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Effects of a Wildfire on Seed Rain and Soil Seed Reserve Dynamics of a Good Condition Sagebrush-Grass Rangeland in Central Utah

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EFFECTS OF A WILDFIRE ON SEED RAIN AND SOIL SEED RESERVE DYNAMICS OF A GOOD CONDITION SAGEBRUSH-GRASS RANGELAND IN CENTRAL UTAH

by

Mohamed Ali Hassan

A thesis submitted in partial fulfillment
of the requirements for the degree

of

MASTER OF SCIENCE

in

Range Science

Approved:

UTAH STATE UNIVERSITY
Logan, Utah

1983

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To my wife, Ateyat, and my children, Suad and Abdell Gadir, and my brother Fathi, for their love and forbearance, I dedicate this piece of work.

Mohamed Ali Hassan

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ABSTRACT

Effects of a Wildfire on Seed Rain and Soil Seed Reserve Dynamics of a Good Condition Sagebrush-Grass Rangeland In Central Utah

by

Mohamed Ali Hassan, Master of Science

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Major Professor: Neil E. West
Department: Range Science

The objectives of this research were to investigate the ecological importance of soil seed reserves and seed rain on regeneration of a good condition sagebrush-grass range vegetation after a wildfire and draw conclusions leading to better understanding and management of such ecosystems. Investigations were conducted for two successive years on a community where major plants were neither rhizomatous nor sprouting. In such cases soil seed reserves and seed rain have to be the main source of regeneration. In addition to monitoring soil seed reserves and seed rain, vegetation changes during the past two years and the historical conditions of the study area were examined.

Study of germinable soil seed reserve dynamics showed

that fire can have a destructive effect on this portion of the community. Cheatgrass soil seed reserves were high even in good condition sagebrush-grass vegetation. Although fire reduced the Bromus tectorum seed bank by half, the cover of this grass increased to almost twice the level observed on the control (unburned) plots a year later. This shows the enormous reproductive capacity of this highly competitive weed species following a wildfire.

Even though the pre-burn vegetation contained a high proportion of native perennial plants, soil seed reserves and seed rain had very small proportions of their germinable seeds.

Timing of the fire is likely important in controlling undesirable range plants and their seeds. Had the fire occurred earlier when more seeds were attached to the culms, greater reduction in cheatgrass probably would have been obtained. Timing of the fire was just right to control sagebrush, because it occurred before their seed set and complete destruction of this species was achieved. Mormon tea was the only shrub to reestablish its cover relatively rapidly. This was related to its strong ability to sprout from root crowns.

Greater germinable soil seed reserves were found under shrub canopies than in the interspaces. This is probably

related to the semi-logarithmic dispersal of seed where seed fall is greatest closest to mother plants (Harper 1977). Since flammable fuel follows the same pattern, it was found that fire has a serious impact on soil seed reserves at "hot" points, but temperatures were apparently not hot enough to cause much damage on seed banks at "cold" points in the former interspaces.

Since soil seed reserves accumulate in significantly higher proportions in the surface 0-2 cm, fire has a more serious impact on the seeds in surface soil than those lower lower down.

Variance of the germinable seed rain was so high that none of the grand totals, life forms totals and species values were statistically significant at alpha <0.05 between treatments. The numerical differences observed may be due to wind moving more seeds to the seed traps in the bare, burned plots.

(141 pages)

INTRODUCTION

Although much information exists on the effects of fire on the aboveground portions of most perennial grasses, shrubs and on soil in the sagebrush-grass range type (Beardall and Sylvester 1976, Blaisdell 1953, Blaisdell et al. 1982, Tisdale and Hironaka 1981, Uresk et al. 1976, Wright 1971, Wright et al. 1979, Young and Evans 1977,...and many others), there is very little information on the effects of fire on soil seed reserves in such ecosystems. Understanding these phenomena is important in understanding how vegetation recovers following fire. For instance, the observation that cheatgrass (Bromus tectorum L.) is favored after fire (Young et al. 1976, 1981, West 1983) may be a function of poor seed reserves of native perennials. Studies of buried seed reserves have shown them to be of significant importance in replenishment of vegetation following wildfire elsewhere (Thompson 1978). This is especially true where major plants are non-rhizomatous or non sprouting. In such cases soil seed reserves and seed rain have to be the main source of regeneration. However, most native perennial grasses of the Great Basin are known to be poor seed producers (West 1983).

Seed of some species can be completely absent from seed banks, in spite of those species being abundant in the extant vegetation (Golubeva 1962, Zenenchuk 1961). This may be an important reason for lack of perennial grass recovery following fire. It is likely that the degree of regeneration of perennial grass species may be a function of vegetative reproduction, since that portion can escape fire destruction and regenerate regardless of how low seed rain or soil seed reserves are. Generally the post-burning season is very critical in determining future forage production of burned areas.

Regeneration can be predicted by comparing soil seed reserves to the vegetation emerging after any disturbance (Barbour and Lange 1967, Koniak and Everett 1982, Nelson and Chew 1977). Previous studies indicate that soil seed reserves are an important ecological component in modeling succession (Kellman 1970, Livingston and Allessio 1968, Major and Pyott 1966). Other studies found that soil seed reserves decrease in density and diversity from early to late successional stages (Koniak and Everett 1982, Livingston and Allesio 1968, Olmsted and Curtis 1947, Oosting and Humphreys 1940, Quick 1956).

Numerous studies have been conducted on the emerging vegetation following cultivation (Roberts and Dowkins 1967, Roberts and Feast 1973, Roberts and Richetts 1979,...and many others), or following other types of disturbances (Beauchamp et al. 1975, Bormann and Likens 1979).

Pechanec et al. (1954) reported that big sagebrush (*Artemisia tridentata* Nutt.), although a non-sprouter, will rapidly reoccupy sites following fire. Whether this is due to seed already in the soil or those blown in is not known. Winward (1983) recently reported that *Artemisia tridentata* ssp. *vaseyana* seed germination is stimulated by burning. In contrast, Young and Evans (1974) concluded that sprouters like *Chrysothamnus viscidiflorus* (Hook) Nutt. and *Tetradymia canescens* D.C. will rapidly reoccupy burned sites from sprouts coming from root crowns. Robocher et al. (1965) indicated that burning controls cheatgrass, presumably because of seed destruction. Countryman and Cornelius (1957) found that even if a few cheatgrass seeds are available, this species can rapidly reoccupy a burned area. Young et al. (1976) found a 80-90 percent reduction in germinable cheatgrass seeds following fire, depending on the intensity of burning.

Since soil seed reserves are concentrated under shrubs and grasses with few seeds on bareground or "interspaces" (Koniak and Everett 1982, Knipe and Springfield 1972, Nelson and Chew 1977), and since accumulation of flammable fuel follows the same pattern, fire could have an accentuated destructive effect on soil seed reserves on such microsites.

Therefore the impact probably differs according to microsite because of differences in the heat generated. Also, since most soil seed reserves are concentrated in the top 2-3 cm of soil surface (Child and Goodall 1973, Floyd 1966, Strickler and Edgerton 1976, Wesson and Wareing 1969), and heat generated from the fire will probably diminish with soil depth, that is there could be a differentially destructive effect of fire on soil seed reserves by depth.

The following research addresses the ecological importance of soil seed reserves and seed rain for regeneration of the vegetation of a good condition sagebrush-grass rangeland near Mills, Utah. The question of what was the differential impact of fire on soil seed reseves at different microsites or in different soil sampling depths was addressed. Another purpose of this work was to develop management guidelines to increase forage production of such burned rangeland.

OBJECTIVES

The specific objectives of this study were:

(1) To monitor for at least one year the seed rain and soil seed reserves on control(unburned) and burned plots of the same range site near Mills, Utah, in order to determine the ecological significance of soil seed reserves and seed rain for regeneration of a good condition sagebrush-grass range vegetation following fire destruction.

(2) To compare germinable soil seed reserves under canopy and in the interspaces of the control plots and "hot spots", which were formerly under canopy, and "cold spots" which were formerly interspaces within the burned plots. The data obtained may provide information on the destructive effect of fire on germinable soil seed reserves at different microsites.

(3) To compare the variation of germinable soil seed reserves found at different soil depths within the control plots and compare them with those at the same depths in the burned plots. This may provide an answer to a third question of what was the differentially destructive

effect of fire on soil seed reserves at different sampling depths.

HYPOTHESES

H_{o1} There will be no significant differences in the total and species germinable soil seed reserves (numbers per unit area) and total and species seed rain (number per unit area) on the control (unburned) and burned plots over time on a good condition phase of a sagebrush-grass range site near Mills, Utah.

H_{o2} There will be no significant differences in the germinable seeds per unit area between the "under canopy" and interspaces within the control plots and the "hot spots" and "cold spots" within the burned plots or between any pairing of these combinations over time.

H_{o3} There will be no significant differences in the germinable soil seed reserves between equal depths of soil within or between the unburned and burned plots over time.

STUDY SITE

An opportunity to study the phenomena mentioned earlier was afforded by the unintentional and unplanned treatment of a wildfire sweeping through a suitable study site on July 26, 1981. This lightning-caused wildfire spread over 32,000 ha. (80,000 acres) of juniper and sagebrush-grass range (Figure 1). Strong southerly winds, accumulations of litter and dryness and density of the vegetation (Figure 2) contributed to rapid spreading of the wildfire. The cover of the burn was not complete however and some small patches of unburned vegetation remained (Figures 3a and b).

All field work for this study was conducted at the northeastern corner of the Oak Creek Mountains, Juab County, Utah (Figure 4). The elevation of this area is 1617-1622 meters. The slope and exposure of the pediment remnant on which it is located is 1-2 percent east.

This area was chosen because the great distance to water (about 8 km) had allowed the area to remain in apparently good range condition. The study site was used in past winters by sheep, and more recently by cattle. Intensity of livestock grazing has been light during at least the past two decades. The result is that the prefire vegetation had a high proportion of native perennial grasses.

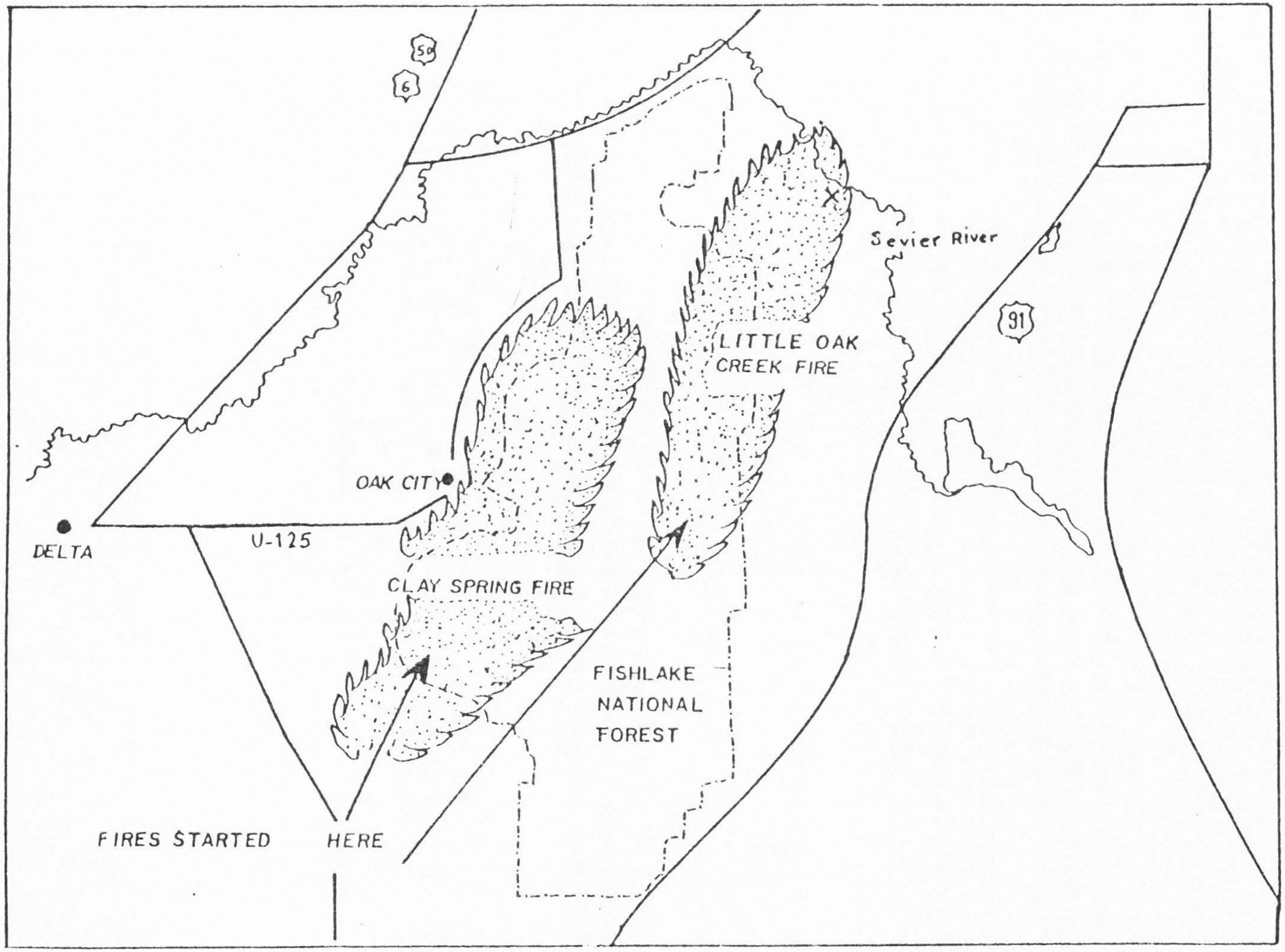


Figure 1. Map of the wildfire occurring around the Oak Creek Mountain on July 24, 1981 (X=approximate location of study area).

Figure 2. Photograph of a portion of the study area a few days before the fire.

Figure 3.

a. Photograph of one of the small patches which escaped the fire and was used as one of control plots.

b. Photograph of the study area just after the fire.

(Figure 3a)

(Figure 3b)

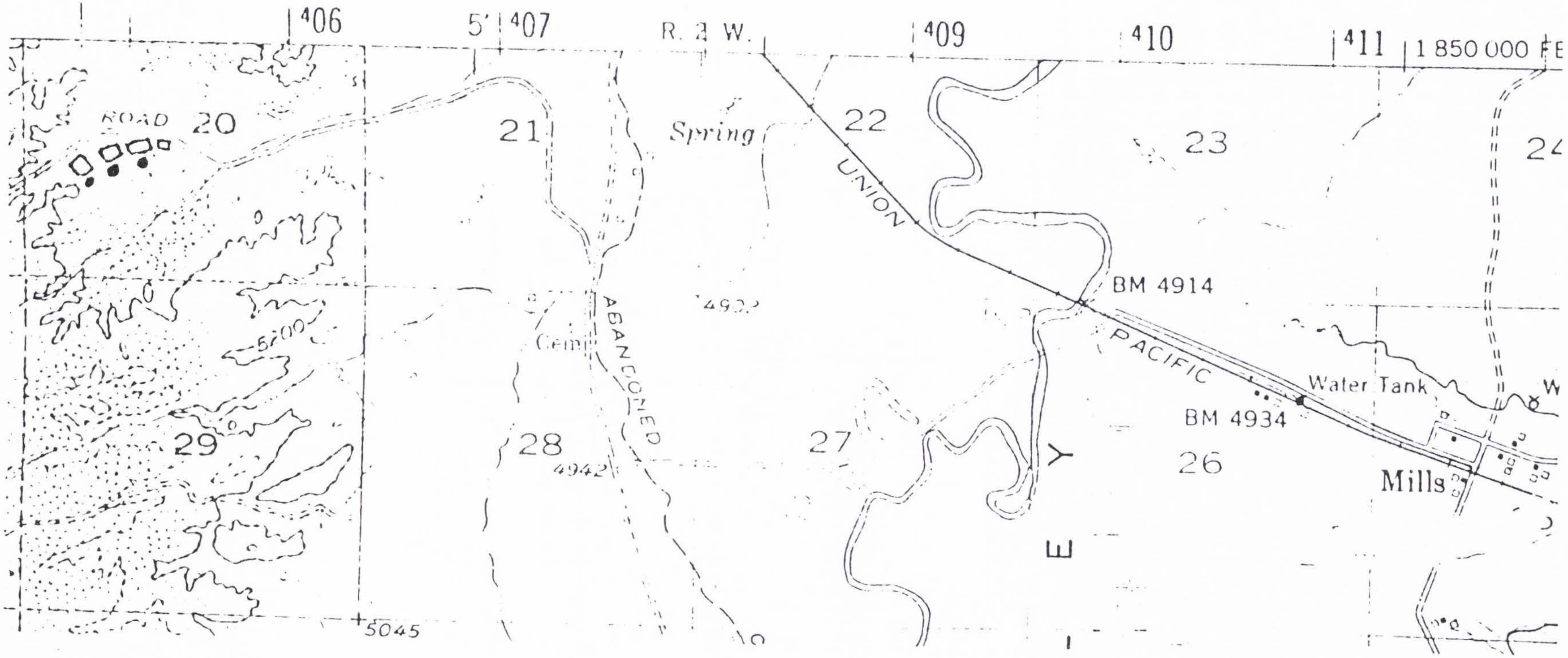


Figure 4. Location of study plots in relation to physical and cultural features (• =paired plots in relation to the previous intended study=□).

Identification of the site and the range condition were determined from the Soil Conservation Service (SCS) Range Site Guidelines (Soil Conservation Service 1976) using data gathered a few days before the fire for another intended study. The ecological site or potential community has been named "Upland Shallow Hardpan (Juniper Savannah)". Prefire vegetation analysis revealed that the study area had a "good" condition rating (57 percent native grass composition by dry weight, Table 1).

Scarcity of such good condition sagebrush-grass range may be attributed to the historical impact on vast areas of the western United States following settlement by European man. The settlers' livestock populations quickly built up in the ninteenth century (Griffiths 1902) and abused the native vegetation. The intensity of grazing was so great that the native bunchgrasses gave way in a relatively short period to native shrubs (West 1983). Dominance of cheatgrass over vast areas of the western United States did not take place until the 1950's (Young et al. 1979).

Bunch grasses in the sagebrush-grass ecosystem type are usually subjected to heavy spring and fall grazing because of their high nutritive value and palatability during those seasons (Rittenhouse and Vavra 1979). Stoddart (1946) reported that these native bunchgrasses can disappear from

Table 1. Percent composition of native perennial grasses obtained using dry weights (grams per m^2) examined in ten 9.6 ft^2 quadrats per plot seven days prior to the wildfire

	Control plots (pre-burn data)				
Grass species	Plot#1	Plot#2	Plot#3	Total	Mean
*Agropyron spicatum**	62.5	30.9	21.5	114.9	38.3
Agropyron smithii	2.5	6.7	12.1	21.3	7.1
Poa spp.	4.1	3.4	1.4	8.9	3.0
Oryzopsis hymenoides	3.2	3.9	14.6	21.7	7.3
Stipa comata	0.0	2.0	1.7	3.7	1.2
Total of means					56.9

* = Plant nomenclature follows Welsh et al. 1981

the vegetation even under moderate use.

Vegetation abuse by livestock grazing has led, in the absence of fire, to plant communities dominated by sagebrush. Attempts to alter these communities back to higher condition by changes in animal numbers, class, or season of use have not resulted in quick trend shifts. West (1983) believes that the primary reason for slow recovery of grasses is that sagebrush does not give up its dominance without fire interference. The lack of grass recovery may also be related to low input of native perennial grass propagules.

The climate in the study area is temperate and semi-arid according to the SCS (1976).

The ridgetop where the study plots were located has shallow soil over a hard pan and conglomerate layer. Surface soils on the site have fairly uniform silt loam texture which can be classified as coarse silty, mixed, mesic, Xerollic Calciorthid (SCS, personal communication). The SCS description for this site says that this is a shallow, somewhat excessively drained soil on alluvial fans. It was formed on a layer dominantly composed of limestone and sandstone. The surface layer is dark grayish brown cobbly loam approximately 23 centimeters thick underlain by very strong calcareous pale brown and very gravelly loam which is approximately 25 centimeters thick. At about 45-50 centimeters a carbonate-cemented hardpan about 18-20 centimeters thick typically occurs. The hardpan depth ranges from 25-50 centimeters. Below one meter, stratified layers of very gravelly loam and indurated hard pan exist.

Permeability of the soils associated with this range site is moderate and available water ranges between 3.8 to 6.4 centimeters. Water supplying capacity is 7.6-12.7 centimeters. The effective rooting depth is 25.4-50.8 centimeters. The organic content is about 1-2 percent. The runoff and water erosion are moderate. For more details see "Upland shallow site" Soil Conservation Service Range Site Description (Soil Conservation Service, 1976).

The high silt and very low clay fraction means the soil does not to shrink when dry or swell when wet, resulting in an almost crack-free soil.

METHODS

Selection of field plots

Three paired (burned and unburned) rectangular (15X23 meter) plots were chosen after the fire.

Similarity of exposure and elevation leads one to believe that all plots probably had and have a similar microclimate. Examination of prefire aerial photographs (black and white taken on August 27, 1964, scale 1:1,800, and color photographs which were taken by the Apollo mission on July 1, 1975, scale 1:8,000) indicated similar plant cover (Figure 5). To make sure that the initial impression of plot similarity was valid, vegetation and soil data were taken.

Field sampling

Plant cover on four nearby plots (20X50 m^2), located for the previously intended study, was determined one week before the fire with a sighting tube device (Winkworth and Goodall 1962). A metal metric tape was strung between the center east-west, long dimensions of each macroplot. Another tape was strung out along the west boundary of each plot. Five random numbers to the nearest one-tenth of a meter were drawn per plot.

The gimbled tube (sighting device) was suspended by wire from a iron staff at about eye height. A transect was

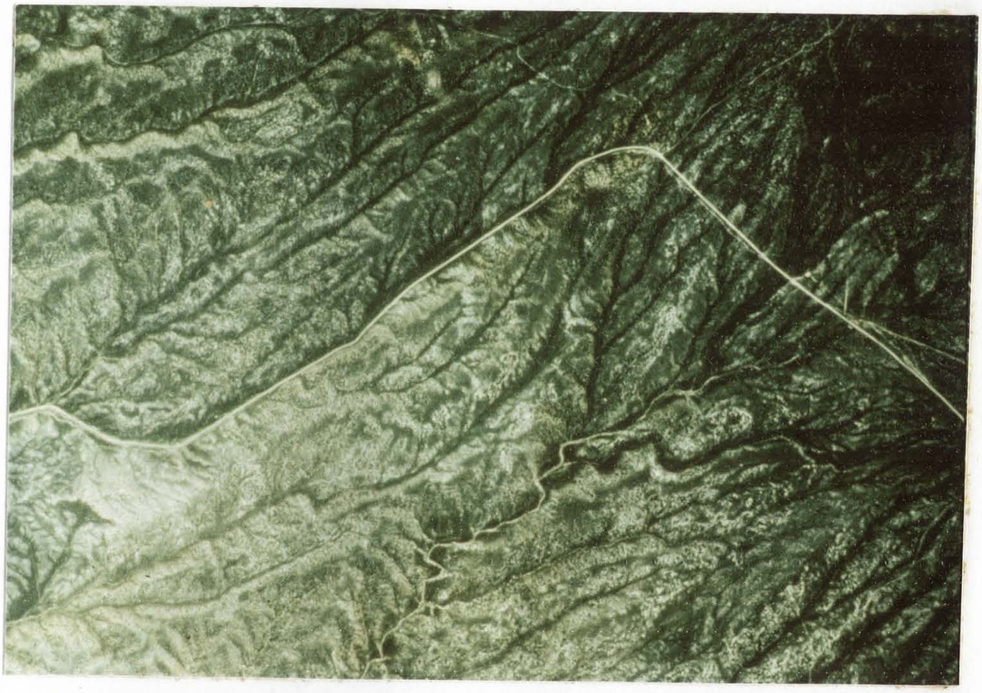


Figure 5. Enlargement (1:8,000 scale)of a color aerial photograph taken during the Apollo mission (July 1, 1975) showing the study area before the fire.

started at one of the random points on the west boundary and the observer started pacing eastward across the macroplot trying to stay parallel to the center tape. The staff was driven into the ground in front of the observer on every second pace. The gimble was allowed to stop swinging. When it came to rest, the observer sighted through the tube and lined up the two sets of cross-wires. The objects intersected in the line of sight from the cross-wires were recorded as plant species or other categories stated in Table 2.

Two readings per point were possible. If plant canopy was intersected, it was first recorded, and then the canopy moved aside to reveal what was on the ground surface. A second reading was taken in the instances when live plant canopy was present. This process was continued until 100 points had been sampled on the 4-5 lines. This same process was also applied six weeks after the fire on the plots of this study.

