

Warm Pretreatment Effects on Antelope Bitterbrush (*Purshia tridentata*) Germination Response to Chilling

Abstract

Antelope bitterbrush occurs over a wide range of habitats in the West, yet laboratory germination requirements for fresh seed collections are remarkably similar. The seeds are dormant when dispersed in midsummer and require four to six weeks of moist chilling to become germinable. Laboratory experiments were conducted to test the hypothesis that warm dry summer conditions at low elevation sites would tend to make seeds less dormant at the beginning of winter chill, while warm moist conditions at higher elevation sites would tend to lengthen the winter chill required to break dormancy. Warm-dry seed pretreatments for short periods (4-8 weeks) at moderate temperature (15 and 30°C) significantly increased germination response to an otherwise inadequate (2-week) chill. Warm-moist seed pretreatments (2 weeks at 15 or 30°C) significantly decreased germination response to an otherwise adequate (4-week) chill. These results suggest that conditions experienced during summer and fall by rodent-cached antelope bitterbrush seeds in the field may change their chill requirements. The resulting increased dormancy at sites with longer winters and decreased dormancy at sites with shorter winters would increase the chances for correctly timed emergence and thus for seedling survival in different habitats. These findings have implications for artificial seeding of antelope bitterbrush, since conditions experienced in dry storage prior to fall seeding may be different from postdispersal conditions in the field.

Introduction

Antelope bitterbrush (*Purshia tridentata*) is an important shrub species in the restoration of depleted big game habitat through artificial seeding (Tiedemann and Johnson 1983). Its germination and establishment ecology have been the subject of numerous studies (Basile and Holmgren 1957, Sherman and Chilcote 1972, Young and Evans 1976, Evans and Young 1977). Seeds ripen from June to August, depending on habitat type, with populations at warmer, drier lowland sites maturing seed first. The seeds are completely dormant at the time of dispersal and require a period of moist chilling to become germinable (Young and Evans 1976). The dormancy is coat-imposed, since excised embryos germinate readily (Nord 1956). Dormancy serves to postpone emergence until late winter/spring, when reduced risk from frost coincides with favorable soil moisture for seedling establishment. The large seeds are a preferred food of rodents and are quickly gathered, stripped of their pericarps, and cached after dispersal from the plant (Sherman and Chilcote 1972, Everett *et al.* 1978, Evans *et al.* 1983). Most seedling emergence under natural conditions is from rodent caches (Sanderson 1962, West 1968).

Antelope bitterbrush occurs over a wide range of habitats (Hormay 1943, Nord 1965). It may dominate warm summer-dry shrublands along the

Columbia River, where annual precipitation is less than 250 mm. It occurs as the understory dominant in ponderosa pine and lodgepole pine forests with heavy winter snowpack. It also has a wide geographic range, occurring in predominantly winter precipitation areas in the Northwest and in California but also in summer precipitation areas of the Southwest.

Because of its great ecological amplitude, one might expect antelope bitterbrush seed germination requirements to vary from one population to another and to be correlated with salient climatic features of the habitat. Such climate-correlated variation in germination pattern and more specifically in the chill requirement for breaking dormancy has been found in other genera of woody Rosaceae (Westwood and Bjornstad 1968, Kester 1969, Barclay and Crawford 1984). The concept of ecotypic differentiation in germination strategy for species of wide ecological amplitude is generally well accepted (Thompson 1981).

In contrast with these examples, seed collections of antelope bitterbrush from contrasting habitats show remarkably little variation in germination characteristics, and the variation that does exist is not correlated in any intuitively obvious way with habitat characteristics (Meyer and Monsen 1989). Researchers working with antelope bitterbrush seedlots have generally found that

a four-week chill is adequate to break dormancy in most or all of the seeds in a lot, regardless of provenance (McConnell 1960, McHenry and Jensen 1967, Young and Evans 1976). This relative lack of variation between seed collections is puzzling, and prompted the experiments reported here.

