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Effects of Afterripening on Cheatgrass (Bromus tectorum) and Squirreltail (Elymus elymoides) Germination

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Effects of Afterripening on Cheatgrass (*Bromus tectorum*) and Squirreltail (*Elymus elymoides*) Germination

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Abstract—Cheatgrass or downy brome (*Bromus tectorum*), an exotic facultatively fall-germinating annual, is displacing native plant communities throughout the Intermountain West. Squirreltail (*Elymus elymoides*), a native facultatively fall-germinating perennial, can reestablish naturally in rangelands infested by cheatgrass. This study was conducted to determine whether cheatgrass and squirreltail afterripen during dry storage in preparation for possible fall-germination and to compare between-population differences in response to afterripening. Seeds of four populations of each species were stored at 0, 10, 20, 30, and 40 °C over a period of four months and then incubated at four temperature regimes. Afterripening in dry storage resulted in complete loss of dormancy and faster germination. In general, afterripened squirreltail collections never germinated as rapidly as cheatgrass. Between-population differences in afterripening patterns were habitat-correlated and ecologically relevant. Artificial seed bank experiments showed that both species fall emerge, although cheatgrass consistently germinated earlier than squirreltail. Our results indicate that both species afterripen in dry storage; this can permit fall-germination when it is advantageous for survival. Early fall seeding of squirreltail into cheatgrass-infested rangelands could be effective in future restoration projects.

Cheatgrass or downy brome (*Bromus tectorum*; Poaceae) was introduced into the Intermountain West through contaminated grain from Eurasia in the late 1800's. Deteriorating range conditions in the early 1900's fostered the initial invasion and widespread establishment of this exotic weed (Mack 1981). Cheatgrass is an effective competitor for soil water resources, enabling it to infest the more arid regions of Washington, Idaho, Oregon, Nevada, Utah, and British Columbia. Currently it is displacing various native plant communities. Billings (1990) reports that millions of acres of sagebrush and pinyon-juniper are now dominated by cheatgrass. Other habitat types invaded by cheatgrass include salt desert shrub, mountain brush, and some mountain meadows. Studies also show that cheatgrass invasion has increased frequency and intensity of fires in the Intermountain West, disrupting the entire natural ecosystem (Whisenant 1990). Overall, invasion by cheatgrass and associated fires affect at least 40 million hectares, making this perhaps the most significant plant invasion in North America (D'Antonio and Vitousek 1992). Thus, restoration of lands dominated by cheatgrass has become an important issue in the Intermountain West.

Squirreltail (*Elymus elymoides*; Poaceae; previously *Sitanion hystrix*) is a perennial bunchgrass native to the Intermountain West. It is a natural invader of disturbed areas in deserts, valleys, foothills, and mountain meadows. Squirreltail can reestablish naturally in rangelands infested by cheatgrass and medusahead (Hironaka and Sindelar 1973). Therefore, squirreltail is a logical native species to examine for possible restoration of degraded rangelands. To understand the successful long-term persistence of cheatgrass and the ability of squirreltail to reestablish in cheatgrass-infested rangelands, the germination strategies of both species must be considered.

Cheatgrass is an exotic winter annual that facultatively fall-germinates; squirreltail is a perennial bunchgrass that is also known to facultatively fall-germinate (Hironaka and Sindelar 1973). Squirreltail, like cheatgrass, flowers in spring or early summer. Seeds of both species from lower elevation populations mature in early June, while seeds from high montane populations do not ripen until late July. Dispersal occurs a few weeks after seed maturation. While cheatgrass seeds are dispersed over long distances by becoming attached to animals or over short distances by wind, squirreltail seeds are dispersed primarily by wind. As an annual, cheatgrass relies entirely on seeds for population replacement and invasion of new habitats. As a nonclonal perennial, squirreltail relies on seeds for population expansion as well as for invasion of new habitats.

Cheatgrass and squirreltail, like many summer-ripening and facultatively fall-emerging species, have safeguards against early summer germination (seed dormancy and/or slow germination), losing these protective mechanisms through afterripening. A variety of definitions of afterripening are used in the literature (Vegis 1964; Taylorson and Brown 1977; Baskin and Baskin 1986). For the purpose of this paper, afterripening will be defined as a process that takes place in dry seeds and results in a reduction of dormancy and/or decrease in mean germination time (days to 50% germination). In other words, afterripening is the mechanism by which fall germination becomes possible.