A cover-weighted index of similarity (Sorenson's K.) for the cover data collected before and after the fire was calculated (Mueller-Dombois and Ellenberg 1974).

Use of Soil Conservation Service range condition and trend rating guides requires herbage weight estimates. Accordingly, herbage weight was sampled ten days before the

Table 2. Summary of plant and ground cover (%) on the plots near Mills, Utah where soil seed reserves and seed rain data were collected.

Category/Species	Pre-burn	Post-burn			
	Just before the fire	Unburned 1981	Unburned 1982	Burned 1981	Burned 1982
Shrubs:					
Artemisia tridentata wyomingensis	6.5	2.3	3.7	0.0	0.0
Chrysothamnus viscidiflorus	7.3	8.0	6.3	0.0	0.0
Ephedra nevadensis	2.5	1.8	4.3	0.0	1.3
Subtotal	16.3	12.1	14.3	0.0	1.3
Grasses					
Agropyron spicatum	14.8	13.3	16.0	0.0	5.3
Agropyron smithii	3.5	1.5	1.0	0.0	0.0
Stipa comata	2.8	4.9	2.0	0.0	1.0
Poa secunda	2.4	5.6	4.0	0.0	1.0
Sitanion hystrix	2.8	0.4	1.3	0.0	0.7
Oryzopsis hymenoides	11.9	11.6	6.3	0.0	8.0
Bromus tectorum	6.3	6.8	11.0	0.0	35.7
Subtotal	44.5	44.1	41.6	0.0	51.7
Forbs					
Erigeron engelmannii	0.4	1.5	1.3	0.0	0.7
Eriogonum cernuum	0.4	0.0	1.0	0.0	0.4
Phlox spp.	0.8	0.0	3.0	0.0	0.4
Antennaria spp.	1.6	0.0	0.0	0.0	0.0
Descurainia pinnata	0.0	0.0	0.7	0.0	1.0
Subtotal	3.2	1.5	6.0	0.0	2.5
Total plant cover	64.0	57.7	61.9	0.0	55.5
Others					
Standing dead	0.8	0.0	1.3	2.7	0.0
Litter	7.4	15.4	18.3	9.3	10.3
Rock	0.0	0.0	0.3	0.0	0.0
Gravel	12.0	11.3	12.3	13.3	8.3
Bareground	14.2	14.7	14.7	77.3	27.3
Moss	11.5	12.8	9.3	0.0	0.0
Lichen	1.0	0.0	1.7	0.0	0.0
Subtotal	56.9	54.2	57.9	102.6	45.9
Grand total	120.9	111.9	119.8	102.6	101.4

fire, after spring and summer growth had ceased. This procedure involved selection of ten random locations per macroplot. A 9.6 ft^2 circular quadrat was centered on these locations and all living herbaceous plant material within the quadrat was harvested to 5 cm stubble height and all new growth taken on shrubs. These current year's standing crops were separated by species. The samples were placed in paper bags and allowed to air-dry for 5-7 days, depending on the dryness of the vegetation. The samples were then weighed to the nearest one tenth of a gram so as to determine percent composition by dry weight. Using the percentage composition in the climax condition for the "Upland Shallow Hardpan (Juniper savannah)", the condition of this site was determined (SCS 1976). The plots established after the fire were too small to allow destructive measurements of vegetation.

At each plot corner and center a soil pit was dug and examined in September 1981. In order to consider a plot homogeneous, four out of the five soil pits should have highly similar soil characteristics like soil color, texture, reaction, rooting depth, hardpans etc.

A meterological station was established at the southwest corner of the study area on July 7, 1981, to monitor air temperature, relative humidity and precipitation

Temperature and relative humidity were measured just above the shrub canopy height.

All data on soil seed reserves and seed rain were collected from the three paired (unburned and burned) plots established after the fire (Figure 4). Collection of soil seed reserve data began on September 22, 1981, and continued every three months over a period of 15 months. Traps to catch seed rain were put in at the same time, but sample collection began 3 months later (December 11, 1981) and continued for 15 months.

The three rectangular paired plots were located south of the four plots established prior to the burn (Figure 4). These plots were gridded at one meter intervals with plastic twine (Figure 6a). Coordinates were chosen randomly to place twenty seed traps (75.8 cm^2 surface area each) per plot (40 per plot pair). The grid helped in locating the exact positions of seed traps and sampling points for soil seed reserves.

The seed traps were constructed of 20 cm long pieces of 15.2 cm (6 inch) diameter plastic irrigation pipe and 240 ml (8 oz.) plastic funnels. One end of the pipe was buried flush with the ground surface. A funnel was then placed in the pipe and filled with well-washed pea-sized gravel to prevent turbulence around and in the trap and hold it down

Figure 6.

a. Photograph of a seed trap (at one of the control plots). Exact location was determined by using random coordinates within a grid.

b. Close-up photograph of a seed trap at a burned plot a year after the fire.

(Figure 6a)

(Figure 6b)

in the wind. A cotton thread had been inserted through the funnel neck. The neck was plugged with cotton. The cotton thread aided in drainage of rain water from the funnel to the soil so as to prevent germination of trapped seeds in the interspaces of the gravel and on the top of the cotton plug. The cotton plug prevented the loss of seeds, but allowed water drainage to the soil. Traps were emptied of seed and other sediments on December 11, 1981; March 25, 1982; June 2, 1982; September 11, 1982; and December 12, 1982.

Seed and other sediment were separated from the gravel in the field using a 0.25 centimeter mesh sieve. The separated seeds and other sediment were carefully placed in individual ziplock plastic bags, labeled, and transported to the laboratory.

The soil seed reserves were sampled for the first time on September 22, 1981, and repeated on the same dates as seed rain was sampled. A 5.4 centimeter diameter soil bulk density sampler (Soil Moisture Inc, Model 200) was used to obtain known soil volume. Soil cores were separated into the upper 2 and next 3 centimeter depths (45.8 and 68.7 cubic centimeters respectively) using a sharp scraper. An arbitrary sample size was determined to be 20 samples per plot. In order to avoid the impact of walking and associated disturbances on the site, a portable platform was used to stand on during the sampling of soil seed reserves and seed rain (Figure 7).

If the soil was dry it was pre-wetted to 5 cm or greater depth. This was done by hammering a piece of iron pipe (10 cm diameter and 20 cm length) into the soil leaving a part of its height above the soil surface to help in holding water. The hammered pipes were left holding water overnight. This was done in order to obtain stable soil cores of more exact volumes than was possible in dry soils.

Each soil seed reserve sample was carefully placed in an individual plastic ziplock bag, labeled and transported to the laboratory.

The distance relationship of seed traps and soil cores to the surrounding plants or "hot points" was determined from a sketch map which depicted to scale the surface cover of different plots immediately after the fire. This allowed soil seed reserves and seed rain analysis data to be related to the distance to nearby plants or "hot" points.

Laboratory operations

In the laboratory, all seed rain and soil seed reserve samples were air-dried for two days to prevent seed germination in the period during which the samples were stored in a cold room. Samples were stored at 0±2 degrees C for a maximum of three months.

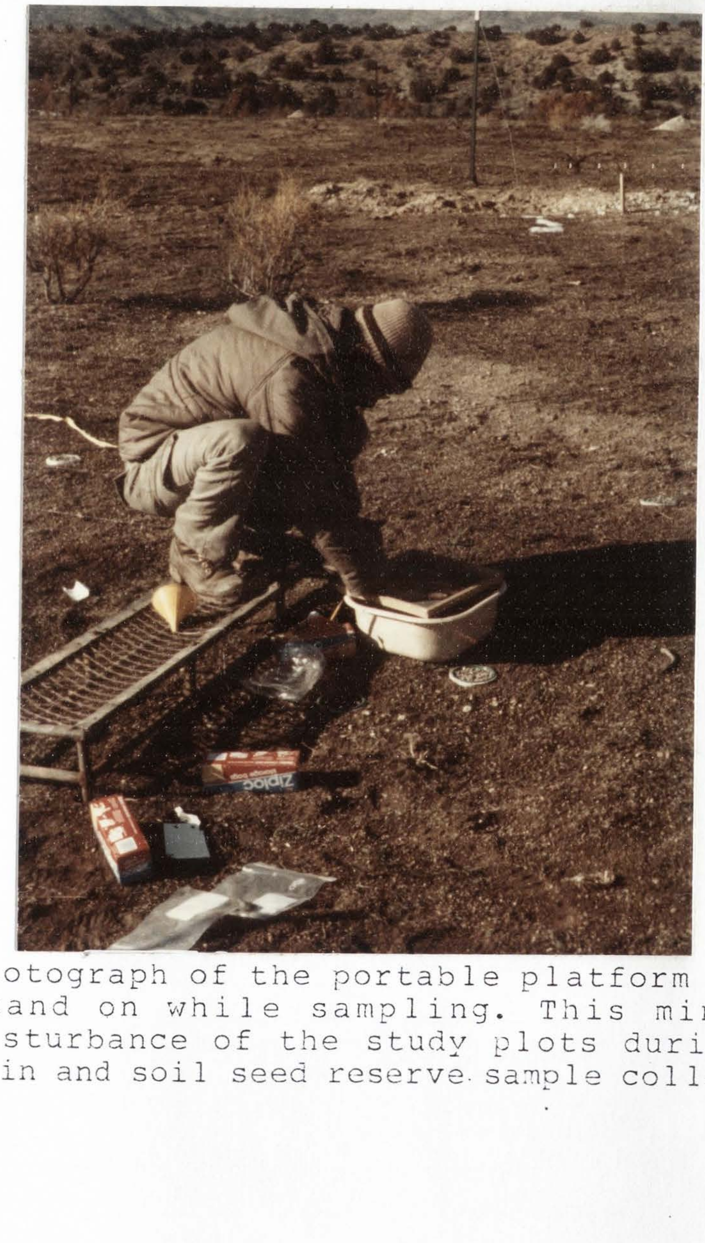


Figure 7. Photograph of the portable platform used to stand on while sampling. This minimized disturbance of the study plots during seed rain and soil seed reserve sample collections.

Soil seed reserve samples were thoroughly mixed and sieved through a 0.5 centimeter mesh sieve to separate out pebbles and large organic debris. One third of the thoroughly mixed and sieved soil seed reserve sample was mixed with a solution of 10 grams of sodium hexametaphosphate, 5 grams of sodium bicarbonate and 25 grams of magnesium sulphate dissolved in 200 ml of tap water (Malone 1967). The soil sample in the salt solution was then agitated for 2-3 minutes to facilitate separation of organic material trapped between mineral particles. Flotation of the organic material was achieved by leaving the solution undisturbed for 2 minutes. The floating organic material, which may include seeds, was skimmed from the solution and rinsed in a 0.025 mm mesh sieve with tap water for about 15 minutes. This reduced the possible adverse effect of highly concentrated salt solution on the viability of the recovered seeds. The flotation operation was repeated several times by reusing the salt solution until complete recovery of the organic material was achieved (Child and Goodall 1973). The recovered organic material was then dried under room temperature for 48 hours.

Efficiency of this flotation procedure in extracting seeds from soil samples was reported by Malone (1967) to be as high as 100 percent for the seeds of most plant species.

For the purpose of testing the efficiency of this procedure in extracting seeds of range plant species, 100 seeds per species of *Artemisia tridentata*, *Chrysothamnus viscidiflorus*, *Bromus tectorum* and *Descurainia pinnata* gathered from the study site were mixed with clean vermiculite and carried through the same steps of the procedure. The result of the test proved that the first step of the procedure was 98-100 percent efficient in extraction of these seeds. By repeating the flotation again, the efficiency increased to 100 percent or complete seed recovery.

The same flotation procedure was used to separate organic material from other sediment in seed rain samples.

Seeds in the separated organic material of soil seed reserve and seed rain samples were separated with bodkins and tweezers under a binocular zoom microscope with 10-30 X magnification. The seeds in both soil seed reserves and seed rain samples were then sorted by species. Species identification was facilitated by use of a binocular zoom microscope and a seed herbarium.

The seed herbarium had been formed by collecting seeds directly from their parent plants over the two years of field work. Seeds dissimilar in morphological and anatomical characteristics were successfully identified to species, but those which were highly similar were identified only to the generic level, e.g. Artemisia.

Seed viability was indexed by a tetrazolium chloride test (Colbry et al. 1961). This test required soaking of separated seed from the soil seed reserve and seed rain collections for enough time (2-3 days) in vials containing tap water. The soaking period depended on the hardness of seed testa or in the case of grasses, the lemma and palea.

The objective of soaking the seeds was to facilitate the increase of biological activity in the embryos so as to enhance the secretion of enzymes in the embryos and thus increase the likelihood of obtaining a positive tetrazolium test. In addition, it eased splitting of the seeds into halves by use of a scalpel. Two to three drops of 0.5 gram tetrazolium chloride crystals dissolved in 200 ml of distilled water were added to the vials which contained split seeds. These vials were then kept under darkness for 4-7 days after which time embryos taking on a reddish coloration were classified as live seeds. Others were classified as dead (Figures 8a, b and c).

Figure 8.

a. Photograph of intact seed of <u>Chrysothamnus</u> spp. under a binocular zoom microscope (magnified 10X).

b. Photograph of intact and two halves of <u>Oryzopsis</u> <u>hymenoides</u> seeds after a tetrazolium test. The half on the left is alive and the other is dead.

(Figure 8a)

(Figure 8b)

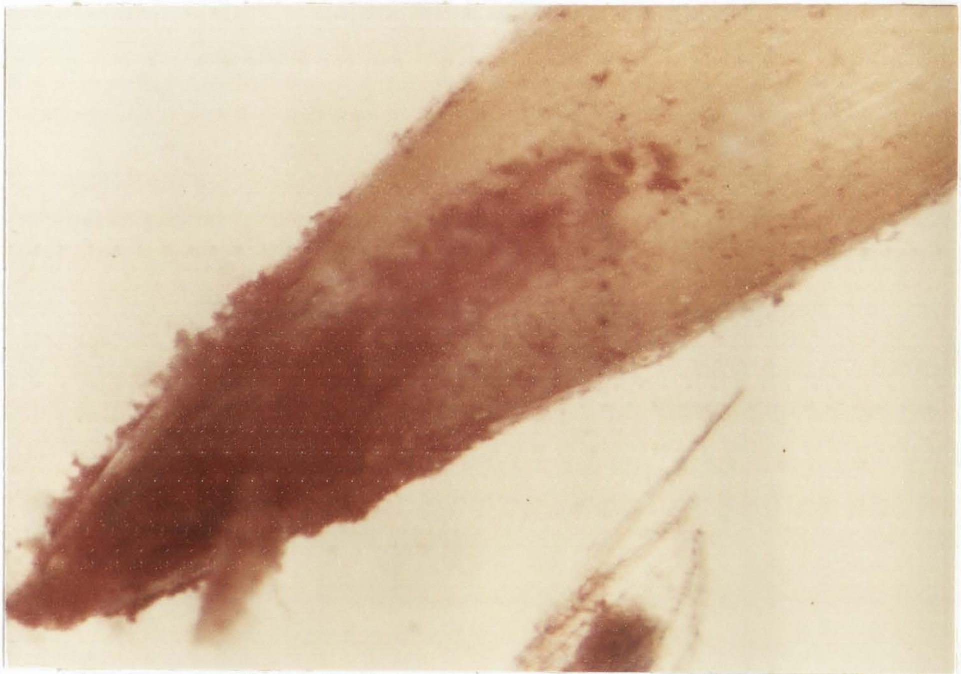


Figure 8c. Photograph of live *Bromus tectorum* embryo showing reddish coloration from application of the tetrazolium test to rapidly respiring tissue.

PROBLEMS IN DETERMINING THE ECOLOGICAL IMPORTANCE OF BURIED SEED BANKS

The process of determining the ecological importance of buried viable seed banks is surrounded by the following problems:

(1) Many perennial species evidently reproduce entirely vegetatively or at least rarely from seeds (Chippindale and Milton 1934, Milton 1936, 1939, 1943, Rabotnov 1956, Zenenchuk 1961, Golubeva 1962, Harberd 1958, 1961, 1962). This may also be the case for some species involved in this study.

(2) Seeds are generally aggregated around parent plants. Aggregated populations are difficult to sample in a satisfactory manner since conventional experimental design usually requires random placement of samples. Square root transformation can be used to normalize skewed data and stabilize the variance (Roberts 1958, Sokal and Rohlf 1969), but that can complicate interpretation of the data. For instance, if one transforms the raw data, then addition of square roots will not add to the square root of the total.

(3) Determination of appropriate sample size frequently leads to sampling efforts too great to be practical (Rabotnov 1958, 1964, Champness 1949). Statistical

analysis of the first samples in the present study showed there should be 317 samples of soil seed reserves in order to show any significance (at alpha ≤ 0.05). This was impractical, thus 20 samples per each plot were arbitrarily taken.

(4) Not all seeds can be easily recovered by a flotation procedure. Small dusty seeds will pass through the sieve mesh in this process. It becomes impossible to recover all seeds without catching fine soil particles as well. This makes the identification process even more difficult. The sieve mesh chosen for this study is a little smaller than any important plant seeds known to occur on the study site.

(5) The possibility of seeds being trapped inside folded organic matter or attached to soil minerals is high. Such seeds can be easily lost and disappear from the analysis. In order to reduce such errors in this study, careful examination of organic material was done under a binocular zoom microscope and the flotation process was done twice.

(6) There is some difficulty in identifying the species of seeds which are similar in their morphological features. Such seeds can be grown in the green house

for successful identification but time considerations precluded this. Consequently, such seeds were identified only to genus.

Statistical analysis

Analysis of variance was performed on the total and individual taxon means of soil seed reserves and seed rain density data aggregated for the different dates of collection, various treatments, and different sampling locations. In addition to these data aggregation methods, density data for soil seed reserves were aggregated by growth form and depth (Figure 9).

Tests for normality of the data were performed, revealing than all data were not normally distributed. In order to fulfil the analysis of variance assumption concerning normality, square root transformations were performed on the data before application of the analysis. That is, the raw values obtained from each sample were transformed before addition into treatment totals. This is the required in order to perform analysis of variance (see page 35).

The alpha level of significance was chosen to be equal to or less than 0.05 for type two error. Least significant differences were used to separate significantly different pairs under comparison. If the difference between the means

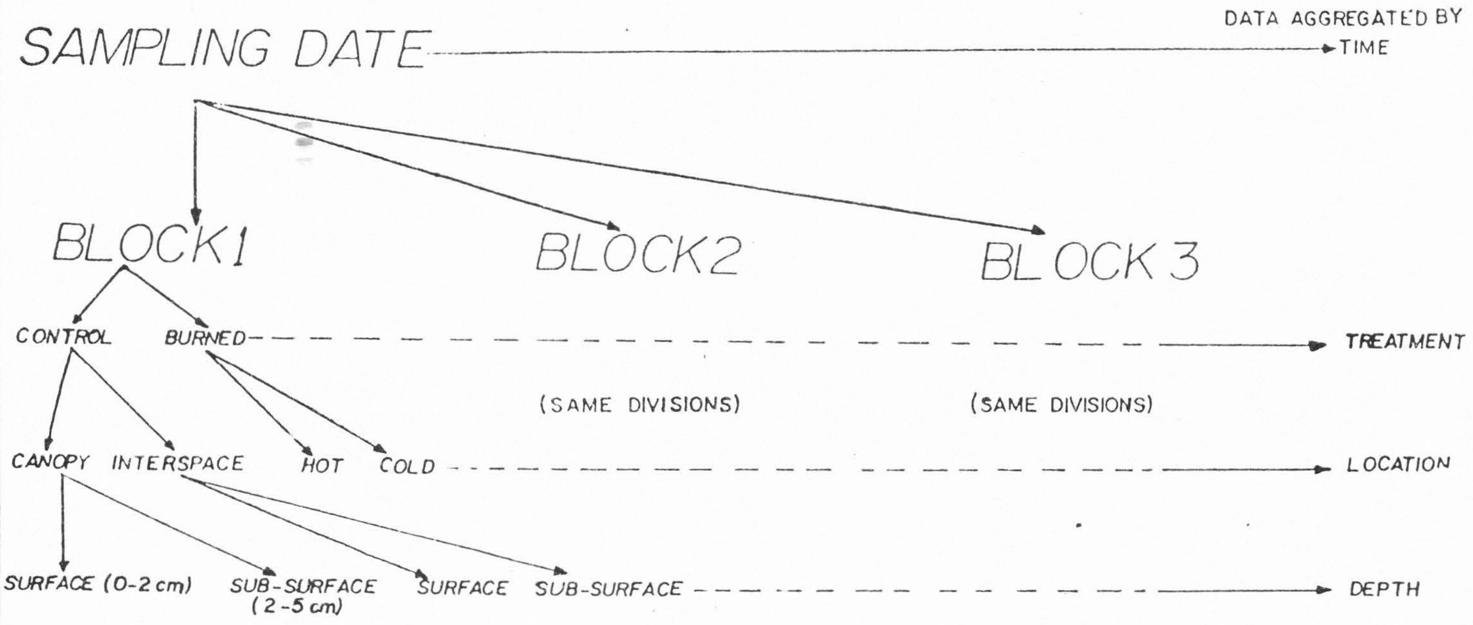


Figure 9. Diagram illustrating the fashion in which data were aggregated.

is higher than the least signicant difference, the difference between the pair was considered statistically significant.

The experimental design of this study was a factorial complete randomized block. The existing statistical packages available for processing unbalanced data fail to separate error terms (PS and PDS, Appendices A and B) possessing more than 400 degrees of freedom. The best estimation of these errors, considering the existing computational limitations, was BPTLD (error d, Appendix B) for soil seed reserves and PBTL (error C Appendix A) for seed rain. These next best error term that were computationally available are larger than the ideal one. Therefore the calculation of the F-tests here should be slightly smaller and the results of the test slightly conservative compared to the ideal models. Analysis of variance tables are shown in Appendices C to H.

RESULTS AND DISCUSSION

Vegetation

Vegetation inventoried before the fire and in the control plots selected after the fire for this study were similar. Cover-weighted comparisons of vegetation data gave similarity indices of 80 to 96 percent. Thus, it is highly probable that the unburned plots escaped the fire not because they had different vegetation from the burned or the previous study plots, but because of random factors controlling wind conditions at the time of the fire. The prefire plant community of the site had an average point cover composition of 10.2 percent shrubby species, 39.7 percent herbaceous species and 1.5 percent forbs (see details in table 2).

Soils

Sixty profiles were examined. Nearly all can be characterized as shallow and have fairly uniform silt loam surface textures. All profiles can be classified as coarse silty, mixed mesic, Xerollic Calciorthids. The epipedon is ochric ranging from brown to dark brown in color. This layer is 4-12 cm thick with loam texture. The coarse fragments are 0-35 percent. Lime distribution is slightly to moderately calcic.

The sub-surface horizon (8-26 cm thick) is cambic. Its texture ranges from loam to silt loam with 0-35 percent coarse fragments.

The substratum (76 cm thick) is calcic or duric. The texture of this layer ranges from loamy sand to sandy loam. The coarse fragments are 0-75 percent. Lime is present as coatings, soft masses or filaments. Silica is present in durinodes or laminar cap shapes.

Directly under the soil surface these soils display a moderately platy vesicular horizon when dry. This makes the soil fluffy with high porosity (Blackburn and Skau 1974, Hugie and Passey 1964). The mean soil bulk density of the surface soil in the control (unburned) plots was found to be 1.28 (0.13, standard error of the mean) grams per cubic centimeter, whereas at the burned plots it was found to be a little higher, 1.35 (0.11) grams per cubic centimeter. These differences were not statistically significant (alpha 0.05).

Study of the soil profiles and pre-fire aerial photographs gave corroborating evidence that these burned plots located next to the unburned plots were similar to the unburned and nearby plots studied prior to the fire.

Climate

The study site received about 38.6 cm precipitation from July, 1981 to July, 1982, making that period wetter than normal (Table 3 and Figure 10). This site received

Table 3. Summary of short term precipitation recorded at the study site compared to short and long-term precipitation at the closest comparable permanent station (Levan).