Because antelope bitterbrush seeds are dispersed in midsummer, they spend a considerable time (2 to 5 months) in the dormant state prior to the beginning of field chilling, which requires a coincidence of soil temperatures between -2° and 5°C with high levels of soil moisture (Young and Evans 1981). The seeds are nongerminable prior to chill, but this does not mean that their level of dormancy (as measured by their response to chilling) remains constant. The hypothesis tested here is that seeds which experience warm, dry conditions during this summer-fall period will become less dormant, while those which experience warm, moist conditions will become more dormant. This would mean that seeds at warm, dry sites, which are less likely to provide long chill periods, would be less dormant at the beginning of chill than at the time of dispersal. Seeds at higher elevation sites would be more likely to spend part of the summer-fall period imbibed and thus would be more dormant at the beginning of the chill period than at the time of dispersal. These sites would in turn be able to provide longer chill periods. These predictions are based on earlier observations showing (1) that bitterbrush seeds dry-afterripen, i.e., become less dormant in dry storage, and (2) that bitterbrush seeds whose chill period is interrupted by a warm-moist treatment become more dormant, i.e., require a longer total chill period to break dormancy (Meyer and Monsen 1989).

In the present work, antelope bitterbrush seeds were subjected to various warm-moist and warm-dry pretreatments, and the effect of these pretreatments on response to chill was observed.

Methods

Seed collections were made in the summers of 1986 and 1987. The seeds were hand-threshed on a rubbing board to remove the papery pericarps, cleaned in a table model fanning mill, and stored in manila envelopes under laboratory conditions (20° to 22°C , 7 to 9% moisture content) until use. Seeds used in the experiments were hand-selected

to eliminate shrivelled, insect-damaged, or otherwise unsound seeds.

For each experimental treatment, four replications of 25 seeds each were used. Seeds were incubated in 100 mm plastic petri dishes between two standard germination blotter disks kept moist as necessary. Radicle protrusion to 5 mm was the criterion for germination. Completely randomized experimental designs were used.

1986 Seed Experiment

In the first experiment five 1986 collections were used which were approximately 12 months old at test initiation (Table 1). Experiments on these lots at 2 and 10 months of age have been reported elsewhere (Meyer and Monsen 1989). A factorial combination of warm-imbibed and warm-dry pretreatments and chill treatments was used. Warm pretreatments were carried out for two weeks in darkness at either 15° or 30°C . For the dry pretreatments, dry seeds were placed in unsealed petri dishes, while for the imbibed pretreatments the seeds were placed between moistened blotters as described above. At the end of the warm pretreatment period, dry seeds were also placed between moistened blotters, and the chill periods were initiated. Seeds were chilled in darkness at 1°C in order to simulate conditions under snowpack for two weeks and for four weeks. No germination occurred during chilling. At the end of the chill treatments, seeds were placed in darkness at 15°C for two weeks and germination percentages were recorded.

Seeds remaining at the end of the germination period were examined using tetrazolium staining techniques to determine viability. The imbibed seeds were slit open at the cotyledon end, and the embryos were excised by squeezing and immersed in a buffered 1 percent solution of tetrazolium chloride for 24 hours at room temperature. They were then evaluated according to established procedures (Grabe 1972).

1987 Seed Experiment

In the second experiment, six 1987 seed collections were used (Table 1). Tests were started approximately two months after harvest. Four replications of 25 seeds from each collection were tested for initial viability using tetrazolium staining techniques as described above. Air-dry seeds

TABLE 1. Collection information and initial viability percentage (ITV) estimated using tetrazolium staining techniques for antelope bitterbrush seed accessions used in the study.

Accession	Year	ITV	Lat	Long	Alt (m)	
Celilo	OR	1986	90	45°38'N	120°58'W	120
Middleton	ID	1986	87	43°49'N	116°40'W	770
Reynolds						
Creek	ID	1986	98	43°07'N	116°46'W	1510
St. Anthony	ID	1986	95	44°03'N	111°57'W	1780
Red Canyon	UT	1986	97	37°43'N	112°16'W	2430
Stansbury						
Mtn.	UT	1987	97	40°33'N	112°35'W	1840
Wells	NV	1987	96	41°07'N	114°48'W	1850
Ftn. Green	UT	1987	86	39°37'N	111°37'W	1850
Pinto	UT	1987	96	37°32'N	113°32'W	1860
Ruby Valley	NV	1987	98	40°40'N	115°27'W	1910
Lake Mtn.	UT	1987	95	40°15'N	111°57'W	2220