There are conflicting reports concerning the afterripening of cheatgrass and squirreltail. Most studies involved

investigations of only one plant population per species. Young and Evans (1977) suggested that cheatgrass and squirreltail seeds do not have afterripening requirements dependent on temperature. Other researchers, however, have shown that afterripening is often a characteristic of fall-germinating grass species (Laude 1956; Taylorson and Brown 1977; Thill and others 1980; Baskin and Baskin 1986). Afterripening at high storage temperatures has occurred in cheatgrass, reducing the initial level of dormancy (Laude 1956; Thill and others 1980) and decreasing the mean germination time (Milby and Johnson 1987). A variety of grass seeds showed increased germination percentage when stored at 50 °C for 14 days (Taylorson and Brown 1977). Afterripening not only increased seed germination percentage, but also the temperature range over which seeds could germinate (Thill and others 1980; Baskin and Baskin 1989). Currently published research is not in agreement as to whether cheatgrass and squirreltail seeds afterripen.

The objectives of this study were to: (1) determine whether cheatgrass and squirreltail seeds afterripen during dry storage; (2) investigate the effects of storage and incubation temperatures on germination percentage and mean germination time (days to 50% germination); (3) relate changes in the mean germination time to species and habitat; and (4) evaluate fall germination of cheatgrass and squirreltail through artificial field seed bank experiments.

Materials and Methods

Afterripening Storage Treatments

Mature fully ripened seeds (caryopses with associated lemma and palea) were hand stripped from four populations each of cheatgrass and squirreltail in the summer of 1992. Collections were cleaned using a rubber seed cleaning board and a small fanning mill. Seeds were hand-selected to improve fill. Collection sites represented four distinct habitats: two low-elevation sites, one cold desert and the other salt desert; and two high-elevation sites, one mountain brush and the other mountain meadow (Table 1). Elevation was determined from topographic maps for each collection site.

Storage

Within 2 weeks of harvest, seeds (7-8% moisture content) were placed in controlled dry storage treatments. Squirreltail and cheatgrass seeds were stored at 0, 10, 20, 30, and 40 °C for 16 weeks, except for cheatgrass seeds from mountain brush and mountain meadow collections, which were stored at 0, 20, and 40 °C only.

Incubation

Germination experiments were conducted when storage treatments began (recently harvested seeds) and at 4-week intervals afterward. For each species collection and storage temperature treatment, four replications of 25 seeds were placed in 100- x 10-mm plastic petri dishes on two germination blotters (Anchor Paper, St. Paul, MN) saturated with tap water. Petri dishes were grouped and randomly stacked in plastic bags closed with rubber bands to retard water loss. Dishes were rewetted as needed. A blank dish was placed on each stack to ensure that all dishes received equal light. Dishes were incubated in controlled-environment chambers under cool-white fluorescent lights with a 12-hour photoperiod. Temperatures corresponded to possible field temperatures for germination: 5/15, 10/20, 15/25, and 20/30 °C (5 °C during darkness, 15 °C during light, for instance). Seeds were classified as germinated when the radicle had elongated to 1 mm. Dishes were inspected for germination on days 2, 4, 7, 11, 14, 21, and 28 after incubation began. Dormant seeds were defined as seeds that did not germinate within 28 days, but were viable. At the end of the 4-week incubation period, the viability of ungerminated seeds in each dish was determined using a cut test to examine the tissue of the seeds. Fully developed, firm tissue with the normal coloring was considered viable while shriveled, decayed, and discolored tissue, or seed lacking an embryo, were considered nonviable (Association of Official Seed Analysts 1988).

Germination percentage (viable seed basis) and mean germination time (calculated as days to 50% of total germination) were determined for each replication. Analysis of variance (ANOVA) was used to test for the effects of species, habitat type, storage temperature, storage duration, and incubation temperature. Linear regression was used to examine progressive changes in mean germination time as a function of storage duration for each collection by storage temperature by incubation temperature combination.

General weather information for each seed collection site was examined to evaluate conditions seeds naturally undergo during ripening and after dispersal. Mean monthly temperature and monthly precipitation were obtained for each collection by interpolating on isotherm maps, supplemented with information from nearby weather stations when available (Water Information Center 1974; Stevens and others 1983).

Table 1—Species and habitat information for seed collection sites.