Month	Short Term		Long Term*
	Total Precipitation (cm)		
	Study Site	Levan	Levan
1981			
July	2.80	3.63	1.73
August	2.17	2.26	2.31
September	2.00	2.36	2.67
October	9.80	9.88	2.76
November	2.28	1.50	3.15
December	3.19	3.07	3.48
1982			
January-March	9.80	10.41	8.54
April	0.21	0.69	4.22
May-June	4.66	5.11	5.31
July	1.72	2.87	1.63
Total	38.63	41.78	37.80
August	3.01	3.05	2.31
September	7.35	15.88	2.67
October	3.68	5.89	2.77
November	2.03	2.41	3.15
December	2.63	4.04	3.49
Total	18.70	31.27	14.38

*=Fifty year average

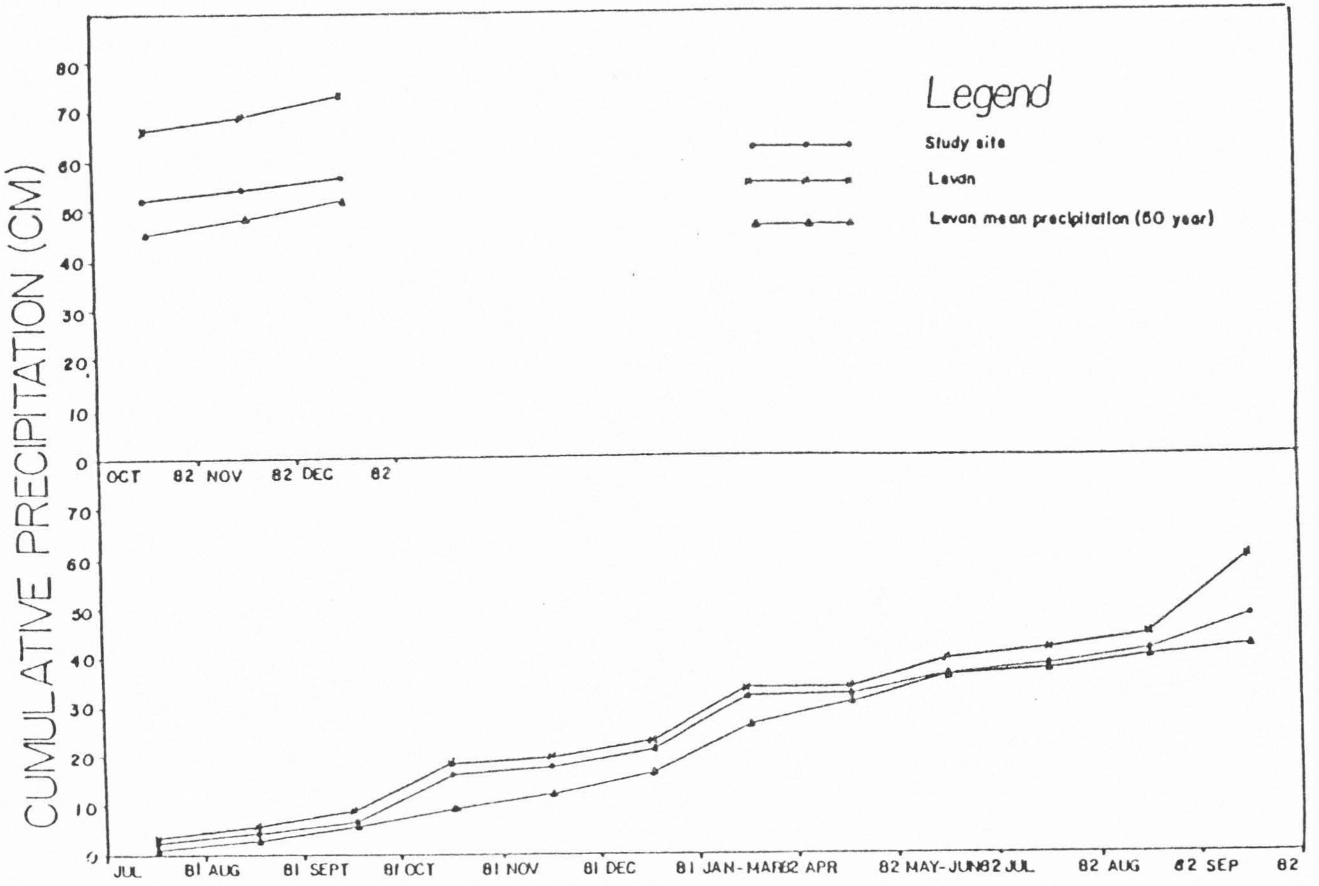


Figure 10. Graphical relationship of precipitation collected at the short-term study site with that recorded at Levan (U.S. Weather service).

about 18.7 cm during the rest of the study period. The precipitation during the whole study period was consistent with long and short term records with the closest comparable station (Levan, see Figure 10) and with the SCS site description. Temperature and humidity data are summarized in Figures 11 and 12, respectively.

Vegetation differences due to fire

Comparison of percent cover of plants and ground cover materials on the burned and unburned plots from the data collected in 1981, shows that the fire was hot enough to have destroyed all the aboveground vegetation on the burned plots. The vegetation and ground cover were highly similar between the plots studied prior to the burn (just one week before the fire) and the unburned plots selected and inventoried six weeks after the fire (Table 2).

Bare ground increased from 14.2% before the fire to 77.3% six weeks after the fire. Standing dead was 0% on the plots examined before the fire, but increased to 2.7% soon after the fire. Most of this component was skeletons of the burned shrubs left standing after the fire. Litter decreased from an average 15.4% before the fire to 9.3% soon after. The percent gravel remained almost the same before and soon after the fire.

Cover of microphytic crusts cover was 12.8% before the

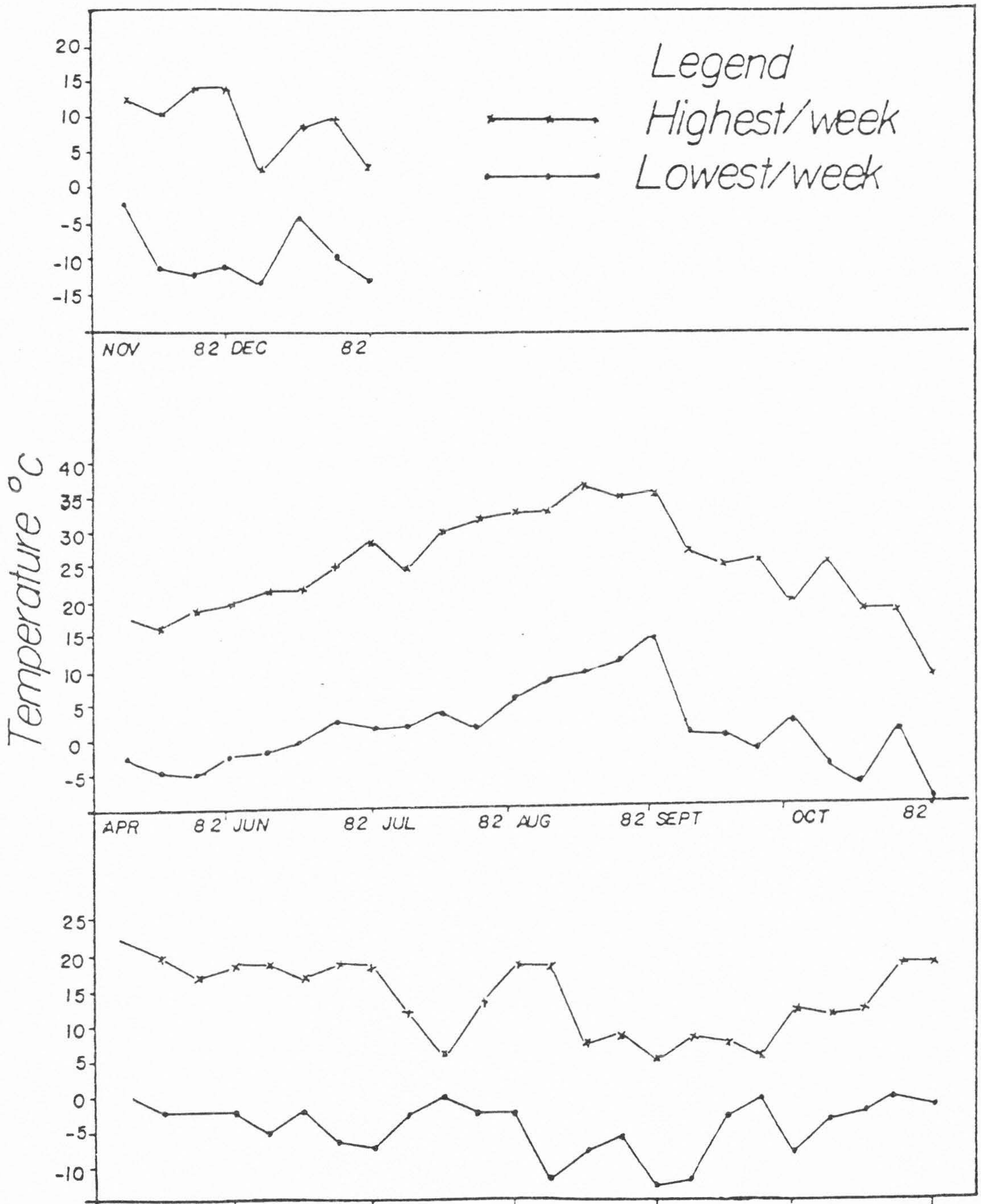


Figure 11. Graph of the highest and lowest daily temperatures (°C) recorded at the study site.

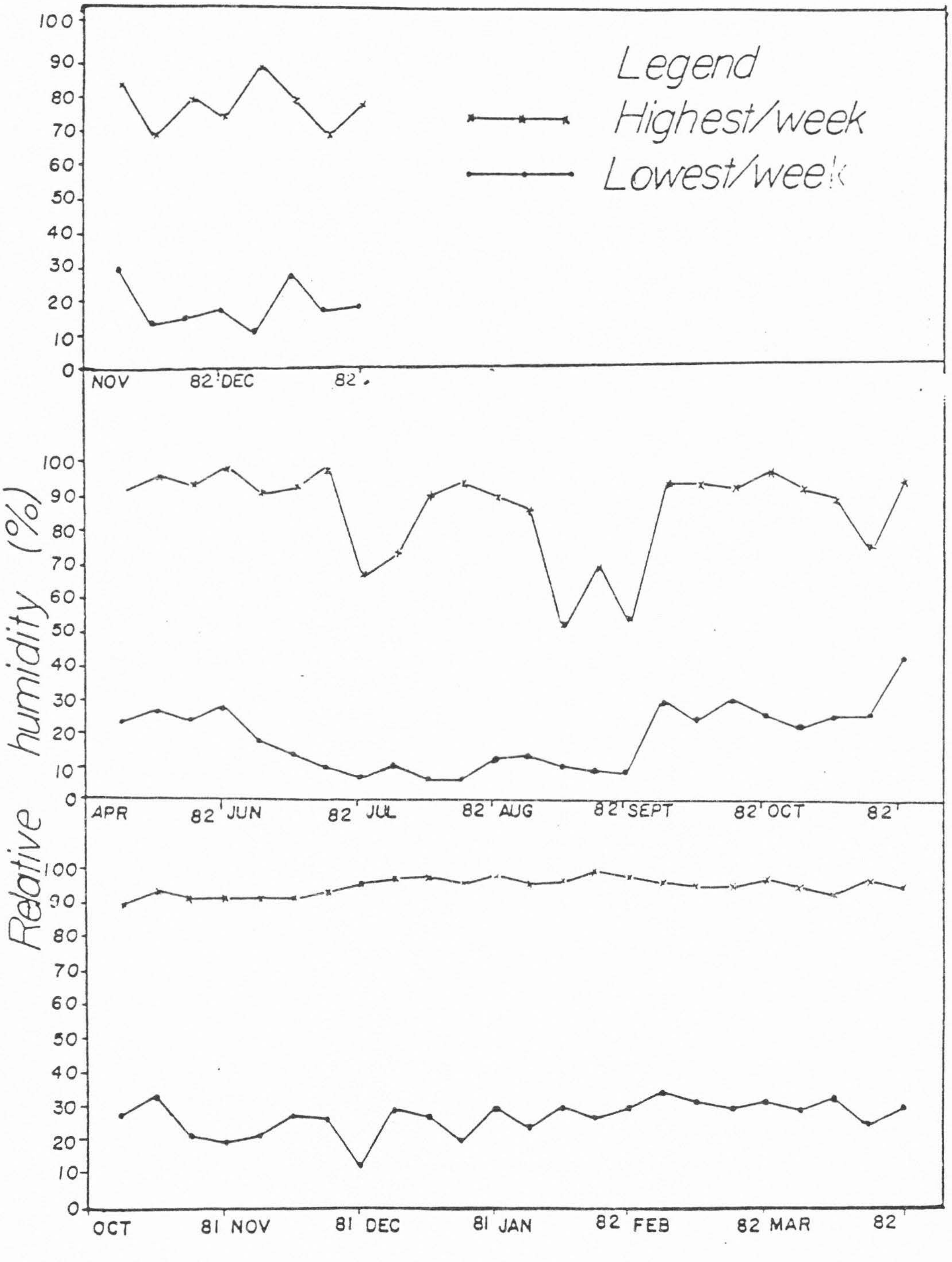


Figure 12. Highest and lowest relative humidity (%) recorded at the study site.

fire, but declined to zero shortly after the fire. The microphytic crust was comprised of only mosses.

One year after the fire, vegetation and ground cover were greatly different than the year before (Table 2, Figures 13 and 14). Total live vegetal cover had recovered by 1982 to a level higher than the pre-burn status (51.7% vs. 44.5%). This was, however, almost solely a function of the profound increase in Bromus tectorum. This annual grass contributed 6.3% to total vegetal cover prior to the burn, but contributed 35.7% to total vegetal cover one year after the fire. The perennial bunch grasses collectively contributed 30% to the total vegetal cover prior to the burn, but made up only 16.0% of the total vegetal cover in the burned plots one year after the fire.

Brush cover, mostly Wyoming big sagebrush (Artemisia tridentata ssp. wyomingensis), prior to the fire was 6.5%. One year later it contributed no cover to the burned plots. Sticky flowered rabbitbrush (Chrysothamnus viscidiflorus) decreased from 7.3% cover in 1981 prior to the fire to zero cover in the burned plots one year later. Mormon tea (Ephedra nevadensis) was the only shrub to reestablish its cover relatively rapidly. Its cover in 1981, prior to the fire was 2.5%, and 1.3% one year later. This recovery is apparently related to its strong ability to sprout from root crowns.

Figure 13. Photograph of a control (unburned) plot a year after the fire.

Figure 14. Photograph of the study area a year after the fire.

The fire effects on germinable soil seed reserves (GSSR) regardless of the microsite or sampling depth

The first GSSR sample of September 1981 should have had minimal errors associated with wind movement. Timing of the fire was important because it occurred after all plant species but sagebrush and rabbitbrush had set and dispersed their seeds. There was not enough time for allochthonous sagebrush and rabbitbrush seeds to be incorporated into the soil since, the first sampling occurred before they set their their seeds.

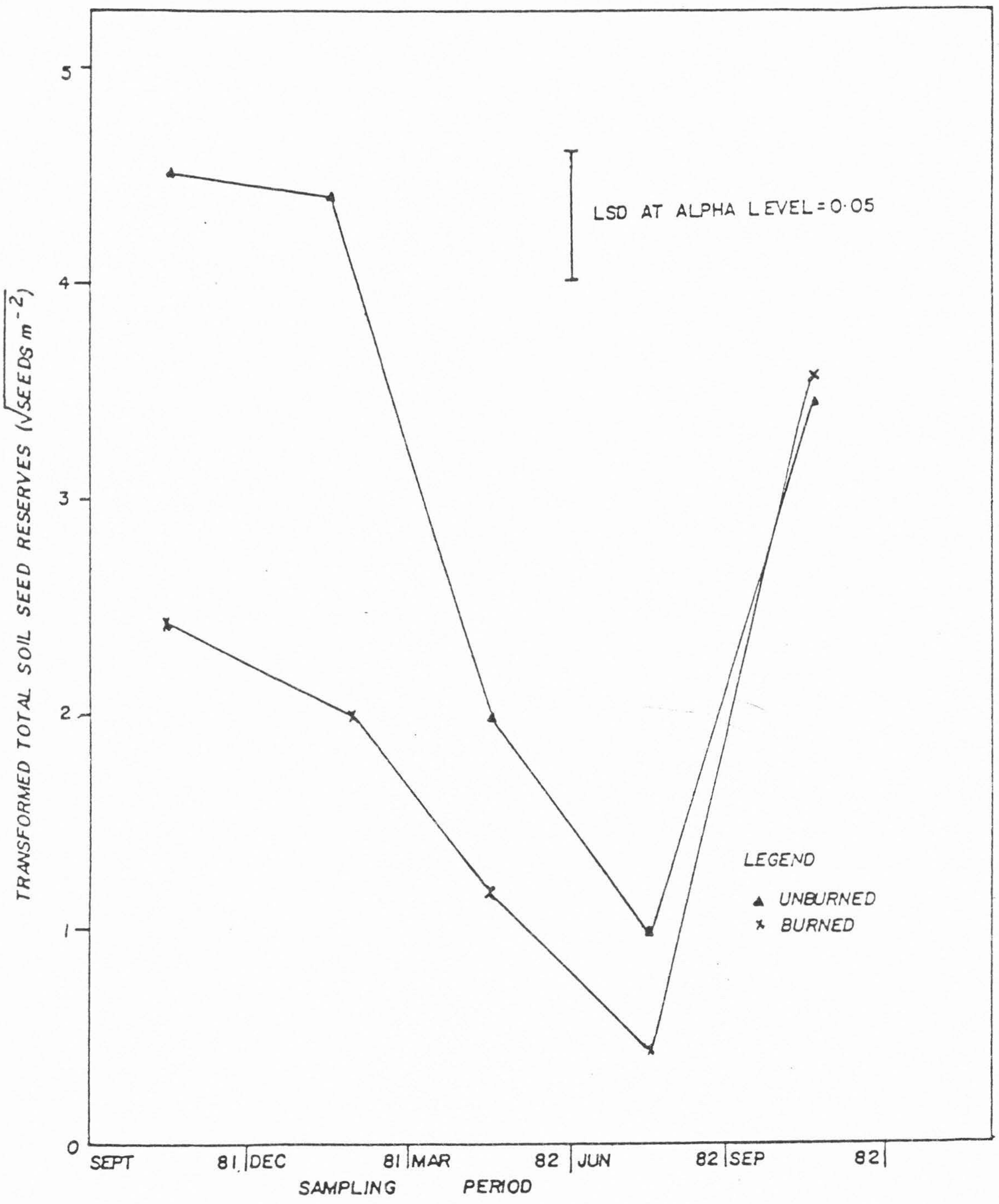
In September 1981, six weeks after the fire, the GSSR of the burned plots was significantly (alpha ≤ 0.05) less (Figure 15a) than that of the unburned plots (38.7 seeds m^{-2}; vs. 85.5 seeds m^{-2}; Table 4). Thus, it was concluded that fire can have a significant impact on the seed reserves of the plant community.

Bromus tectorum, *Agropyron* spp. and *Poa* spp. were the only taxon level differences showing significantly (alpha $\leq$ 0.05, Table 5) lower densities of germinable seeds on the burned plots. *Bromus tectorum* made up 51.2 percent of the seed bank on these burned plots and 45.8 percent on the unburned plot during September 1981 (Figure 15b).

No significant change in total GSSRs over that observed in September was detected in December 1981, in either the burned or unburned plots.

Figure 15.

a. Graph of mean total germinable soil seed reserves of transformed data (square root of seed m^{-2}), with LSD (alpha=0.05) on the unburned and burned plots.


TRANSFORMED TOTAL SOIL SEED RESERVES ($\sqrt{SEEDS\ m^{-2}}$)
0
1
2
3
4
5
LSD AT ALPHA LEVEL=0·05
LEGEND
▲ UNBURNED
× BURNED
SEPT
81 DEC
81 MAR
82 JUN
82 SEP
82
SAMPLING PERIOD

(Figure 15a)

Table 4. Summary of mean soil seed reserve densities (germinable seed per m^2) in the surface 5 cm of soil on unburned (control) and burned sites near Mills, Utah, for several collection dates (Number in parentheses=one standard error of the mean).

#	Growth form and Species	Unburned				
		Sept 1981	Dec 1981	Mar 1982	Jun 1982	Sept 1982
	Grasses:					
1	*Bromus tectorum*	39.2 (9.4)	45.5 (13.9)	14.1 (5.3)	8.8 (4.9)	41.5 (13.7)
2	*Agropyron* spp.	5.0 (2.5)	4.4 (2.1)	1.3 (1.4)	0.0	2.7 (2.0)
3	*Poa* spp.	5.4 (3.8)	5.0 (2.4)	3.8 (2.2)	1.3 (1.0)	4.4 (1.9)
4	*Oryzopsis hymenoides*	1.9 (1.7)	3.9 (2.0)	3.1 (2.0)	0.6 (0.7)	3.9 (1.9)
5	*Stipa comata*	0.0	0.4 (0.7)	0.3 (0.6)	0.0	1.6 (1.1)
6	*Sitanion hystrix*	0.0	0.0	0.3 (0.5)	0.0	1.3 (1.0)
	Forbs:					
7	*Descurainia pinnata*	15.1 (5.9)	15.5 (5.1)	2.2 (1.4)	1.3 (1.2)	4.5 (2.3)
8	*Erigeron* spp	5.2 (8.2)	0.0	0.6 (0.8)	0.0	1.2 (0.9)
9	*Eriogonum cernuum*	0.2 (0.4)	3.1 (1.9)	0.3 (0.5)	0.0	1.2 (0.9)
10	*Allium acuminatum*	1.3 (1.1)	0.9 (1.1)	0.0	0.0	0.3 (0.5)
11	*Sphaeralcea* spp.	0.5 (0.6)	0.0	0.0	0.0	0.0
12	*Phlox* spp.	0.0	4.7 (2.8)	NON	0.7 (1.1)	4.4 (03.8)
13	*Mentzelia albicaulis*	0.4 (0.6)	0.0	0.0	0.0	0.0
14	*Cordaria draba*	0.4 (0.6)	0.0	0.0	0.0	0.0
15	*Helianthus* spp.	0.0	0.0	0.0	0.0	0.0
16	*Senecio* spp:	0.0	0.0	0.3 (0.6)	0.0	3.7 (4.6)
	Shrubs:					
17	*Artemisia* spp.	3.7 (1.9)	5.8 (4.0)	1.5 (1.2)	0.3 (0.3)	0.7 (0.7)
18	*Chrysothamnus* spp.	1.8 (2.0)	0.9 (0.9)	0.4 (0.6)	0.0	2.1 (1.2)
19	*Ephedra* spp	0.0	0.0	0.0	0.0	0.5 (0.6)
20	*Purshia tridentata*	0.0	0.5 (0.8)	0.0	0.0	0.3 (0.4)
21	*Juniperus osteosperma*	0.0	0.6 (1.0)	0.0	0.0	0.0
22	Unidentified	5.4 (2.5)	0.4 (0.7)	NON	0.0	0.0
23	Total	85.5 (29.8)	91.5 (19.0)	28.2 (8.1)	13.0 (6.1)	74.3 (19.4)

#	Growth Form and Species	Burned				
		Sept 1981	Dec 1981	Mar 1982	Jun 1982	Sept 1982
	Grasses:					
1	*Bromus tectorum*	19.8 (5.3)	16.9 (6.2)	9.3 (3.9)	2.2 (1.3)	71.9 (20.9)
2	*Agropyron* spp.	0.4 (0.6)	2.0 (1.4)	0.6 (1.0)	0.0	3.5 (1.4)
3	*Poa* spp.	2.4 (2.2)	0.9 (1.0)	1.4 (1.2)	0.1 (0.2)	0.7 (0.7)
4	*Oryzopsis hymenoides*	2.4 (1.4)	3.7 (2.3)	1.3 (1.1)	0.1 (0.3)	0.5 (0.5)
5	*Stipa comata*	0.0	0.0	0.6 (0.9)	0.0	0.0
6	*Sitanion hystrix*	0.0	0.0	0.2 (0.3)	0.0	0.3 (0.4)
	Forbs:					
7	*Descurainia pinnata*	6.8 (2.6)	3.6 (1.7)	1.0 (0.8)	0.6 (0.6)	1.6 (1.0)
8	*Erigeron* spp.	0.0	0.8 (0.9)	0.0	0.0	0.0
9	*Eriogonum cernuum*	0.5 (0.8)	0.5 (0.8)	1.2 (0.9)	0.0	0.3 (0.4)
10	*Allium acuminatum*	0.4 (0.6)	0.0	0.0	0.0	0.0
11	*Sphaeralcea* spp.	0.0	0.0	0.0	0.0	0.0
12	*Phlox* spp.	0.8 (0.9)	0.9 (1.4)	0.2 (0.3)	0.3 (0.5)	0.6 (0.6)
13	*Mentzelia albicaulis*	1.4 (1.0)	0.0	0.0	0.0	0.0
14	*Cordaria draba*	0.5 (0.7)	0.0	0.0	0.0	0.0
15	*Helianthus* spp.	0.4 (0.6)	0.0	0.0	0.0	0.0
16	*Senecio* spp.	0.0	0.0	0.0	0.0	0.0
	Shrubs:					
17	*Artemisia* spp.	1.8 (1.5)	0.0	0.3 (0.5)	0.0	0.3 (0.5)
18	*Chrysothamnus* spp.	0.0	0.9 (1.0)	0.2 (0.4)	0.0	0.0
19	*Ephedra* spp.	0.0	0.0	0.0	0.0	0.0
20	*Purshia tridentata*	0.0	0.0	0.0	0.0	0.0
21	*Juniperus osteosperma*	0.0	0.6 (0.7)	0.0	0.0	0.0
22	Unidentified	1.1 (1.0)	0.0	0.0	0.0	0.0
23	Total	38.7 (8.5)	30.8 (7.7)	16.3 (5.4)	3.3 (1.5)	79.7 (21.8)

NON=Detected but not alive.