of each collection were placed in sealed vials and subjected to a series of six warm-dry pretreatments. Preliminary trials showed that seed moisture loss from the sealed vials was negligible. The dry pretreatments were two and four weeks at 50°C, two, four and eight weeks at 30°C, and eight weeks at 15°C. A control treatment in which seeds were placed directly into chill with no additional dry storage period was also included. At the end of each dry pretreatment, seeds were counted into petri dishes, placed between moistened blotters and subjected to one of four chill treatments. These treatments were no chill, two or four weeks of chill at 1°C, or a two-week period imbibed at 15°C followed by a four-week chill. No germination occurred during chilling. At the end of each chill period, seeds were incubated at 15°C for two weeks and germination percentages were recorded. Since the four-week 50°C pretreatment was the only treatment suspected of causing any loss of viability, four replications of 25 seeds of each collection from this treatment were evaluated using tetrazolium staining techniques as described earlier.

The data from each experiment were arcsine transformed for analysis of variance. The Student-Newman-Keuls means separation test was used to evaluate the significance of differences between means. In the first experiment, germination percentage in each experimental unit (petri dish) was expressed as a percentage of total viable seeds in that unit. In the second experiment, initial viability percentage for each collection as

determined by tetrazolium staining was included as an additional treatment value for comparison in the analysis.

Results

1986 Seed Experiment

Seeds exposed to two-week dry pretreatments at 15° and 30°C showed nearly identical responses to two or four weeks of chill (Figure 1). Averaged across collections, germination after the four-week chill was 94 percent, while germination after the two-week chill averaged 42 percent. In contrast, seeds exposed to two-week warm pretreatments while imbibed showed a marked decrease in response to both two and four weeks of chill when compared with dry pretreated seeds (Figure 1). Imbibed pretreatment at 15°C was almost as effective as the 30°C pretreatment in increasing dormancy.

Seeds from Red Canyon, Utah, were the least dormant, while seeds from Celilo, Oregon, and Middleton, Idaho, were the most dormant, a result similar to those reported for these lots in earlier experiments (Meyer and Monsen 1989). Reduction in germination response to a two-week chill as a consequence of imbibed warm-pretreatment compared to a dry warm-pretreatment was greater for high elevation northern collections, while reduction in response to a four-week chill was greater for low elevation collections (Table 2).

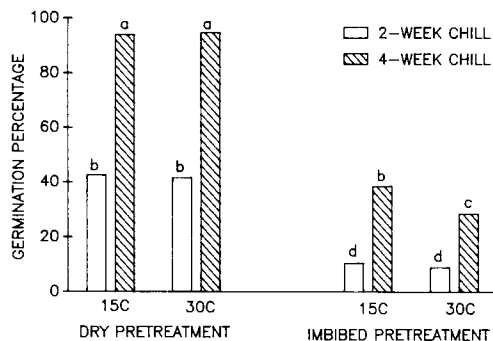


Figure 1. Treatment effects (averaged across seed accessions) in the factorial experiment combining 15° and 30°C dry and imbibed 2-week pretreatments with 2- and 4-week chill treatments. Seeds were incubated at 15°C for 2 weeks following chilling. Bars headed by the same letter represent means not significantly different at the $p < .05$ level.

TABLE 2. Effect of factorial combinations of warm pretreatments and chill treatments on relative germination percentage for 5 antelope bitterbrush seed accessions collected in 1986. Within an accession (row), means followed by the same letter are not significantly different at the $p < .05$ level.

