure were assessed to verify habitat types and seral stages. Subsequent visits to sites in 1989 and 1990, during which aboveground vegetation was quantified, confirmed all previous identifications.

A total of 60 sites were sampled during the period from 15 September to 15 November 1988. The Zone 12 Universal Transverse Mercator coordinates for each site are provided in Appendix C.

Soil Sample Collection

At each sampling site, representative subsites were chosen in both the burned and unburned areas. A single 25 m transect was laid out in each treatment area. Burned transects were deliberately placed to sample the most severely affected area available at the site. Overstory

canopies above these transects had been completely burned in all of the forested habitat types sampled. Transects were not, however, laid out to follow the deep ash "ghosts" of burned downfall. These areas were considered unrepresentative of the overall burn treatment which the site had received. In many cases, it was possible to locate burned and unburned transects within a few meters of each other, but in no case were they separated by more than 100 m.

Five sampling stations were located at 5 m intervals along each transect. Bulb planters with a diameter of 5.5 cm and a height of 10 cm were used to collect soil cores. The litter and duff layers, which were generally very shallow, were collected along with the mineral soil.

On the burned transects, 5 cores, 1 from each of the 5 sampling stations, were collected and placed in a doubled paper bag to constitute sample #1. Cores for sample #2 were collected immediately adjacent to the holes produced by coring for sample #1 at each sampling station. This procedure was repeated for samples #3, #4, and #5, so that each sample consisted of 5 cores taken at 5 m intervals. The total volume of soil collected along the burned transect was 5,939.6 cm^3 (0.0059 m^3/site, 0.0178 m^3/h.t. or seral stage).

On the unburned transects, a similar design was used, except that 15 cores, 3 from each of the 5 sampling stations, were collected per sample. Larger samples were collected to provide sufficient quantities of soil to later divide the unburned samples into the control and oven-heated treatment subsamples. The total volume of soil collected along the unburned transect was 17,818.7 cm^3 (0.0178 m^3/site, 0.0535 m^3/h.t. or seral stage).

All soil samples were transferred to a cold-storage facility within one week of collection and stratified at 4°C for a minimum of five months (Wareing and Phillips 1984). During this period, each soil sample was briefly removed and passed through a 3 mm x 3 mm sieve in order to remove stones, root and rhizome fragments, fecal pellets, and other coarse material. The sieving process also mixed the separate cores into homogenous soil.

Subsample Treatment

Germination flats (17.8 cm long x 13.3 cm wide x 5.9 cm deep, and perforated for drainage) were obtained and labeled with sequentially numbered color-coded transport tape. Each subsample per site was thus given a unique number and each of five treatments was given a different color. A paper towel was placed in the bottom of each flat and 400 cm^3 of sterilized (250°C) sand was added, giving a 2 cm deep layer to promote drainage.

Beginning with the first sample series, the unburned soil sample from each site was thoroughly mixed and four 500 cm^3 subsamples were removed. One 500 cm^3 subsample was removed from the burned soil sample. One of the unburned subsamples was placed in a control-labeled flat and the burned subsample was placed in a burn-labeled flat. The three remaining unburned subsamples were each placed in a 29.5 cm long x 19.5 cm wide x 3.0 cm deep aluminum cake pan and evenly spread to a depth of 9 mm. Each of these subsamples was then given a treatment of one-hour oven heating at a temperature of either 50°C, 100°C, or 150°C. Temperatures within the ovens were monitored with glass-bulb mercury

thermometers, and temperature-sensitive labels were initially buried in subsamples at a depth of 4 mm to verify that even heating of the entire soil volume occurred. Heated subsamples were then placed in appropriately labeled germination flats and all treatment flats were taken to the greenhouse. This procedure was then repeated for sample series two through five.

Any seeds present in the original unburned soil cores had an equal probability of being placed in the control, 50°C, 100°C, and 150°C treatment subsamples, and seeds present in the burned soil cores had the same probability of occurring in the burn treatment subsample. This may be obvious to some, but since 4 subsamples were extracted from 15 cores in the case of unburned samples, and 1 subsample was extracted from 5 cores in the case of burned samples, I feel it is helpful to present the following proof: Let us say a given species has a true seedbank density of 8 seeds per soil core, so that 120 seeds would occur in 15 cores and 40 seeds would occur in 5 cores. If four 500 cm^3 subsamples are removed from the well-mixed 3564 cm^3 contained in 15 cores, each subsample would be expected to contain 500/3564 x 120 = 17 seeds. Similarly, if one 500 cm^3 subsample is removed from the well-mixed 1188 cm^3 contained in 5 cores, that subsample would be expected to contain 500/1188 x 40 = 17 seeds. Therefore, no bias was introduced by the subsampling procedure.

The 500 cc volume of each treatment subsample represented 1/200 of the soil contained in a representative 1 m^2 x 10 cm deep volume of soil at a given site. A single germinant in a treatment flat was therefore equivalent to a density of 200 seeds/m^2 at that site. The densities of each species in each subsample of a treatment were totaled and the sum

was divided by 5 (number of subsamples) to obtain the mean species density for each treatment at a site. The mean densities at each site were then totaled and the sum was divided by 3 (number of replicate sites per h.t.) in order to obtain the mean species density for each treatment in a h.t. or seral stage of a h.t.

Each sample collected for this study was a composite of systematically dispersed soil cores. The five 500 cm^3 subsamples from which germinants were innumerated for each treatment were not treated as replicate samples (Hurlbert 1984). The purpose of the five subsamples was to increase the accuracy of species density estimates for each treatment, but they did not increase the precision (ie., decrease the standard error) of these estimates.

Artificial heat treatments were used in order to refine the interpretation of natural burn treatment effects on seeds of individual species.

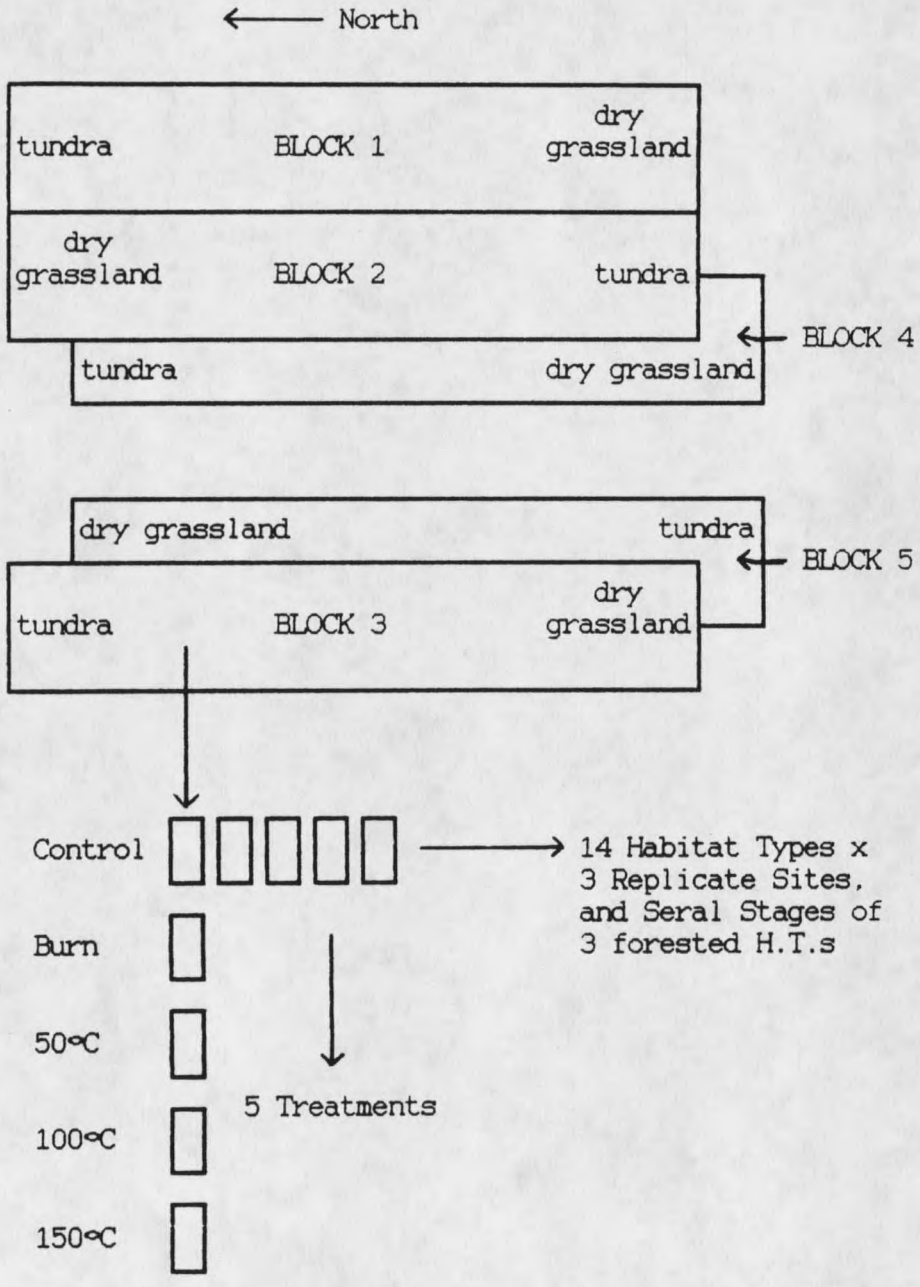
The null hypothesis that the populations of burned seed banks within a h.t. were equal to the populations of unburned seed banks of that h.t. was tested against the alternative hypothesis that burned seed bank populations were less than undisturbed seed bank populations by one-way analysis of variance. All p-values reported are thus one-tailed probabilities. Since variances of subsample densities were proportional to the means, all density estimates were square-root transformed to equalize variances. The transformation used was of the form: X'= SQRT(X+0.5), as recommended by Zar (1984) for data sets containing some zero values.

Greenhouse Procedures

The greenhouse facility and the benches within it were oriented on a north-south axis, which raised the possibility of slightly unequal exposure of germination flats to temperature and lighting conditions. Ideally, all treatment flats should have been randomly dispersed on the greenhouse benches; it was decided, however, that this would make the frequent inventories of germinants difficult and subject to error. As an alternative to random dispersal, flats were systematically placed on benches along the same altitudinal gradient as the sites from which they came. This gradient was reversed, however, for each of the five subsample blocks. Thus block #1 was arranged with the alpine tundra sites at the north end of the bench and progressed to the dry grassland sites at the south end. Block #2 had the alpine tundra sites at the south end and progressed to the dry grassland sites at the north end. Block #3 was arranged identically to block #1. Due to limited bench space, blocks #4 and #5 were placed upon corrugated fiberglass panels below the benches. The height and positioning of the benches provided adequate lighting for these germination flats (Figure 4).

Fifteen flats were placed on the greenhouse benches to control for contamination; they were prepared with 400 cm^3 of sterilized sand and 500 cm^3 of sterilized potting soil, and served as a test for contaminant seeds within the greenhouse. Three flats were located within each block. Two were placed at opposite ends of each block, and one was placed near the center.

Figure 4. Arrangement of germination flats on greenhouse benches.



When all of the sites of a block had been given heat treatments and were properly located in the greenhouse, all germination flats were immersed in water to provide a thorough initial soaking. This wetting procedure began on 1 April 1989 and was completed on 25 April 1989. After the inital wetting, water was provided as needed with a fine mist nozzle, to prevent the splashing of soil or seeds. The flats were sprayed with a dilute mixture of commercial fertilizer (15% N--30% P--15% K) 2-3 weeks after seedlings began to emerge, and every 2-3 weeks thereafter. No artificial lighting was provided at any time.

Seedlings were formally inventoried once every two weeks, although they were inspected daily while watering and identifying them. References used for identification were Hitchcock and Cronquist (1955), Hitchcock and Cronquist (1973), Dorn (1984), Despain (1975), Booth (1966), Booth (1972), and Shaw (1976). Herbarium specimens contained in the Montana State University and Yellowstone National Park herbariums were also used. Plant nomenclature follows Hitchcock and Cronquist (1973). By 15 November 1989, all germinants had either been identified, transplanted to pots for future identification, or classified as dead unknowns.

To maximize seedling emergence, the germination procedure was repeated. Seedling emergence from soil samples can continue for years (Major and Pyott 1966, Strickler and Edgerton 1976, Graber and Thompson 1978, Roberts 1986). The long-term emergence of seedlings in these studies strongly suggested that it would be prudent to continue germination trials. The depth of subsample soils within the flats was slightly more than 2 cm, which was probably too deep to provide all

seeds with the appropriate light and temperature conditions required for germination (Strickler and Edgerton 1976). All treatment subsample soils were therefore moistened and once again thoroughly mixed in order to provide a phytochrome-activating light flash to enhance seed germination (Wareing and Phillips 1984).

The second germination trial began on 29 November 1989, and the same watering, fertilization, inventory, and identification procedures were followed as was outlined above. By 18 March 1990, all new germinants had been identified, potted, or classified as dead unknowns.

A surprisingly large number of seedlings germinated during the second trial, and therefore a third (and final) germination trial was initiated on 20 March 1990. Once again, all treatment subsample soils were moistened and mixed, and all of the same procedures were followed as in the first and second trials. All new germinants had been identified, potted, or classified as dead unknowns by 1 June 1990.

As potted seedlings matured, their identities were gradually established. All possible identifications were completed by January 1991.

Voucher specimens were collected, pressed, and mounted throughout the germination trial periods. For many species, it was possible to collect a series of specimens ranging from the appearance of the first true leaves through flowering and/or fruiting. The voucher specimens were a valuable aid in identifying subsequent germinants of these species. The voucher collection is deposited in the Montana State University herbarium.

RESULTS

Two contaminant species were found during the germination trials. These were Oxalis corniculata and Clematis ligusticifolia. The Oxalis was common throughout the greenhouse, and its distinctive foliage allowed rapid identification and removal of this species. A large Clematis vine grew outside the entrance to the greenhouse, and although the plumose achenes produced by this plant were sometimes found on the surface of subsamples, they were easily identified and removed prior to germination.

A total of 10681 seedlings germinated in the greenhouse. Positive identifications were obtained for 165 species. The total number of seedlings which died prior to being identified was 63 (0.6%).

The first germination trial yielded 7099 seedlings, the second trial produced 1981 seedlings, and the third trial produced 1601 seedlings. Additional viable seeds were probably present in the soils; extrapolation of a logarithmic curve fit to the germinants per trial tallies suggests that continued trials might have eventually yielded another 850 seedlings. The tendency of germination tests to underestimate seed density is due to an inability to provide appropriate stimuli for the seeds of all species (Simpson et al. 1989). The fact that 1988 was a year of drought and probably low seed production may have further reduced the density and richness of seed banks. The results reported in this study are therefore conservative estimates.