Table 5. Summary of means of transformed data on observed germinable soil seed reserves (square root of seed m^{-2}) of the most important taxa (those that showed up more than twice during the whole study period) at both unburned and burned plots. Last column shows LSDs (alpha =0.05) for the species showing significant differences.

Species	Unburned					Burned					LSD
	Sept 81	Dec 81	Mar 82	Jun 82	Sept 82	Sept 81	Dec 81	Mar 82	Jun 82	Sept 82	
Bromus tectorum	2.65	2.50	1.49	0.68	2.36	1.42	1.05	0.72	0.24	3.09	0.54
Agropyron spp.	0.47	0.43	0.11	0.0	0.47	0.03	0.19	0.04	0.0	0.39	0.22
Poa spp.	0.36	0.44	0.36	0.15	0.46	0.16	0.08	0.14	0.02	0.07	0.12
Oryzopsis hymenoides	0.19	0.39	0.34	0.07	0.40	0.24	0.29	0.13	0.02	0.06	0.12
Stipa comata	0.0	0.04	0.04	0.0	0.18	0.0	0.0	0.04	0.0	0.0	0.04
Sitanion hystrix	0.0	0.0	0.03	0.0	0.15	0.0	0.0	0.02	0.0	0.03	0.06
Descurainia pinnata	1.12	1.17	0.24	0.13	0.42	0.62	0.36	0.12	0.08	0.20	0.31
Erigeron spp.	0.05	0.0	0.07	0.0	0.14	0.0	0.07	0.0	0.0	0.0	0.07
Eriogonum cernuum	0.03	0.29	0.03	0.0	0.14	0.04	0.04	0.11	0.0	0.03	0.12
Artemisia spp.	0.37	0.39	0.16	0.03	0.08	0.02	0.0	0.03	0.0	0.03	0.19

Table 6. Summary of means of transformed data on observed germinable soil seed reserves (square root of seed m^{-2}) of the most important taxa (those that showed up more than twice during the whole study period) at both unburned and burned microsites (see appendix I.1-I.10 for LSD of each pair in comparison)

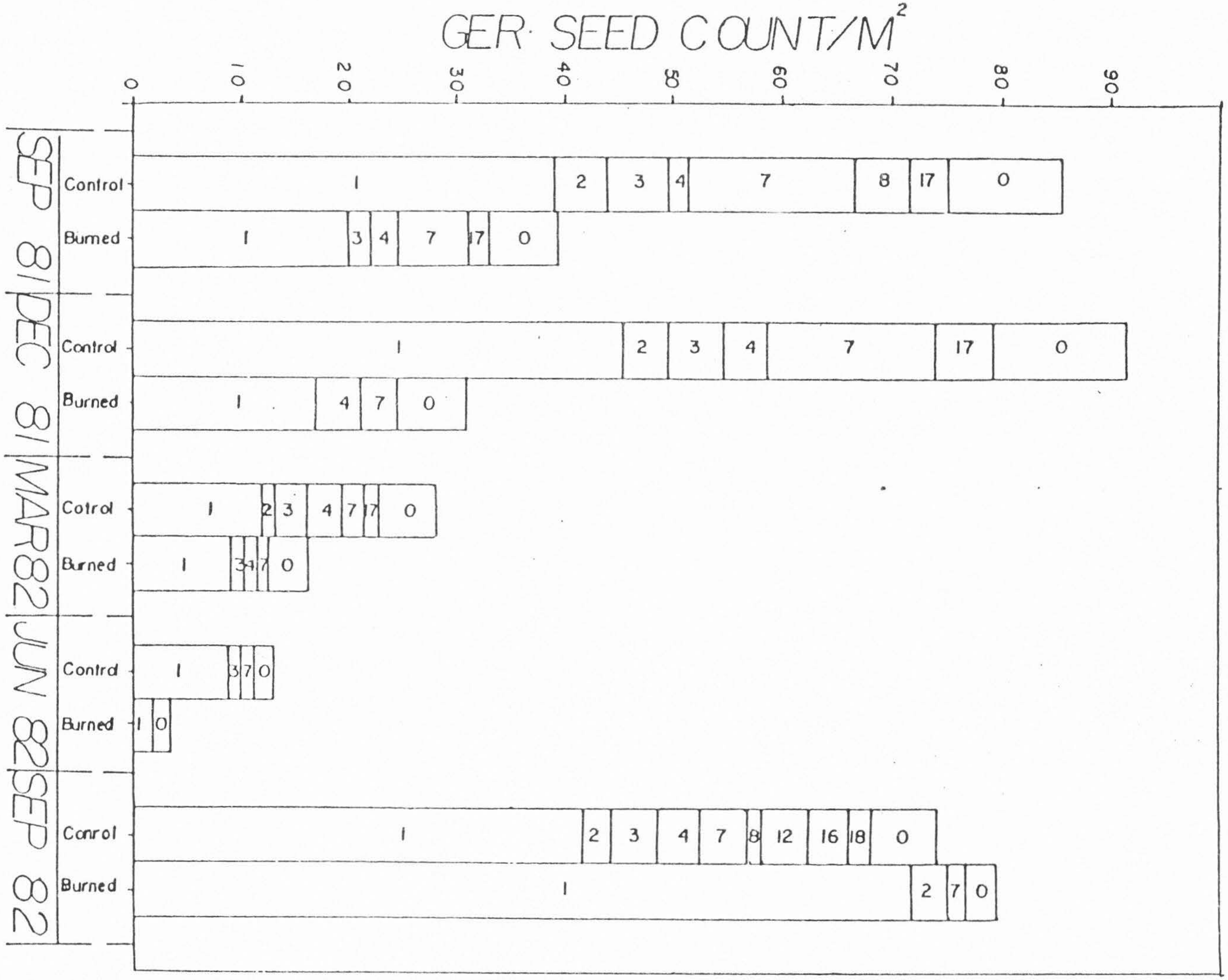
Species	Unburned									
	Canopy					Interspace				
	Sept 81	Dec 81	Mar 82	Jun 82	Sept 82	Sept 81	Dec 81	Mar 82	Jun 82	Sept 82
Bromus tectorum	3.62	3.90	1.50	0.38	3.48	1.95	1.43	0.81	0.91	1.13
Agropyron spp.	0.82	0.67	0.23	0.0	0.78	0.22	0.25	0.0	0.0	0.0
Poa spp.	0.77	0.46	0.68	0.06	0.67	0.07	0.44	0.09	0.23	0.23
Oryzopsis hymenoides	0.28	0.56	0.66	0.0	0.58	0.12	0.26	0.07	0.13	0.14
Stipa comata	0.0	0.0	0.02	0.0	0.26	0.0	0.06	0.06	0.0	0.07
Sitanion hystrix	0.0	0.0	0.07	0.0	0.20	0.0	0.0	0.0	0.0	0.07
Descuirania pinnata	1.61	1.68	0.25	0.06	0.70	0.78	0.79	0.23	0.19	0.0
Erigeron spp.	0.09	0.0	0.14	0.0	0.24	0.02	0.0	0.0	0.0	0.0
Eriogonum cernuum	0.08	0.34	0.07	0.0	0.13	0.0	0.26	0.0	0.0	0.0
Artemisia spp.	0.40	0.53	0.15	0.07	0.10	0.35	0.29	0.17	0.0	0.07

Species	Burned									
	"Hot"					"Cold"				
	Sept 81	Dec 81	Mar 82	Jun 82	Sept 82	Sept 81	Dec 81	Mar 82	Jun 82	Sept 82
Bromus tectorum	0.93	0.83	0.53	0.0	4.88	1.79	1.27	0.81	0.41	1.05
Agropyron spp.	0.0	0.15	0.10	0.0	0.52	0.69	0.23	0.0	0.0	0.26
Poa spp.	0.22	0.78	0.12	0.0	0.06	0.12	0.07	0.16	0.03	0.07
Oryzopsis hymenoides	0.16	0.31	0.24	0.0	0.10	0.31	0.27	0.05	0.04	0.0
Stipa comata	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.08	0.0	0.0
Sitanion hystrix	0.0	0.0	0.06	0.0	0.05	0.0	0.0	0.0	0.0	0.0
Descurainia pinnata	0.36	0.34	0.09	0.0	0.21	0.81	0.38	0.14	0.14	0.19
Erigeron spp.	0.0	0.14	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Eriogonum cernuum	0.09	0.0	0.15	0.0	0.07	0.0	0.80	0.08	0.0	0.0
Artemisia spp.	0.19	0.0	0.0	0.0	0.0	0.12	0.0	0.05	0.0	0.07

Figure 15.

b. Bar graph showing the total and taxa level germinable soil seed reserve dynamics at the control (unburned) and burned plots. Numbers indicate different taxa (see Table 4 for numerical codes).

Legend
O=all trace species (see table 4)


GER. SEED COUNT/M²
0
10
20
30
40
50
60
70
80
90
SEP 81
Control
1 2 3 4 7 8 17 0
Burned
1 3 4 7 17 0
DEC 81
Control
1 2 3 4 7 17 0
Burned
1 4 7 0
MAR82
Cotrol
1 2 3 4 7 17 0
Burned
1 3 4 7 0
JUN 82
Contrd
1 3 7 0
Burned
1 0
SEP 82
Conrol
1 2 3 4 7 8 12 16 18 0
Burned
1 2 7 0

(Figure 15b)

found on both burned and unburned plots in March and June of 1982 (Table 4) compared to earlier sampling periods. This decline is presumably related to lack of seed rain and depletion of the seed bank via germination, decomposition and granivory during this part of the year. The minimum total GSSRs on both burned and unburned plots was reached in June 1982. These minima were found to be significantly lower than GSSRs collected during all previously mentioned sampling periods.

Total GSSRs on both types of plots increased significantly between June and September 1982. Peak total GSSRs were reached in September on both burned and unburned plots (Figure 15a). The profound increase in total GSSR on the burned plots was almost entirely due to cheatgrass (Table 5), which underwent a rapid expansion in the year following the fire. Its cover increased from zero to 35.7 percent on the burned plots (Table 2). The differences in total GSSRs between burned and unburned sites were not statistically significant by September 1982. Bromus tectorum comprised 90.2 percent of the total GSSR detected on the burned plot in September 1982, showing the enormous reproductive capacity of this species shortly a year after fire. Although the vegetation on the unburned plots was rich in bunchgrass cover (Table 2), the GSSR contained few of their seeds at all sampling periods. The recovery of these species may come from vegetative reproduction via portions which escaped the fire.

Because the fire occurred before seed set, timing of the fire was important in the way it affected seed of undesirable shrubby species, especially sagebrush. Significantly fewer sagebrush seed per square meter were detected on the burned plots in September 1981 compared to the unburned plots during the same sampling period (see Tables 4 and 5 and Figure 15b).

Fire effects on GSSR at different microsites in burned and unburned plots

Highest mean GSSR density was found in the undercanopy compared to all other types of microsites in unburned and burned plots in September 1981. Significantly greater *Bromus tectorum*, *Agropyron* spp., *Poa* spp., *Oryzopsis hymenoides* and *Descurainia pinnata* GSSRs were found in the undercanopy microsite on the unburned plots than in the interspace microsite in this sampling period (Tables 6 and 7, Figures 16a and b). Other taxa which did not show significant differences were either not detected in both unburned microsites or were present in very low densities in the interspaces. This is evidence that seeds accumulated where shrubs were growing (canopy), with few seed found in bare areas (interspace). Apparently this is related to the semi-

Table 7. Summary of mean soil seed densities (germinable seed count m^{2}) in the surface 5 cm under canopy and in interspaces on unburned (control) sites near Mills, Utah, at several collection dates (Numbers in parentheses=one standard error of the mean).

Growth Form and Species	Canopy				
	Sept 1981	Dec 1981	Mar 1982	Jun 1982	Sept 1982
Grasses:					
Bromus tectorum	61.9 (12.1)	79.4 (18.8)	20.3 (7.0)	3.8+(2.3)	55.2 (13.7)
Agropyron spp.	8.9 (3.3)	6.9 (2.6)	2.7 (2.0)	ND	7.5 (2.5)
Poa spp.	11.9 (5.7)	5.4 (2.7)	7.1 (2.9)	0.5+(0.5)	6.4 (2.3)
Oryzopsis hymenoides	3.2 (2.3)	5.7 (2.4)	11.1 (8.3)	0.0	5.7 (02.3)
Stipa comata	0.0	0.0	5.7 (6.7)	0.0	2.2 (1.3)
Sitanion hystrix	0.0	0.0	0.6 (0.7)	0.0	1.8 (1.2)
Forbs:					
Descurainia pinnata	25.5 (7.8)	23.1 (6.0)	2.6 (1.7)	0.5 (0.5)	7.4 (3.0)
Erigeron spp.	1.0 (1.0)	0.0	1.4 (1.2)	0.0	2.1 (1.2)
Eriogonum cernuum	0.5 (0.6)	3.7 (2.0)	0.6 (0.7)	0.0	1.9 (01.1)
Allium acuminatum	1.8 (1.4)	0.0	0.0	0.0	0.5 (00.6)
Sphaeralcea spp.	0.0	0.0	0.0	0.0	0.0
Phlox spp.	0.0	6.9 (03.6)	NON	0.0	6.9 (4.8)
Mentzelia albicaulis	0.8 (1.0)	0.0	0.0	0.0	0.0
Cordaria draba	0.0	0.0	0.0	0.0	0.0
Helianthus spp.	0.0	0.0	0.0	0.0	0.0
Senecio spp.	0.0	0.0	0.0	0.0	5.7 (6.0)
Shrubs:					
Artemisia spp.	3.7 (1.9)	8.3 (5.1)	1.3 (1.1)	0.7 (0.8)	0.8 (0.8)
Chrysothamnus spp	10.2 (11.3)	0.4 (0.4)	0.8 (0.8)	0.0	2.6 (1.4)
Ephedra spp.	0.0	0.0	0.0	0.0	0.8 (0.8)
Purshia tridentata	0.0	0.0	0.0	0.0	0.5 (0.6)
Juniperus osteosperma	0.0	1.3 (1.5)	0.0	0.0	0.0
Unidentified	8.1 (2.9)	NON	0.0	0.0	0.0
Total	137.5 (43.5)	141.1 (24.5)	54.2 (10.5)	5.5 (3.5)	108.5 (21.0)

Growth Form and Species	Interspace				
	Sept 1981	Dec 1981	Mar 1982	Jun 1982	Sept 1982
Grasses:					
Bromus tectorum	22.9 (5.6)	19.7 (6.1)	8.4 (2.9)	12.5 (6.2)	21.1 (13.2)
Agropyron spp.	2.2 (1.4)	2.5 (1.6)	0.0	0.0	NON
Poa spp.	0.8 (1.1)	4.7 (2.2)	0.8 (1.1)	2.1 (1.3)	1.3 (1.0)
Oryzopsis hymenoides	1.0 (1.0)	2.6 (1.6)	0.7 (0.9)	1.0 (1.0)	1.2 (0.9)
Stipa comata	0.0	0.8 (0.9)	0.5 (0.7)	0.0	0.6 (0.7)
Sitanion hystrix	0.0	0.0	0.0	0.0	0.6 (0.7)
Forbs:					
Descurainia pinnata	9.1 (3.8)	9.7 (4.1)	1.9 (1.1)	1.9 (1.5)	NON
Erigeron spp.	NON	0.0	0.0	0.0	0.0
Eriogonum cernuum	0.0	2.8 (1.8)	0.0	0.0	0.0
Allium acuminatum	1.0 (0.9)	1.5 (1.4)	0.0	0.0	0.0
Sphaeralcea spp.	0.8 (0.7)	0.0	0.0	0.0	0.0
Phlox spp	0.0	3.1 (2.0)	NON	1.3 (1.4)	0.6 (0.7)
Mentzelia albicaulis	NON	0.0	0.0	0.0	0.0
Cordaria draba	0.6 (0.8)	0.0	0.0	0.0	0.0
Helianthus spp.	0.0	0.0	0.0	0.0	0.0
Senecio spp.	0.0	0.0	0.6 (0.8)	0.0	NON
Shrubs:					
Artemisia spp.	3.7 (1.9)	3.8 (2.8)	1.7 (1.3)	0.0	0.6 (0.6)
Chrysothamnus spp.	0.7 (0.8)	1.3 (1.2)	0.0	0.0	1.2 (0.9)
Ephedra spp.	0.0	0.0	0.0	0.0	0.0
Purshia tridentata	0.0	0.8 (01.1)	0.0	0.0	0.0
Juniperus osteosperma	0.0	0.0	0.0	0.0	0.0
Unidentified	3.5 (2.1)	0.7 (0.9)	NON	0.0	0.0
Total	46.3 (7.7)	54.0 (10.9)	14.6 (4.1)	18.8 (7.2)	27.2 (14.1)

ND =Not detected.

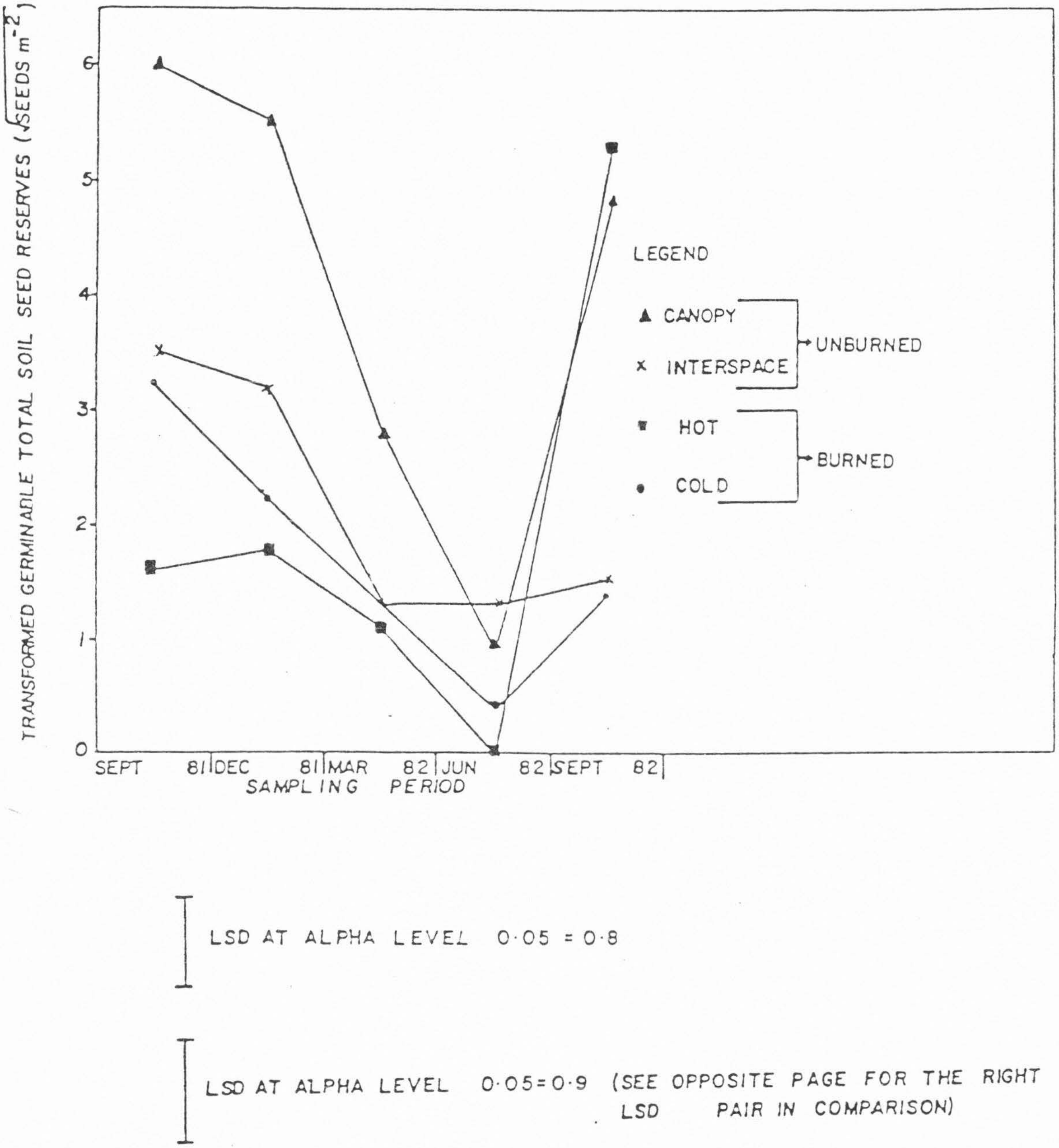


Figure 16a Graph of total germinable soil seed reserves of transformed data (square root of seed m^{-2}), with LSD (alpha=0.05) at different microsites of the unburned and burned plots.

LSDs AT ALPHA LEVEL = 0.05 FOR CODED PAIRS WHICH SHOWED SIGNIFICANCES WITH CODINGS NUMBERS.

CODES	LSD	CODES	LSD
111-113	0.9	113-115	0.8
111-114		121-123	
111-115		115-124	
111-121		122-123	
111-211		122-124	
112-113		122-222	
112-114		221-222	
112-122		221-223	
112-212		221-224	
113-114		222-223	
113-123		222-224	
113-213			
114-115			
114-124			
115-125			
121-125			
111-225			
122-125			
211-214			
211-215			
211-221			
212-214			
212-215			
213-214			
213-215			
214-215			
215-225			
221-225			
222-225			

LEGEND FOR CODES

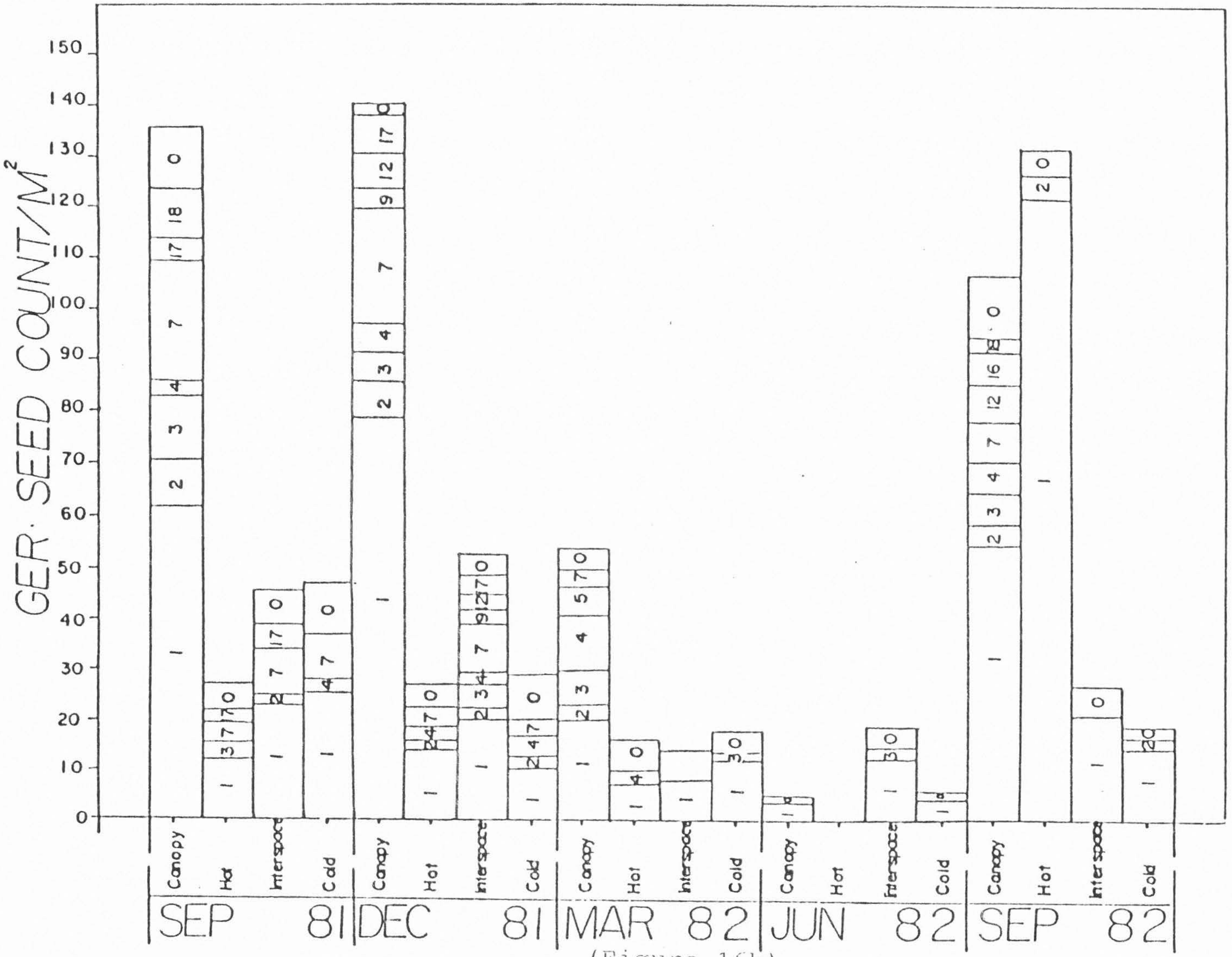
FIRST DIGIT = TREATMENT (1-2)
1=UNBURNED
2=BURNED
SECOND DIGIT = LOCATIONS
WITHIN UNBURNED (1-2)
1=CANOPY AND 2=INTERSPACES
WITHIN BURNED PLOTS (1-2)
1="HOT" POINT AND 2="COLD" POINT
THIRD DIGIT = SAMPLING DATE
1=SEPTEMBER 81, 2=DECEMBER 81,
3=MARCH 82, 4=JUNE 82, AND
5=SEPTEMBER 82

(Figure 16a. continued)

Figure 16.

b. Bar graph of mean total and taxa level germinable soil seed reserves dynamics at the different microsites on control and burned plots. Numbers indicate different taxa (see Table 4 for numerical codes).