Accession		2-week moist chill (percentage)				4-week moist chill (percentage)			
		Imbibed		Dry		Imbibed		Dry	
		15°C	30°C	15°C	30°C	15°C	30°C	15°C	30°C
Celilo	OR	6d	8cd	22bc	26b	20bcd	18bcd	80a	88a
Middleton	ID	8b	9b	14b	12b	16b	15b	94a	87a
Reynolds Creek	ID	9c	5c	49b	47b	43b	40b	100a	99a
St. Anthony	ID	4e	11de	48b	35bc	41bc	20cd	96a	100a
Red Canyon	UT	24d	13d	80b	88b	74b	49c	100a	100a

1987 Seed Experiment

In the second experiment, warm dry pretreatments were largely ineffective in eliminating the chill requirement of fresh seeds (Figure 2A). Some warm pretreatments significantly affected germination response to a two-week chill (Figure 2B). The two-week pretreatments at 30° and 50°C were not significantly different from the control percentage value. Four weeks at 30°C gave the highest germination percentage, a value nearly double the control value. However, extending the 30°C pretreatment to eight weeks did not result in further dormancy reduction. Storage at 15°C for eight weeks resulted in a significant germination increase relative to the control, while storage at 50°C for four weeks gave a significant decrease.

Differences among warm pretreatments became relatively insignificant when seeds were subjected to four weeks of chill, because a four-week chill was effective in breaking most of the dormancy even in the control (Figure 2C). A slight but significant increase over the control value was seen after four and eight weeks of storage at 30°C.

A notable exception to the above trend was the sharp decrease in response to a four-week chill after four weeks of storage at 50°C. This reduction was due mostly to some sort of secondary dormancy induction and not to reduced viability of the seeds (Table 3). Different collections showed different degrees of sensitivity to the four-week 50°C treatment. Reduction in response to a four-week chill ranged from 23 to 79 percent (Table 3).

A fourth chill treatment was included to find out if warm dry pretreatments would change the effect of a two-week imbibed pretreatment at 15°C on response to chill. This treatment (2

weeks imbibed at 15°C) greatly decreased the response of one-year-old seed collections to a four-week chill in the first experiment. Averaged across collections in the second experiment, the two-week 15°C imbibed pretreatment decreased the control response to a four-week chill from 93 to 55 percent (Figure 2C, 2D). Warm dry pretreatments generally ameliorated the dormancy-inducing effects of the 15°C imbibed pretreatment (Figure 2D). Longer and warmer dry pretreatments were more effective. This included the four-week 50°C pretreatment, which had a mean germination percentage of 74 after the warm imbibed/chill treatment sequence, a value not significantly different from the maximum. This is a puzzling result, since this pretreatment followed directly by a four-week chill resulted in only 48 percent germination. The warm imbibition period apparently overcame whatever dormancy-inducing effects had been imposed by the high temperature dry pretreatment, even though it tended to induce dormancy in seeds not exposed to the high temperature pretreatment.

Different collections responded quite differently to this series of treatments (Table 3). The Lake Mountain collection once again was most dormant, with the greatest depression in response to four-week chill as a result of the warm imbibition treatment and little ameliorating effect from the four-week 50°C dry pretreatment. The Pinto collection was again least dormant and was little affected by the warm imbibition treatment.

Discussion

A period of warm-imbibition prior to the beginning of chill increased dormancy for all seed accessions in both experiments. These results