The biological significance (Krebs 1989, Yoccoz 1991) of these results should be considered by reviewers of this data. Due to the small number of replicate sites sampled (N=3), and the sampling of an essentially invisible (but presumably aggregated) population, a large degree of variability occurs in the data set, particularly at the individual species level. This is a common finding in the seed bank literature. Thus, since the time and expense required to collect and process larger samples is beyond the means of most investigators, some conclusions must be drawn from statistically insignificant trends.

As an example, for 80% of the plant communities the 50°C oven heat treatment resulted in the highest seed bank density estimates. The estimates were never statistically different from the control samples within a habitat type, however, nor across all h.t. sites, when tested by one-way analysis of variance (N=60, p=0.16). The consistency of this finding across the entire altitudinal/moisture gradient, however, strongly suggests that exposure to moderate heat enhances the germination rates of most species. The nonparametric sign test (Daniel 1990), in which sample variance is not considered, supported (p=0.01) the hypothesized germination enhancement effect of moderate heating.

An obvious dilemma arose as to which value (control or 50°C) to report as the undisturbed seed bank density estimate for each h.t. The larger of the two possibilities was given in the text, although all means, and their associated standard errors, are provided in the appendix tables (Tables 4-24, Appendix A).

Seed Bank Composition, Density, and Treatment Effects

Stipa comata/Bouteloua gracilis

The mean seed bank density of the undisturbed needle-and-thread/blue grama h.t. was 437 seeds/m^2 (Table 4, Appendix A). A total of 12 species were identified, and the average species richness was 5 taxa/site. Only one species, Poa sandbergii, occurred in densities greater than 100/m^2. Plantago patagonica alone was present in the seed banks of all three sites. All seed bank species were found in the aboveground vegetation. The seeds of 4 species occurring in the vegetation were absent from the seed bank (Appendix B).

The 50°C treatment had 82% more germinants than the control, and the 100°C treatment had 61% fewer germinants than the control. No seedlings emerged in the 150°C treatment.

Agropyron spicatum/Poa sandbergii-Stipa comata

The bluebunch wheatgrass/Sandberg bluegrass-needle-and-thread h.t. had a mean undisturbed seed bank density of 318 seeds/m^2 (Table 5, Appendix A). A total of 20 species were identified; species richness averaged 10 taxa/site. No species occurred in densities greater than 100/m^2. Alyssum alyssoides, Draba reptans, and Achillea millefolium were present in the seed banks of all three sites. All seed bank species were present in the aboveground vegetation. Four species found in the vegetation were not present in the seed bank (Appendix B).

The 50°C, 100°C, and 150°C treatments had 17%, 45%, and 87% fewer germinants than the control, respectively. Germinants of Melilotus officinalis were found only in the 150°C treatment.

Festuca idahoensis/Agropyron spicatum

The mean seed bank density of the undisturbed Idaho fescue/bluebunch wheatgrass h.t. was 3011 seeds/m^2 (Table 6, Appendix A). A total of 31 species were identified; species richness averaged 14 taxa/site. Poa pratensis, Alyssum alyssoides, Androsace septentrionalis, Arabis glabra, Arenaria serpyllifolia, and Filago arvensis occurred in densities greater than 100/m^2. The seeds of Poa pratensis, Androsace septentrionalis, Arabis glabra, and Achillea millefolium were found in the seed banks of all three sites. Two seed bank species were not present in the aboveground vegetation. Ten species present in the vegetation were not found in the seed bank (Appendix B).

The 50°C treatment had 12% more germinants than the control, and the 100°C and 150°C treatments had 77% and 98% fewer germinants than the control, respectively. The largest number of Melilotus officinalis germinants were found in the 150°C treatment.

Deschampsia caespitosa/Carex spp.

The tufted hairgrass/sedge spp. h.t. had a mean undisturbed seed bank density of 13707 seeds/m^2 (Table 7, Appendix A). A total of 44 species were identified; species richness averaged 22 taxa/site. Twenty species occurred in densities greater than 100/m^2. Species present in the seed banks of all three sites were Agrostis idahoensis, Deschampsia caespitosa, Juncus balticus, and Barbarea orthocerus. Three species occurred in the seed bank, but were not present in the aboveground

vegetation. Two species were found in the vegetation, but not in the seedbank (Appendix B).

The 50°C treatment had 18% more germinants than the control, and the 100°C and 150°C treatments had 60% and over 99% fewer germinants than the control, respectively. The burn treatment had 41% fewer germinants than the control ($p=0.21$). Erysimum cheiranthoides, Potentilla norvegica, Ranunculus uncinatus, Cerastium arvense, Cirsium scariosum, Geum macrophyllum, Potentilla diversifolia, Potentilla gracilis, and Solidago multiradiata attained their highest densities in the burn treatment.

Pseudotsuga menziesii/Calamagrostis rubescens

The mean seed bank density of the undisturbed Douglas fir/pinegrass h.t. was 3158 seeds/m^2 (Table 8, Appendix A). A total of 40 species were identified; species richness averaged 20 taxa/site. Carex geyeri, Carex rossii, Phleum pratense, Poa nervosa, Androsace septentrionalis, Geranium bicknellii, Iliamna rivularis, and Trifolium hybridum occurred in densities greater than 100/m^2. Carex rossii, Poa interior, Poa nervosa, Androsace septentrionalis, Arabis glabra, and Potentilla glandulosa were present in the seed banks of all three sites. Fourteen species were found only in the seed bank, and 8 species were present only in the aboveground vegetation (Appendix B).

The 50°C treatment had 27% more germinants than the control, and the 100°C and 150°C treatments had 24% and 96% fewer germinants than the control, respectively. The burn treatment had 76% fewer germinants than the control ($p=0.03$). Geranium bicknellii, Iliamna rivularis, and Trifolium hybridum attained their highest densities in the 100°C

treatment. Ceanothus velutinus, Arabis holboellii, Chenopodium fremontii, and Dracocephalum parviflorum were present in the burn treatment only, although each of these species occurred there in very low densities.

Pseudotsuga menziesii/Symphoricarpos albus

The Douglas fir/common snowberry h.t. had a mean undisturbed seed bank density of 3117 seeds/m^2 (Table 9, Appendix A). A total of 38 species were identified; species richness averaged 22 taxa/site. Poa interior, Poa nervosa, Androsace septentrionalis, Arabis glabra, Phacelia franklinii, Antennaria microphylla, Campanula rotundifolia, Conimitella williamsii, Penstemon procerus, and Potentilla glandulosa occurred in densities greater than 100/m^2. Species present in the seed banks of all three sites were Agropyron dasystachyum, Carex rossii, Poa nervosa, Androsace septentrionalis, Arabis divaricarpa, Arabis glabra, Phacelia franklinii, Potentilla glandulosa, and Taraxacum officinale. Eleven seed bank species were not found in the aboveground vegetation, and 17 species present in the vegetation were absent from the seed bank (Appendix B).

The 50°C treatment had 6% more germinants than the control, and the 100°C and 150°C treatments had 88% and 98% fewer germinants than the control, respectively. The burn treatment had 69% fewer germinants than the control ($p=0.02$). Iliamna rivularis attained its highest density in the 150°C treatment. The highest density of Conimitella williamsii occurred in the burn treatment.

Populus tremuloides/Calamagrostis rubescens

The aspen/pinegrass c.t. had a mean undisturbed seed bank density of 6850 seeds/m^2 (Table 10, Appendix A). A total of 40 species were identified; species richness averaged 21 taxa/site. Twelve species occurred in densities greater than 100/m^2. Carex geyeri, Carex rossii, Phleum pratense, Poa interior, Poa nervosa, and Potentilla glandulosa were present in the seed banks of all three sites. Twelve species occurred only in the seed bank, and 21 species were present only in the aboveground vegetation (Appendix B).

The 50°C treatment had 26% more germinants than the control, and the 100°C and 150°C treatments had 45% and over 99% fewer germinants than the control, respectively. The burn treatment had 88% fewer germinants than the control ($p=0.00$). Medicago lupulina, Melilotus officinalis, Astragalus alpinus, and Oxytropis deflexa were present in the 100°C treatment only; each occurred in very low densities. Trifolium hybridum attained its highest density in the 100°C treatment. Iliamna rivularis was present only in the burn and 100°C treatments.

Artemisia tridentata/Festuca idahoensis

The big sagebrush/Idaho fescue h.t. had a mean undisturbed seed bank density of 3678 seeds/m^2 (Table 11, Appendix A). A total of 38 species were identified; species richness averaged 17 taxa/site. Artemisia tridentata, Phleum pratense, Androsace septentrionalis, Arabis glabra, Thlaspi arvense, Arabis nuttallii, Campanula rotundifolia, Cerastium arvense, Oxytropis deflexa, and Trifolium hybridum occurred in densities greater than 100/m^2. The seeds of Artemisia tridentata,

Arabis glabra, and Taraxacum officinale were present at all three sites. Seven seed bank species were not found in the aboveground vegetation, and 8 species were present in the vegetation only (Appendix B).

The 50°C treatment had 27% more germinants than the control, and the 100°C and 150°C treatments had 90% and 97% fewer germinants than the control, respectively. There were 10% fewer germinants in the burn treatment than in the control ($p=0.34$). Four species attained their highest densities in the burn treatment. These were Androsace septentrionalis, Campanula rotundifolia, Oxytropis deflexa, and Penstemon procerus.

Abies lasiocarpa/Calamagrostis rubescens

The mean undisturbed seed bank density of the seral stages comprising the subalpine fir/pinegrass sere were 5400 seeds/m^2 in the LP0 (one site only), 2160 seeds/m^2 in the LP1, 1171 seeds/m^2 in the LP2, and 1465 seeds/m^2 in the LP3. The seed bank richness of each stage was 18 species in the LP0, 28 species in the LP1 (averaging 14 taxa/site), 29 species in the LP2 (averaging 15 taxa/site), and 30 species in the LP3 (averaging 15 taxa/site). Thus, while seed bank density declined with stand age, the richness of the seed bank remained quite constant across the sere.

The LP0 stage had 5 species present in densities greater than 100/m^2 (Table 12, Appendix A). These were Agrostis scabra, Carex rossii, Androsace septentrionalis, Collomia linearis, and Potentilla diversifolia. Twelve species were found only in the seed bank, and 7 species were present only in the aboveground vegetation (Appendix B).

The 50°C treatment had 21% more germinants than the control.

The 100°C and 150°C treatments had 34% and 99% fewer germinants than the control, respectively. The burn treatment also had 99% fewer germinants than the control; Pinus contorta was the only species which appeared in this treatment.

The LP1 stage had 6 species occurring in densities greater than 100/m^2 (Table 13, Appendix A). These were Agrostis scabra, Carex rossii, Poa nervosa, Androsace septentrionalis, Collinsia parviflora, and Campanula rotundifolia. Agrostis scabra, Carex geyeri, Carex rossii, Poa nervosa, and Antennaria microphylla were found at all three sites. The number of species found only in the seed bank was 16, and 30 species were present only in the aboveground vegetation (Appendix B).

The 50°C, 100°C, and 150°C treatments had 3%, 76%, and 98% fewer germinants than the control, respectively. The burn treatment had 84% fewer germinants than the control ($p=0.07$). Danthonia intermedia and Trifolium hybridum attained their highest densities in the 100°C treatment. Arabis glabra, Arenaria serpyllifolia, Astragalus alpinus, and Epilobium glaberrimum attained their highest densities in the burn treatment.

The LP2 stage had 2 species, Carex rossii and Poa nervosa, which occurred in densities greater than 100/m^2 (Table 14, Appendix A). The seeds of Pinus contorta, Carex rossii, Poa nervosa, Campanula rotundifolia, and Taraxacum officinale were present at all three sites. Fourteen species occurred only in the seed bank, and 30 species occurred only in the aboveground vegetation (Appendix B).

The 50°C treatment had 66% more germinants than the control, and the 100°C and 150°C treatments had 58% and 91% fewer germinants than the

control. The burn treatment had 53% fewer germinants than the control ($p=0.20$). Trifolium hybridum attained its highest density in the 100°C treatment. Ceanothus velutinus occurred only in the 150°C treatment. Pinus contorta and Carex rossii attained their highest densities in the burn treatment.

The LP3 stage had 6 species which occurred in densities greater than 100/m^2 (Table 15, Appendix A). These were Pinus contorta, Carex rossii, Poa nervosa, Androsace septentrionalis, Collinsia parviflora, and Campanula rotundifolia. The seeds of Carex rossii and Fragaria virginiana were present at all three sites. Fourteen species were found only in the seed bank, and 18 species were present only in the aboveground vegetation (Appendix B).

The 50°C treatment had 13% more germinants than the control, and the 100°C treatment had 55% fewer germinants than the control. No seeds germinated in the 150°C treatment. The burn treatment had 80% fewer germinants than the control ($p=0.00$). Neither of the higher heat treatments, nor the burn treatment, appeared to enhance the germination rate of any species.

Festuca idahoensis/Agropyron caninum

The mean undisturbed seed bank density of the Idaho fescue/bearded wheatgrass h.t. was 2200 seeds/m^2 (Table 16, Appendix A). A total of 44 species were identified, and species richness averaged 24 taxa/site. Koeleria cristata, Poa pratensis, Androsace septentrionalis, Arabis glabra, Collomia linearis, Descurainia richardsonii, Arabis nuttallii, Campanula rotundifolia, Cerastium arvense, Penstemon procerus, and Potentilla glandulosa were present in densities greater than 100/m^2.

Agropyron caninum, Phleum pratense, Androsace septentrionalis, Arabis divaricarpa, Arabis glabra, Collomia linearis, and Arabis nuttallii occurred at all three sites. Eleven species were present only in the seed bank. Four species were present only in the aboveground vegetation (Appendix B).

The 50°C, 100°C, and 150°C treatments had 4%, 92%, and over 99% fewer germinants than the control, respectively. The burn treatment had 83% more germinants than the control. This increase in the number of germinants in the burn treatment occurred at each site, and was significant for the h.t. ($p=0.02$). Dracocephalum parviflorum was found only in the 100°C treatment. Pinus contorta, Agropyron dasystachyum, Poa interior, Descurainia richardsonii, Thlaspi arvense, Erigeron peregrinus, and Potentilla glandulosa were present only in the burn treatment. Agropyron caninum, Danthonia intermedia, Festuca idahoensis, Koeleria cristata, Phleum pratense, Androsace septentrionalis, Arabis divaricarpa, Arabis glabra, Campanula rotundifolia, Hackelia floribunda, Penstemon procerus, and Potentilla gracilis attained their highest densities in the burn treatment.