Legend
O=all trace species (see table 4)


GER. SEED COUNT/M^2
0
10
20
30
40
50
60
70
80
90
100
110
120
130
140
150
Canopy
Hot
Interspace
Cold
SEP 81
DEC 81
MAR 82
JUN 82
SEP 82
1
2
3
4
7
12
16
17
18
0

(Figure 16b)

logarithmic seed dispersal pattern of most plants (Harper 1977), where seed fall is greatest closest to mother plants.

The total GSSR of the canopy microsite in September 1981 was composed of 45 percent cheatgrass, 17.4 percent bunchgrass seeds, 21.5 percent forbs, and 13.9 percent shrubs (Table 7 and Figure 16b). The rest was composed of 1-2, at most, unidentified species. Cheatgrass contributions to the total GSSR were relatively high even in this good condition sagebrush grass rangeland, although it comprised only a small proportion of the vegetation (Table 2).

In the interspace microsites in September 1981, fifty percent of the total GSSR was cheatgrass, 8.6% was bunchgrasses, 11.5% was forbs and 4.4% was shrubs (Table 7 and Figure 16b).

Only Eriogonum cernuum in both microsites of unburned plots and Poa species in the interspaces showed significant increases in December 1981 compared to the previous sampling interval within the same type of microsite. Increases in these and other taxa were too slight to cause any significant change in total GSSR by December 1981 at both unburned microsites (Figure 16a, Table 6).

Significantly less total GSSRs were found on both unburned microsites (canopy and interspaces) in March of 1982 compared to previous periods (Figure 16a). This decline is presumably related to an absence of seed rain, as well as depletion of the seed bank via germination, decomposition and granivory during the fall and winter. Total GSSR continued to decrease signicantly at the canopy microsites until it reached its minimum in June 1982 (5.5 seeds per square meter) (Figure 16a,table 7). It then increased significantly to reach its peak (108.5 seeds per square meter) in September 1982, after almost all plants had dispersed their seeds. This increase was found to be significantly higher than March and June total GSSRs, but not significantly different from the level found a year before. The same is true for *Bromus tectorum*.

Stipa and *Sitanion* spp. showed up in the GSSR of September 1982 at the canopy microsite, whereas a year before they were undetected. *Descurainia pinnata* and *Artemisia* spp. decreased significantly (Table 6) in September 1982 at the same microsite compared to the levels a year before. This may be related to fire destruction of parent plants around the relatively small unburned plots.

Total GSSR in the interspace microsite on the unburned plots decreased significantly to reach the minimum (14.6 seeds per square meter) in March 1982 (Table 7, Figure 16a). This GSSR density was also found to be significantly different from GSSR density in the canopy microsites for the same sampling interval (Table 16a). Total GSSR in the canopy microsite decreased significantly to reach the same level as the interspace microsite total GSSR by June 1982. The 1982 peak total GSSR for the interspace microsites was reached in September (27.2 seeds per square meter). This total GSSR was significantly lower than that observed for the first two sampling periods (September and December 1981).

Fire on the "hot" spots (where shrubs had been growing) reduced total and most taxon GSSRs significantly compared to canopy microsites in September 1981 (Figure 16a, Table 8). The reduction in the total GSSR at these spots was 80.6 percent of the levels at canopy microsites. The reduction of cheatgrass, bunchgrass, forb and shrub GSSRs were 80, 5.5, 6.6 and 82 percent, respectively, compared to their GSSRs at the canopy microsite in September, 1981 (Table 8, Figure 16b).

Artemisia spp., Bromus tectorum, Agropyron spp. and Descurainia pinnata GSSRs were significantly lower on the "hot" points compared to canopy microsites in September 1981 (Table 6).

The changes in total and all taxa GSSRs at the "hot" points were not significant in December 1981 compared to their GSSRs in the previous sampling period at the same type of microsite. This was also true for March 1981 totals and

Table 8. Summary of mean soil seed reserve densities (germinable seed per m^2) in the surface 5 cm of soil in "hot" and "cold" spots on burned sites near Mills, Utah, at several collection dates (Numbers in parentheses=one standard error of the mean).

Growth Form and Species	"Hot" spot				
	Sept 1981	Dec 1981	Mar 1982	Jun 1982	Sept 1982
Grasses:					
Bromus tectorum	12.1 (3.9)	14.4 (6.2)	7.6 (4.4)	0.0	122.4 (25.9)
Agropyron spp.	0.0	1.6 (1.4)	1.3 (1.5)	0.0	4.8 (1.7)
Poa spp.	3.7 (3.1)	1.0 (1.1)	1.0 (1.1)	0.0	0.6 (0.6)
Oryzopsis hymenoides	1.8 (1.8)	3.3 (1.8)	2.7 (1.6)	NON	0.9 (0.7)
Stipa comata	0.0	0.0	0.0	0.0	0.0
Sitanion hystrix	0.0	0.0	0.4 (0.5)	0.0	0.5 (0.5)
Forbs:					
Descurainia pinnata	3.9 (2.0)	3.7 (1.9)	0.7 (0.8)	0.0	1.9 (1.1)
Erigeron spp.	0.0	1.7 (1.3)	0.0	0.0	0.0
Eriogonum cernuum	1.1 (1.1)	0.0	1.6 (1.1)	0.0	0.5 (0.5)
Allium acuminatum	0.0	0.0	0.0	0.0	0.0
Sphaeralcea spp.	0.0	0.0	0.0	0.0	0.0
Phlox spp.	0.0	0.0	0.5 (0.5)	0.0	1.1 (0.8)
Mentzelia albicaulis	0.8 (0.8)	0.0	0.0	0.0	0.0
Cordaria draba	0.0	0.0	0.0	0.0	0.0
Helianthus spp.	0.8 (0.9)	0.0	0.0	0.0	0.0
Senecio spp.	0.0	0.0	0.0	0.0	0.0
Shrubs:					
Artemisia spp.	2.5 (1.8)	0.0	0.0	0.0	0.0
Chrysothamnus spp.	0.0	0.9 (1.0)	0.4 (0.4)	0.0	0.0
Ephedra spp.	0.0	0.0	0.0	0.0	0.0
Purshia tridentata	0.0	0.0	0.0	0.0	0.0
Juniperus osteosperma	0.0	0.4 (0.4)	0.0	0.0	0.0
Unidentified	NON	0.0	0.0	0.0	0.0
Total	26.7 (9.2)	27.0 (7.8)	16.2 (6.2)	NIL	132.7 (27.1)

Growth Form and Species	"Cold" spot				
	Sept 1981	Dec 1981	Mar 1982	Jun 1982	Sept 1982
Grasses:					
Bromus tectorum	25.6 (6.1)	10.6 (3.6)	12.1 (3.6)	3.8 (1.6)	14.2 (6.4)
Agropyron spp.	0.7 (6.8)	2.5 (1.6)	0.0	0.0	2.0 (1.0)
Poa spp.	1.3 (1.6)	0.8 (0.9)	1.7 (1.4)	0.2 (0.2)	0.4 (0.4)
Oryzopsis hymenoides	2.9 (1.5)	4.1 (2.8)	0.4 (0.4)	0.3 (0.4)	0.0
Stipa comata	0.0	0.0	1.1 (1.3)	0.0	0.0
Sitanion hystrix	0.0	0.0	0.0	0.0	0.0
Forbs:					
Descurainia pinnata	9.0 (3.0)	3.5 (1.6)	1.1 (0.8)	1.1 (0.8)	1.3 (0.8)
Erigeron spp.	0.0	0.0	0.0	0.0	0.0
Eriogonum cernuum	0.0	1.1 (1.1)	0.6 (0.6)	0.0	0.0
Allium acuminatum	0.6 (0.7)	0.0	0.0	0.0	0.0
Sphaeralcea spp.	0.0	0.0	0.0	0.0	0.0
Phlox spp.	1.4 (1.2)	1.8 (2.0)	0.0	0.5 (0.6)	0.0
Mentzelia albicaulis	1.8 (1.1)	0.0	0.0	0.0	0.0
Cordaria draba	NON	0.8 (01.0)	0.0	0.0	0.0
Helianthus spp.	0.0	0.0	0.5 (0.6)	0.0	0.0
Senecio spp.	0.0	0.0	0.0	0.0	0.0
Shrubs:					
Artemisia spp.	1.3 (1.1)	0.0	0.5 (0.6)	0.0	0.6 (0.6)
Chrysothamnus spp.	0.0	0.9 (1.0)	0.0	0.0	0.0
Ephedra spp.	0.0	0.0	0.0	0.0	0.0
Purshia tridentata	0.0	0.0	0.0	0.0	0.0
Juniperus osteosperma	0.0	0.8 (0.9)	0.0	0.0	0.0
Unidentified	02.0 (1.3)	0.0	0.0	0.0	0.0
Total	46.6 (7.7)	26.9 (7.7)	18.0 (4.6)	5.9 (1.8)	18.5 (3.4)

NON=detected but not alive.

almost all taxa compared to the preceding period. The change in the GSSRs associated with canopy between December 1981 and March 1982 were significant (Figure 16).

Total GSSR at the "hot" spots in June 1982 was the lowest level of GSSRs achieved in the whole study period. Because these sites are probably more favorable to seed germination via greater soil organic matter, nutrients, infiltration and soil moisture (West 1983), the seed bank is apparently depleted more readily here.

Within only one year after the fire, the vegetation cover on the burned plot had increased greatly. A great proportion of the regenerated vegetation was found to be cheatgrass (35.7% of the mean total plant cover, see Table 2). This rebound in cover was followed by a significant increase of the total GSSR, reaching its peak in September 1982 (132.7 seeds per square meter). This increase may be related to the great increase of cheatgrass in the seed bank (92.2%). The GSSR of other taxa remained significantly lower or not signicantly different from other sampling intervals. The great increase of cheatgrass resulted in total GSSR in September 1982 reaching even the total GSSR of unburned plots during the first sampling period. Seed populations of other species, including undesirable species (e.g. Artemisia spp.), remained significantly lower than their GSSR at under canopy microsites in September 1981 (Table 6). This indicated that fire was a good treatment for controlling some undesirable range plant seeds, but timing of the fire was very important.

Although cheatgrass seed density was reduced immediately after the fire, this species had increased approximately ten fold in its total GSSR a year later. Seeds of most native perennial grasses had significantly lower densities on "hot" spots in September 1982 compared to their densities in the undercanopy microsite (Table 6). Recovery of these plant species may come from vegetative portions which escaped the fire rather than by seeds. Seeds of sagebrush and other shrubby species were absent from the total GSSR on the "hot" spots even a year after fire (Table 8 and Figures 16a and b).

No significant differences between total GSSR at the "cold" spots and interspaces were found in September 1981, but there was a significant decrease in the total GSSR of the "cold" spots in December 1982 compared to the previous sampling interval at the same microsite (Figure 16b).

Total and taxa GSSRs continued to decrease at "cold" and interspace microsites until they reached their minima in June 1982. Total GSSR at these microsites increased to reach their 1982 highs in September. These values were significantly lower than their GSSRs in the first two sampling periods and not significantly different than the rest (Table 8 and Figures 16a and b). There were no significant differences in most GSSRs of different taxa between the "cold" and interspace microsites during similar sampling periods.

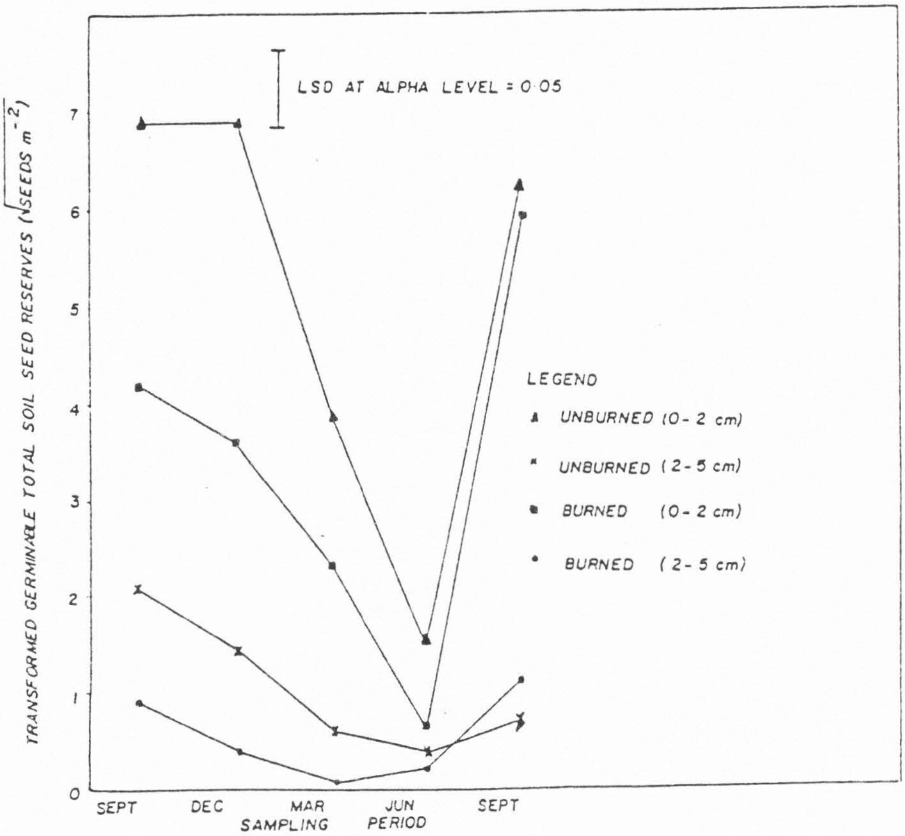
Fire effects on GSSR at different sampling depths

Comparison of total and taxon GSSR densities at two soil depths showed that the destructive effect of fire on seeds was greater in the surface 0-2 cm than sub-surface soil (2-5 cm depth). That is, because there are more seeds in the surface layer, more are there to be distroyed (Figure 17a). Six weeks after the wildfire, total GSSR in the surface layer of the burned plots was only 45.7% of that found in the unburned plots (Tables 10, 11 and Figure 17b). Total GSSR in the deeper depth (2-5 cm) of the burned plots was 34.4% of that found in comparable depths in the unburned plots. However, because there were few there, fewer were destroyed in absolute terms. The total GSSR for both depths combined in the burned plots was 56.3% less than for both depths in the unburned plots. About 82 and 86% of the total GSSR occurs in the upper layer of the unburned and burned soils, respectively.

A great proportion of total GSSR detected at the surface sampling depth was found to be cheatgrass seeds, even in September 1981 at the unburned plots (Table 10). This indicated that even on good condition rangeland, cheatgrass seed density was high. Although the vegetation was relatively rich in bunchgrass (38% cover), their GSSR was found to be low, comprising only 15 percent of the total GSSR found at the surface sampling depth in the unburned

Figure 17.

a. Graph of mean total germinable soil seed reserves, of transformed data (square root of seed m^{-2}) with LSD (alpha=0.05) in the different sampling depth of the control and burned plots.


LSD AT ALPHA LEVEL = 0·05
TRANSFORMED GERMINABLE TOTAL SOIL SEED RESERVES ($\sqrt{\text{SEEDS m}^{-2}}$)
7
6
5
4
3
2
1
0
SEPT
DEC
MAR
JUN
SEPT
SAMPLING PERIOD
LEGEND
▲ UNBURNED (0-2 cm)
× UNBURNED (2-5 cm)
■ BURNED (0-2 cm)
• BURNED (2-5 cm)

(Figure 17a)

Table 9. Summary of means of transformed data on observed germinable soil seed reserves (square root of seed m^{-2}) of the most important taxa (those that showed up more than twice during the whole study period) in both unburned and burned plots at two sampling depths. Last column shows LSDs (alpha =0.05) for the taxa showing significant differences.

Species	Unburned										
	Surface (0-2 cm)					Sub-surface (2-5 cm)					LSD
	Sept 81	Dec 81	Mar 82	Jun 82	Sept 82	Sept 81	Dec 81	Mar 82	Jun 82	Sept 82	
Bromus tectorum	4.17	4.27	2.17	1.13	4.25	1.13	0.74	0.13	0.22	0.46	0.76
Agropyron spp.	0.79	0.63	0.22	0.0	0.89	0.15	0.21	0.0	0.0	0.06	0.31
Poa spp.	0.73	0.89	0.51	0.24	0.92	0.0	0.0	0.22	0.08	0.0	0.33
Oryzopsis hymenoides	0.23	0.58	0.55	0.14	0.81	0.14	0.20	0.13	0.0	0.0	0.33
Stipa comata	0.0	0.07	0.07	0.0	0.30	0.0	0.0	0.0	0.0	0.07	0.12
Sitanion hystrix	0.0	0.0	0.06	0.0	0.29	0.0	0.0	0.0	0.0	0.0	0.10
Descurainia pinnata	2.03	2.10	0.32	0.20	0.72	0.22	0.25	0.15	0.06	0.07	0.44
Erigeron spp.	0.10	0.10	0.0	0.13	0.0	0.28	0.0	0.0	0.0	0.0	0.11
Eriogonum cernuum	0.0	0.51	0.06	0.0	0.28	0.07	0.07	0.0	0.0	0.0	0.18
Artemisia spp.	0.58	0.79	0.24	0.06	0.17	0.16	0.0	0.84	0.0	0.0	0.27

Species	Burned										
	Surface (0-2 cm)					Sub-surface (2-5)					LSD
	Sept 81	Dec 81	Mar 82	Jun 82	Sept 82	Sept 81	Dec 81	Mar 82	Jun 82	Sept 82	
Bromus tectorum	2.62	2.03	1.44	0.39	5.35	0.21	0.07	0.0	0.09	0.83	0.76
Agropyron spp.	0.07	0.21	0.09	ND	0.66	0.0	0.17	0.0	0.0	0.14	0.31
Poa spp.	0.15	0.28	0.04	0.13	0.0	0.0	0.0	0.0	0.0	0.0	0.33
Oryzopsis hymenoides	0.34	0.58	0.26	0.05	0.11	0.15	0.0	0.0	0.0	0.0	0.33
Stipa comata	0.0	0.0	0.09	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.12
Sitanion hystrix	0.0	0.0	0.05	0.0	0.06	0.0	0.0	0.0	0.0	0.0	0.10
Descurainia pinnata	0.84	0.59	0.16	0.09	0.28	0.39	0.13	0.08	0.07	0.11	0.44
Erigeron spp.	0.0	0.14	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.11
Eriogonum cernuum	0.08	0.08	0.23	0.0	0.0	0.0	0.0	0.0	0.0	0.23	0.18
Artemisia spp.	0.30	0.0	0.06	0.0	0.05	0.0	0.0	0.0	0.0	0.0	0.27

Table 10. Summary of mean soil seed reserve densities (germinable seed per m^2) in the surface 0-2 cm and sub-surface 2-5 cm soil sampling depths on the unburned (control) plots near Mills, Utah, at several collection dates (Numbers in parentheses= one standard error of the mean.

Growth Form and Species	Surface (0-2 cm)				
	Sept 1981	Dec 1981	Mar 1982	Jun 1982	Sept 1982
Grasses:					
Bromus tectorum	25.6 (10.7)	30.5 (13.2)	11.0 (6.9)	6.4 (6.7)	31.7 (17.4)
Agropyron spp.	3.5 (3.2)	3.0 (2.8)	1.0 (1.9)	0.0	3.5 (2.7)
Poa spp.	4.4 (5.3)	4.0 (3.2)	2.3 (2.7)	0.9 (1.3)	3.5 (2.5)
Oryzopsis hymenoides	1.2 (2.2)	2.6 (2.6)	1.6 (1.3)	0.5 (1.0)	3.1 (2.5)
Stipa comata	0.0	0.3 (1.0)	2.4 (2.8)	0.0	1.1 (1.4)
Sitanion hystrix	0.0	0.0	0.2 (0.7)	0.0	1.1 (1.4)
Forbs:					
Descurainia pinnata	11.4 (7.8)	11.6 (6.4)	1.3 (1.8)	0.8 (1.6)	3.4 (3.2)
Erigeron spp.	4.2 (11.6)	0.0	0.5 (1.1)	0.0	1.0 (1.3)
Eriogonum cernuum	0.0	2.4 (2.6)	0.2 (0.7)	0.0	1.0 (1.2)
Allium acuminatum	0.6 (1.3)	0.7 (1.5)	0.0	0.0	0.2 (0.7)
Sphaeralcea spp.	0.0	0.0	0.0	0.0	0.0
Phlox spp.	0.0	3.3 (3.6)	NON	0.6 (1.5)	3.5 (5.3)
Mentzelia albicaulis	0.3 (0.9)	0.0	0.0	0.0	0.0
Cordaria draba	0.3 (0.9)	0.0	0.0	0.0	0.0
Helianthus spp.	0.0	0.0	0.0	0.0	0.0
Senecio spp.	0.0	0.0	0.3 (0.8)	0.0	2.7 (6.5)
Shrubs:					
Artemisia spp.	2.4 (2.4)	4.6 (5.5)	0.9 (1.4)	0.2 (0.7)	0.6 (1.0)
Chrysothamnus spp.	1.5 (4.0)	0.6 (1.3)	0.3 (0.3)	0.0	1.6 (1.6)
Ephedra spp.	0.0	0.0	0.0	0.0	0.3 (0.7)
Purshia tridentata	0.0	0.4 (1.1)	0.0	0.0	0.2 (0.6)
Juniperus osteosperma	0.0	0.4 (1.4)	0.0	0.0	0.0
Unidentified	3.7 (3.2)	0.3 (0.9)	NON	0.0	NON
Total	59.1 (18.7)	64.7 (20.7)	22.0 (10.0)	9.4 (8.2)	58.5 (22.3)

Growth Form and Species	Sub-surface 2-5 cm				
	Sept 1981	Dec 1981	Mar 1982	Jun 1982	Sept 1982
Grasses:					
Bromus tectorum	7.3 (5.2)	7.9 (12.9)	0.5 (0.8)	0.7 (1.1)	2.2 (1.9)
Agropyron spp.	0.8 (1.0)	0.9 (1.1)	0.0	0.0	0.2 (0.4)
Poa spp.	0.0	0.0	1.1 (1.4)	0.4 (0.7)	0.0
Oryzopsis hymenoides	0.6 (0.8)	0.9 (1.0)	0.6 (0.8)	0.0	0.0
Stipa comata	0.0	0.0	0.0	0.0	0.3 (0.5)
Sitanion hystrix	0.0	0.0	0.0	0.0	0.0
Forbs:					
Descurainia pinnata	1.0 (1.2)	1.3 (1.6)	0.7 (1.0)	NON	0.3 (0.5)
Erigeron spp.	0.0	0.0	0.0	0.0	0.0
Eriogonum cernuum	0.3 (0.5)	0.3 (0.5)	0.0	0.0	0.0
Allium acuminatum	0.7 (1.0)	0.0	0.0	0.0	0.0
Sphaeralcea spp.	0.6 (0.8)	0.0	0.0	0.0	0.0
Phlox spp.	0.0	0.7 (1.4)	0.0	0.0	0.0
Mentzelia albicaulis	0.0	0.0	0.0	0.0	0.0
Cordaria draba	0.0	0.0	0.0	0.0	0.0
Helianthus spp.	0.0	0.0	0.0	0.0	0.0
Senecio spp	0.0	0.0	0.0	0.0	0.0
Shrubs:					
Artemisia spp.	0.8 (1.1)	0.0	0.4 (0.9)	0.0	0.0
Chrysothamnus spp.	0.0	0.2 (0.4)	0.0	0.0	0.0
Ephedra spp.	0.0	0.0	0.0	0.0	0.2 (0.5)
Purshia tridentata	0.0	0.0	0.0	0.0	0.0
Juniperus osteosperma	0.0	0.0	0.0	0.0	0.0
Unidentified	0.7 (1.1)	NON	0.0	0.0	0.0
Total	12.8 (4.2)	12.2 (6.2)	3.3 (2.4)	1.1 (1.1)	3.2 (2.2)

NON=Detected but not alive.