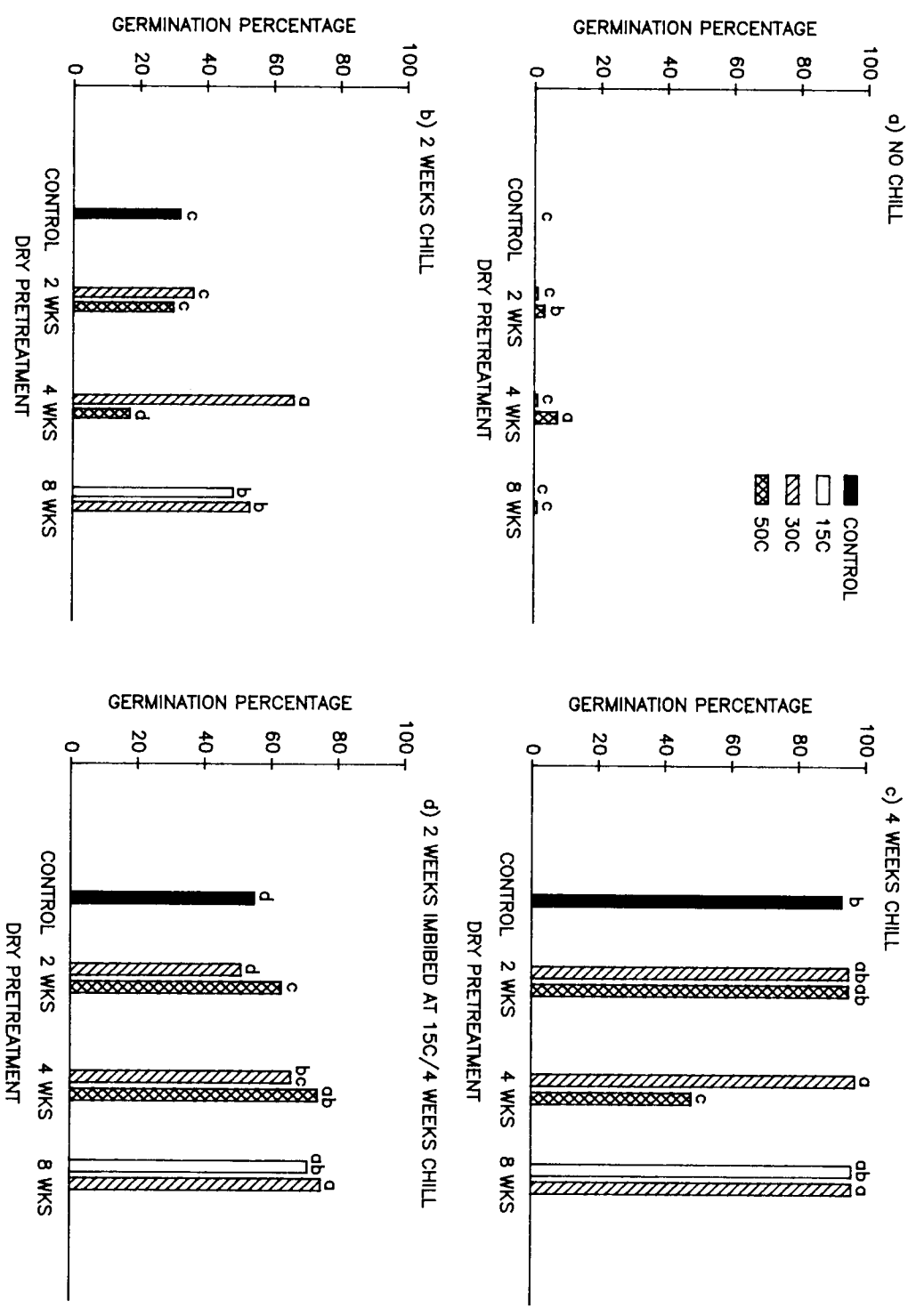


Figure 2. Dry pretreatment effects (averaged across seed accessions) for each of 4 chill treatments: (a) no chill, (b) 2-week chill, (c) 4-week chill, (d) 2 weeks at 15°C followed by a 4-week chill. Seeds were incubated at 15°C for 2 weeks following chill treatments. Within a chill treatment, bars headed by the same letter represent means not significantly different at the $p < .05$ level.

TABLE 3. Effect of a 4-week, 50°C dry pretreatment on response to chill treatments for six antelope bitterbrush seed accessions collected in 1987. Chill treatments are 0, 2, and 4 weeks at 1°C, and 2 weeks imbibed at 15°C (2-week prewarm) followed by 4 weeks at 1°C. Control values (Ctr) are for seeds not subjected to a dry pretreatment. Initial total viable seed percentage (ITV) is included for comparison. Within an accession (row), means followed by the same letter are not significantly different at the $p < .05$ level.