Abies lasiocarpa/Vaccinium scoparium

The mean undisturbed seed bank densities of the seral stages comprising the subalpine fir/grouse whortleberry sere were 2920 seeds/m^2 in the LP0 (2 sites only), 640 seeds/m^2 in the LP1, 399 seeds/m^2 in the LP2, and 199 seeds/m^2 in the LP3. The seed bank richness of each stage was 9 species in the LP0 (averaging 6 taxa/site), 16 species in the LP1 (averaging 7 taxa/site), 5 species in the LP2 (averaging 3 taxa/site), and 8 species in the LP3 (averaging 3 taxa/site). As in the Abla/Caru

sere, seed bank density decreased with stand age, and there may also be a trend toward fewer taxa with stand age.

The LP0 stage had 3 species occurring in densities greater than 100/m^2 (Table 17, Appendix A). These were Carex rossii, Spergularia rubra, and Epilobium glaberrimum. No species were common to the seed banks of all three sites. Four species were present only in the seed bank. There were 24 species which occurred only in the aboveground vegetation (Appendix B).

The 50°C and 100°C treatments had 60% and 33% more germinants than the control, respectively, and the 150°C treatment had 87% fewer germinants than the control. The burn treatment had 98% fewer germinants than the control ($p=0.14$). No enhancement of germination in the higher heat treatments, nor in the burn treatment, was found for any species.

The LP1 stage had 2 species, Carex rossii and Festuca rubra, which occurred in densities greater than 100/m^2 (Table 18, Appendix A). Carex rossii and Campanula rotundifolia were the only species present in the seed banks of all three sites. Ten species were present only in the seed bank, and 21 species occurred only in the vegetation (Appendix B). The 50°C treatment had 38% more germinants than the control, and the 100°C treatment had 57% fewer germinants than the control. No seeds germinated in the 150°C treatment. The burn treatment had 51% fewer germinants than the control ($p=0.28$). Juncus bufonius and Penstemon procerus were found only in the burn treatment.

The LP2 stage had only one species, Carex rossii, which occurred with a density greater than 100/m^2 (Table 19, Appendix A). Pinus

contorta and Carex rossii were present in the seed banks of all three sites. Three species occurred only in the seed bank, and 18 species were found only in the vegetation (Appendix B).

The 50°C and 100°C treatments had 43% and 47% fewer germinants than the control. The 150°C treatment produced no germinants. The burn treatment had 80% fewer germinants than the control ($p=0.05$). Agrostis scabra was present only in the burn treatment.

The LP3 stage had only Carex rossii present in densities greater than 100/m^2, and Carex rossii was also the only species found in the seed banks of all three sites (Table 20, Appendix A). Two species occurred only in the seed bank, and 16 species were present only in the aboveground vegetation (Appendix B).

The 50°C treatment had 36% more germinants than the control, and the 100°C treatment had 73% fewer germinants than the control. There were no germinants in the 150°C treatment. The burn treatment had 46% fewer germinants than the control ($p=0.24$). Astragalus alpinus and Hieracium gracile occurred only in the burn treatment.

Abies lasiocarpa/Vaccinium globulare

The mean seed bank density of the undisturbed subalpine fir/blue huckleberry h.t. (LP3) was 305 seeds/m^2 (Table 21, Appendix A). A total of 18 species were identified, and species richness averaged 7 taxa/site. No species occurred with densities greater than 100/m^2, and only Epilobium glaberrimum was found at all three sites. Five species were present only in the seed bank, and 5 species occurred only in the aboveground vegetation (Appendix B).

The 50°C treatment had 29% more germinants than the control, and the 100°C treatment had 61% fewer germinants than the control. The 150°C treatment had no germinants. Iliamna rivularis occurred only in the 100°C treatment, and Poa nervosa attained its highest density in this treatment.

Abies lasiocarpa/Vaccinium scoparium-Pinus albicaulis

The two seral stages of the subalpine fir/grouse whortleberry-whitebark pine sere had mean undisturbed seed bank densities of 2986 seeds/m^2 in the WB2, and 892 seeds/m^2 in the WB3. The seed bank richness was 26 species in the WB2 (averaging 13 taxa/site), and 19 species in the WB2 (averaging 9 taxa/site). Although these two stages are an incomplete sample of the sere, they conform to the density declines with stand age found in the other forested seres. Again, there was an indication that species richness may decrease in older stands.

The WB2 stage had 7 species which occurred in densities greater than 100/m^2 (Table 22, Appendix A). These were Agrostis scabra, Carex capitata, Carex rossii, Juncus parryi, Poa nervosa, Androsace septentrionalis, and Hieracium gracile. The species present at all three sites were Agrostis scabra, Carex rossii, Juncus parryi, Poa nervosa, Hieracium gracile, and Sibbaldia procumbens. Fourteen species were found only in the seed bank, and 15 species occurred only in the aboveground vegetation (Appendix B).

The 50°C treatment had 45% more germinants than the control, and the 100°C and 150°C treatments had 31% and 98% fewer germinants than the control, respectively. The burn treatment had 95% fewer germinants than the control ($p=0.01$). Oxytropis deflexa was found only in the 100°C

treatment, which also contained the highest density of Androsace septentrionalis. Epilobium angustifolium occurred only in the burn treatment.

The WB3 stage had 3 species which occurred in densities greater than 100/m^2 (Table 23, Appendix A). These were Carex rossii, Juncus parryi, and Astragalus alpinus. The first two of these were the only species found at all three sites. Thirteen species were present only in the seed bank, and 17 species occurred only in the aboveground vegetation (Appendix B).

The 50°C treatment had 24% more germinants than the control, and the 100°C treatment had 55% fewer germinants than the control. No seedlings emerged in the 150°C treatment. The burn treatment had 81% fewer germinants than the control ($p=0.05$). Hieracium gracile attained its highest density in the 100°C treatment. Draba stenoloba occurred only in the 100°C and burn treatments, and Arenaria serpyllifolia was found only in the latter treatment.

To ease comparison, a summary of the mean undisturbed seed bank density and mean number of taxa/site for each seral stage sampled in the Abla/Caru, Abla/Vasc, and Abla/Vasc-Pial habitat types is provided (Table 1).

Festuca ovina/Poa alpina

The mean undisturbed seed bank density of the sheep fescue/alpine bluegrass tundra communities was 6038 seeds/m^2 (Table 24, Appendix A). A total of 25 species were identified; species richness averaged 15 taxa/site. Agrostis scabra, Carex capitata, Carex phaeocephala, Juncus parryi, Poa alpina, Poa grayana, Androsace septentrionalis, Draba

Table 1. Mean seed bank density (#/m^2 ± SE) and mean number of taxa/site in seral stages of the Abla/Caru, Abla/Vasc, and Abla/Vasc-Pial habitat types.

HABITAT TYPE	LP0	LP1	LP2/WB2	LP3/WB3
Abla/Caru (1 site only in the LP0)	5400 18 spp.	2160±1139 14 spp.	1171±782 15 spp.	1465±87 15 spp.
Abla/Vasc (2 sites only in the LP0)	2920±2040 6 spp.	640±289 7 spp.	399±237 3 spp.	199±80 3 spp.
Abla/Vasc-Pial	---	---	2986±512 13 spp.	892±354 9 spp.

stenoloba, Cerastium beeringianum, Epilobium glaberrimum, and Sagina saginoides were present in densities greater than 100/m^2. Species which occurred at all three sites were Juncus parryi, Poa alpina, Poa grayana, Androsace septentrionalis, Draba stenoloba, Sagina saginoides, and Sibbaldia procumbens. Three species were found only in the seed bank, and 6 species occurred only in the aboveground vegetation (Appendix B).

The 50°C treatment had 14% more germinants than the control, and the 100°C treatment had 84% fewer germinants than the control. No seedlings emerged in the 150°C treatment. The burn treatment had 31% fewer germinants than the control ($p=0.18$). The highest densities of Arabis drummondii, Astragalus alpinus, Hieracium gracile, and Oxytropis deflexa, and the only occurrences of Epilobium angustifolium and Saxifraga rhomboidea were in the burn treatment.

Comparison of Vegetation and Seed Bank Composition

Sorenson's (1948) similarity index was used to compare the correspondence between species in the vegetation and in the seed bank.

The index (S) is the number of species in common (C) divided by the average number of species in the seed bank (A) and in the vegetation (B). Thus

$$S = \frac{C}{\frac{A + B}{2}}$$

where A = the number of species in sample A (the seed bank)

B = the number of species in sample B (the aboveground vegetation)

C = the number of species common to both samples

The correspondence between seed banks and vegetation declined from grasslands to Douglas fir and subalpine fir zones (Table 2). The nonforested habitat types (dry grasslands, shrubland, and high grasslands) were all characterized by a relatively high degree of correspondence (0.81-0.94) between the aboveground vegetation and the species in the seed bank. The open communities of the Douglas fir zone were in a group with an intermediate degree of correspondence (0.61-0.68). In the closed forests of the Abla/Caru and Abla/Vasc seres, similarity was consistently low (0.14-0.41) throughout the early seral stages, although it did increase in the final stage of each sere (0.50-0.60). The LP3 stage of the Abla/Vagl sere also exhibited moderately good correspondence of aboveground and seed bank taxa (0.72). The Abla/Vasc-Pial sere was unique in showing a decline in correspondence in the older stands.

Heat Tolerance in Lifeform Guilds

While the seeds of most species are able to tolerate exposure to a temperature of 50°C, seeds of many species survive 100°C, and a few--usually annual/biennial forbs and less often perennial forbs--survive

Table 2. Values of Sorenson's similarity index for habitat types and seral stages.

HABITAT TYPE	SORENSON'S SIMILARITY INDEX
Nonforested	
Stco/Bogr	0.87
Agsp/Posa-Stco	0.91
Feid/Agsp	0.83
Artr/Feid	0.82
Feid/Agca	0.81
Deca/Carex	0.94
Feov/Poal	0.83
Forested	
Potr/Caru	0.61
Psme/Caru	0.68
Psme/Syal	0.66
Abla/Caru	
LP0	0.39
LP1	0.34
LP2	0.41
LP3	0.50
Abla/Vasc	
LP0	0.26
LP1	0.28
LP2	0.14
LP3	0.60
Abla/Vagl	
LP3	0.72
Abla/Vasc-Pial	
WB2	0.45
WB3	0.29

150°C (Table 3). About 95% of the species of all lifeform guilds emerged in the 50°C heat treatment. The low percentage for shrubs is probably due to their rarity in the seed banks of most habitat types. Over 60% of the species in the shrub, graminoid, annual/biennial forb, and perennial forb lifeform guilds emerged in the 100°C heat treatment. While nearly 15% of the species in the shrub and graminoid guilds emerged in the 150°C heat treatment, the proportion of species emerging

in the 150°C treatment was doubled for annual/biennial forbs and halved for perennial forbs. The two tree species found in the seed bank (*Pinus contorta* and *Pseudotsuga menziesii*) did not germinate in the higher heat treatments.

Table 3. The percentage of lifeform guild species which germinated in the 50°C, 100°C, and 150°C heat treatments.

LIFEFORM GUILD	50°C	100°C	150°C
Trees	100%	0%	0%
Shrubs	71%	57%	14%
Graminoids	100%	66%	15%
Annual/Biennial Forbs	94%	64%	33%
Perennial Forbs	92%	63%	6%
ALL GUILDS	95%	63%	13%

DISCUSSION

This study demonstrated that soil seed banks are maintained by all plant communities across the full spectrum of environmental types occurring in the Greater Yellowstone ecosystem. While this should not necessarily excite wonder, the ubiqitous nature of propagule storage is noteworthy. Alternative reproductive strategies do exist, including vegetative propagation (perennials) and long-distance dispersal of seeds (annuals and perennials), but they have some disadvantages in regard to post disturbance revegetation. Vegetative propagation is limited by its inability to colonize distant sites, and in its lack of the genetic variability required for adaptation to changing conditions. If the timing of disturbance and dispersal do not coincide, or if the disturbance is large, long-distance dispersal may be less efficient than a residual seed reserve.

Seed bank species richness and density are correlated with the richness and density of the aboveground vegetation. The dry grassland environments, where moisture is limited, and the dense coniferous forest environments, where light is limited and the soils are poor in nutrients, are each characterized by depauperate vegetation. The seed banks of these habitats are also depauperate, with densities of 300-1500 seeds/m^2, and 10-20 taxa/h.t. The moist Carex meadows and Populus tremuloides groves, rich in resources and aboveground vegetation, contain large and diverse seed banks (14000 and 7000 seeds/m^2, 44 and 40 taxa/h.t). The mesic grasslands and shrubland, where moisture stress is

moderate, and the relatively open forests dominated by Pseudotsuga menziesii and Pinus albicaulis, hold seed reserves of intermediate density and richness. These findings correlate well with the results of studies in similar environments (Major and Pyott 1966, Hassan and West 1986, and Coffin and Lauenroth 1989 in semi-arid regions; Olmsted and Curtis 1947, Kellman 1970 and 1974, Johnson 1975, Strickler and Edgerton 1976, Whipple 1978, Morin and Payette 1987, and Fyles 1989 in coniferous forests; McCarthy 1987 and McGraw 1987 in wetlands; Rabinowitz 1981 and Archibold 1981 in mesic grasslands; Pratt et al. 1982 in open forests).

The large seed banks (over 5000 seeds/m^2, see Table 24, Appendix A) found in the alpine tundra communities seem contrary to the pattern of low densities in stressful environments. Seed bank densities of about 3000 seeds/m^2 have been measured in arctic tundra soils by McGraw (1980) and Fox (1983), and a density of nearly 22000 seeds/m^2 was reported for a dry alpine meadow in Alberta (Archibold 1984). The sites which were sampled seemed to epitomize the stressful, stable environments expected to favor vegetative propagation and small, transient seed bank populations (Donelan and Thompson 1980). Several factors may contribute to the high seed bank populations of cold sites: 1) An overestimation of the stress experienced by alpine plants growing in the microclimate within a few centimeters of the soil surface may underestimate seed production. 2) Low soil temperatures might extend seed dormancy and viability. 3) It is possible that exclusively alpine species produce seeds with long-term viability, as might alpine ecotypes of widespread

species. 4) The shallow, rocky soils and lack of cover of alpine ridges may provide poor granivore habitat, so seed predation may be low.

Stable climax communities may be indicated by the consistently high vegetation/seed bank correspondence found in the nonforested habitat types, while a lack of stability is suggested by the lower correspondence in the forested habitat types (Table 2). This seems especially true for the Abies lasiocarpa successional series, in which correspondence is generally highest in the oldest seral stage sampled. I can offer no explanation for the decrease in vegetation/seed bank correspondence found in the final stage of the Abla/Vasc-Pial sere.