Species	Location	Elevation (m)	Habitat type
Cheatgrass	Whiterocks, UT	1,450	Cold Desert
Cheatgrass	East of Green River, UT	1,280	Salt Desert
Cheatgrass	East of Salina, UT	2,040	Mountain Brush
Cheatgrass	North of Helper, UT	2,070	Mountain Meadow
Squirreltail	Whiterocks, UT	1,450	Cold Desert
Squirreltail	South of Price, UT	1,340	Salt Desert
Squirreltail	East of Salina, UT	2,040	Mountain Brush
Squirreltail	Strawberry, UT	2,400	Mountain Meadow

Location	Elevation (m)	Habitat type	Annual precipitation (cm)
Whiterocks	1,450	Cold Desert	18
Point of the Mountain	1,480	Mountain Brush	43
Strawberry	2,400	Mountain Meadow	65

Artificial Seed Bank Experiment

Artificial field seed bank experiments were carried out with two of the four cheatgrass collections and three of the four squirreltail collections. Before being placed in the field experiment, seeds were stored at 20 °C. Groups of about 100 seeds (determined by weight) were placed in flat nylon mesh packets. In mid-August, the packets were buried at a depth of 0.5 cm, with the exception of the squirreltail collection from Strawberry, which was buried in mid-September. Each group of packets was protected with a hardware cloth cone. Cones were arranged in three blocks at each of three field sites: a cold desert site (Whiterocks), a mountain brush site (Point of the Mountain), and a high-elevation mountain meadow site (Strawberry) (Table 2). At monthly intervals through mid-November, mid-March (mid-May at Strawberry), and mid-June, three sets of packets were retrieved from each site and transported to the laboratory in an insulated chest. Within 6 hours, germinated seeds in each packet were counted, and remaining seeds were placed in petri dishes, incubated at 10/20 °C for 4 weeks, and scored at least weekly for germination as described previously. Seeds that germinated during post-field incubation were classified as ungerminated but laboratory-germinable, while any viable seeds remaining at the end of 4 weeks were classified as dormant.

Results

Afterripening Storage Treatments

Storage temperature and duration had a dramatic effect on both germination percentage and mean germination time. Recently harvested seeds (before afterripening storage treatments) showed some dormancy and germinated slowly. Fully afterripened seeds came out of dormancy and germinated much faster than recently harvested seeds (Table 3).

Although recently harvested cheatgrass and squirreltail collections showed dormancy, squirreltail was less dormant than cheatgrass. Following the dry afterripening treatment, cheatgrass and squirreltail seeds for all collections reached 100% germination. Recently harvested cheatgrass and squirreltail collections showed a relatively long mean germination time, contrasting with a shorter mean germination time for fully afterripened seeds. Squirreltail collections never germinated as rapidly as cheatgrass.

Recently harvested desert collections had higher levels of dormancy than did mountain collections. Fully afterripened seeds from all habitats came out of dormancy. Seeds from all habitats germinated faster when fully afterripened, although seeds from the mountain meadow population had the slowest germination.

Table 3—Mean germination percentage and mean germination time (days to 50% total germination) for recently harvested and fully afterripened seeds. Main effects and interactions are averaged across different treatments (species, habitat, incubation temperature). All main effects and interactions were highly significant ($p < 0.0001$) for both response variables.

	Recently harvested seeds		Fully afterripened seeds	
Effects and interactions	Mean germination Percent	Mean germination Time (Days)	Mean germination Percent	Mean germination Time (Days)
Afterripening Main Effect (Averaged Across Species-Habitat-Incubation Temperature)	63	13.4	100	4.4
Averaged Across Habitat-Incubation Temperature				
Cheatgrass	50	15.7	100	3.0
Squirreltail	77	11.3	100	5.9
Averaged Across Species-Incubation Temperature				
Cold Desert Habitat	44	15.4	100	4.2
Salt Desert Habitat	52	13.9	100	4.1
Mountain Brush Habitat	77	11.3	99	4.0
Mountain Meadow Habitat	78	13.2	100	5.5
Averaged Across Species-Habitat				
5/15 °C Incubation Temperature	59	13.2	99	7.4
10/20 °C Incubation Temperature	83	10.9	100	4.1
15/25 °C Incubation Temperature	70	12.8	100	3.2
20/30 °C Incubation Temperature	40	17.2	100	3.1

Incubation Temperature Effects

The optimum incubation temperature for recently harvested seeds for both germination percentage and time was 10/20 °C (Table 3). The least favorable incubation temperature was 20/30 °C. However, when seeds were fully afterripened, the optimum incubation temperature for mean germination time occurred at 20/30 °C. All fully afterripened collections came out of dormancy across the tested range of incubation temperatures.