Table 11. Summary of mean soil seed reserve densities (germinable seed per m^2) in the surface 0-2 cm and subsurface 2-5 cm soil sampling depths on the burned plots near Mills, Utah, at several collection dates (Numbers in parentheses=one standard error of the mean).

Growth Form and Species	Surface 0-2 cm				
	Sept 1981	Dec 1981	Mar 1982	Jun 1982	Sept 1982
Grasses:					
Bromus tectorum	15.0 (6.4)	13.3 (8.1)	7.5 (5.2)	1.5 (1.6)	53.3 (26.2)
Agropyron spp.	0.3 (0.8)	0.9 (1.5)	0.5 (1.4)	0.0	2.2 (1.8)
Poa spp.	1.9 (3.1)	1.1 (1.4)	1.7 (1.7)	0.1 (0.3)	0.4 (0.5)
Oryzopsis hymenoides	1.3 (1.7)	2.7 (3.2)	0.6 (1.7)	0.1 (0.4)	0.4 (0.7)
Stipa comata	0.0	0.0	0.5 (1.3)	0.0	0.0
Sitanion hystrix	0.0	0.0	0.2 (0.4)	0.0	0.2 (0.6)
Forbs:					
Descurainia pinnata	4.1 (3.3)	2.5 (2.8)	0.5 (0.8)	0.3 (0.6)	1.0 (1.2)
Erigeron spp.	0.0	0.7 (1.3)	0.0	0.0	0.0
Eriogonum cernuum	0.4 (1.1)	0.4 (1.1)	0.8 (1.2)	0.0	0.0
Allium acuminatum	0.3 (0.8)	0.0	0.0	0.0	0.0
Sphaeralcea spp	0.0	0.0	0.0	0.0	0.0
Phlox spp.	0.7 (1.3)	0.7 (2.0)	0.2 (0.5)	0.2 (0.7)	0.4 (0.9)
Mentzelia albicaulis	0.8 (1.2)	0.0	0.0	0.0	0.0
Cordaria draba	0.4 (1.0)	0.0	0.0	0.0	0.0
Helianthus spp.	0.3 (0.9)	0.0	0.2 (0.7)	0.0	0.0
Senecio spp	0.0	0.0	0.0	0.0	0.0
Shrubs:					
Artemisia spp.	1.5 (2.0)	0.0	0.3 (0.7)	0.0	0.3 (0.7)
Chrysothamnus spp.	0.0	0.7 (1.4)	0.1 (0.4)	0.0	0.0
Ephedra spp.	0.0	0.0	0.0	0.0	0.0
Purshia tridentata	0.0	0.0	0.0	0.0	0.0
Juniperus osteosperma	0.0	0.3 (0.9)	0.0	0.0	0.0
Unidentified	NON	0.0	0.0	0.0	0.0
Total	27.0 (9.9)	23.3 (9.3)	13.1 (6.9)	2.2 (1.8)	58.2 (17.1)

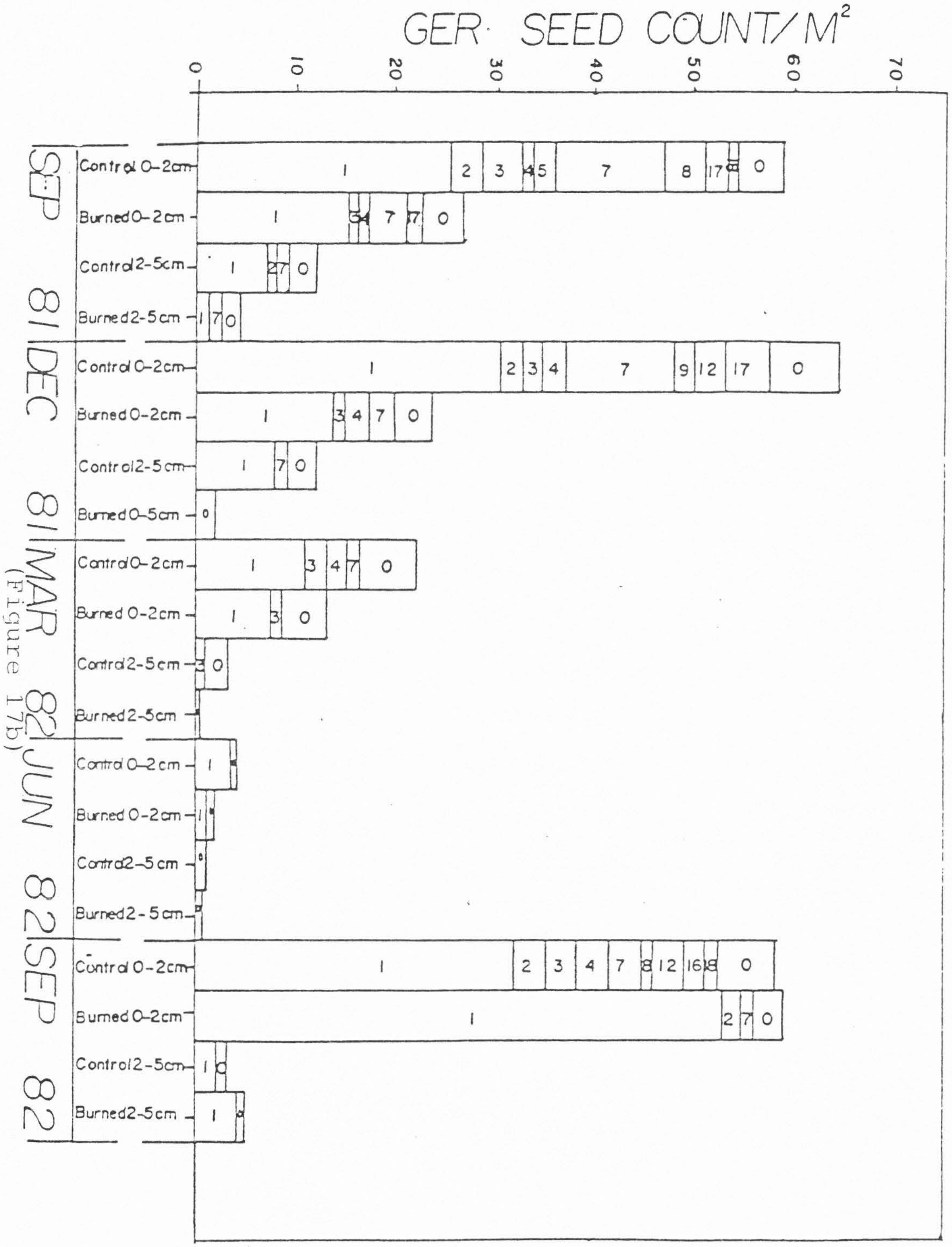
Growth Form and Species	Sub-surface 2-5 cm				
	Sept 1981	Dec 1981	Mar 1982	Jun 1982	Sept 1982
Grasses:					
Bromus tectorum	1.2 (1.7)	0.3 (0.5)	0.0	0.5 (0.8)	4.6 (6.5)
Agropyron spp.	0.0	1.0 (1.3)	0.0	0.0	0.6 (0.8)
Poa spp.	0.0	0.0	0.0	0.0	0.0
Oryzopsis hymenoides	0.7 (0.9)	0.0	0.0	0.0	0.0
Stipa comata	0.0	0.0	0.0	0.0	0.0
Sitanion hystrix	0.0	0.0	0.0	0.0	0.0
Forbs:					
Descurainia pinnata	1.9 (1.6)	0.5 (0.7)	0.4 (0.7)	0.3 (0.6)	0.4 (0.6)
Erigeron spp.	0.0	0.0	0.0	0.0	0.0
Eriogonum cernuum	0.0	0.0	0.0	0.0	0.3 (0.6)
Allium acuminatum	0.0	0.0	0.0	0.0	0.0
Sphaeralcea spp.	0.0	0.0	0.0	0.0	0.0
Phlox spp.	0.0	0.0	0.0	0.0	NON
Mentzelia albicaulis	0.6 (0.7)	0.0	0.0	0.0	0.0
Cordaria draba	0.0	0.0	0.0	0.0	0.0
Helianthus spp.	0.0	0.0	0.0	0.0	0.0
Senecio spp.	0.0	0.0	0.0	0.0	0.0
Shrubs:					
Artemisia spp.	0.0	0.0	0.0	0.0	0.0
Chrysothamnus spp.	0.0	0.0	0.0	0.0	0.0
Ephedra spp.	0.0	0.0	0.0	0.0	0.0
Purshia tridentata	0.0	0.0	0.0	0.0	0.0
Juniperus osteosperma	0.0	0.2 (0.4)	0.0	0.0	0.0
Unidentified	NON	0.0	0.0	0.0	0.0
Total	4.4 (2.3)	2.0 (1.5)	0.4 (0.7)	0.8 (1.3)	5.9 (2.1)

NON=Detected but not alive.

Figure 17.

b. Bar graph of mean total and taxa level germinable soil seed reserves dynamics in the different sampling depths at the control and burned plots. Numbers indicate different taxa (see Table 4 for numerical codes).

Legend
0=all trace species (see Table 4)


GER. SEED COUNT/M²
0
10
20
30
40
50
60
70
SEP 81
Control 0–2cm
1 2 3 4 5 7 8 17 18 0
Burned 0–2cm
1 5 4 7 17 0
Control 2–5cm
1 2 7 0
Burned 2–5cm
1 7 0
DEC 81
Control 0–2cm
1 2 3 4 7 9 12 17 0
Burned 0–2cm
1 3 4 7 0
Control 2–5cm
1 7 0
Burned 0–5cm
0
MAR 82
Control 0–2cm
1 3 4 7 0
Burned 0–2cm
1 3 0
Control 2–5cm
3 0
Burned 2–5cm
JUN 82
Control 0–2cm
1
Burned 0–2cm
1
Control 2–5cm
0
Burned 2–5cm
SEP 82
Control 0–2cm
1 2 3 4 7 8 12 16 18 0
Burned 0–2cm
1 2 7 0
Control 2–5cm
1 0
Burned 2–5cm
1 0

(Figure 17b)

plots. Forb GSSR contributed a higher proportion than shrubs (28.4% vs. 6.6%) to the total GSSR in September 1981.

The changes in total and taxon GSSRs were not significant between September and December 1981 at the surface sampling depth within the unburned plots, except for Eriogonum spp. which was completely absent from the first sampling period, but showed up in December 1981 GSSR (Table 9).

Significantly less total GSSR were found in the surface sampling depths of both burned and unburned plots in March 1982 compared to all earlier dates. These continued to decrease until minima were reached in June 1982. This decline was presumably related to germination, decomposition, and granivory during a period of no new seed rain (Table 9).

Total GSSR at the surface sampling depths increased significantly to reach their 1982 peaks in September, presumably because seed dispersal occurs primarily between June and September. This September value was found to be significantly higher than March and June 1982 total GSSR.

A high proportion of the total GSSR detected in the surface 0-2 cm in September 1982 was cheatgrass (54.2 percent). Sagebrush seed density was significantly lower (Table 9) than its seed density a year before at the same sampling depth in the same plots (Table 10). The decrease in sagebrush seed was probably a function of destruction of parent plants by fire around the relatively small control plots.

In sub-surface (2-5 cm) depths within the unburned plots in September 1981, 56 percent of the total GSSRs were cheatgrass, 13 percent were bunchgrasses, 26 percent were forbs and 5.6 percent were shrubs (Table 10). As mentioned before, the sub-surface layer contained only about 21.7 percent of the total GSSR in the surface layer.

Total GSSR in the sub-surface samples from the unburned plots in December 1981 were not significantly different from the previous sampling period at the same plots and depth. There were, however, significant differences between the surface and sub-surface sampling depths at this date (Figure 17a).

Total GSSR in the sub-surface sampling depth continued to decrease through time until it reached its minimum in June 1982 (1.1 seeds per square meter). This minimum was significantly different from the first sample (September 1981) (Figure 17a).

The peak 1982 total GSSR in the sub-surface sampling depth was reached in September (3.2 seeds per square meter). This peak was not significantly different from December 1981 to June 1982 readings, but was significantly lower than the level observed on the same plots during September 1981 (Tables 10, 11 and Figures 17a, b). Higher peaks perhaps may be achieved if more time were given for incorporation of seed from the surface to the sub-surface sampling depth, provided trampling by grazing animals was allowed.

Fire apparently caused significant reduction in total GSSR in the surface 0-2 cm samples in September 1981 (Figure 17a). Reductions of the GSSR in burned plots for individual taxa as compared to similar samples from the unburned sites were: cheatgrass, 41.4 percent; bunchgrasses, 61.5 percent; forbs, 58.3 percent and; shrubs, 38.5 percent (Table 11, Figure 17b).

Total and taxon GSSRs in surface samples from the burned plots did not change significantly from September 1981 to December 1981. The differences between total (Figure 17a), Bromus tectorum, Agropyron spp., Poa spp., Descurainia pinnata, Eriogonum cernuum and Artemisia spp. GSSRs were significantly lower, however, on the burned than unburned plots in December 1981 (Table 9).

On or before March 1982, temperature increased sharply (Figure 11) followed by snow melt, both of which promoted germination from the seed bank and exhaustion of the total GSSR in the surface sampling depth in the burned plots. This continued until total GSSR reached its minimum value in June 1982. Other reasons which can result in exhaustion of the seed bank were mentioned before.

Total GSSRs in the upper sampling depth in the burned plots in September 1982 were not significantly different from GSSRs at comparable sampling depths and periods in the unburned plots, but significantly higher than all previous sampling periods within the burned plots (Tables 10 and 11, Figure 17a). Cheatgrass composed a large proportion of the total GSSR in September 1982 in the surface sample from the burned plots (91.6 percent of the total, see Figure 17b). This indicates a quick increase of the total GSSR by the relatively high participation of cheatgrass seed. The other species, including undesirable ones, contributed less to the seed banks in September 1982 than earlier (Tables 9 and 11, Figure 17b). This indicated that fire was a good treatment to control some undesirable range plant seeds (e.g. sagebrush). Cheatgrass, however, made up most of the increased GSSR. Timing of the fire was important. If this fire had occurred earlier, before cheatgrass dispersed its seed, damage to cheatgrass seed would probably have been greater.

Fire reduced the total GSSR significantly in the sub-surface sampling depth compared to the GSSR in the unburned plots at the same sampling depth in September 1981 (Figure 17a).

Total and taxon GSSRs did not change significantly from September to December 1981 in the surface depth of both burned and unburned plots (Figures 17a and b, Table 9). The surface total GSSRs were significantly (Figure 17a) lower in the burned plots in December 1981 and March 1982 than unburned GSSRs for the same sampling depth and periods. None of the taxon differences between burned and unburned plots were significant in December 1981, March 1982 or June 1982.

Total and taxon sub-surface GSSR levels declined through the spring. These depletions were probably due to germination, decomposition and herbivory during a period of no seed rain.

The September 1982 peak in surface GSSRs in both burned and unburned plots was not significantly different from the March and June 1982 values (Figure 17a), but the value for unburned samples was significantly lower than total GSSR in September 1981 (Figures 17a and b). If more time were involved or trampling by grazing animals were allowed, a higher peak total GSSR may have been achieved in the sub-surface (2-5 cm) sampling depth. The formation of soil crusts and lack of soil cracks (see page 17), may be the reason for low incorporation of soil seed reserves into deeper soil depths.

Fire effects on germinable seed rain (GSR)

One of the main questions of this study was to investigate whether the wildfire had any significant effect on seed rain. Data analysis showed that this treatment had no significant effect on seed rain between burned and unburned plots throughout the study period. One of the reasons for the lack of significant difference may be lack of physical separation or a buffer zone between burned and unburned plots due to limitation of unburned areas, i.e., the fire could have been affecting control plots as well. Lack of buffer zones could also result in free local movement of seed accross both kinds of plots. Unfortunately, seed movement may be unequal on all seed traps in the control plots. Seed traps located on the borders of these plots could catch more seeds than the inner ones. This cannot be addressed here because of the complex interactions produced by a design focused on other questions.

Even though seed traps on burned plots had trapped 4.4 times the total GSR density as that recorded on unburned plots by December 1981 (Table 12) these differences were not significant (Figure 18) due to high variation. This may be related to the early lack of vegetation at the burned plots which facilitated easy movement of seeds toward the traps. Vegetation on unburned plots may have acted as a wind break preventing easy movement of seeds to the traps (Parmenter and MacMahon 1983). The total GSR density in the burned plots at this sampling period was higher (but not statistically so) than the GSR density in the unburned plots (see Table 12, Figure 18).

In the burned plots during the first collection, 82.6 percent of the total GSR was cheatgrass (340.9 seeds per square meter), 12.9 percent bunchgrass seeds (53.1 seeds per square meter), and 4.5 percent forbs (18.6 seeds per square meter). Shrub seeds were completely absent. The reason for this may be that the heat around these relatively small control plots could have killed the flowering buds of shrubs. Cheatgrass GSR density at the burned plots, although 8.6 times that in the unburned plots, was still not statistically different. Mean total and all other taxon GSR were also not significantly different in burned vs. unburned plots (Table 12 and Figure 18). This may be related to the previously mentioned reasons.

Mean total GSR density within the unburned plots did not increase significantly (99.7 seed per square meter) by March 1982 compared to the previous sampling period (Table 12 and Figure 18). Similarly GSR density of the burned plots in March 1982 (431.6 seeds per square meter) was not significantly different from total GSR densities detected in

Table 12. Summary of mean germinable seed rain densities per meter^2 (number of seed accumulated in the traps over 3-month intervals, for 15 months) on unburned (control) and burned plots near Mills, Utah (Numbers in parentheses=one standard error of the mean).

Growth Forms and Species	Unburned				
	Dec 1981	Mar 1982	Jun 1982	Sept 1982	Dec 1982
Grasses:					
Bromus tectorum	39.8 (78.3)	43.8 (102.1)	114.1 (339.6)	5881.4 (4350.7)	5881.4 (4350.7)
Agropyron spp.	2.7 (17.2)	2.7 (17.2)	13.3 (87.5)	378.0 (681.8)	378.0 (681.8)
Poa spp,	4.0 (23.9)	4.0 (23.9)	8.0 (47.8)	392.6 (681.8)	395.1 (692.4)
Oryzopsis hymenoides	4.0 (23.9)	4.0 (23.9)	6.6 (41.1)	37.1 (92.9)	37.1 (92.9)
Stipa comata	2.7 (17.2)	2.7 (17.2)	2.7 (17.2)	13.3 (61.0)	13.3 (92.9)
Sitanion hystrix	0.0	0.0	0.0	0.0	0.0
Forbs:					
Descurainia pinnata	23.9 (61.3)	23.9 (062.3)	47.8 (185.7)	65.0 (230.8)	69.7 (232.9)
Eriogonum cernuum	0.0	0.0	0.0	2.7 (17.2)	2.7 (17.2)
Allium acuminatum	0.0	0.0	0.0	2.7 (17.2)	2.7 (17.2)
Sphaeralcea spp.	0.0	0.0	0.0	0.0	0.0
Phlox spp.	9.3 (33.2)	9.3 (33.2)	9.3 (33.2)	15.9 (71.6)	15.9 (71.6)
Senecio spp.	2.7 (17.2)	5.3 (34.5)	5.3 (34.5)	8.0 (51.7)	8.0 (51.7)
Shrubs:					
Artemisia spp.	0.0	0.0	0.0	6.6 (29.2)	6.6 (29.2)
Chrysothamnus spp.	0.0	0.0	0.0	9.3 (33.2)	12.7 (38.6)
Purshia tridentata	0.0	0.0	2.7 (17.2)	2.7 (17.2)	2.7 (17.2)
Juniperus osteosperma	0.0	0.0	0.0	0.0	0.0
Unknown	4.0 (26.9)	4.0 (26.9)	4.4 (26.9)	4.0 (26.9)	4.0 (26.9)
Total	93.1 (124.7)	99.7 (099.5)	213.8 (213.6)	6819.3 (4257.1)	6829.9 (4259.2)

Growth Forms and Species	Burned				
	Dec 1981	Mar 1982	Jun 1982	Sept 1982	Dec 1982
Grasses:					
Bromus tectorum	340.9 (229.5)	351.5 (273.2)	420.5 (388.6)	10286.5 (6686.6)	10286.5 (6686.6)
Agropyron spp.	10.6 (37.1)	13.3 (54.4)	37.1 (156.5)	206.9 (408.5)	206.9 (408.5)
Poa spp.	19.9 (47.8)	22.5 (45.1)	45.1 (143.3)	47.8 (160.5)	47.8 (160.5)
Oryzopsis hymenoides	15.9 (42.4)	18.6 (59.7)	21.2 (69.0)	47.8 (149.9)	47.8 (149.9)
Stipa comata	2.7 (17.2)	2.7 (17.2)	2.7 (17.2)	9.3 (69.0)	9.3 (69.0)
Sitanion hystrix	4.0 (23.9)	4.0 (023.9)	4.0 (23.9)	4.0 (23.9)	4.0 (23.9)
Forbs:					
Descurainia pinnata	9.3 (33.2)	9.3 (33.2)	19.9 (76.9)	26.5 (106.1)	26.5 (106.1)
Eriogonum cernuum	0.0	0.0	0.0	NON	NON
Allium accuminatum	0.0	NON	4.0 (23.9)	4.0 (23.9)	4.0 (23.9)
Sphaeralcea spp.	0.0	0.0	0.0	0.0	0.0
Phlox spp.	9.3 (33.2)	9.3 (33.2)	11.9 (62.3)	11.9 (62.3)	11.9 (62.3)
Senecio spp.	0.0	0.0	0.0	2.7 (17.2)	2.7 (0017.2)
Shrubs:					
Artemisia spp.	0.0	0.0	NON	2.7 (17.2)	2.7 (17.2)
Chrysothamnus spp.	0.0	0.0	0.0	0.0	2.7 (17.2)
Purshia tridentata	0.0	0.0	2.7 (17.2)	2.7 (17.2)	2.7 (17.2)
Juniperus osteosperma	0.0	0.0	0.0	0.0	0.0
Unknown	0.0	0.0	0.0	0.0	0.0
Total	412.6 (266.6)	431.2 (176.4)	569.1 (185.7)	10652.8 (5962.3)	10655.5 (5962.3)

NON=Detected but not alive

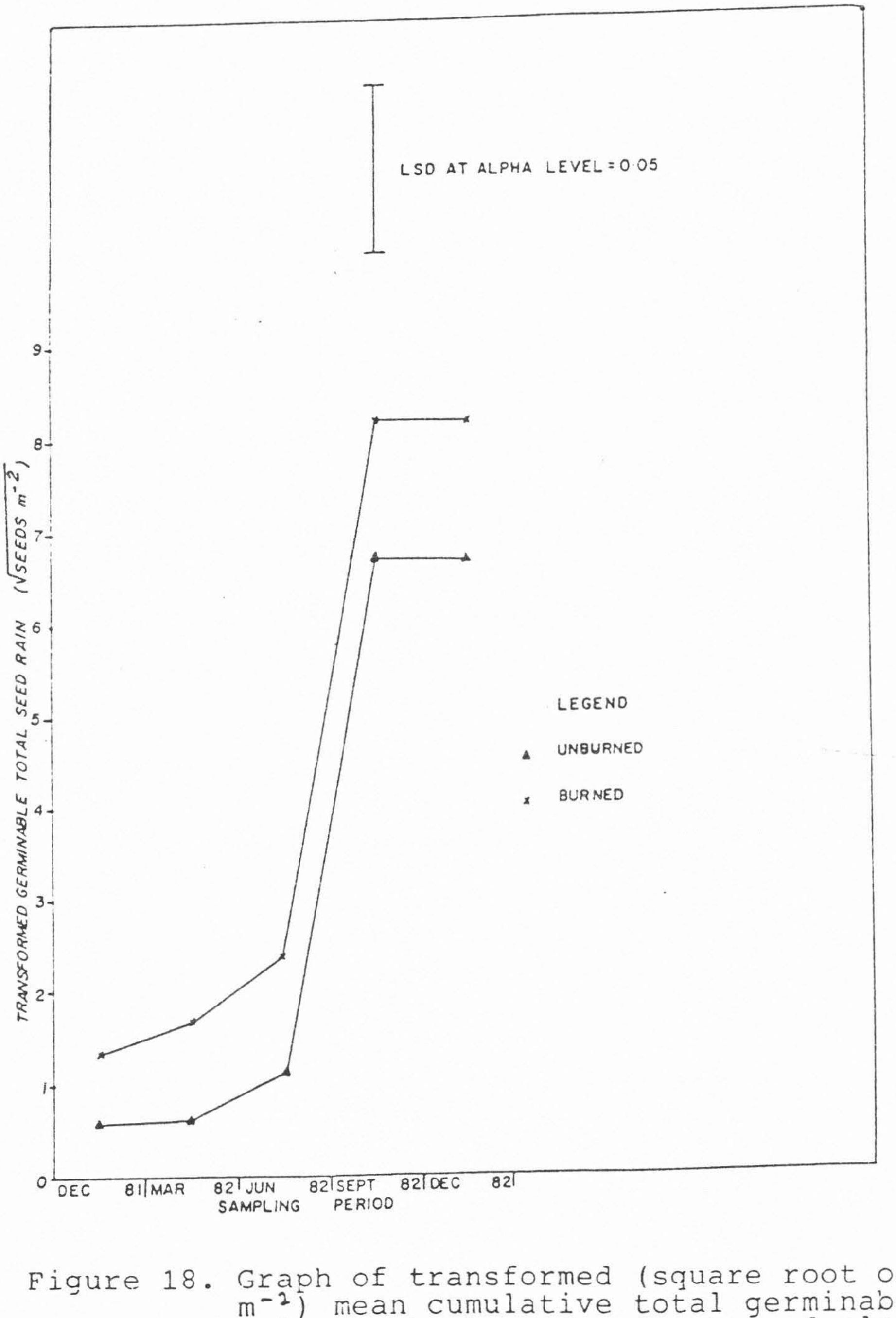


Figure 18. Graph of transformed (square root of seed m^{-2}) mean cumulative total germinable seed rain at the burned and unburned plots (sum of square root transformed individual plot data used).

burned and unburned plots for the previous sampling periods.