A decrease in seed bank density with stand age was found in all three of the Abies lasiocarpa seres investigated (Table 1). This decrease may be due primarily to dominance of conifers in the overstory, which results in the production of few seed bank seeds in the overstory and competitive exclusion of other seed producers from the understory. Similar density declines across seres have been reported for eastern U.S. forests (Oosting and Humphreys 1940, Livingston and Allessio 1968) and English woodlands (Donelan and Thompson 1980), and are suggested by the work of Conn et al. (1984) for Alaskan forests.

Seed bank species richness showed little or no tendency to decrease across successional series. These results agree with the findings of the studies cited in the eastern U.S. and England, and also with results obtained in Swedish forests (Granström 1982). The consistency of insignificant decreases in species richness across seres may serve as a reminder that, regardless of our attempts to classify seral stages, secondary succession is a continuum. As an example, the species

composition of sites classified as a late LP1 stage and an early LP2 stage may be more similar than the species composition of sites classified as an early LP2 stage and a late LP2 stage.

Long-term seed viability may be uncommon in the Abies lasiocarpa seres. If persistent seeds were of major importance in these forests, one would expect to find especially poor vegetation/seed bank correspondence during the LP1 stage, when aboveground vegetation is depauperate, and large numbers of viable seeds produced during the LP0 stage would presumably remain in the seed bank. The correspondence of aboveground vegetation and seed bank taxa remains relatively constant in the early stages of each sere (Table 2), and in two of the three seres studied, increases in the final stage. This suggests that the seeds of most species do not persist for many years. My interpretation is that input to the seed bank of most early and mid-seral species gradually decreases with time, as the seed production and, eventually, the aboveground occurrence of these taxa decreases due to competitive stress. Plants which have the capability of vegetative propagation finally dominate the understory of these stands, as the seed population, the seedling establishment potential, and the presence of plants without this capability declines.

The density and diversity of postfire seed banks seem more than adequate to provide for revegetation of nonforested sites. Fire resulted in an average seed bank density reduction of about 20%, and a net reduction in species richness of 15%, in the nonforested habitat types (the postfire density increase found in the Festuca idahoensis/Agropyron caninum h.t. is here regarded as a 0% decrease).

The mean postfire seed bank density for non-forested sites was about 4200 seeds/m^2. This decrease is similar to the 16% reduction in seed bank density reported for a tall-grass prairie subjected to 4-year burn intervals (Abrams 1988).

The effect of fire on the seed banks of sites dominated by Pseudotsuga menziesii and Populus tremuloides was more severe. The mean seed bank density was reduced by about 78%, and a net reduction in species richness of 58% occurred. The mean postfire seed bank density of the Douglas fir zone was about 700 seeds/m^2. These reductions represent significant losses of viable seeds, but again, seed bank densities seem more than sufficient for the postfire revegetation of these habitat types. Fire effects in the Douglas fir zone were more significant than the effects documented in a Saskatchewan mixed forest spring burn (Archibold 1978).

The reductions incurred by seed banks of the Abies lasiocarpa series as a result of fire were very similar to those of the Douglas fir zone, but the overall impact of the disturbance was greater. The mean reduction in seed bank density was about 77%, and there was a net reduction of 72% in species richness. The mean postfire seed bank density was about 120 seeds/m^2. Since the undisturbed seed banks of these habitat types were relatively poor in species and density, comparable losses had more severe effects.

No evidence of postburn "soil sterilization" was found in any of the habitat types sampled, despite the fact that samples were collected from the most severely burned areas of sampling sites. The postfire seed bank densities of burned sites in the subalpine fir zone seem only

marginally adequate for revegetation, however, considering the vagaries of actual germination and establishment in the field. Vegetative propagules and offsite colonizers must account for a significant portion of the postfire revegetation in these stands.

Heat tolerance of seeds was measured for a large number of species. A relatively large percentage of annual/biennial forb species, and few perennial forb species, survived the 150°C heat treatments (Table 3). While the seeds of several taxa germinated only in the burn treatments, this does not necessarily imply that their seeds are heat tolerant. Seeds may have been present only on the burned subsites, particularly if the species was found at only one site. Preburn densities may have been larger than the postburn densities which were measured, and seeds may have been insulated from intense heat by deep burial. Thus, ostensible heat tolerance in a species may reflect sampling error. Seeds which germinated in either the 100°C or 150°C treatments, however, provide evidence of heat tolerance (Tables 4-24, Appendix A). The full hour of heat exposure which seeds received in the laboratory met or exceeded heat exposure periods occurring in most fires (Heyward 1938, Norton and McGarity 1965, Stinson and Wright 1969, DeBano et al. 1977), except possibly in the Abies lasiocarpa/Vaccinium globulare habitat type, where deep duff layers continued to smoulder for weeks after stands burned.

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APPENDICES

APPENDIX A

SEED BANK COMPOSITION, BY TREATMENT, FOR EACH HABITAT TYPE

Table 4. Mean seed bank density (#/m^2 ± SE) by treatment for the *Stipa comata/Bouteloua gracilis* habitat type. N=3 for all treatments. The "SITES" column indicates the number of sites from which germinants were obtained. All seed bank species were present in the aboveground vegetation.

SPECIES	SITES	CONTROL	50°C	100°C	150°C
Shrubs					
Artemisia frigida	1	0	0	13±13	0
Graminoids					
Carex stenophylla	1	40±40	0	0	0
Distichlis stricta	2	13±13	40±23	0	0
Poa pratensis	1	27±27	13±13	0	0
Poa sandbergii	1	120±120	173±173	53±53	0
Stipa comata	1	0	13±13	0	0
unidentified graminoid	1	0	13±13	0	0
Subtotals		200±140	252±135	53±53	0
Annual/Biennial Forbs					
Descurainia pinnata	1	0	13±13	0	0
Melilotus officinalis	1	13±13	27±27	27±27	0
Plantago patagonica	3	27±27	80±40	0	0
Tragopogon dubius	1	0	13±13	0	0
Subtotals		40±23	133±48	27±27	0
Perennial Forbs					
Antennaria microphylla	1	0	13±13	0	0
Gaillardia aristata	1	0	13±13	0	0
unid. Monocot sp.	1	0	13±13	0	0
Subtotals		0	39±23	0	0
unidentified forb	1	0	13±13	0	0
TOTALS		240±162	437±180	93±48	0

Table 5. Mean seed bank density (#/m^2 ± SE) by treatment for the *Agropyron spicatum/Poa sandbergii-Stipa comata* habitat type. N=3 for all treatments. The "SITES" column indicates the number of sites from which germinants were obtained. All seed bank species were present in the aboveground vegetation.

SPECIES	SITES	CONTROL	50°C	100°C	150°C
Shrubs					
Artemisia frigida	1	13±13	0	0	0
Graminoids					
Agropyron spicatum	2	0	27±13	0	0
Carex stenophylla	1	0	27±27	27±27	0
Koeleria cristata	1	0	13±13	0	0
Poa pratensis	1	13±13	0	27±27	0
Poa sandbergii	1	13±13	0	13±13	0
Stipa comata	1	0	13±13	0	0
Stipa viridula	1	13±13	13±13	0	0
Subtotals		39±23	93±48	67±67	0
Annual/Biennial Forbs					
Alyssum alyssoides	3	67±48	27±13	27±27	13±13
Amaranthus albus	1	0	13±13	0	0
Cerastium vulgatum	1	13±13	0	0	0
Draba reptans	3	40±23	67±13	0	0
Melilotus officinalis	1	0	0	0	27±27
Plantago patagonica	1	13±13	13±13	27±27	0
Subtotals		93±13	120±0	54±27	40±23
Perennial Forbs					
Achillea millefolium	3	40±23	13±13	27±13	0
Arabis nuttallii	1	13±13	0	0	0
Gaillardia aristata	1	0	13±13	0	0
Linum perenne	2	40±23	0	0	0
Taraxacum officinale	1	13±13	0	0	0
Xylorhiza glabriuscula	1	0	13±13	0	0
Subtotals		106±35	39±23	27±13	0
unidentified forbs	1	27±27	13±13	27±27	0
TOTALS		318±69	265±53	175±119	40±23

Table 6. Mean seed bank density (#/m^2 ± SE) by treatment for the Festuca idahoensis/Agropyron spicatum habitat type. N=3 for all treatments. The "SITES" column indicates the number of sites from which germinants were obtained. Asterisks denote species which were not present in the aboveground vegetation.

SPECIES	SITES	CONTROL	50°C	100°C	150°C
Shrubs					
Gutierrezia sarothrae	1	13±13	13±13	13±13	0
Graminoids					
Agropyron spicatum	1	13±13	40±40	0	0
Danthonia intermedia	2	67±48	67±67	0	0
Poa pratensis	3	267±170	600±363	200±180	0
Poa sandbergii	1	27±27	0	0	0
Stipa viridula	1	27±27	13±13	13±13	0
Subtotals		401±151	720±302	213±194	0
Annual/Biennial Forbs					
Alyssum alyssoides	2	120±61	120±83	67±48	0
Amaranthus albus	1	0	13±13	0	0
Androsace septentrionalis	3	400±321	307±267	40±40	0
Arabis glabra*	3	413±219	427±188	53±13	13±13
Arenaria serpyllifolia	1	840±840	973±973	160±160	0
Collinsia parviflora	1	67±67	13±13	13±13	0
Cryptantha torreyana	1	53±53	13±13	0	0
Filago arvensis	1	213±213	227±227	40±40	0
Matricaria matricarioides	1	13±13	0	0	0
Medicago lupulina	1	13±13	0	27±27	40±40
Melilotus officinalis	1	0	27±27	0	0
Orthocarpus luteus	1	0	13±13	0	0
Plantago patagonica	1	0	0	13±13	0
Sisymbrium altissimum	1	53±53	53±53	13±13	0
Tragopogon dubius	1	13±13	0	0	0
Subtotals		2198±1501	2186±536	426±227	53±53
Perennial Forbs					
Achillea millefolium	3	13±13	40±23	13±13	0
Arabis nuttallii	1	0	13±13	0	0
Artemisia ludoviciana	1	0	13±13	0	0
Cirsium arvense	1	0	0	13±13	0
Gaillardia aristata	1	0	13±13	0	0

Table continues on next page.

Table 6--Continued. Mean seed bank density (#/m^2 ± SE) by treatment for the Festuca idahoensis/Agropyron spicatum habitat type. N=3 for all treatments. The "SITES" column indicates the number of sites from which germinants were obtained. Asterisks denote species which were not present in the aboveground vegetation.

SPECIES	SITES	CONTROL	50°C	100°C	150°C
Perennial Forbs					
Oxytropis deflexa*	1	13±13	0	0	0
Phlox hoodii	1	13±13	0	0	0
Solidago multiradiata	1	13±13	0	0	0
Sonchus sp.	1	13±13	13±13	0	0
Taraxacum officinale	1	0	0	13±13	0
Subtotals		65±13	92±58	39±0	0
TOTALS		2677±1361	3011±1416	691±207	53±53

Table 7. Mean seed bank density (#/m^2 ± SE) by treatment for the Deschampsia caespitosa/Carex spp. habitat type. N=3 for all treatments. The "SITES" column indicates the number of sites from which germinants were obtained. Asterisks denote species which were not present in the aboveground vegetation.

SPECIES	SITES	CONTROL	BURN	50°C	100°C	150°C
Trees						
Pinus contorta*	1	13±13	0	0	0	0
Graminoids						
Agropyron smithii	2	27±13	0	40±23	0	0
Agrostis idahoensis	3	173±119	67±35	240±151	80±61	27±27
Bromus ciliatus	1	13±13	0	0	0	0
Carex lanuginosa	2	0	40±23	93±74	40±40	0
Carex microptera	1	400±400	213±213	293±293	67±67	0
Carex praegracilis	1	53±53	0	40±40	13±13	0
Carex praticola	1	253±253	27±27	120±120	13±13	0
Danthonia intermedia	1	0	0	13±13	0	0
Deschampsia caespitosa	3	440±231	253±215	507±343	400±360	0
Juncus balticus	3	1667±1394	493±249	2267±1878	1187±108	0
Luzula campestris	1	133±133	0	267±267	40±40	0
Phleum pratense	2	80±80	40±23	40±23	0	0
Poa interior	1	0	0	53±53	0	0
Poa palustris	2	3120±2165	1413±898	4213±2802	1920±999	0
Poa pratensis	1	0	13±13	0	0	0
Subtotals		6359 ±2386	2559 ±1358	8186 ±3213	3747 ±1990	27±27
Annual/Biennial Forbs						
Androsace sept.	1	0	27±27	0	0	0
Barbarea orthocerus	3	653±614	307±307	907±847	147±93	0
Erysimum cheiranthoides	2	27±27	240±240	27±27	0	0
Potentilla norvegica	1	0	453±453	13±13	13±13	0
Ranunculus uncinatus*	2	320±320	627±587	307±307	40±40	0
Subtotals		1000±960	1654±847	1254±1174	200±129	0
Perennial Forbs						
Allium spp.	2	0	13±13	13±13	0	0
Antennaria microphylla	1	160±160	0	120±120	0	0
Cerastium arvense	1	40±40	80±80	27±27	0	0
Cirsium scariosum	1	0	27±27	0	0	0
Epilobium angustifolium*	2	13±13	0	13±13	0	0
Epilobium glaberrimum	2	947±669	1027±668	1107±614	227±188	0
Epilobium watsonii	1	13±13	0	0	0	0

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Table 7--Continued. Mean seed bank density (#/m^2 ± SE) by treatment for the Deschampsia caespitosa/Carex spp. habitat type. N=3 for all treatments. The "SITES" column indicates the number of sites from which germinants were obtained. Asterisks denote species which were not present in the aboveground vegetation.

SPECIES	SITES	CONTROL	BURN	50°C	100°C	150°C
Perennial Forbs						
Erigeron peregrinus	1	0	0	27±27	0	0
Galium trifidum	2	453±245	307±199	667±340	13±13	0
Geum macrophyllum	2	67±48	213±157	27±27	0	0
Mentha arvensis	1	93±93	40±40	227±227	173±173	0
Polygonum bistortoides	2	67±67	40±40	67±48	0	0
Potentilla diversifolia	1	0	13±13	0	0	0
Potentilla gracilis	1	0	27±27	0	0	0
Pyrola asarifolia	2	53±53	0	106±87	27±27	0
Saxifraga oregana	2	0	0	13±13	13±13	0
Solidago multiradiata	1	0	80±80	13±13	13±13	0
Stellaria crassifolia	1	467±467	0	560±560	27±27	0
Taraxacum officinale	1	27±27	0	0	0	0
Trifolium hybridum	1	0	0	53±50	67±67	0
Veronica serpyllifolia	1	1493±1493	627±627	947±947	40±40	0
Viola adunca	1	40±40	0	0	0	0
Viola palustris	2	267±267	53±53	240±220	27±27	0
Subtotals		4200±2090	2547±1553	4227±2498	627±442	0
unidentified forbs	2	0	13±13	40±40	13±13	0
TOTALS		11572 ±5232	6773 ±3727	13707 ±5886	4587 ±2474	27±27

Table 8. Mean seed bank density (#/m^2 ± SE) by treatment for the Pseudotsuga menziesii/Calamagrostis rubescens habitat type. N=3 for all treatments. The "SITES" column indicates the number of sites from which germinants were obtained. Asterisks denote species which were not present in the aboveground vegetation.