Recently harvested cold desert and salt desert cheatgrass populations were quite dormant and germination was reduced at some incubation temperatures (Figure 1). Furthermore, salt desert cheatgrass germination was extremely restricted at both 15/25 and 20/30 °C. In contrast, the recently harvested cold desert and salt desert squirreltail populations showed less restriction in germination, although dormancy was greatest at 20/30 °C for the cold desert squirreltail and at both 5/15 and 20/30 °C for the salt desert squirreltail. Recently harvested mountain cheatgrass and squirreltail populations showed less dormancy than the desert populations. Mountain squirreltail collections were less dormant than mountain cheatgrass collections at high incubation temperatures. Mountain cheatgrass dormancy was most pronounced at 20/30 °C; mountain squirreltail dormancy was most pronounced at 5/15 °C.

Mean germination time of fully afterripened seeds was shorter than that of recently harvested seeds for all incubation temperatures for both species (Figure 2). The optimal incubation temperature for fast germination was reversed as a result of afterripening for cheatgrass collections. While recently harvested cheatgrass seeds germinated fastest at 5/15 °C, fully afterripened seeds germinated fastest at 20/30 °C. Squirreltail populations did not reverse optimal incubation temperature following storage. Afterripened squirreltail populations germinated more quickly, but not to the degree that the cheatgrass populations did. Recently harvested squirreltail seeds did show a higher initial germination time across the incubation temperatures.
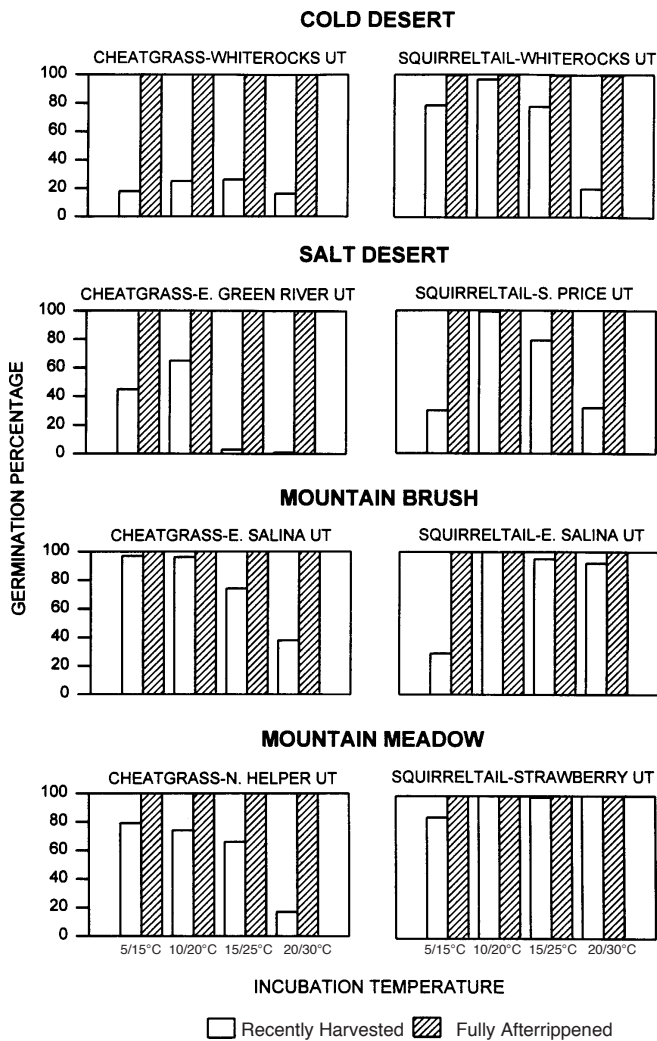