Cumulative mean total GSR density started to increase in June 1982 on the unburned plots because early seed maturing species started to shed their seeds. Cumulative total GSR increased sharply by September 1982 (6819.3 seeds per square meter). This increase was found to be significantly different from all previous sampling periods, but only within the same type of treatment (Figure 18).

Cumulative total GSR did not significantly increase in December 1982 over the September 1982 total, probably because most species had already ended their life cycle. The sharp increase in cumulative GSR of cheatgrass in the unburned plots (147.8 times GSR of December 1981) at this sampling period was probably due to the increase of cheatgrass in the burned areas around those plots in the year after the fire. That is, the control plots were small "islands" in a "sea" of cheatgrass.

Similarly, the cumulative total GSR density at the burned plots increased from June 1982 until it reached its peak in September 1982, with no significant change over the following three months. The maintenance of the September peak was probably because almost all species had ended their life cycle and no extra seeds were added to the seed rain density, except those moved locally from the surrounding areas.

The GSR density in the burned plots during September and December 1982 was found to be significantly different from all other sampling periods (Figure 18). December 1982 Cheatgrass GSR was 258.5 times that of unburned plots a year earlier. Similarly the cumulative GSR of all other species were lower in September and December, 1982, compared to their values at the same sampling period in the unburned plots, but the differences were not statistically significant because of the high variability within and between the GSR densities on these two kinds of plots (Table 13).

Fire effects on GSR at different microsites within burned and unburned plots

Interspaces within the unburned plots had mean cumulative total GSR densities which were 13 percent higher than the mean canopy cumulative total GSR in December 1981 (Table 13). The difference is not statistically significant (Table 14), which is surprising because the higher wind turbulence in the interspaces where no vegetation was growing could result in seed rain movements towards this microsite. Shrubs on the unburned plots should slow wind force greatly at the soil surface (Parmenter and MacMahon 1983).

Cheatgrass seed composed the highest proportion of the cumulative total GSR in both canopy (44.8 percent or 35.8 seeds per square meter) and interspace (47 percent or 42.4 seeds per square meter) microsites. Canopy vs. interspace differences for cheatgrass, bunchgrasses and forb GSR were not significant (Table 14). Seeds of shrubby species were completely absent (Table 13).

Total and all taxon GSR were not significantly different between unburned microsites in the first three comparable sampling periods. This may be related to the earlier mentioned reasons which can lead to high internal variability.

Table 13. Summary of mean germinable seed rain densities per meter^2 (number of seed accumulated in the traps over 3-month intervals for 15 months) in undercanopy and interspace microsites where seed traps were placed on unburned (control) sites near Mills, Utah (Numbers in parentheses=one standard error of the mean).

Growth Forms and Species	Canopy Dec 1981	 Mar 1982	 Jun 1982	 Sept 1982	 Dec 1982
Grasses:					
Bromus tectorum	35.8 (88.9)	41.1 (115.4)	91.5 (200.3)	8442.8 (4153.1)	8442.8 (4153.1)
Agropyron spp.	5.3 (26.6)	5.3 (26.6)	25.2 (130.0)	514.7 (947.1)	514.7 (947.1)
Poa spp.	0.0	0.0	5.3 (26.5)	622.1 (1555.9)	623.1 (1556.7)
Oryzopsis hymenoides	5.3 (26.6)	5.3 (26.6)	10.6 (53.1)	35.8 (118.1)	35.8 (118.1)
Stipa comata	0.0	0.0	0.0	10.6 (51.7)	10.6 (51.7)
Sitanion hystrix	0.0	0.0	0.0	0.0	0.0
Forbs:					
Descurainia pinnata	25.2 (53.1)	25.2 (53.1)	30.5 (96.8)	41.1(132.6)	41.1 (132.6)
Eriogonum cernuum	0.0	0.0	0.0	NON	NON
Allium acuminatum	0.0	0.0	0.0	0.0	0.0
Sphaeralcea spp.	0.0	0.0	0.0	0.0	0.0
Phlox spp.	0.0	0.0	0.0	0.0	0.0
Senecio spp.	5.3 (26.6)	10.6 (53.1)	10.6 (53.1)	10.6 (53.1)	10.6 (53.1)
Shrubs:					
Artemisia spp.	0.0	0.0	0.0	0.0	0.0
Chrysothamnus spp.	0.0	0.0	0.0	10.6 (53.1)	10.6 (53.1)
Purshia tridentata	0.0	0.0	0.0	0.0	0.0
Juniperus osteosperma	0.0	0.0	0.0	0.0	0.0
Unknown	0.0	0.0	0.0	0.0	0.0
Total	79.9 (33.2)	87.5 (035.8)	168.4 (149.9)	9688.3 (4085.4)	9689.3 (4085.7)

Growth Forms and Species	Interspaces Dec 1981	 Mar 1982	 Jun 1982	 Sept 1982	 Dec 1982
Grasses:					
Bromus tectorum	42.4 (70.3)	46.4 (92.9)	132.6 (399.3)	3924.9 (3098.9)	3924.9 (3098.9)
Agropyron spp.	0.0	0.0	8.0 (45.1)	374.1 (386.0)	374.1 (3098.9)
Poa spp.	0.0	0.0	4.0 (22.5)	273.2 (344.9)	274.8 (349.7)
Oryzopsis hymenoides	4.0 (22.5)	4.0 (22.5)	4.0 (22.5)	38.5 (98.2)	38.5 (98.2)
Stipa comata	4.0 (22.5)	4.0 (22.5)	4.0 (22.5)	15.9 (61.0)	15.9 (61.0)
Sitanion hystrix	0.0	0.0	0.0	0.0	0.0
Forbs:					
Descurainia pinnata	23.9 (69.0)	23.9 (69.0)	62.3 (230.8)	86.2 (282.5)	86.2 (282.5)
Eriogonum cernuum	0.0	0.0	0.0	4.0 (22.5)	4.0 (22.5)
Allium acuminatum	0.0	0.0	0.0	4.0 (22.5)	4.0 (22.5)
Sphaeralcea spp	NON	NON	NON	NON	NON
Phlox spp.	8.0 (31.8)	8.0 (31.8)	8.0 (31.8)	19.9 (67.6)	19.9 (67.6)
Senecio spp.	0.0	0.0	0.0	4.0 (22.5)	4.0 (22.5)
Shrubs:					
Artemisia spp.	0.0	0.0	0.0	6.6 (31.8)	6.6 (31.8)
Chrysothamnus spp.	0.0	0.0	0.0	8.0 (31.8)	8.0 (31.8)
Purshia tridentata	0.0	0.0	4.0 (22.5)	4.0 (22.5)	4.0 (22.5)
Juniperus osteosperma	0.0	0.0	0.0	0.0	0.0
Unknown	8.0 (31.8)	8.0 (31.8)	8.0 (31.8)	8.0 (31.8)	8.0 (31.8)
Total	90.3 (114.1)	94.3 (119.4)	234.9 (344.9)	4771.3 (2818.7)	4772.9 (2818.7)

NON=Detected but not alive

Table 14. LSD of significant tranformed differences of seed rain means in comparison at different micosites of the unburned and burned plots.

Code	Difference	LSD
111-114	7.7458	0.7580
111-115	7.6347	0.7572
112-114	8.1690	0.7520
112-115	8.1659	0.7519
113-114	7.7590	0.7520
113-115	7.7558	0.7518
211-221	1.4773	0.6213
211-214	6.9495	0.6215
211-215	6.9384	0.6215
212-214	8.4268	0.6218
212-215	8.2617	0.4120
213-214	7.8865	0.6550
213-215	7.8853	0.6343
221-224	6.1696	0.8306
221-225	6.8679	1.6109
222-224	7.6839	0.8199
222-225	7.6011	0.8201
223-224	7.0363	0.8202
223-225	6.9534	0.8194

LEGEND FOR CODES

First digit =Treatment (1-2)
1=Unburned, 2=Burned
Second digit =Locations
Within unburned
1=Canopy and 2=Interspace
Within burned
1="Hot" point and 2="cold" point
Third digit =Sampling date
1=December 81, 2=March 82, 3=June 82,
4=September 82 and 5=December 82

In September 1982 total GSR increased sharply and was found to be significantly different from all previous earlier sampling periods for the same microsite on unburned plots (Table 14).

The changes in total and taxon GSR in December 1982 were too small to cause any significant difference between this sampling period and the previous one within the same unburned microsite.

In the burned plots, seed rain was distributed quite evenly between the "hot" and "cold" microsites (Table 15). The early absence of the vegetation at the burned plots and later more uniform grass swards may have allowed the wind dispersal of seeds to be more uniform. Total GSR at the "hot" microsite was significantly higher (425.7 seeds per square meter) than "cold" microsites (387.2 seeds per square meter) in December 1981 (Table 14). All taxon GSR densities were not significantly different at the "hot" microsite compared to their GSR at interspaces.

Peak total GSR was achieved at both microsites within burned plots in September 1982. These GSRs values were significantly higher (Table 14) from all other sampling periods, but there were no significant differences between microsites of burned and unburned plots. This peak was maintained through December 1982 and no significant

Table 15. Summary of mean germinable seed rain densities per meter^2 (number of seeds accumulated in the traps over 3-month intervals for 15 months) in "hot" and "cold" microsites where seed traps were located on burned sites near Mills, Utah (Numbers in parentheses=one standard error of the mean).

Growth Form and Species	"Hot" spot				
	Dec 1981	Mar 1982	Jun 1982	Sept 1982	Dec 1982
Grasses:					
Bromus tectorum	355.5 (232.1)	370.1 (285.2)	421.8 (394.0)	10971.0 (6694.5)	10971.0 (6694.5)
Agropyron spp.	14.6 (41.1)	18.6 (62.3)	53.1 (188.4)	209.6 (412.5)	209.6 (412.5)
Poa spp.	21.2 (49.1)	21.2 (49.1)	49.1 (136.6)	49.1 (136.6)	49.1 (136.6)
Oryzopsis hymenoides	17.2 (45.1)	19.9 (66.3)	23.9 (87.5)	51.7 (149.9)	51.7 (149.9)
Stipa comata	0.0	0.0	0.0	9.3 (65.4)	9.3 (65.4)
Sitanion hystrix	6.6 (30.5)	6.6 (30.5)	6.6 (30.5)	6.6 (30.5)	6.6 (30.5)
Forbs:					
Descurainia pinnata	6.6 (30.5)	6.6 (30.5)	23.9 (84.9)	27.9 (106.1)	27.9 (106.1)
Eriogonum cernuum	0.0	0.0	0.0	0.0	NON
Allium acuminatum	0.0	0.0	6.6 (30.5)	6.6 (30.5)	6.6 (30.5)
Sphaeralcea spp	0.0	0.0	0.0	0.0	0.0
Sphlox spp.	4.0 (21.2)	4.0 (21.2)	4.0 (21.2)	4.0 (21.2)	4.0 (21.2)
Senecio spp.	0.0	0.0	0.0	4.0 (21.2)	4.0 (21.2)
Shrubs:					
Artemisia spp.	0.0	0.0	NON	NON	NON
Chrysothamnus spp.	0.0	0.0	0.0	0.0	0.0
Purshia tridentata	0.0	0.0	4.0 (21.2)	4.0 (21.2)	4.0 (21.2)
Juniperus osteosperma	0.0	0.0	0.0	0.0	0.0
Unknown	NON	NON	NON	NON	NON
Total	425.7 (281.2)	447.0 (323.7)	593.0 (427.5)	11343.8 (5872.1)	11343.8 (5872.1)

Growth Form and Species	"Cold" spot				
	Dec 1981	Mar 1982	Jun 1982	Sept 1982	Dec 1982
Grasses:					
Bromus tectorum	313.0 (226.8)	319.7 (254.7)	416.5 (379.4)	9104.7 (6637.5)	9104.7 (6637.5)
Agropyron spp.	6.6 (27.9)	6.6 (27.9)	13.3 (55.7)	205.6 (352.8)	205.6 (352.8)
Poa spp.	18.6 (46.4)	25.2 (74.3)	38.5 (131.3)	43.8 (151.2)	43.8 (159.2)
Oryzopsis hymenoides	11.9 (38.5)	11.9 (38.5)	11.9 (38.5)	35.8 (87.5)	35.8 (87.5)
Stipa comata	6.6 (27.9)	6.6 (27.9)	6.6 (27.9)	6.6 (27.9)	27.9 (27.9)
Sitanion hystrix	0.0	0.0	0.0	0.0	0.0
Forbs:					
Descurainia pinnata	11.9 (38.5)	11.9 (38.5)	11.9 (38.5)	11.9 (38.5)	11.9 (38.5)
Eriogonum cernuum	0.0	0.0	0.0	0.0	0.0
Allium acuminatum	0.0	NON	NON	NON	NON
Sphaeralcea spp.	0.0	0.0	0.0	0.0	0.0
Phlox spp.	18.6 (46.4)	18.6 (46.4)	30.5 (84.9)	30.5 (84.9)	30.5 (84.9)
Senecio spp.	0.0	0.0	0.0	0.0	0.0
Shrubs:					
Artemisia spp.	0.0	0.0	0.0	6.6 (27.9)	6.6 (27.9)
Chrysothamnus spp.	0.0	0.0	0.0	6.6 (27.9)	6.6 (27.9)
Purshia tridentata	0.0	0.0	0.0	0.0	0.0
Juniperus osteosperma	NON	NON	NON	NON	NON
Unknown	NON	NON	NON	NON	NON
Total	387.2 (245.4)	400.5 (282.5)	529.2 (339.6)	9452.1 (6186.5)	9473.4 (6198.6)

NON=Detected but not alive

increases were noticed over the last sampling interval. Variances are so high, however, that most of the differences between the two microsites in totals, life form and species values were not statistically significant at alpha ≤ 0.05.

SUMMARY AND CONCLUSIONS

The objectives of this research were to investigate the ecological importance of soil seed reserves and seed rain in regeneration of vegetation on a good condition sagebrush-grass range after a severe wildfire and draw conclusions leading to better management of such ecosystems. Investigations were conducted in two successive years on a community composed mainly of non-rhizomatous and non-sprouting species. In such cases soil seed reserves and seed rain have to be the main source of regeneration. In addition to soil seed reserves and seed rain monitoring, vegetation changes during the first two years following the fire and the grazing history of the study area before the fire were studied.

The major findings and conclusions are as follows:

(1) Fire can have a significant destructive impact on soil seed reserves.

(2) Bromus tectorum soil seed reserves were high, even on good condition sagebrush-grass rangeland.

(3) Although fire reduced the Bromus tectorum seed bank by half, it subsequently increased to almost twice the level observed on the unburned areas. This shows the enormous reproductive capacity of

this species.

(4) Despite the fact that the vegetation contained a high proportion of native perennial parent plants, they contributed relatively little germinable seed to the soil seed reserves and seed rain. Such species may have to regenerate vegetatively.

(5) Timing of the fire could be an important factor in controlling some undesirable range plants and their seeds. Although *Bromus tectorum* was certainly not reduced for long, had the fire occurred earlier when more seeds of the species were attached to the culm, greater reduction in cheatgrass seeds would have probably been obtained. Timing of the fire was just right to control sagebrush and most other brush, because it occurred before their seed set.

(6) *Ephedra nevadensis* was the only shrub to reestablish its cover relatively rapidly. This is apparently related to its strong ability to sprout from root crowns.

(7) Significantly greater total and taxon level germinable soil seed reserves were found under the shrub canopies than in the interspaces. This

pattern is apparently related to the semi-logarithmic dispersal of seed, where seed fall is greatest closest to mother plants (Harper 1977). Since flammable fuel follows the same pattern, fire has a serious impact on seed banks at "hot" points and slight impact on "cold" points which were former interspaces.

(8) Since mean soil seed reserve populations were significantly higher in the surface 0-2 cm soil depth, with fewer seeds in the sub-surface 2-5 cm depth, fire has a more serious impact on the surface depth than on the sub-surface.

(9) Variance in the germinable seed rain data were so high that none of the grand totals, life form totals and taxon differences were statistically significant at alpha = 0.05 between the burned and unburned plots at large. Significant differences, however, were found between "cold" and "hot" microsites. More sophisticated experiments would have to be designed to obtain definitive evaluation of hypotheses concerning seed rain variability between treatments.

It can be concluded that soil seed reserve data gave enough evidence to reject the first part of H_{o1} and H_{o2} and all of H_{o3}, but the variances of seed rain data were so high that the second parts of these hypotheses could not be rejected, except that fire had significantly greater effects on hot points points compared to "cold" points.

RECOMMENDATIONS

Some of the management recommendations possible from this and related research are:

(1) Fire is a good treatment to control sagebrush, but timing of the fire is a very important factor to consider. In order to maximize the destructive effect on this species, fire has to occur before seeds are produced or dispersed.

(2) Native perennial grasses are poorly represented in soil seed reserves. Their regeneration success is probably a function of vegetative reproduction. This is why grazing should not be allowed for at least one year after fire in order that the remnants of such species can recover.

(3) Fire is a good treatment for controlling non-sprouting species (most sagebrushes), but not sprouters (mormon tea).

(4) Wildfires are not always an unmitigated evil, but can be a good tool in management of rangelands. Wildfires at certain times on good condition ranges can result in release of perennial grass from sagebrush dominance.

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APPENDICES

Appendix A. Expected mean square (EMS) for seed rain analysis

Item	Symbol	i	j	k	l	m	EMS
Block	B_i	$D_B=1$	t	1	s	p	$\sigma_s^2 + tlsp\ \sigma_b^2$
Treatment	T_j	b	$D_T=0$	1	s	p	$\sigma_s^2 + blsp\ \sigma_T^2$
Location	L_k	b	t	$D_l=0$	s	p	$\sigma_s^2 + btsp\ \sigma_L^2$
T x L	TL_{jk}	b	$D_T=0$	$D_l=0$	s	p	$\sigma_s^2 + sp\ \sigma_{BTL}^2 + bsp\ \sigma_{TL}^2$
Error (a)	BTL_{ijk}	$D_B=1$	$D_T=0$	$D_l=0$	s	p	$\sigma_s^2 + sp\ \sigma_{rtl}^2$
Plots/L	$S_{l(ijk)}$	1	1	1	$D_s=1$	p	σ_s^2
Period	P_m	b	t	1	s	$D_p=0$	$\sigma_{ps}^2 + tls\ \sigma_{bp}^2 + btls\ \sigma_p^2$
Error (b)	BP_{im}	$D_B=1$	t	1	s	$D_p=0$	$\sigma_{ps}^2 + tls\ \sigma_{BP}^2$
PT	PT_{jm}	b	$D_T=0$	1	s	$D_p=0$	$\sigma_{ps}^2 + bls\ \sigma_{pt}^2$
PL	PL_{km}	b	t	$D_l=0$	s	$D_p=0$	$\sigma_{ps}^2 + bls\ \sigma_{pl}^2$
PTL	PTL_{jkm}	b	$D_T=0$	$D_l=0$	s	$D_p=0$	$\sigma_{ps}^2 + s\sigma_{PBTL}^2 + bs\ \sigma_{PTL}^2$
Error (c)	$PBTL_{ijkm}$	$D_B=1$	$D_T=0$	$D_l=0$	s	$D_p=0$	$\sigma_{ps}^2 + s\sigma_{PBTL}^2$
Within	$PS_{ml(ijk)}$	1	1	1	$D_s=1$	$D_p=0$	σ_{ps}^2

Appendix B. Expected mean square (EMS) for siol seed reserve analysis

Item	Symbol	df	i	j	k	l	m	n	EMS
Block	B_i	2	$D_B=1$	t	l	s	d	p	$dp\ \sigma_s^2 + tlsdj\ \sigma_B^2$
Treatment	T_j	1	b	$D_T=0$	l	s	d	p	$dp\ \sigma_s^2 + blsdp\ \sigma_T^2$
Locations	L_k	1	b	t	$D_L=0$	s	d	p	$dp\ \sigma_s^2 + btsdp\ \sigma_L^2$
T x L	TL_{jk}	1	b	$D_T=0$	$D_L=0$	s	d	p	$dp\ \sigma_s^2 + sdp\ \sigma_{BTL}^2 + bsdp\ \sigma_{TL}^2$
Error (a)	BTL_{ijk}	6	$D_B=1$	$D_T=0$	$D_L=0$	s	d	p	$dp\ \sigma_s^2 + sdp\ \sigma_{BTL}^2$
Plots/L	$S_{l(ijk)}$	108	1	1	1	$D_S=1$	d	p	$dp\ \sigma_s^2$
Depths	D_m	1	b	t	l	s	$D_D=0$	p	$P\ \sigma_{Ds}^2 + bllsp\ \sigma_D^2$
TD	TD_{jm}	1	b	$D_T=0$	l	s	$D_D=0$	p	$P\ \sigma_{Ds}^2 + blsp\ \sigma_{TD}^2$
LD	LD_{km}	1	b	t	$D_L=0$	s	$D_D=0$	p	$P\ \sigma_{Ds}^2 + btsp\ \sigma_{LD}^2$
TLD	TLD_{jkm}	1	b	$D_T=0$	$D_L=0$	s	$D_D=0$	p	$P\ \sigma_{DS}^2 + ps\ \sigma_{BTLD}^2 + bsp\ \sigma_{TLD}^2$
Error (b)	$BTLD_{ijkm}$	8	$D_B=1$	$D_T=0$	$D_L=0$	s	$D_D=0$	p	$P\ \sigma_{Ds}^2 + ps\ \sigma_{BTLD}^2$
D x Plots/L	$DS_{ml(ijk)}$	108	1	1	1	$D_S=1$	$D_{D=0}$	p	$P\ \sigma_{Ds}^2$
Period	P_n	4	b	t	l	s	d	$D_p=0$	$d\ \sigma_{ps}^2 + tlsd\ \sigma_{BD}^2 + btlsd\ \sigma_P^2$
Error (c)	BP_{in}	8	$D_B=1$	t	l	s	d	$D_p=0$	$d\ \sigma_{ps}^2 + tlsd\ \sigma_{BD}^2$
PT	PT_{jn}	4	b	$D_T=0$	l	s	d	$D_p=0$	$d\ \sigma_{ps}^2 + blsd\ \sigma_{PT}^2$
PL	PL_{kn}	4	b	t	$D_L=0$	s	d	$D_p=0$	$d\ \sigma_{ps}^2 + btsd\ \sigma_{PL}^2$

Appendix B. Expected mean square (EMS) for siol seed reserve analysis (continued)

Item	Symbol	df	i	j	k	l	m	n	EMS
PTL	PTL_{jkm}	4	b	$D_T=0$	$D_L=0$	s	d	$D_p=0$	$d\ \sigma^2_{ps} + bsd\ \sigma^2_{PTL}$
PD	PD_{mn}	4	b	t	1	s	$D_D=0$	$D_p=0$	$\sigma^2_{PDS} + btls\ \sigma^2_{PD}$
PTD	PTD_{jmn}	4	b	$D_T=0$	1	s	$D_D=0$	$D_p=0$	$\sigma^2_{PDS} + bls\ \sigma^2_{PTD}$
PLD	PLD_{kmn}	4	b	t	$D_L=0$	s	$D_D=0$	$D_p=0$	$\sigma^2_{PDS} + bts\ \sigma^2_{PLD}$
PTLD	$PTLD_{jkmn}$	4	b	$D_T=0$	$D_L=0$	s	$D_D=0$	$D_p=0$	$\sigma^2_{PDS} + s\ \sigma^2_{BPTLD} + bs\ \sigma^2_{PTLD}$
Error (d)	$BPTLD_{ijkmn}$	56	$D_B=1$	$D_T=0$	$D_L=0$	s	$D_D=0$	$D_p=0$	$\sigma^2_{PDS} + s\ \sigma^2_{BPTLD}$
P x P/L	$PS_{nl(ijk)}$	432	1	1	1	$D_S=1$	d	$D_p=0$	$d\ \sigma^2_{ps}$
P x D x P/L	$PDS_{mnl(ijk)}$	432	1	1	1	$D_S=1$	$D_D=0$	$D_p=0$	σ^2_{PDS}
	Total	1199							

Analysis of variance for total soil seed reserve density (number of germinable seed count per m^2) aggregated by treatments, microsites, depths and their different combinations.