SPECIES	SITES	CONTROL	BURN	50°C	100°C	150°C
Shrubs						
Artemisia tridentata	1	13±13	0	0	0	0
Ceanothus velutinus*	1	0	13±13	0	0	0
Subtotals		13±13	13±13	0	0	0
Graminoids						
Agropyron caninum	1	13±13	0	13±13	0	0
Agropyron spicatum*	1	0	0	27±13	0	0
Bromus carinatus	1	0	0	13±13	0	0
Calamagrostis sp.	1	0	0	13±13	0	0
Carex geyeri	2	147±109	0	120±120	147±147	0
Carex rossii*	3	133±48	107±87	280±205	253±196	0
Juncus ensifolius*	1	0	0	13±13	0	0
Phleum pratense	2	613±613	27±13	733±733	280±280	13±13
Poa interior	3	27±27	0	53±13	13±13	0
Poa juncifolia	1	40±40	13±13	27±27	0	0
Poa nervosa	3	733±534	67±48	853±673	467±387	67±67
Subtotals		1706±988	214±93	2145±1188	1160±481	80±80
Annual/Biennial Forbs						
Androsace septentrionalis	3	267±148	120±69	307±167	67±13	0
Arabis glabra*	3	40±23	0	40±23	27±27	0
Arabis holboellii	1	0	13±13	0	0	0
Chenopodium capitatum*	1	13±13	0	0	0	0
Chenopodium fremontii	1	0	13±13	0	0	0
Collinsia parviflora	2	53±53	0	80±61	40±40	0
Collomia linearis	1	27±27	0	0	0	0
Geranium bicknellii*	1	27±27	40±40	67±67	267±267	13±13
Medicago lupulina	1	0	0	13±13	0	0
Monolepsis nuttalliana*	1	13±13	0	0	0	0
Phacelia franklinii*	2	53±35	53±53	80±40	27±27	0
Subtotals		493±164	239±69	587±139	428±289	13±13

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Table 8--Continued. Mean seed bank density (#/m^2 ± SE) by treatment for the Pseudotsuga menziesii/Calamagrostis rubescens habitat type. N=3 for all treatments. The "SITES" column indicates the number of sites from which germinants were obtained. Asterisks denote species which were not present in the aboveground vegetation.

SPECIES	SITES	CONTROL	BURN	50°C	100°C	150°C
Perennial Forbs						
Achillea millefolium	1	0	0	13±13	0	0
Antennaria microphylla	1	13±13	13±13	0	0	0
Arenaria lateriflora*	1	0	0	13±13	0	0
Campanula rotundifolia	2	27±27	0	67±35	13±13	0
Cerastium arvense	2	0	0	53±35	0	0
Conimitella williamsii	1	13±13	0	0	0	0
Dracocephalum parviflorum*	1	0	13±13	0	0	0
Epilobium angustifolium	1	0	0	13±13	0	0
Fragaria virginiana	1	13±13	0	0	0	0
Gaillardia aristata*	1	0	0	0	13±13	0
Iliamna rivularis*	2	0	53±35	0	107±87	13±13
Lychnis drummondii*	2	40±23	13±13	67±48	13±13	0
Potentilla glandulosa	3	53±13	40±23	67±35	0	0
Solidago multiradiata	1	0	0	13±13	0	0
Taraxacum officinale	1	27±27	0	40±40	0	0
Trifolium hybridum	1	67±67	0	53±53	147±147	0
Subtotals		253±74	132±71	399±151	293±122	13±13
unid. Brassicaceae spp.	1	13±13	0	0	0	0
unidentified forbs	2	13±13	0	27±13	0	0
TOTALS		2491±1081	598±227	3158±1459	1881±694	106±87

Table 9. Mean seed bank density (#/m^2 ± SE) by treatment for the Pseudotsuga menziesii/Symphoricarpos albus habitat type. N=3 for all treatments. The "SITES" column indicates the number of sites from which germinants were obtained. Asterisks denote species which were not present in the aboveground vegetation.

SPECIES	SITES	CONTROL	BURN	50°C	100°C	150°C
Trees						
Pseudotsuga menziesii	2	0	0	40±23	0	0
Shrubs						
Artemisia tridentata	2	13±13	0	27±27	13±13	0
Graminoids						
Agropyron caninum	1	13±13	0	0	0	0
Agropyron dasystachyum	3	67±67	0	80±40	27±27	0
Agropyron spicatum	1	13±13	0	13±13	0	0
Carex geyeri	1	27±27	0	13±13	0	0
Carex rossii*	3	27±13	13±13	53±27	13±13	0
Elymus glaucus	1	13±13	0	13±13	0	0
Phleum pratense	2	13±13	0	53±35	0	0
Poa interior	2	93±48	0	120±101	27±27	0
Poa nervosa	3	320±92	80±40	320±106	53±35	13±13
Subtotals		586±187	93±48	665±162	120±61	13±13
Annual/Biennial Forbs						
Androsace septentrionalis	3	467±277	0	453±210	27±13	0
Arabis divaricarpa	3	0	0	53±13	0	0
Arabis drummondii	1	0	0	13±13	0	0
Arabis glabra	3	120±23	13±13	133±58	0	0
Collinsia parviflora	2	80±46	0	13±13	0	0
Collomia linearis	1	27±27	0	13±13	0	0
Geranium bicknellii*	2	13±13	0	0	0	13±13
Phacelia franklinii*	3	493±473	107±10	640±600	53±53	0
Subtotals		1200±280	120±12	1318±460	80±40	13±13
Perennial Forbs						
Antennaria microphylla	2	120±101	13±13	147±147	0	0
Arabis nuttallii	2	13±13	0	27±13	0	0
Arenaria lateriflora*	2	0	27±27	27±27	0	0
Campanula rotundifolia	1	413±413	187±18	440±440	13±13	0
Conimitella williamsii	2	40±23	187±16	0	0	0
Epilobium angustifolium	1	0	0	27±27	0	0
Erigeron peregrinus	1	27±27	0	0	0	0
Fragaria virginiana	1	0	13±13	0	0	0

Table continues on next page.

Table 9--Continued. Mean seed bank density (#/m^2 ± SE) by treatment for the Pseudotsuga menziesii/Symphoricarpos albus habitat type. N=3 for all treatments. The "SITES" column indicates the number of sites from which germinants were obtained. Asterisks denote species which were not present in the aboveground vegetation.

SPECIES	SITES	CONTROL	BURN	50°C	100°C	150°C
Perennial Forbs						
Iliamna rivularis*	1	0	13±13	0	13±13	27±27
Lychnis drummondii*	1	40±40	0	27±27	0	0
Penstemon procerus*	1	147±147	53±53	133±133	67±67	0
Polemonium pulcherrimum*	1	40±40	0	27±27	13±13	0
Potentilla glandulosa	3	227±148	187±104	93±74	13±13	0
Potentilla gracilis*	1	13±13	0	13±13	0	0
Ranunculus sp.*	1	0	0	13±13	0	0
Sedum lanceolatum*	1	0	0	13±13	0	0
Solidago missouriensis	1	27±27	0	0	0	0
Taraxacum officinale	3	27±13	0	40±23	13±13	0
Trifolium hybridum	1	0	13±13	0	0	0
Subtotals		1134±563	693±485	1027±691	132±81	27±27
unidentified forbs	2	13±13	13±13	40±23	0	0
TOTALS		2946±915	919±655	3117±1284	345±170	53±53

Table 10. Mean seed bank density (#/m^2 ± SE) by treatment for the Populus tremuloides/Calamagrostis rubescens community type. N=3 for all treatments. The "SITES" column indicates the number of sites from which germinants were obtained. Asterisks denote species which were not present in the aboveground vegetation.

SPECIES	SITES	CONTROL	BURN	50°C	100°C	150°C
Shrubs						
Spirea betufolia	1	0	0	13±13	0	0
Graminoids						
Bromus carinatus	2	80±80	0	107±87	40±40	0
Carex geyeri	3	40±23	0	53±13	13±13	0
Carex rossii*	3	0	27±27	53±35	27±13	0
Carex xerantica	1	0	0	27±27	0	0
Juncus parryi*	1	0	0	13±13	0	0
Phleum pratense	3	2920±1340	387±367	3253±1297	1613±652	27±27
Poa interior	3	107±58	0	267±93	120±40	0
Poa nervosa	3	653±538	13±13	853±581	427±327	0
Poa palustris	1	187±187	0	133±133	93±93	0
Subtotals		3987±1714	427±407	4759±1473	2333±881	27±27
Annual/Biennial Forbs						
Androsace septentrionalis	2	293±235	40±23	400±231	40±23	0
Arabis divaricarpa	2	27±13	0	53±53	13±13	0
Arabis glabra	2	227±114	53±35	360±183	67±35	0
Arabis holboellii	1	40±40	0	13±13	13±13	0
Artemisia biennis*	1	0	0	13±13	0	0
Chenopodium fremontii	1	13±13	0	67±67	0	0
Collinsis parviflora	1	0	0	27±27	0	0
Collomia linearis	2	120±69	0	107±53	13±13	0
Linanthus septentrionalis	1	13±13	0	0	0	0
Medicago lupulina	1	0	0	0	13±13	0
Melilotus officinalis*	1	0	0	0	13±13	0
Phacelia franklinii*	2	13±13	27±27	40±23	13±13	0
Thlaspi arvense	1	13±13	0	0	0	0
Subtotals		759±409	120±69	1080±528	185±58	0
Perennial Forbs						
Achillea millefolium	2	27±13	0	0	0	0
Antennaria microphylla	1	13±13	0	13±13	0	0
Arenaria lateriflora*	2	13±13	40±40	67±67	40±40	0
Astragalus alpinus*	1	0	0	0	13±13	0
Campanula rotundifolia	2	160±160	13±13	293±293	40±40	0
Cerastium arvense	1	27±27	0	53±53	13±13	0

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Table 10--Continued. Mean seed bank density (#/m^2 ± SE) by treatment for the Populus tremuloides/Calamagrostis rubescens community type. N=3 for all treatments. The "SITES" column indicates the number of sites from which germinants were obtained. Asterisks denote species which were not present in the aboveground vegetation.

SPECIES	SITES	CONTROL	BURN	50°C	100°C	150°C
Perennial Forbs						
Cirsium arvense	1	0	0	13±13	0	0
Dracocephalum parviflorum*	1	0	0	13±13	0	0
Epilobium watsonii	1	0	13±13	0	0	0
Iliamna rivularis*	1	0	13±13	0	27±27	0
Lychnis drummondii*	1	0	0	13±13	0	0
Oxytropis deflexa*	1	0	0	0	13±13	0
Potentilla glandulosa	3	213±96	0	227±207	27±27	0
Taraxacum officinale	2	120±61	27±13	120±83	67±48	0
Trifolium hybridum	2	80±40	13±13	40±23	213±175	0
Urtica dioica*	1	0	0	13±13	0	0
Viola adunca	1	0	13±13	40±40	0	0
Subtotals		653±319	132±96	905±670	453±254	0
unid. Brassicaceae spp.	1	0	0	40±40	0	0
unidentified forbs	2	40±23	0	53±53	13±13	0
TOTALS		5439±1804	679±441	6850±1682	2984±1086	27±27

Table 11. Mean seed bank density (#/m^2 ± SE) by treatment for the Artemisia tridentata/Festuca idahoensis habitat type. N=3 for all treatments. The "SITES" column indicates the number of sites from which germinants were obtained. Asterisks denote species which were not present in the aboveground vegetation.

SPECIES	SITES	CONTROL	BURN	50°C	100°C	150°C
Shrubs						
Artemisia tridentata	3	53±53	133±67	187±35	13±13	0
Graminoids						
Agropyron spicatum	1	13±13	0	0	0	0
Agrostis scabra	1	0	27±27	93±93	0	0
Carex geyeri	1	13±13	13±13	13±13	0	0
Carex rossii*	1	13±13	0	0	0	0
Carex sp.	1	13±13	0	0	0	0
Danthonia intermedia	1	53±53	0	67±67	0	0
Festuca idahoensis	1	0	0	13±13	0	0
Juncus tenuis	1	13±13	0	0	0	0
Koeleria cristata	1	13±13	0	93±93	0	0
Phleum pratense	2	453±433	13±13	533±494	27±27	0
Poa juncifolia	1	13±13	0	13±13	0	0
Stipa occidentalis	1	0	13±13	0	0	0
unidentified graminoid	1	0	0	0	13±13	0
Subtotals		597±500	66±48	1012±747	53±23	0
Annual/Biennial Forbs						
Androsace sept.	2	773±753	1200±1200	827±827	13±13	0
Arabis divaricarpa	1	13±13	40±40	53±53	0	0
Arabis drummondii	1	13±13	0	40±40	0	0
Arabis glabra*	3	347±308	0	213±194	27±27	0
Arabis holboellii*	2	27±27	0	40±40	0	0
Chenopodium capitatum	1	0	40±40	0	0	0
Chenopodium fremontii	1	13±13	0	0	0	0
Cirsium vulgare*	2	13±13	13±13	0	0	0
Draba nemorosa	1	0	0	40±40	0	0
Melilotus officinalis*	1	13±13	0	0	0	0
Orthocarpus luteus	2	0	0	27±27	0	0
Thlaspi arvense	1	133±133	40±40	267±267	0	0
Subtotals		1345±842	1333±1333	1507±1061	40±23	0
Perennial Forbs						
Antennaria microphylla	2	53±53	27±27	40±40	0	0
Arabis nuttallii	2	200±162	147±147	333±210	0	0
Arenaria lateriflora*	1	13±13	0	0	0	0

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Table 11--Continued. Mean seed bank density (#/m^2 + SE) by treatment for the Artemisia tridentata/Festuca idahoensis habitat type. N=3 for all treatments. The "SITES" column indicates the number of sites from which germinants were obtained. Asterisks denote species which were not present in the aboveground vegetation.