Figure 1—Germination percentages at four incubation temperatures for recently harvested and fully afterripened cheatgrass and squirreltail seeds from four habitats.
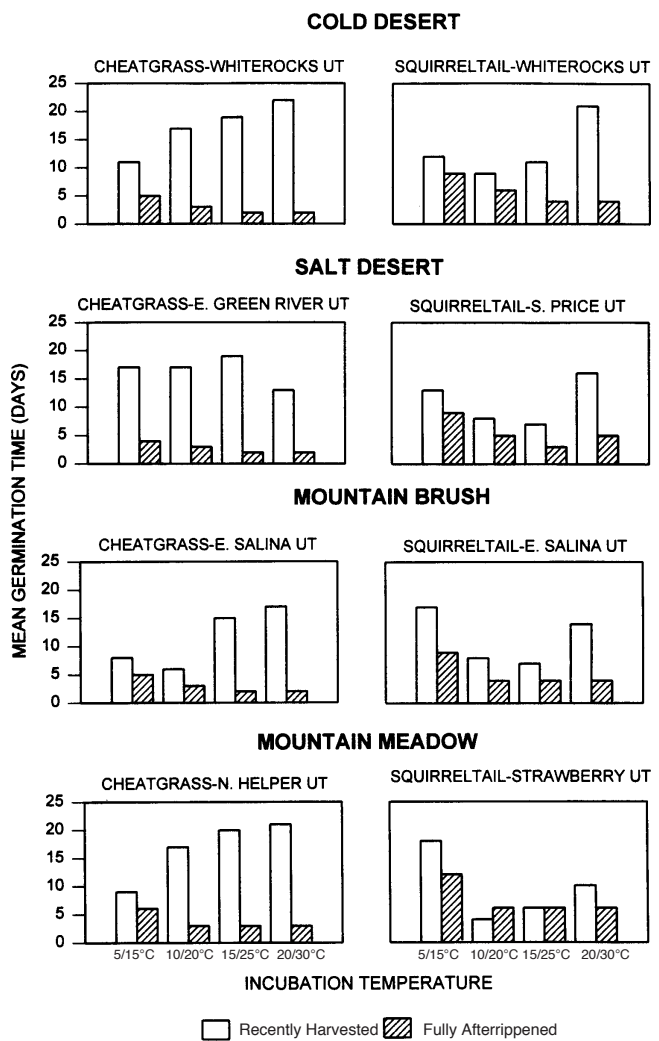

Figure 2—Mean germination time (days to 50% total germination) at four incubation temperatures for recently harvested and fully afterripened cheatgrass and squirreltail seeds from four habitats.
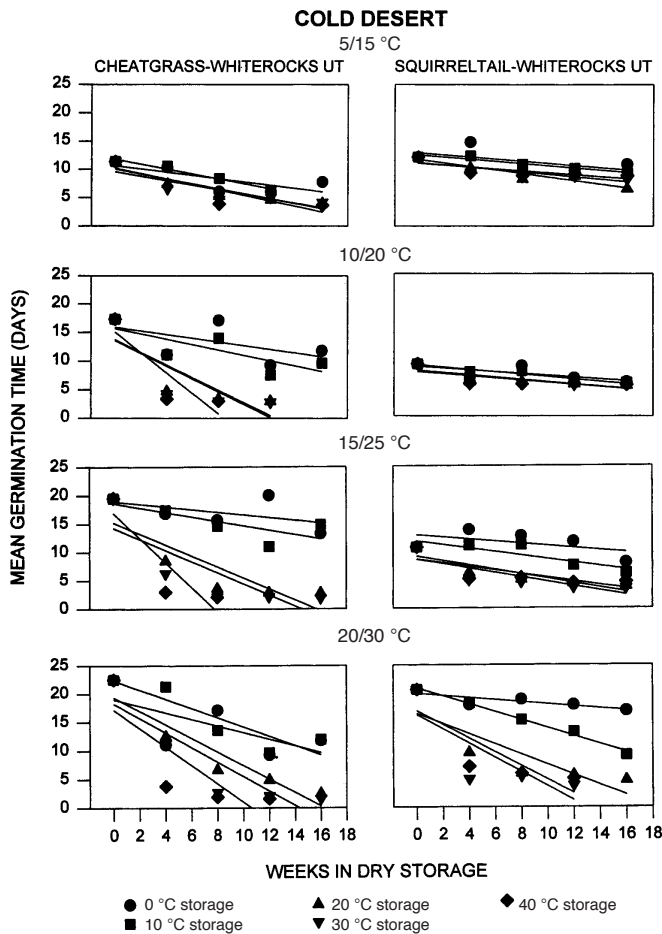
COLD DESERT

Figure 3—The effect of storage duration and temperature on mean germination time (days to 50% total germination) at four incubation temperatures for cold desert cheatgrass and squirreltail collections.

Storage Temperature Effects

Comparing changes in mean germination time across weeks in dry storage revealed clear patterns for both species. Cold desert (Figure 3) and mountain meadow populations (Figure 4) represented the two extreme habitat types. The mean germination time changed less at incubation temperatures of 5/15 and 10/20 °C than the mean germination times at 15/25 and 20/30 °C for both habitat types. In general, the negative relationship between mean germination time and weeks in dry storage for each collection was significant ($p < 0.05$) at 10, 20, 30, and 40 °C storage temperatures. Changes during storage at 0 °C usually were minimal; changes in mean germination time became greater at higher storage temperatures. The mountain cheatgrass and squirreltail populations are an exception to this pattern; 40 °C storage resulted in minimal or increased germination time. This effect was possibly due to loss of vigor resulting from extended storage at high temperature, unlikely conditions for mountain populations. Comparing habitat types, mountain populations showed less change in mean germination time following afterripening than desert populations.