Source	DF	MS	F	Significance at alpha 0.05
Block (B)	2	0.4657	0.0765	NS
Treatment (T)	1	36.4618	5.9894	S
Location (L)	1	34.7329	5.7054	S
TXL	1	71.7632	6.9267	NS
BXTXL (Error A)	2	10.3604		
Plot/L (S)	138	6.0877		
Depth (D)	1	286.8972	40.6994	S
TXD	1	10.2681	1.4566	NS
LXD	1	2.5893	0.3673	NS
TXLXD	1	7.8841	1.7595	NS
BXTXLXD (Error B)	2	4.4809		
DXS	140	7.0492		
Periods (P)	4	135.8966	36.1877	S
BXP (Error C)	8	3.7755		
TXP	4	76.0124	31.9612	S
LXP	4	141.6263	59.5501	S
TXLXP	4	49.0975	20.6441	S
DXP	4	156.0909	65.6320	S
TXDXP	4	12.1031	5.0893	S
LXDXP	4	80.6771	33.9226	S
TXLXDXP	4	15.4901	6.5132	S
BXTXLXDXP (Error D)	8	2.3783		
Exp.Error	860	1.9785		
Total	1199			

Appendix D. Analysis of variance

Analysis of variance table for Artemisia spp. mean soil seed reserve density (number of germinable seed count per m^2) data aggregated by treatment, microsite, depth and their different compinations.

Source	DF	MS	F	Significace at alpha 0.05
Block (B)	2	0.0631	0.1433	NS
Treatment (T)	1	0.8550	1.9450	NS
Location (L)	1	0.1067	0.0101	NS
TXL	1	0.3809	0.6726	NS
BXTXL (Error A)	2	0.5662		
Plot/L (S)	138	0.4400		
Depth (D)	1	0.3897	0.8736	NS
TXD	1	0.4030	0.9035	NS
LXD	1	0.0301	0.0674	NS
TXLXD	1	0.0618	3.1339	NS
BXTXLXD (Error B)	2	0.0197		
DXS	140	0.4461		
Period (P)	4	0.6916	4.0112	NS
BXP (Error C)	8	0.1724		
TXP	4	1.4476	14.5855	S
LXP	4	0.2539	2.5579	NS
TXLXP	4	0.1363	1.3733	NS
DXP	4	1.3628	13.7310	S
TXDXP	4	1.8669	18.8102	S
LXDXP	4	0.7282	7.3368	S
TXLXDXP	4	0.7585	7.6420	S
BXTXLXDXP (Error D)	8	0.0993		
Exp. Error	860	0.0566		
Total	1199			

Appendix E. Analysis of variance

Analysis of variance table for Bromus tectorum soil seed reserve density (number of germinable seed count per m^2) data aggregated by treatments, microsites, depths and their different compinations.

Source	DF	MS	F	Significanc at alpha 0.05
Block (B)	2	1.0210	0.1760	NS
Treatment (T)	1	9.1496	1.5779	NS
Location (L)	1	11.9573	2.0620	NS
TXL	1	18.6071	2.9866	NS
BXTXL (Error A)	2	6.2303		
Plot/L (S)	138	5.7988		
Depth (D)	1	240.3174	46.6593	S
TXD	1	20.2485	3.9314	S
LXD	1	8.2289	1.5977	NS
TXLXD	1	22.5854	3.4601	NS
BXTXLXD (Error B)	2	6.5274		
DXS	140	5.1505		
Periods (P)	4	60.6252	13.4925	S
BXP (Error C)	8	4.4933		
TXP	4	46.7667	13.2402	S
LXP	4	88.4608	25.0443	S
TXLXP	4	53.7394	15.2143	S
DXP	4	85.5902	24.2316	S
TXDXP	4	18.8911	5.3485	S
LXDXP	4	51.7065	14.6387	S
TXLXDXP	4	21.3474	6.0437	S
BXTXLXDXP (Error D)	8	3.5322		
Exp. Error	860	4.4933		
Total	1199			

Appendix F. Analysis of variance

Analysis of variance table for total seed rain density (Number of germinable seed count per m^2) data aggregated by treatments, microsites, depths and their different compinations.

Source	DF	MS	F	Significance at alpha 0.05
Block (B)	2	3.6664	2.0844	NS
Treatment (T)	1	4.4093	2.5067	NS
Location (L)	1	7.3828	4.1972	S
TXL	1	3.8523	2.0115	NS
BXTXL (Error A)	2	1.9149		
PLOT/L	113	1.7590		
Periods (P)	4	434.0567	389.2536	S
BXP (Error B)	8	1.1151		
TXP	4	10.2927	4.7029	NS
LXP	4	22.0523	10.0523	S
TXLXP	4	6.9834	3.1908	NS
BXTXLXP (Error C)	8	2.1886		
Exp. Error	447	1.6031		
Total	599			

Appendix G. Analysis of variance

Analysis of veriance table for Bromus tectorum seed rain density (number of germinable seed count per m^2) data aggregated by treatments, microsites, depths and their different compinations.

Source	DF	MS	F	Significance at alpha 0.05
Block (B)	2	3.3993	2.1351	NS
Treatment (T)	1	5.3938	3.3879	NS
Location (L)	1	5.7839	3.6329	NS
TXL	1	5.1346	1.8792	NS
BXTXL (Error A)	2	2.7323		
Plot/L	113	1.5921		
Peroids (P)	4	420.6454	155.9110	S
BXP (Error B)	8	2.6980		
TXP	4	17.9488	5.4933	S
LXP	4	21.9428	6.7160	S
TXLXP	4	7.5486	2.3103	NS
BXTXLXP (Error C)	8	3.2674		
Exp. Error	447			
Total	599			

Appendix H. Analysis of Variance

Artemisia spp. seed density (number of germinable seed count per m^2) data aggregated by treatments, microsites, depths and their different compinations.

Source	DF	MS	F	Significance at alpha 0.05
Block (B)	2	0.0010	000.1667	NS
Treatment (T)	1	0.0000001	000.000002	NS
Location (L)	1	0.0000001	000.01667	NS
TXL	1	0.0000001	000.0001	NS
BXTXL (Error A)	2	0.001		
Plot/L	113	0.006		
Periods (P)	4	0.0001	000.0060	NS
BXP (Error B)	8	0.0166		
TXP	4	0.0003	003.0000	NS
LXP	4	0.0189	189.0000	S
TXLXP	4	0.000002	000.0200	NS
BXTXLXP(Error C)	8	0.0001		
Exp. Error	447	0.0060		
Total	599			

Appendix I.1. Table of LSDs

LSDs of significant transformed observed means (square root of seeds m^{-2}) of Bromus tectorum soil seed reserves at different microsites on unburned and burned plots. Numbers between brackets identify the right LSD for the observed pair of means (see Table 6 for the observed means).

			UNBURNED (1)										BURNED (2)									
			CANOPY (1)					INTERSPACE (2)					"HOT" (1)					"COLD" (2)				
			SEPT 81 (1)	DEC 81 (2)	MAR 82 (3)	JUN 82 (4)	SEPT 82 (5)	SEPT 81 (1)	DEC 81 (2)	MAR 82 (3)	JUN 82 (4)	SEPT 82 (5)	SEPT 81 (1)	DEC 81 (2)	MAR 82 (3)	JUN 82 (4)	SEPT 82 (5)	SEPT 81 (1)	DEC 81 (2)	MAR 82 (3)	JUN 82 (4)	SEPT 82 (5)
(1)	(1)	(1)																				
		(2)																				
		(3)	0.81	0.81																		
		(4)	0.82	0.82	0.80																	
		(5)			0.73	0.75																
	(2)	(1)	0.76	0.76		0.75	0.69															
		(2)	0.76	0.76		0.76	0.70															
		(3)	0.78	0.78			0.73	0.72														
		(4)	0.76	0.76			0.70	0.71														
		(5)	0.84	0.84		0.84	0.76															
(2)	(1)	(1)	0.82	0.82			0.75	0.75														
		(2)	0.79	0.79			0.72	0.73														
		(3)	0.82	0.81	0.73		0.75	0.75	0.79													
		(4)	0.83	0.81	0.81		0.75	0.75	0.77	0.78	0.78		0.82	0.79								
		(5)			0.76	0.77		0.72	0.72	0.73	0.72	0.84	0.77	0.75	0.81	0.78						
	(2)	(1)	0.76	0.76		0.76	0.71			0.72		0.77			0.76	0.76	0.72					
		(2)	0.79	0.80		0.79	0.72									0.79	0.75					
		(3)	0.77	0.76			0.73	0.73								0.76	0.72	0.71				
		(4)	0.76	0.75	0.74		0.69	0.71	0.71								0.72	0.71	0.73			
		(5)	0.83				0.75	0.75								0.83	0.77					

Appendix I.2. Table of LSDs

LSDs of significant transformed observed means (square root of seeds m^{-2}) of Agropyron spp. soil seed reserves at different microsites on unburned and burned plots. Numbers between brackets identify the right LSD for the observed pair of means (see Table 6 for the observed means).

			UNBURNED (1)										BURNED (2)									
			CANOPY (1)					INTERSPACE (2)					"HOT" (1)					"COLD" (2)				
			SEPT 81 (1)	DEC 81 (2)	MAR 82 (3)	JUN 82 (4)	SEPT 82 (5)	SEPT 81 (1)	DEC 81 (2)	MAR 82 (3)	JUN 82 (4)	SEPT 82 (5)	SEPT 81 (1)	DEC 81 (2)	MAR 82 (3)	JUN 82 (4)	SEPT 82 (5)	SEPT 81 (1)	DEC 81 (2)	MAR 82 (3)	JUN 82 (4)	SEPT 82 (5)
(1)	(1)	(1)																				
		(2)																				
		(3)	0.33	0.33																		
		(4)	0.33	0.33																		
		(5)			0.29	0.30																
	(2)	(1)	0.31	0.31			0.28															
		(2)	0.32	0.31			0.29															
		(3)	0.31	0.33			0.29															
		(4)	0.31	0.32			0.29															
		(5)	0.33	0.33			0.31															
(2)	(1)	(1)	0.33	0.33			0.30															
		(2)	0.32	0.32			0.29															
		(3)	0.33	0.32			0.30															
		(4)	0.33	0.33			0.31															
		(5)				0.31				0.29	0.29	0.32	0.31	0.30	0.31	0.31						
	(2)	(1)			0.30	0.31			0.29	0.29	0.29	0.31	0.31	0.29	0.31	0.31						
		(2)	0.32	0.32			0.29						0.29									
		(3)	0.31	0.31			0.29					0.29	0.30									
		(4)	0.31	0.31			0.28					0.29	0.29									
		(5)	0.33	0.32			0.29						0.30									

Appendix I.3. Table of LSDs

LSDs of significant transformed observed means (square root of seeds m^{-2}) of Poa spp. soil seed reserves at different microsites on unburned and burned plots. Numbers between brackets identify the right LSD for the observed pair of means (see Table 6 for the observed means).

			UNBURNED (1)										BURNED (2)									
			CANOPY (1)					INTERSPACE (2)					"HOT" (1)					"COLD" (2)				
			SEPT 81 (1)	DEC 81 (2)	MAR 82 (3)	JUN 82 (4)	SEPT 82 (5)	SEPT 81 (1)	DEC 81 (2)	MAR 82 (3)	JUN 82 (4)	SEPT 82 (5)	SEPT 81 (1)	DEC 81 (2)	MAR 82 (3)	JUN 82 (4)	SEPT 82 (5)	SEPT 81 (1)	DEC 81 (2)	MAR 82 (3)	JUN 82 (4)	SEPT 82 (5)
(1)	(1)	(1)																				
		(2)																				
		(3)																				
		(4)	0.35	0.34	0.34																	
		(5)				0.31																
	(2)	(1)	0.32	0.32	0.32		0.30															
		(2)				0.32		0.31														
		(3)	0.33	0.33	0.34		0.31		0.31													
		(4)	0.33		0.32		0.31															
		(5)	0.35		0.35		0.32															
(2)	(1)	(1)	0.35		0.34		0.32															
		(2)	0.34	0.34	0.33		0.31															
		(3)	0.35		0.34		0.32															
		(4)	0.36	0.34	0.35		0.32															
		(5)	0.35	0.33	0.32		0.31		0.31													
	(2)	(1)	0.33		0.32		0.30															
		(2)	0.34	0.34	0.33		0.31		0.31													
		(3)	0.33		0.32		0.30		0.31													
		(4)	0.32	0.32	0.32		0.30		0.31													
		(5)	0.35	0.34	0.34		0.31		0.31													

Appendix I.4. Table of LSDs

LSDs of significant transformed observed means (square root of seeds m^{-2}) of Oryzopsis hymenoides soil seed reserves at different microsites on unburned and burned plots. Numbers between brackets identify the right LSD for the observed pair of means (see Table 6 for the observed means).

			UNBURNED (1)										BURNED (2)									
			CANOPY (1)					INTERSPACE (2)					"HOT" (1)					"COLD" (2)				
			SEPT 81 (1)	DEC 81 (2)	MAR 82 (3)	JUN 82 (4)	SEPT 82 (5)	SEPT 81 (1)	DEC 81 (2)	MAR 82 (3)	JUN 82 (4)	SEPT 82 (5)	SEPT 81 (1)	DEC 81 (2)	MAR 82 (3)	JUN 82 (4)	SEPT 82 (5)	SEPT 81 (1)	DEC 81 (2)	MAR 82 (3)	JUN 82 (4)	SEPT 82 (5)
(1)	(1)	(1)																				
		(2)																				
		(3)	0.36																			
		(4)	0.36		0.34																	
		(5)				0.31																
	(2)	(1)	0.33		0 31		0.29															
		(2)			0.31																	
		(3)	0.33		0.34		0.32															
		(4)	0.34				0.29															
		(5)	0.35		0.35		0.34															
(2)	(1)	(1)	0.35		0.34		0.31															
		(2)																				
		(3)			0.34																	
		(4)	0.35		0.35		0.33															
		(5)	0.33		0.34		0.32															
	(2)	(1)																				
		(2)	0.34		0.31		0.29															
		(3)	0.34		0.31		0.29															
		(4)	0.33		0.31		0.29															
		(5)	0.34		0.33		0.32															

Appendix I.5. Table of LSDs

LSDs of significant transformed observed means (square root of seeds m^{-2}) of Poa spp. soil seed reserves at different microsites on unburned and burned plots. Numbers between brackets identify the right LSD for the observed pair of means (see Table 6 for the observed means).

			UNBURNED (1)										BURNED (2)									
			CANOPY (1)					INTERSPACE (2)					"HOT" (1)					"COLD" (2)				
			SEPT 81 (1)	DEC 81 (2)	MAR 82 (3)	JUN 82 (4)	SEPT 82 (5)	SEPT 81 (1)	DEC 81 (2)	MAR 82 (3)	JUN 82 (4)	SEPT 82 (5)	SEPT 81 (1)	DEC 81 (2)	MAR 82 (3)	JUN 82 (4)	SEPT 82 (5)	SEPT 81 (1)	DEC 81 (2)	MAR 82 (3)	JUN 82 (4)	SEPT 82 (5)
(1)	(1)	(1)																				
		(2)																				
		(3)																				
		(4)																				
		(5)	0.12	0.11	0.11	0.11																
	(2)	(1)					0.11															
		(2)					0.11															
		(3)					0.11															
		(4)					0.11															
		(5)					0.12															
(2)	(1)	(1)					0.12															
		(2)					0.11															
		(3)					0.12															
		(4)					0.12															
		(5)					0.11															
	(2)	(1)					0.11															
		(2)					0.11															
		(3)					0.11															
		(4)					0.11															
		(5)					0.12															

Appendix I.6. Table of LSDs

LSDs of significant transformed observed means (square root of seeds m^{-2}) of <u>Sitanion hystrix</u> soil seed reserves at different microsites on unburned and burned plots. Numbers between brackets identify the right LSD for the observed pair of means (see Table 6 for the observed means).

			UNBURNED (1)										BURNED (2)									
			CANOPY (1)					INTERSPACE (2)					"HOT" (1)					"COLD" (2)				
			SEPT 81 (1)	DEC 81 (2)	MAR 82 (3)	JUN 82 (4)	SEPT 82 (5)	SEPT 81 (1)	DEC 81 (2)	MAR 82 (3)	JUN 82 (4)	SEPT 82 (5)	SEPT 81 (1)	DEC 81 (2)	MAR 82 (3)	JUN 82 (4)	SEPT 82 (5)	SEPT 81 (1)	DEC 81 (2)	MAR 82 (3)	JUN 82 (4)	SEPT 82 (5)
(1)	(1)	(1)																				
		(2)																				
		(3)																				
		(4)																				
		(5)	0.10	0.10	0.10	0.09																
	(2)	(1)					0.10															
		(2)					0.10															
		(3)					0.10															
		(4)					0.10															
		(5)					0.10															
(2)	(1)	(1)					0.09															
		(2)					0.09															
		(3)					0.10															
		(4)					0.10															
		(5)					0.09															
	(2)	(1)					0.09															
		(2)					0.09															
		(3)					0.09															
		(4)					0.09															
		(5)					0.10															

Appendix I.7. Table of LSDs

LSDs of significant transformed observed means (square root of seeds m^{-2}) of *Descurainia pinnata* soil seed reserves at different microsites on unburned and burned plots. Numbers between brackets identify the right LSD for the observed pair of means (see Table 6 for the observed means).

			UNBURNED (1)										BURNED (2)									
			CANOPY (1)					INTERSPACE (2)					"HOT" (1)					"COLD" (2)				
			SEPT 81 (1)	DEC 81 (2)	MAR 82 (3)	JUN 82 (4)	SEPT 82 (5)	SEPT 81 (1)	DEC 81 (2)	MAR 82 (3)	JUN 82 (4)	SEPT 82 (5)	SEPT 81 (1)	DEC 81 (2)	MAR 82 (3)	JUN 82 (4)	SEPT 82 (5)	SEPT 81 (1)	DEC 81 (2)	MAR 82 (3)	JUN 82 (4)	SEPT 82 (5)
(1)	(1)	(1)																				
		(2)																				
		(3)	0.47	0.47																		
		(4)	0.48	0.47																		
		(5)	0.44	0.43		0.43																
	(2)	(1)	0.44	0.44	0.43	0.44																
		(2)	0.45	0.44	0.43	0.44																
		(3)	0.45	0.45					0.42													
		(4)	0.45	0.44			0.41	0.41	0.42													
		(5)	0.49	0.48			0.44	0.45	0.45													
(2)	(1)	(1)	0.48	0.47						0.42												
		(2)	0.46	0.46																		
		(3)	0.48	0.47			0.43	0.44	0.44													
		(4)	0.48	0.48			0.44	0.44	0.45													
		(5)	0.45	0.45			0.42	0.42	0.42													
	(2)	(1)	0.45	0.44	0.44						0.42	0.45	0.44	0.43	0.44	0.45	0.42					
		(2)	0.46	0.46														0.42				
		(3)	0.45	0.45			0.41	0.41	0.42									0.42				
		(4)	0.44	0.44			0.41	0.41	0.41									0.41				
		(5)	0.48	0.48			0.41	0.41	0.45									0.45				

Appendix I.8. Table of LSDs

LSDs of significant transformed observed means (square root of seeds m^{-2}) of *Erigeron* spp. soil seed reserves at different microsites on unburned and burned plots. Numbers between brackets identify the right LSD for the observed pair of means (see Table 6 for the observed means).

			UNBURNED (1)										BURNED (2)									
			CANOPY (1)					INTERSPACE (2)					"HOT" (1)					"COLD" (2)				
			SEPT 81 (1)	DEC 81 (2)	MAR 82 (3)	JUN 82 (4)	SEPT 82 (5)	SEPT 81 (1)	DEC 81 (2)	MAR 82 (3)	JUN 82 (4)	SEPT 82 (5)	SEPT 81 (1)	DEC 81 (2)	MAR 82 (3)	JUN 82 (4)	SEPT 82 (5)	SEPT 81 (1)	DEC 81 (2)	MAR 82 (3)	JUN 82 (4)	SEPT 82 (5)
(1)	(1)	(1)																				
		(2)																				
		(3)																				
		(4)																				
		(5)	0.11	0.11		0.11																
	(2)	(1)					0.10															
		(2)					0.10															
		(3)					0.10															
		(4)					0.10															
		(5)					0.11															
(2)	(1)	(1)					0.11															
		(2)																				
		(3)					0.11															
		(4)					0.11															
		(5)					0.10															
	(2)	(1)					0.10															
		(2)					0.11															
		(3)					0.10															
		(4)					0.10															
		(5)					0.11															

Appendix I.9. Table of LSDs

LSDs of significant transformed observed means (square root of seeds m^{-2}) of *Eriogonum cernuum* soil seed reserves at different microsites on unburned and burned plots. Numbers between brackets identify the right LSD for the observed pair of means (see Table 6 for the observed means).

			UNBURNED (1)										BURNED (2)									
			CANOPY (1)					INTERSPACE (2)					"HOT" (1)					"COLD" (2)				
			SEPT 81 (1)	DEC 81 (2)	MAR 82 (3)	JUN 82 (4)	SEPT 82 (5)	SEPT 81 (1)	DEC 81 (2)	MAR 82 (3)	JUN 82 (4)	SEPT 82 (5)	SEPT 81 (1)	DEC 81 (2)	MAR 82 (3)	JUN 82 (4)	SEPT 82 (5)	SEPT 81 (1)	DEC 81 (2)	MAR 82 (3)	JUN 82 (4)	SEPT 82 (5)
(1)	(1)	(1)																				
		(2)	0.19																			
		(3)		0.19																		
		(4)		0.19																		
		(5)				0.18																
	(2)	(1)		0.18			0.17															
		(2)				0.18		0.17														
		(3)		0.18			0.17		0.17													
		(4)		0.18			0.17		0.17													
		(5)		0.20			0.18		0.18													
(2)	(1)	(1)		0.19																		
		(2)		0.19			0.17		0.17													
		(3)																				
		(4)		0.20			0.18		0.18													
		(5)		0.18					0.17													
	(2)	(1)		0.18			0.17		0.17													
		(2)		0.19																		
		(3)		0.18																		
		(4)		0.18			0.17		0.17													
		(5)		0.20			0.18		0.18													

Appendix I.10. Table of LSDs

LSDs of significant transformed observed means (square root of seeds m^{-2}) of Artemisia spp. soil seed reserves at different microsites on unburned and burned plots. Numbers between brackets identify the right LSD for the observed pair of means (see Table 6 for the observed means).

			UNBURNED (1)										BURNED (2)									
			CANOPY (1)					INTERSPACE (2)					"HOT" (1)					"COLD" (2)				
			SEPT 81 (1)	DEC 81 (2)	MAR 82 (3)	JUN 82 (4)	SEPT 82 (5)	SEPT 81 (1)	DEC 81 (2)	MAR 82 (3)	JUN 82 (4)	SEPT 82 (5)	SEPT 81 (1)	DEC 81 (2)	MAR 82 (3)	JUN 82 (4)	SEPT 82 (5)	SEFT 81 (1)	DEC 81 (2)	MAR 82 (3)	JUN 82 (4)	SEPT 82 (5)
(1)	(1)	(1)																				
		(2)																				
		(3)		0.28																		
		(4)	0.29	0.29																		
		(5)	0.27	0.27																		
	(2)	(1)																				
		(2)																				
		(3)		0.27																		
		(4)	0.27	0.27			0.25															
		(5)	0.30	0.29																		
(2)	(1)	(1)		0.29																		
		(2)	0.28	0.28			0.26															
		(3)	0.29	0.29			0.27															
		(4)	0.29	0.29			0.27															
		(5)	0.28	0.27			0.25															
	(2)	(1)		0.27																		
		(2)	0.28	0.28			0.26															
		(3)	0.27	0.27			0.25															
		(4)	0.27	0.27			0.25															
		(5)	0.29	0.28																		

VITA

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