SPECIES	SITES	CONTROL	BURN	50°C	100°C	150°C
Perennial Forbs						
Campanula rotundifolia	1	0	107±107	27±27	0	0
Cerastium arvense	2	53±53	27±27	160±83	13±13	0
Epilobium glaberrimum*	1	0	0	13±13	0	0
Erigeron peregrinus	1	0	13±13	0	0	0
Linum perenne	1	13±13	0	0	0	0
Oxytropis deflexa	2	187±104	427±427	240±183	213±213	13±13
Penstemon procerus	1	0	240±240	0	0	0
Potentilla diversifolia*	1	0	27±27	0	0	0
Taraxacum officinale	3	147±58	0	13±13	13±13	0
Trifolium hybridum	2	226±207	40±40	320±320	53±53	80±80
Subtotals		892±485	1055±1053	1146±669	292±274	93±93
unidentified forb	1	0	0	13±13	0	0
TOTALS		2887±2498	2587±2467	3678±2580	385±287	93±93

Table 12. Seed bank density (#/m^2) by treatment for the LPO seral stage of the Abies lasiocarpa/Calamagrostis rubescens habitat type. N=1 for all treatments. There is no "SITES" column, as only one site representing this seral stage was located and sampled. Asterisks denote species which were not present in the aboveground vegetation.

SPECIES	CONTROL	BURN	50°C	100°C	150°C
Trees					
Pinus contorta	0	40	0	0	0
Graminoids					
Agropyron dasystachyum*	0	0	80	0	0
Agrostis scabra	3840	0	4120	2760	40
Carex rossii	320	0	80	80	0
Subtotals	4160	0	4280	2840	40
Annual/Biennial Forbs					
Androsace septentrionalis*	0	0	120	0	0
Arabis glabra*	0	0	40	0	0
Collomia linearis*	120	0	400	0	0
Gayophytum diffusum*	0	0	40	0	0
Phacelia franklinii*	80	0	0	0	0
Subtotals	200	0	600	0	0
Perennial Forbs					
Antennaria microphylla	0	0	40	0	0
Arabis nuttallii*	0	0	80	0	0
Campanula rotundifolia*	0	0	40	40	0
Epilobium angustifolium*	0	0	0	40	0
Fragaria virginiana	0	0	40	0	0
Penstemon procerus*	0	0	40	0	0
Potentilla diversifolia*	0	0	120	0	0
Sagina saginoides*	0	0	80	0	0
Taraxacum officinale	40	0	0	40	0
Subtotals	40	0	440	120	0
unidentified forbs	80	0	80	0	0
TOTALS	4480	40	5400	2960	40

Table 13. Mean seed bank density (#/m^2 ± SE) by treatment for the LP1 seral stage of the Abies lasiocarpa/Calamagrostis rubescens habitat type. N=3 for all treatments. The "SITES" column indicates the number of sites from which germinants were obtained. Asterisks denote species which were not present in the aboveground vegetation.

SPECIES	SITES	CONTROL	BURN	50°C	100°C	150°C
Trees						
Pinus contorta	2	0	13±13	13±13	0	0
Graminoids						
Agrostis scabra	3	573±338	0	507±270	40±23	13±13
Carex geyeri	3	40±23	27±27	80±80	27±27	0
Carex rossii	3	160±140	67±35	120±40	107±35	0
Deschampsia caespitosa*	1	0	0	13±13	0	0
Danthonia intermedia*	2	27±27	0	27±27	40±40	0
Juncus ensifolius*	1	0	0	13±13	0	0
Juncus parryi*	1	0	0	13±13	13±13	0
Poa nervosa	3	213±141	27±27	173±119	80±61	0
Stipa occidentalis	1	27±27	0	0	0	0
Subtotals		1040±534	121±35	946±486	307±119	13±13
Annual/Biennial Forbs						
Androsace sept.*	1	440±440	0	387±387	40±40	13±13
Arabis glabra*	2	13±13	80±80	0	0	0
Arenaria serpyllifolia*	1	0	27±27	0	0	0
Cerastium vulgatum*	1	40±40	13±13	40±40	0	0
Collinsia parviflora*	1	93±93	0	107±107	0	0
Veronica arvensis*	1	27±27	27±27	67±67	0	0
Subtotals		613±463	147±147	601±450	40±40	13±13
Perennial Forbs						
Antennaria microphylla	3	67±67	0	67±27	13±13	0
Astragalus alpinus	1	0	27±27	0	13±13	0
Campanula rotundifolia	1	320±320	0	373±373	67±67	0
Cerastium arvense	1	0	0	27±27	0	0
Epilobium glaberrimum*	2	13±13	27±13	13±13	0	0
Erigeron compositus*	1	0	0	13±13	0	0
Fragaria virginiana	1	27±27	0	0	0	0
Penstemon procerus*	1	13±13	0	0	0	0
Taraxacum officinale	1	0	0	13±13	0	0
Trifolium hybridum*	1	27±27	0	0	80±80	27±27

Table continues on next page.

Table 13--Continued. Mean seed bank density (#/m^2 ± SE) by treatment for the LP1 seral stage of the Abies lasiocarpa/Calamagrostis rubescens habitat type. N=3 for all treatments. The "SITES" column indicates the number of sites from which germinant were obtained. Asterisks denote species which were not present in the aboveground vegetation.

SPECIES	SITES	CONTROL	BURN	50°C	100°C	150°C
Perennial Forbs						
Viola adunca*	1	27±27	0	27±27	0	0
unid. Liliaceae sp.*	1	13±13	0	13±13	0	0
Subtotals		507±411	54±35	546±448	173±154	27±27
TOTALS		2160±1139	335±140	2106±1102	520±295	53±35

Table 14. Mean seed bank density (#/m^2 ± SE) by treatment for the LP2 seral stage of the Abies lasiocarpa/Calamagrostis rubescens habitat type. N=3 for all treatments. The "SITES" column indicates the number of sites from which germinants were obtained. Asterisks denote species which were not present in the aboveground vegetation.

SPECIES	SITES	CONTROL	BURN	50°C	100°C	150°C
Trees						
Pinus contorta	3	40±23	53±35	0	0	0
Shrubs						
Ceanothus velutinus*	1	0	0	0	0	27±27
Graminoids						
Agropyron caninum	1	13±13	0	27±27	0	0
Agrostis scabra	2	13±13	0	27±13	13±13	13±13
Carex geyeri	2	0	0	93±74	0	0
Carex rossii	3	133±27	173±133	107±58	120±101	13±13
Danthonia intermedia	1	13±13	0	13±13	0	0
Juncus bufonius*	1	0	0	13±13	0	0
Juncus ensifolius*	2	0	0	13±13	13±13	0
Juncus parryi*	1	0	0	67±67	0	0
Juncus tenuis*	1	27±27	0	53±53	0	0
Phleum pratense	1	0	0	53±53	0	0
Poa interior*	2	0	0	13±13	13±13	0
Poa nervosa	3	187±81	80±80	280±260	27±13	13±13
Sitanion hystrix	1	27±27	13±13	53±53	0	0
Subtotals		413±148	266±127	812±554	186±93	39±39
Annual/Biennial Forbs						
Androsace septentrionalis*	1	53±53	0	40±40	0	0
Arabis glabra*	1	0	0	0	13±13	0
Cerastium vulgatum*	1	40±40	0	53±53	0	0
Collinsia parviflora*	1	27±27	0	67±67	0	0
Phacelia franklinii*	1	13±13	0	0	0	0
Spergularia rubra	1	27±27	0	53±53	0	0
Subtotals		160±83	0	213±107	13±13	0
Perennial Forbs						
Achillea millefolium	1	0	0	13±13	27±27	0
Antennaria microphylla	1	0	0	13±13	0	0
Campanula rotundifolia	3	27±13	13±13	40±23	0	0
Cerastium arvense*	1	13±13	0	0	0	0
Epilobium glaberrimum*	2	13±13	0	27±13	0	0

Table continues on next page.

Table 14--Continued. Mean seed bank density (#/m^2 ± SE) by treatment for the LP2 seral stage of the Abies lasiocarpa/Calamagrostis rubescens habitat type. N=3 for all treatments. The "SITES" column indicates the number of sites from which germinants were obtained. Asterisks denote species which were not present in the aboveground vegetation.

SPECIES	SITES	CONTROL	BURN	50°C	100°C	150°C
Perennial Forbs						
Rumex acetosella*	1	13±13	0	27±27	0	0
Taraxacum officinale	3	27±13	0	13±13	0	0
Trifolium hybridum	1	0	0	13±13	67±67	0
Subtotals		93±27	13±13	146±71	94±94	0
TOTALS		706±236	332±131	1171±782	293±131	66±66

Table 15. Mean seed bank density (#/m^2 ± SE) by treatment for the LP3 seral stage of the Abies lasiocarpa/Calamagrostis rubescens habitat type. N=3 for all treatments. The "SITES" column indicates the number of sites from which germinants were obtained. Asterisks denote species which were not present in the aboveground vegetation.

SPECIES	SITES	CONTROL	BURN	50°C	100°C	150°C
Trees						
Pinus contorta	1	120±120	0	13±13	0	0
Graminoids						
Agropyron caninum	2	40±23	0	27±13	0	0
Agropyron dasystachyum	2	27±27	0	53±35	13±13	0
Agrostis scabra	1	40±40	0	40±40	0	0
Carex geyeri	2	13±13	0	27±27	27±13	0
Carex rossii	3	107±58	27±27	307±148	227±148	0
Danthonia intermedia	2	27±13	0	13±13	0	0
Juncus parryi*	1	13±13	0	27±27	0	0
Juncus tenuis*	1	13±13	0	40±40	0	0
Poa interior*	2	13±13	0	13±13	0	0
Poa nervosa	2	213±141	93±48	200±106	133±67	0
unidentified graminoid	1	0	0	0	13±13	0
Subtotals		506±107	120±69	747±210	413±187	0
Annual/Biennial Forbs						
Androsace septentrionalis	2	200±162	0	187±131	40±40	0
Arabis divaricarpa*	1	0	0	13±13	0	0
Arabis drummondii*	1	13±13	0	13±13	13±13	0
Arabis holboellii*	1	13±13	13±13	27±27	0	0
Collinsia parviflora*	2	107±107	0	40±23	27±27	0
Phacelia franklinii*	2	13±13	0	53±35	0	0
Spergularia rubra*	1	0	0	13±13	0	0
Subtotals		346±141	13±13	346±154	80±40	0
Perennial Forbs						
Antennaria microphylla	1	0	0	27±27	0	0
Arabis nuttallii*	2	13±13	0	40±23	0	0
Campanula rotundifolia	2	147±147	93±48	120±120	13±13	0
Cerastium arvense*	1	13±13	0	13±13	0	0
Fragaria virginiana	3	53±35	0	27±27	0	0
Hieracium gracile	1	80±80	0	13±13	0	0
Lychnis drummondii*	1	0	0	13±13	0	0
Potentilla glandulosa*	2	13±13	0	27±27	13±13	0
Potentilla gracilis	1	0	0	13±13	0	0

Table continues on next page.

Table 15--Continued. Mean seed bank density (#/m^2 ± SE) by treatment for the LP3 seral stage of the Abies lasiocarpa/Calamagrostis rubescens habitat type. N=3 for all treatments. The "SITES" column indicates the number of sites from which germinants were obtained. Asterisks denote species which were not present in the aboveground vegetation.

SPECIES	SITES	CONTROL	BURN	50°C	100°C	150°C
Perennial Forbs						
Sedum lanceolatum	1	0	0	13±13	0	0
Taraxacum officinale	1	0	0	0	13±13	0
Viola adunca*	1	0	13±13	0	0	0
Subtotals		319±122	106±53	306±107	39±23	0
unidentified forbs	1	0	13±13	53±53	53±53	0
TOTALS		1291±139	252±81	1465±87	585±93	0

Table 16. Mean seed bank density (#/m^2 ± SE) by treatment for the Festuca idahoensis/Agropyron caninum habitat type. N=3 for all treatments. The "SITES" column indicates the number of sites from which germinants were obtained. Asterisks denote species which were not present in the aboveground vegetation.

SPECIES	SITES	CONTROL	BURN	50°C	100°C	150°C
Trees						
Pinus contorta*	1	0	13±13	0	0	0
Graminoids						
Agropyron caninum	3	27±13	80±40	27±27	0	0
Agropyron dasystachyum	1	0	13±13	0	0	0
Agrostis scabra	1	67±67	40±40	13±13	0	0
Carex rossii*	1	13±13	13±13	40±40	13±13	0
Carex stenophylla	2	0	0	40±23	0	0
Danthonia intermedia	2	40±40	67±48	0	0	0
Festuca idahoensis	1	13±13	80±80	53±53	0	0
Juncus parryi	2	13±13	13±13	0	0	0
Juncus tenuis	2	0	0	27±13	0	0
Koeleria cristata	2	0	160±92	13±13	0	0
Phleum pratense	3	27±13	53±13	13±13	0	0
Poa interior	1	0	13±13	0	0	0
Poa juncifolia	2	53±35	27±27	0	0	0
Poa pratensis	1	187±187	27±27	253±253	40±40	0
unidentified graminoids	1	0	13±13	13±13	13±13	0
Subtotals		440±197	599±129	492±187	66±27	0
Annual/Biennial Forbs						
Androsace septentrionalis	3	280±241	1000±506	427±294	13±13	0
Arabis divaricarpa	3	27±13	53±13	27±13	0	0
Arabis glabra*	3	187±147	360±360	133±81	80±80	0
Arabis holboellii*	1	27±27	0	13±13	0	0
Chenopodium capitatum*	1	27±27	13±13	13±13	0	0
Chenopodium fremontii	2	67±35	13±13	27±27	0	0
Collomia linearis	3	173±154	173±93	200±83	0	0
Descurainia richardsonii	2	0	267±150	0	0	0
Draba nemorosa	1	0	0	13±13	0	0
Lactuca serriola	1	0	0	0	0	13±13
Lappula redowskii	1	40±40	27±27	27±27	0	0
Thlaspi arvense	2	0	67±35	0	0	0
Tragopogon dubius	1	13±13	0	0	0	0
Subtotals		841±311	1973±67	879±162	93±74	13±13

Table continues on next page.

Table 16--Continued. Mean seed bank density (#/m^2 ± SE) by treatment for the Festuca idahoensis/Agropyron caninum habitat type. N=3 for all treatments. The "SITES" column indicates the number of sites from which germinants were obtained. Asterisks denote species which were not present in the aboveground vegetation.