Change was most pronounced in cheatgrass populations, although squirreltail cold desert populations also showed a slight change in mean germination time.

Artificial Seed Bank Experiment

Results from the artificial seed bank experiments showed that both species do facultatively fall germinate (Figure 5). At the cold desert Whiterocks site, both cheatgrass collections reached 100% germination by mid-November, but only the south of Price squirreltail collection germinated (60%) by this time. The other two squirreltail collections postponed germination until late winter. When packets were excavated from beneath the snow in mid-March, squirreltail germination percentages ranged from 80% for the Strawberry collection to 98% for the south of Price collection.

At the mountain brush Point of the Mountain site, both cheatgrass collections had reached between 70% (east of Green River) to 90% (Whiterocks) germination by mid-September. By mid-November, cheatgrass collections reached 100% germination. All three squirreltail collections reached 100% germination by mid-November, although there was no field germination before seed packets were retrieved in mid-November.
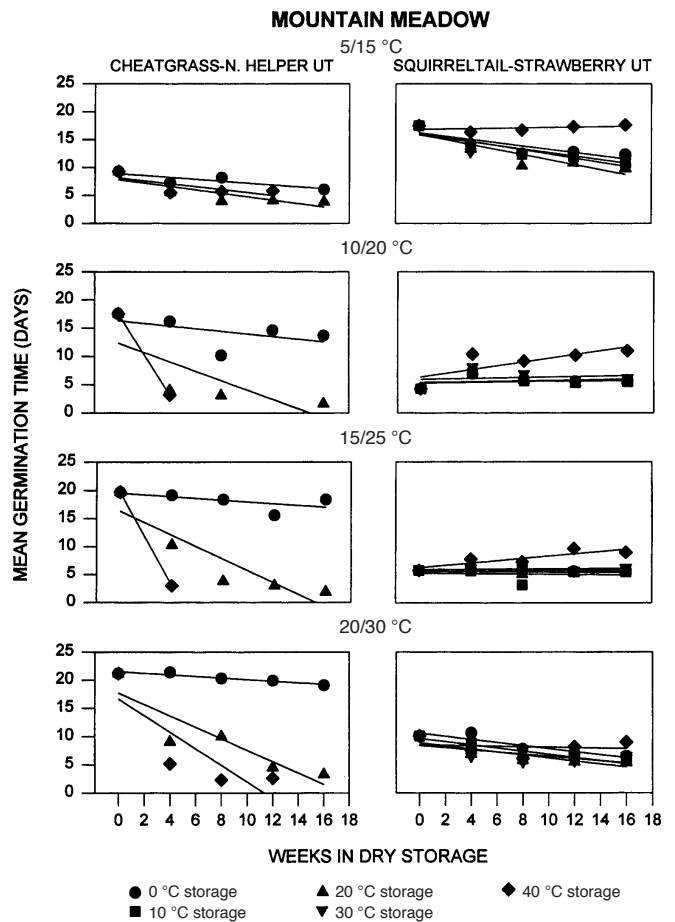
MOUNTAIN MEADOW

Figure 4—The effect of storage duration and temperature on mean germination time (days to 50% total germination) at four incubation temperatures for mountain meadow cheatgrass and squirreltail collections.
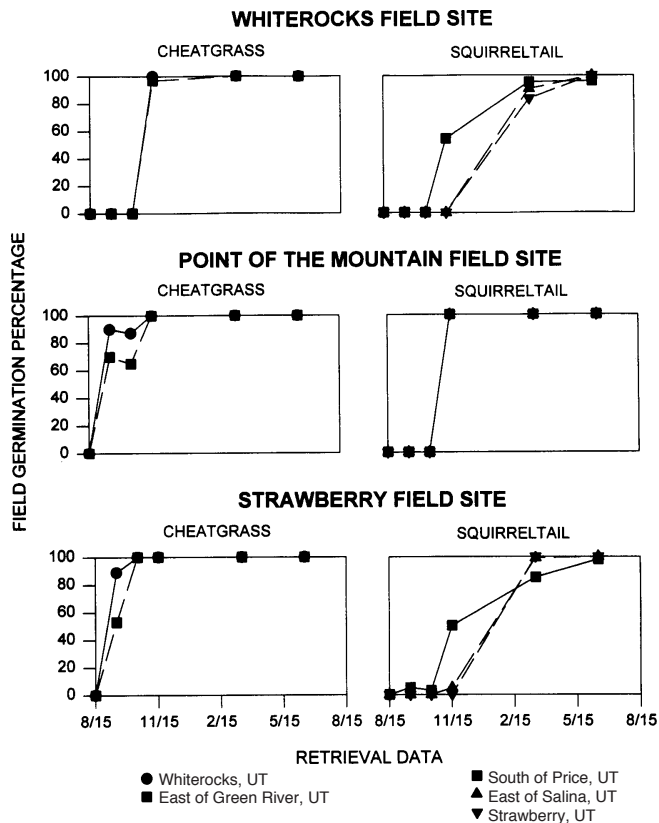
WHITEROCKS FIELD SITE