Accession	Chill period (Germination percentage)									
	ITV		0-week		2-week		4-week		4-week (2-week pw)	
	Ctr	4/50	Ctr	4/50	Ctr	4/50	Ctr	4/50	Ctr	4/50
Stansbury Mtn.	98a	96a	0e	4e	25d	21d	96a	44c	65bc	81b
Wells	99a	92ab	0e	14d	53c	20d	97a	56c	52c	84b
Ftn. Green	89a	83a	0d	3d	30c	17c	86a	59b	59b	58b
Pinto	97a	95a	0f	16e	40c	29d	99a	76b	86b	82b
Ruby Valley	99a	96a	0f	3f	24d	10e	90b	41d	39d	73c
Lake Mtn.	99a	91b	1f	1f	22de	2f	92b	13e	28d	63c

support the hypothesis that periods spent in the imbibed state prior to the beginning of chilling in the field would increase the chill period necessary for elimination of dormancy. Processes that operate to reduce dormancy during chilling are known to be reversible at warm temperatures for seeds of many cold temperate woody species including other Rosaceae (Stewart and Semeniuk 1965, Nikolaeva 1977). The ecological significance of this phenomenon has apparently not been previously addressed.

Warm-dry pretreatments significantly affected the response to chill for all six fresh seed accessions tested, but these effects were not unidirectional. In general, treatments of intermediate length and at intermediate temperatures tended to make the seeds less dormant. But when either temperature or time periods were increased, the effect was reversed. The physiological processes which underlie these changes in dormancy are unknown. In traditional seed physiology, rate of dry-afterripening (dormancy reduction in dry storage) is considered to be directly related to temperature of storage, and reports of increased dormancy in dry storage under any conditions are difficult to find (Bewley and Black 1982). Dry pretreatments in this experiment were carried out in sealed vials to maintain the seeds at a constant moisture content. Under field conditions, seeds would tend to lose moisture at high temperatures. This might obviate both the afterripening and the dormancy induction effects observed here, because physiological processes in "dry" seeds require a minimum moisture content to proceed (Bewley and Black 1982).

Seeds on the soil surface in bitterbrush habitats may experience temperatures in excess of 50°C, but the mean temperature would certainly be much lower (Ferguson 1972). In a rodent cache only a few centimeters beneath the surface, extremes would be greatly damped by the insulating effects of soil. Thus, the effect of 50°C constant temperature may not have much field relevance unless the seeds are unburied and the dormancy-inducing effects of high temperature are cumulative.

The case for 30°C as a mean summer temperature inside a rodent cache is easier to make, at least for low elevation sites where dry-afterripening is likely to be more important. The temperature for dry-afterripening may not have to be high for the seeds to undergo significant dormancy reduction. This is indicated by the significant effects of eight weeks of storage at 15°C, a temperature probably well below the summer mean in rodent caches.

The experimental results suggest a complex response to temperature by seeds in the dry state. In general the dormancy reduction at moderate temperature over several weeks supports the hypothesis that dry-afterripening in the field would decrease the level of dormancy at the beginning of chill.

Another result with possible ecological relevance is the fact that warm-dry pretreatments had a significant ameliorating effect on the induction of dormancy in the warm-imbibed state. Summer dry-afterripening may function to prevent dormancy induction in the imbibed state

during fall storms. This effect could be as important as direct reduction of dormancy. Even the highly dormancy-inducing four-week 50°C dry pretreatment interacted synergistically in some way with the warm-imbibed treatment to result in a net reduction in dormancy relative to the control.

Without knowing more about temperature and moisture conditions inside rodent caches in various types of antelope bitterbrush habitat, it is unwise to speculate further on the ecological significance of the present results. But the laboratory experiments indicate that field studies on seed dormancy in antelope bitterbrush could yield interesting results. The present findings may also have some practical implications for managers involved in artificial seeding with antelope bitterbrush. Bitterbrush seed is known to retain its viability through many years of storage (Stevens *et al.* 1981). But the effects of storage, and more particularly of storage temperature, on degree of seed dormancy have rarely been considered. Storage of freshly harvested seeds could have indirect effects as well. The normal practice in seeding bitterbrush is to seed as late in the fall as possible to avoid rodent

depredation, a major deterrent to seeding success (Stephen B. Monsen, pers. comm.). This places the seed in the ground roughly at the beginning of the field chilling period, so that processes that would occur in the field between dispersal and chill initiation are largely circumvented. Direct and indirect effects of seed storage and sowing time could condition a response to chill which is inappropriate at the seeding site and result in failure of the seeding. We do not yet know how to predict or manipulate these effects. But continued investigation of germination biology with a focus on field aspects will add to our knowledge of this useful and important wildland shrub.

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