SPECIES	SITES	CONTROL	BURN	50°C	100°C	150°C
Perennial Forbs						
Achillea millefolium	2	13±13	13±13	0	0	0
Antennaria microphylla	2	13±13	13±13	13±13	0	0
Arabis nuttallii	3	107±48	53±35	40±23	0	0
Campanula rotundifolia	1	0	547±547	13±13	0	0
Cerastium arvense	2	360±266	80±40	280±144	0	0
Dracocephalum parviflorum*	1	0	0	0	13±13	0
Epilobium glaberrimum*	2	13±13	13±13	13±13	0	0
Erigeron compositus	1	27±13	0	13±13	0	0
Erigeron peregrinus	1	0	13±13	0	0	0
Hackelia floribunda*	1	13±13	53±53	13±13	0	0
Lychnis drummondii*	1	67±67	53±53	27±27	0	0
Penstemon procerus*	2	227±227	346±346	267±247	13±13	0
Potentilla glandulosa*	2	0	213±194	0	0	0
Potentilla gracilis	1	13±13	27±27	0	0	0
Solidago multiradiata	1	0	0	13±13	0	0
Taraxacum officinale	1	40±40	13±13	0	0	0
Subtotals		893±196	1437±521	692±83	26±13	0
unid. Brassicaceae spp.	1	13±13	0	13±13	0	0
unidentified forbs	2	13±13	13±13	27±27	0	0
TOTALS		2200±703	4035±621	2103±255	185±107	13±13

Table 17. Mean seed bank density (#/m^2 ± SE) by treatment for the LPO seral stage of the Abies lasiocarpa/Vaccinium scoparium habitat type. N=2 for all treatments. The "SITES" column indicates the number of sites from which germinants were obtained. Asterisks denote species which were not present in the aboveground vegetation.

SPECIES	SITES	CONTROL	BURN	50°C	100°C	150°C
Trees						
Pinus contorta	2	20±20	0	0	0	0
Graminoids						
Agrostis scabra	1	0	0	80±80	80±80	20±20
Carex rossii	2	120±40	0	140±60	120±80	0
Subtotals		120±40	0	220±140	200±160	20±20
Annual/Biennial Forbs						
Arabis glabra*	1	20±20	0	0	20±20	0
Arabis holboellii*	1	0	20±20	80±40	20±20	0
Cirsium vulgare*	1	20±20	0	0	0	0
Spergularia rubra*	1	1440±1440	0	2220±2220	2100±2100	220±220
Subtotals		1480±1480	20±20	2300±2260	2140±2140	220±220
Perennial Forbs						
Epilobium glaberrimum	2	200±200	20±20	380±380	60±60	0
Taraxacum officinale	1	0	0	0	20±20	0
Subtotals		200±200	20±20	380±380	80±80	0
unidentified forb	1	0	0	20±20	0	0
TOTALS		1820±1340	40±0	2920±2040	2420±2220	240±240

Table 18. Mean seed bank density (#/m^2 ± SE) by treatment for the LP1 seral stage of the Abies lasiocarpa/Vaccinium scoparium habitat type. N=3 for all treatments. The "SITES" column indicates the number of sites from which germinants were obtained. Asterisks denote species which were not present in the aboveground vegetation.

SPECIES	SITES	CONTROL	BURN	50°C	100°C	150°C
Trees						
Pinus contorta	2	27±27	0	40±23	0	0
Graminoids						
Agrostis scabra	1	0	0	0	13±13	0
Carex geyeri	1	40±40	0	0	0	0
Carex rossii	3	53±13	67±48	267±127	67±23	0
Festuca rubra*	1	253±253	13±13	227±227	40±40	0
Juncus bufonius*	1	0	53±53	0	0	0
Juncus ensifolius*	1	0	0	13±13	0	0
Subtotals		346±289	133±71	507±219	120±46	0
Annual/Biennial Forbs						
Spergularia rubra*	1	0	0	0	13±13	0
Perennial Forbs						
Astragalus alpinus*	1	13±13	0	0	0	0
Campanula rotundifolia	3	40±40	40±40	40±23	0	0
Epilobium angustifolium	1	13±13	40±40	0	0	0
Penstemon procerus*	1	0	13±13	0	0	0
Saxifraga sp.*	1	13±13	0	27±27	53±53	0
Trifolium hybridum*	1	13±13	0	0	13±13	0
Viola adunca*	1	0	0	13±13	0	0
unid. Liliaceae sp.*	1	0	0	13±13	0	0
Subtotals		92±74	93±74	93±58	66±66	0
TOTALS		465±387	226±139	640±289	199±69	0

Table 19. Mean seed bank density (#/m^2 ± SE) by treatment for the LP2 seral stage of the Abies lasiocarpa/Vaccinium scoparium habitat type. N=3 for all treatments. The "SITES" column indicates the number of sites from which germinants were obtained. Asterisks denote species which were not present in the aboveground vegetation.

SPECIES	SITES	CONTROL	BURN	50°C	100°C	150°C
Trees						
Pinus contorta	3	40±23	0	53±35	0	0
Graminoids						
Agrostis scabra*	1	0	13±13	0	0	0
Carex rossii	3	333±218	67±13	160±106	213±96	0
Juncus tenuis*	1	0	0	13±13	0	0
Subtotals		333±218	80±0	173±104	213±96	0
Perennial Forbs						
Hieracium gracile*	1	13±13	0	0	0	0
TOTALS		399±237	80±0	226±71	213±96	0

Table 20. Mean seed bank density (#/m^2 ± SE) by treatment for the LP3 seral stage of the Abies lasiocarpa/Vaccinium scoparium habitat type. N=3 for all treatments. The "SITES" column indicates the number of sites from which germinants were obtained. Asterisks denote species which were not present in the aboveground vegetation.

SPECIES	SITES	CONTROL	BURN	50°C	100°C	150°C
Trees						
Pinus contorta	1	0	0	13±13	0	0
Graminoids						
Carex geyeri	1	0	13±13	13±13	0	0
Carex rossii	3	120±69	13±13	147±58	40±23	0
Subtotals		120±69	26±13	160±69	40±23	0
Perennial Forbs						
Antennaria microphylla*	1	13±13	0	0	0	0
Astragalus alpinus*	1	0	27±27	0	0	0
Epilobium angustifolium	1	0	0	13±13	0	0
Hieracium gracile	1	0	13±13	0	0	0
Thalictrum occidentale	1	13±13	13±13	13±13	0	0
Subtotals		26±13	53±35	26±26	0	0
TOTALS		146±81	79±46	199±80	40±23	0

Table 21. Mean seed bank density (#/m^2 ± SE) by treatment for the Abies lasiocarpa/Vaccinium globulare (LP3) habitat type. N=3 for all treatments. The "SITES" column indicates the number of sites from which germinants were obtained. Asterisks denote species which were not present in the aboveground vegetation.

SPECIES	SITES	CONTROL	50°C	100°C	150°C
Shrubs					
Ribes lacustre	1	0	13±13	0	0
Rubus parviflora	1	13±13	0	0	0
Sambucus racemosa	2	40±23	13±13	0	0
Vaccinium scoparium	1	0	13±13	0	0
Subtotals		53±13	39±23	0	0
Graminoids					
Bromus carinatus	1	80±80	53±53	0	0
Carex rossii*	1	13±13	13±13	0	0
Elymus glaucus	1	0	13±13	0	0
Festuca rubra*	2	0	27±13	13±13	0
Poa nervosa	1	13±13	27±27	40±40	0
Subtotals		106±106	186±114	53±35	0
Perennial Forbs					
Anaphalis margaritacea	1	0	13±13	0	0
Antennaria microphylla	1	13±13	0	0	0
Epilobium glaberrimum*	3	13±13	67±13	13±13	0
Epilobium watsonii*	1	13±13	0	0	0
Fragaria virginiana	1	13±13	0	0	0
Iliamna rivularis	1	0	0	27±27	0
Mimulus lewisii	1	0	53±53	0	0
Mitella pentandra*	1	13±13	0	0	0
Taraxacum officinale	1	13±13	0	0	0
Subtotals		78±40	133±53	40±40	0
TOTALS		237±160	305±104	93±48	0

Table 22. Mean seed bank density (#/m^2 ± SE) by treatment for the WB2 seral stage of the Abies lasiocarpa/Vaccinium scoparium-Pinus albicaulis habitat type. N=3 for the control and oven-heated treatments, and N=2 for the burn treatment. The "SITES" column indicates the number of site from which germinants were obtained. Asterisks denote species which were not present in the aboveground vegetation.

SPECIES	SITES	CONTROL	BURN	50°C	100°C	150°C
Trees						
Pinus contorta	1	13±13	0	0	0	0
Shrubs						
Vaccinium scoparium	1	13±13	0	80±80	0	0
Graminoids						
Agropyron dasystachyum*	1	0	0	27±27	0	0
Agrostis scabra	3	613±441	20±20	413±148	547±432	13±13
Carex capitata*	1	27±27	0	107±107	0	0
Carex geyeri	1	0	0	53±53	0	0
Carex rossii	3	307±58	40±0	333±71	253±87	13±13
Danthonia intermedia*	1	27±27	0	27±27	0	0
Juncus parryi*	3	613±116	20±20	1253±61	307±147	13±13
Poa alpina*	1	13±13	0	13±13	0	0
Poa nervosa	3	133±58	0	107±87	93±93	0
Subtotals		1733±612	80±40	2333±439	1200±733	39±0
Annual/Biennial Forbs						
Androsace septentrionalis*	1	40±40	0	93±93	107±107	0
Draba stenoloba*	1	27±27	0	27±27	0	0
Spergularia rubra*	1	0	0	27±27	0	0
Subtotals		67±67	0	147±147	107±107	0
Perennial Forbs						
Achillea millefolium	1	0	0	13±13	0	0
Antennaria microphylla	1	13±13	0	0	0	0
Astragalus alpinus*	1	13±13	0	0	13±13	0
Cerastium beeringianum*	2	13±13	0	27±13	0	0
Epilobium angustifolium	1	0	20±20	0	0	0
Epilobium glaberrimum*	1	0	0	13±13	13±13	0
Hieracium gracile	3	160±140	0	240±140	27±13	0

Table continues on next page.

Table 22--Continued. Mean seed bank density (#/m^2 ± SE) by treatment for the WB2 seral stage of the Abies lasiocarpa/Vaccinium scoparium-Pinus albicaulis habitat type. N=3 for the control and oven-heated treatments, and N=2 for the burn treatment. The "SITES" column indicates the number of sites from which germinants were obtained. Asterisks denote species which were not present in the aboveground vegetation.

SPECIES	SITES	CONTROL	BURN	50°C	100°C	150°C
Perennial Forbs						
Oxytropis deflexa*	1	0	0	0	13±13	0
Polemonium pulcherrimum*	1	27±27	0	40±40	27±27	0
Sibbaldia procumbens	3	13±13	0	67±13	27±27	0
Solidago multiradiata	1	0	0	13±13	0	0
Thalictrum occidentale*	1	0	0	13±13	0	0
Subtotals		239±144	20±20	426±127	120±83	0
TOTALS		2065±701	100±20	2986±512	1427±921	39±0

Table 23. Mean seed bank density (#/m^2 ± SE) by treatment for the WB3 seral stage of the Abies lasiocarpa/Vaccinium scoparium-Pinus albicaulis habitat type. N=3 for the control and oven-heated treatments, and N=2 for the burn treatment. The "SITES" column indicates the number of sites from which germinants were obtained. Astersisks denote species which were not present in the aboveground vegetation.

SPECIES	SITES	CONTROL	BURN	50°C	100°C	150°C
~~Trees~~ Shrubs						
Vaccinium scoparium	1	13±13	0	27±27	13±13	0
Graminoids						
Agropyron caninum	1	13±13	0	13±13	0	0
Carex geyeri*	1	27±27	0	27±27	27±27	0
Carex rossii*	3	160±106	0	147±58	67±35	0
Juncus parryi*	3	280±205	80±80	360±340	80±46	0
Luzula spicata*	1	13±13	0	0	0	0
Poa alpina*	1	0	0	13±13	0	0
Poa nervosa	1	0	0	13±13	0	0
Stipa occidentalis	1	13±13	0	13±13	0	0
Subtotals		506±292	80±80	586±375	174±67	0
Annual/Biennial Forbs						
Androsace septentrionalis*	2	27±13	0	13±13	0	0
Arenaria serpyllifolia*	1	0	20±20	0	0	0
Draba stenoloba*	2	0	20±20	0	13±13	0
Subtotals		27±13	40±0	13±13	13±13	0
Perennial Forbs						
Astragalus alpinus*	1	40±40	20±20	107±107	67±67	0
Epilobium angustifolium	2	40±40	0	0	27±27	0
Epilobium glaberrimum*	2	27±27	0	27±27	0	0
Hieracium gracile*	1	13±13	0	13±13	27±27	0
Mitella pentandra*	1	13±13	0	13±13	0	0
Thalictrum occidentale	1	40±40	0	93±93	0	0
Veronica serpyllifolia*	1	0	0	13±13	0	0
Subtotals		173±71	20±20	266±247	121±61	0
TOTALS		719±326	140±60	892±354	321±40	0

Table 24. Mean seed bank density (#/m^2 ± SE) by treatment for the Festuca ovina/Poa alpina community type. N=3 for the control and oven-heated treatments, and N=2 for the burn treatment. The "SITES" column indicates the number of sites from which germinants were obtained. Asterisks denote species which were not present in the aboveground vegetation.

SPECIES	SITES	CONTROL	BURN	50°C	100°C	150°C
Shrubs						
Vaccinium scoparium	1	0	0	13±13	0	0
Graminoids						
Agropyron caninum	1	0	40±40	53±53	13±13	0
Agrostis scabra	2	320±300	20±20	267±228	240±220	0
Carex capitata	2	53±53	60±60	133±114	27±27	0
Carex phaeocephala	1	80±80	0	187±187	0	0
Juncus parryi	3	1387±1387	20±20	1947±1907	107±71	0
Poa alpina	3	293±173	60±21	213±87	13±13	0
Poa grayana	3	107±87	40±0	27±13	0	0
Subtotals		2240±1688	240±120	2827±2149	400±262	0
Annual/Biennial Forbs						
Androsace sept.	3	867±467	1620±540	973±472	147±74	0
Arabis drummondii	1	67±67	80±80	13±13	13±13	0
Draba stenoloba	3	627±530	600±520	747±647	53±53	0
Subtotals		1561±1021	2300±1140	1733±1027	213±127	0
Perennial Forbs						
Antennaria microphylla	1	0	0	13±13	0	0
Astragalus alpinus	1	0	80±80	27±27	27±13	0
Cerastium beeringianum	2	787±430	660±140c	693±350	93±35	0
Epilobium angustifolium	1	0	40±40	0	0	0
Epilobium glaberrimum*	2	120±69	40±40	80±80	0	0
Hackelia floribunda*	1	27±27	20±20	13±13	0	0
Hieracium gracile*	1	0	80±80	27±27	0	0
Oxytropis deflexa	1	0	40±40	13±13	27±27	0
Potentilla diversifolia	2	13±13	20±20	0	0	0
Potentilla gracilis	1	13±13	0	13±13	0	0

Table continues on next page.

Table 24--Continued. Mean seed bank density (#/m^2 ± SE) by treatment for the Festuca ovina/Poa alpina community type. N=3 for the control and oven-heated treatments, and N=2 for the burn treatment. The "SITES" column indicates the number of sites from which germinants were obtained. Asterisks denote species which were not present in the aboveground vegetation.