POINT OF THE MOUNTAIN FIELD SITE

STRAWBERRY FIELD SITE

Whiterocks, UT
East of Green River, UT
South of Price, UT
East of Salina, UT
Strawberry, UT

Figure 5—Field germination percentages for cheatgrass and squirreltail collections retrieved from artificial seed bank at Whiterocks, Point of the Mountain, and Strawberry field sites in late summer.

At the high-elevation Strawberry site the east of Green River collection had reached 50% germination and the Whiterocks collection reached 90% germination by mid-September. By mid-November both cheatgrass collections reached 100% germination. Only one squirreltail collection had germinated by mid-November (south of Price, 50%). All the other squirreltail collections postponed germination until late winter. When packets were excavated from beneath the snow in mid-May, squirreltail germination percentages ranged from 80% for the south of Price collection to 100% for both the east Salina and Strawberry collections.

Discussion

Completion of afterripening can be marked by reduction in dormancy and faster germination (Thill and others 1980; Milby and Johnson 1987). Populations of cheatgrass and squirreltail are at least conditionally dormant when recently harvested and respond to the afterripening treatments by reaching 100% germination, indicating that both species afterripen in dry storage. However, a reduction in dormancy is not the only factor influencing the probability of fall germination; a change in mean germination time is also necessary. Our results show that mean germination

time decreased for both cheatgrass and squirreltail from 13.4 to 4.4 days following afterripening. The afterripening mechanism protects seeds from early summer germination but allows for fall germination (Milby and Johnson 1987). The results of afterripening are clearly indicated by a reduction in dormancy and a decrease in mean germination time; however, mechanisms controlling afterripening are still not fully understood.

Germination of recently harvested squirreltail seeds occurs primarily at moderate incubation temperatures (10/20 and 15/25 °C), while higher incubation temperatures (20/30 °C) inhibit germination. An examination of desert weather patterns (Figure 6) shows that in June and July, when field dispersal occurs, it is unlikely that seeds will experience temperatures of 10/20 and 15/25 °C in combination with adequate moisture. In contrast, mountain sites may experience these temperatures in July. However, seeds collected in the mountains ripen much later than those of desert populations. The critical point is that the recently harvested seeds were dormant at 20/30 °C incubation temperature, which represents conditions seeds will likely experience during June and July. Furthermore, recently harvested squirreltail seeds show a long mean germination time (11.3 days). Therefore, it is unlikely that squirreltail seeds would germinate in early to midsummer.

The annual species, cheatgrass, germinates faster than squirreltail, a perennial. From an ecological standpoint, this implies that cheatgrass benefits more from early fall germination than does squirreltail. This may be due to the total plant reproductive output, which is directly affected by fall germination and subsequent spring seed production for the annual species (Mack and Pyke 1983). The lifetime reproductive output of squirreltail, a perennial, is probably not as dependent on the time of emergence, because plants will have more than one season to produce seed.

Recently harvested seeds from desert populations of both cheatgrass and squirreltail show more dormancy than mountain populations. This difference can partly be explained by the weather data, which show that the earlier ripening desert populations experience a longer period of warm and relatively dry weather before conditions are suitable for fall germination (Figure 6). Mountain populations, which ripen later, have a relatively shorter period to wait for fall germination.

Precipitation, a limiting resource in the desert, is received principally in the winter. It provides seedlings with adequate moisture for growth, increasing their probability of survival. Seedlings in a desert environment face a lower risk of winter mortality if they emerge in the fall. The fact that desert populations show a greater change in the mean germination time in comparison to the mountain populations suggests that fall germination is more important to desert populations.

Low incubation temperatures were optimal for germination of recently harvested cheatgrass and squirreltail seeds; high incubation temperatures were optimal for fully afterripened seed. This study supports others (Thill and others 1980; Baskin and Baskin 1989) in demonstrating that afterripening broadens the range of incubation temperatures at which germination occurs. In addition, the change in the mean germination time across weeks of storage was greater at higher incubation temperatures (20/30 °C).
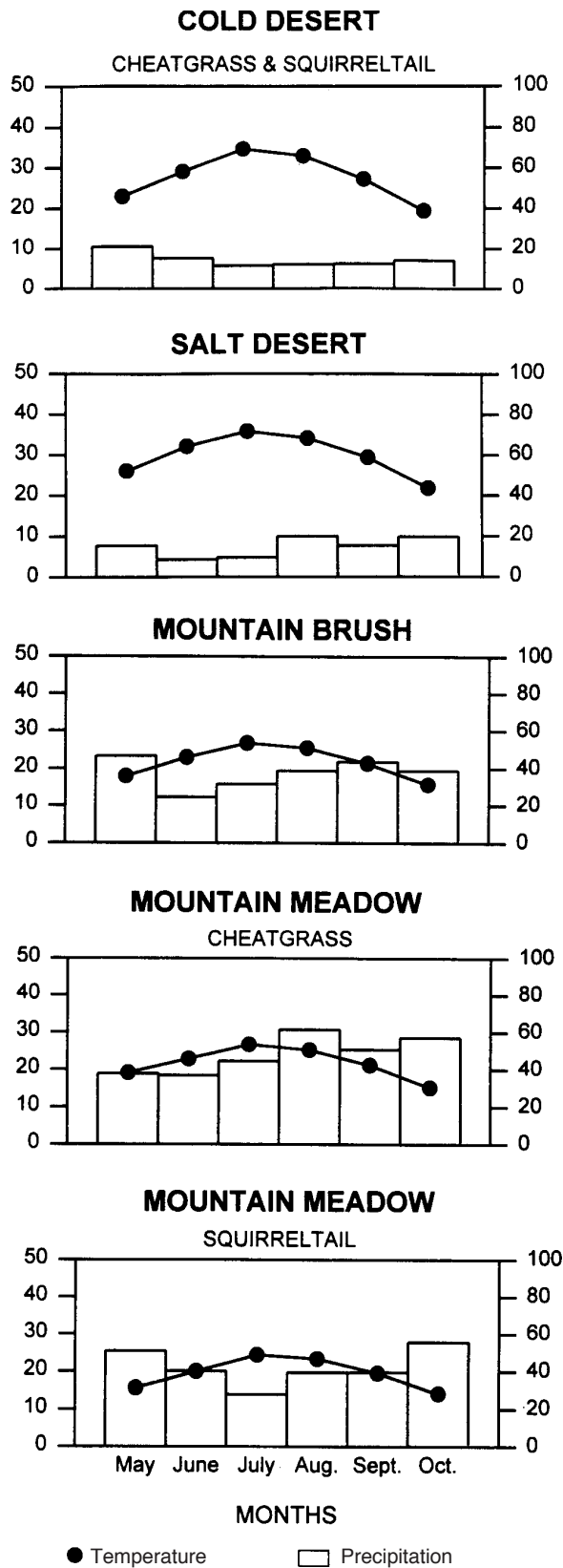
COLD DESERT
CHEATGRASS & SQUIRRELTAIL

SALT DESERT

MOUNTAIN BRUSH

MOUNTAIN MEADOW
CHEATGRASS

MOUNTAIN MEADOW
SQUIRRELTAIL

May June July Aug. Sept. Oct.

MONTHS

● Temperature   □ Precipitation

Figure 6—Climate diagrams for squirreltail seed collection sites: cold desert, salt desert, mountain brush, and mountain meadow.

The artificial seed bank experiment indicates that both species can fall emerge in years of above-average autumn precipitation (such as occurred in 1992). All cheatgrass populations germinated completely by mid-November at all three field sites. Squirreltail populations fall-germinated completely at the mountain brush site, and partially at the other two sites. Cheatgrass consistently germinated earlier than squirreltail.

Results from the artificial seed bank experiments support conclusions from the afterripening laboratory experiments, which showed that afterripened cheatgrass germinates more rapidly than afterripened squirreltail. The germination of squirreltail populations may be too slow to facilitate fall emergence in some habitats. For example, mountain population seeds that fall-emerge face a higher risk of winter mortality; therefore, germination may be postponed to avoid death. These adaptive mechanisms for cheatgrass and squirreltail permit fall emergence when it is advantageous for survival. However, our data suggest that early fall seeding of squirreltail into cheatgrass-infested rangelands could be effective in future restoration projects. Further studies are needed to examine seedling establishment and competition between the two species.

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