SPECIES ~~150°C~~	SITES	CONTROL	BURN	50°C	100°C	150°C
Perennial Forbs						
Sagina saginoides	3	387±253	0	573±441	40±40	0
Saxifraga rhomboidea	1	0	20±20	0	0	0
Sibbaldia procumbens	3	27±27	20±20	13±13	27±27	0
Thalictrum alpinum	1	13±13	0	0	0	0
Subtotals		1387±188	1020±180	1465±196	214±127	0
unidentified forb	1	0	20±20	0	0	0
TOTALS		5188±1292	3580±1220	6038±1709	827±187	0

APPENDIX B

SPECIES PRESENT ONLY IN THE ABOVEGROUND VEGETATION OF EACH HABITAT TYPE

Species present only in the aboveground vegetation of each habitat type.

1. Stco/Bogr

Shrubs: Gutierrezia sarothrae
Graminoids: Agropyron spicatum, Bouteloua gracilis, Koeleria cristata

2. Agsp/Posa-Stco

Shrubs: Gutierrezia sarothrae
Annual/Biennial Forbs: Tragopogon dubius
Perennial Forbs: Antennaria microphylla, Phlox hoodii

3. Feid/Agsp

Shrubs: Artemisia frigida
Graminoids: Agropyron caninum, A. dasystachyum, A. smithii, Carex stenophylla, Festuca idahoensis, Koeleria cristata, Stipa comata
Perennial Forbs: Antennaria microphylla, Lupinus sericeus

4. Deca/Carex

Perennial Forbs: Achillea millefolium, Fragaria virginiana

5. Psme/Caru

Trees: Pinus contorta, Pseudotsuga menziesii
Graminoids: Agropyron dasystachyum, Calamagrostis rubescens, Elymus glaucus, Stipa occidentalis
Perennial Forbs: Erigeron peregrinus, Geranium viscosissimum, Linum perenne, Lupinus argentea

6. Psme/Syal

Trees: Pinus contorta
Shrubs: Spirea betufolia, Symphoricarpos albus
Graminoids: Agropyron dasystachyum, Agrostis scabra, Calamagrostis rubescens, Koeleria cristata, Stipa occidentalis
Annual/Biennial Forbs: Arabis holboellii, Descurainia richardsonii, Draba nemorosa, Linanthus septentrionalis
Perennial Forbs: Achillea millefolium, Aster conspicuus, Geranium viscosissimum, Thalictrum occidentale, Viola adunca

Species present only in the aboveground vegetation of each habitat type--Continued.

7. Potr/Caru

Trees: Populus tremuloides, Pseudotsuga menziesii
Shrubs: Artemisia tridentata, Spirea betufolia
Graminoids: Agropyron caninum, A. dasystachyum, A. spicatum, Agrostis scabra, Bromus anomalous, Calamagrostis canadensis, C. rubescens, Elymus glaucus, Poa juncifolia, Stipa occidentalis
Annual/Biennial Forbs: Polygonum douglasii
Perennial Forbs: Aster conspicuus, Cirsium scariosum, Fragaria virginiana, Lupinus argentea, Potentilla diversifolia, Solidago multiradiata, Thalictrum occidentale

8. Artr/Feid

Shrubs: Artemisia frigida
Graminoids: Agropyron caninum, A. dasystachyum
Annual/Biennial Forbs: Collinsia parviflora, Collomia linearis
Perennial Forbs: Achillea millefolium, Cirsium arvense, Lupinus sericeus, Phlox hoodii, Potentilla glandulosa, P. gracilis, Sedum lanceolatum, Solidago multiradiata

9. Abla/Caru LP0

Graminoids: Bromus carinatus, Calamagrostis rubescens, Danthonia intermedia, Poa nervosa, Trisetum spicatum
Perennial Forbs: Arenaria congesta, Lupinus argentea

10. Abla/Caru LP1

Trees: Abies lasiocarpa
Shrubs: Arctostaphylos uva-ursi, Juniperus communis, Vaccinium scoparium
Graminoids: Agropyron caninum, Bromus anomalous, Calamagrostis rubescens, Elymus canadensis, Phleum pratense, Poa interior, Trisetum spicatum
Annual/Biennial Forbs: Polygonum douglasii
Perennial Forbs: Achillea millefolium, Agoseris glauca, Antennaria racemosa, Arnica cordifolia, Astragalus miser, Castilleja rhexifolia, Epilobium angustifolium, Erigeron peregrinus, Eriogonum umbellatum, Hieracium albiflorum, Lomatium triternatum, Lupinus argentea, Potentilla gracilis, Senecio serra, S. streptanthofolius, Solidago multiradiata, Taraxacum laevigatum

Species present only in the aboveground vegetation of each habitat type--Continued.

11. Abla/Caru LP2

Trees: Abies lasiocarpa, Pinus albicaulis, P. flexelis
Shrubs: Arctostaphylos uva-ursi, Berberis repens, Juniperus communis, Lonicera utahensis, Shepherdia canadensis
Graminoids: Bromus anomalous, B. carinatus, Calamagrostis rubescens, Festuca idahoensis, Stipa occidentalis
Annual/Biennial Forbs: Gayophytum diffusum
Perennial Forbs: Agoseris glauca, Arenaria congesta, Arnica cordifolia, Aster conspicuus, Astragalus miser, Chimaphila umbellata, Epilobium angustifolium, Erigeron peregrinus, Fragaria virginiana, Hieracium albiflorum, Lupinus argentea, Penstemon procerus, Phlox longifolia, Potentilla gracilis, Solidago multiradiata, Taraxacum laevigatum

12. Abla/Caru LP3

Trees: Picea engelmannii, Pinus albicaulis
Shrubs: Berberis repens
Graminoids: Bromus carinatus, Calamagrostis rubescens, Stipa occidentalis
Annual/Biennial Forbs: Collomia linearis, Polygonum douglasii, Tragopogon dubius
Perennial Forbs: Achillea millefolium, Agoseris glauca, Astragalus miser, Epilobium angustifolium, Erigeron peregrinus, Eriogonum umbellatum, Galium boreale, Lupinus argentea, Solidago multiradiata

13. Feid/Agca

Graminoids: Bromus carinatus, Stipa occidentalis
Annual/Biennial Forbs: Spergularia rubra
Perennial Forbs: Lupinus sericeus

14. Abla/Vasc LPO

Trees: Pinus albicaulis
Shrubs: Artemisia tridentata, Berberis repens, Shepherdia canadensis, Spirea betufolia, Vaccinium scoparium
Graminoids: Carex geyeri, Danthonia intermedia, Poa juncifolia, Sitanion hystrix, Stipa occidentalis, Trisetum spicatum
Perennial Forbs: Achillea millefolium, Antennaria microphylla, Arnica cordifolia, Aster foliaceus, Campanula rotundifolia, Cirsium arvense, Epilobium angustifolium, Erigeron peregrinus, Eriogonum umbellatum, Fragaria virginiana, Lupinus argentea, Solidago multiradiata

Species present only in the aboveground vegetation of each habitat type--Continued.

15. Abla/Vasc LP1

Trees: Abies lasiocarpa, Pinus albicaulis
Shrubs: Berberis repens, Lonicera utahensis, Spirea betufolia, Vaccinium globulare, V. scoparium
Graminoids: Calamagrostis rubescens, Poa nervosa, Sitanion hystrix, Stipa occidentalis
Perennial Forbs: Antennaria microphylla, A. racemosa, Arnica cordifolia, Aster conspicuus, Erythronium grandiflorum, Fragaria virginiana, Hieracium albiflorum, H. cynoglossoides, Sedum lanceolatum, Solidago multiradiata

16. Abla/Vasc LP2

Trees: Abies lasiocarpa, Picea engelmannii, Pinus albicaulis
Shrubs: Juniperus communis, Shepherdia canadensis, Vaccinium globulare, V. scoparium
Perennial Forbs: Achillea millefolium, Antennaria racemosa, Arnica cordifolia, Aster conspicuus, Epilobium angustifolium, Lupinus argentea, Pyrola secunda, Solidago multiradiata

17. Abla/Vasc LP3

Trees: Abies lasiocarpa, Picea engelmannii, Pinus albicaulis
Shrubs: Vaccinium globulare, V. scoparium
Graminoids: Calamagrostis rubescens, Poa nervosa
Perennial Forbs: Achillea millefolium, Antennaria racemosa, Arnica cordifolia, A. latifolia, Campanula rotundifolia, Fragaria virginiana, Lupinus argentea, Potentilla diversifolia, Solidago multiradiata

18. Abla/Vagl LP3

Trees: Abies lasiocarpa, Picea engelmannii, Pinus albicaulis, P. contorta
Shrubs: Vaccinium globulare

19. Abla/Vasc-Pial WB2

Trees: Abies lasiocarpa, Picea engelmannii, Pinus albicaulis
Graminoids: Stipa occidentalis, Trisetum spicatum
Perennial Forbs: Agoseris glauca, Arnica cordifolia, A. latifolia, Erigeron peregrinus, Erythronium grandiflorum, Frasera speciosa, Hieracium cynoglossoides, Lupinus argentea, Potentilla diversifolia, Senecio crassulus

Species present only in the aboveground vegetation of each habitat type--Continued.

20. Abla/Vasc-Pial WB3

Trees: Abies lasiocarpa, Picea engelmannii, Pinus albicaulis, P. contorta
Shrubs: Ledum glandulosum
Graminoids: Bromus ciliatus
Perennial Forbs: Antennaria racemosa, Aquilegia flavescens, Arnica cordifolia, A. latifolia, Aster engelmannii, Erigeron peregrinus, Lomatium dissectum, Lupinus argentea, Osmorhiza depauperata, Pedicularis racemosa, Pyrola secunda

21. Feov/Poal

Shrubs: Dryas octopetala
Graminoids: Festuca ovina
Perennial Forbs: Achillea millefolium, Erigeron compositus, Phlox hoodii, Polemonium pulcherrimum

APPENDIX C

SAMPLING SITE LOCATIONS (UTM)

Sampling site locations (UTM coordinates).

Gallatin Valley Locations (Figure 2):

1a.	Three Forks Stco/Bogr	50734 N, 4550 E
1b.	Trident Stco/Bogr	50873 N, 4625 E
1c.	Logan Stco/Bogr	50821 N, 4663 E
2a.	Bear Creek Agsp/Posa-Stco	50786 N, 4912 E
2b.	Foster Agsp/Posa-Stco	50791 N, 4876 E
2c.	Thiesen Agsp/Posa-Stco	50810 N, 4872 E
3a.	Walker Feid/Agsp	50719 N, 4952 E
3b.	East Walker Feid/Agsp	50728 N, 4967 E
3c.	R and R Feid/Agsp	50860 N, 4934 E

Yellowstone N.P., Gallatin and Shoshone N.F. Locations (Figure 3):

1a.	Crystal Bench Deca/Carex	49730 N, 5532 E
1b.	Lamar Deca/Carex	49692 N, 5619 E
1c.	West Canyon Deca/Carex	49521 N, 5388 E
2a.	Bunsen Psme/Caru	49765 N, 5243 E
2b.	Water Plant Psme/Caru	49774 N, 5231 E
2c.	Blacktail Psme/Caru	49743 N, 5416 E
3a.	Terrace Psme/Syal	49787 N, 5213 E
3b.	Floating Island Psme/Syal	49762 N, 5433 E
3c.	Wraith Psme/Syal	49761 N, 5299 E
4a.	Bunsen Potr/Caru	49746 N, 5244 E
4b.	Lamar Potr/Caru	49673 N, 5657 E
4c.	Water Plant Potr/Caru	49776 N, 5230 E
5a.	Washburn Artr/Feid	49660 N, 5450 E
5b.	Frog Rock Artr/Feid	49780 N, 5342 E
5c.	Lamar Artr/Feid	49689 N, 5618 E
6a.	Indian Creek Abla/Caru LP0	49683 N, 5174 E
6b.	Horseshoe Abla/Caru LP1	49298 N, 5145 E
6c.	Roaring Mtn Abla/Caru LP1	49598 N, 5208 E
6d.	Tuff Cliff Abla/Caru LP1	49441 N, 5132 E
6e.	Golden Gate Abla/Caru LP2	49756 N, 5215 E
6f.	Madison Abla/Caru LP2	49440 N, 5015 E
6g.	Grotto Geyser Abla/Caru LP2	49246 N, 5126 E
6h.	South Canyon Abla/Caru LP3	49495 N, 5401 E
6i.	Southeast Swan Abla/Caru LP3	49716 N, 5221 E
6j.	Miller Creek Abla/Caru LP3	49558 N, 5812 E

Sampling site locations (UTM coordinates)--Continued.

7a.	Washburn Feid/Agca	49637 N, 5438 E
7b.	Blacktail Feid/Agca	49764 N, 5395 E
7c.	Specimen Feid/Agca	49720 N, 5574 E
8a.	Canyon-Norris Abla/Vasc LP0	49521 N, 5372 E
8b.	Fan Creek Abla/Vasc LP0	49781 N, 4967 E
8c.	Lulu Pass Abla/Vasc LP1	49865 N, 5866 E
8d.	Willow Park Abla/Vasc LP1	49628 N, 5215 E
8e.	Horseshoe Abla/Vasc LP1	49295 N, 5141 E
8f.	West Thumb Abla/Vasc LP2	49192 N, 5335 E
8g.	Lewis Lake Abla/Vasc LP2	49039 N, 5306 E
8h.	Lewis River Abla/Vasc LP2	48974 N, 5275 E
8i.	Lulu Pass Abla/Vasc LP3	49866 N, 5864 E
8j.	Canyon-Norris Abla/Vasc LP3	49522 N, 5374 E
8k.	Virginia Abla/Vasc LP3	49507 N, 5282 E
9a.	Sylvan Abla/Vagl LP3	49250 N, 5686 E
9b.	Eleanor Abla/Vagl LP3	49243 N, 5732 E
9c.	East Abla/Vagl LP3	49240 N, 5753 E
10a.	Washburn Abla/Vasc-Pial WB2	49618 N, 5443 E
10b.	Observation Abla/Vasc-Pial WB2	49570 N, 5363 E
10c.	Daisy Pass Abla/Vasc-Pial WB2	49877 N, 5834 E
10d.	Dunraven Abla/Vasc-Pial WB3	49596 N, 5435 E
10e.	Sylvan Abla/Vasc-Pial WB3	49275 N, 5638 E
10f.	W Dunraven Abla/Vasc-Pial WB3	49600 N, 5427 E
11a.	Washburn Feov/Poal	49617 N, 5447 E
11b.	Fantan Lake Feov/Poal	49757 N, 6158 E
11c.	Bootjack Gap Feov/Poal	49565 N, 5876 E

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