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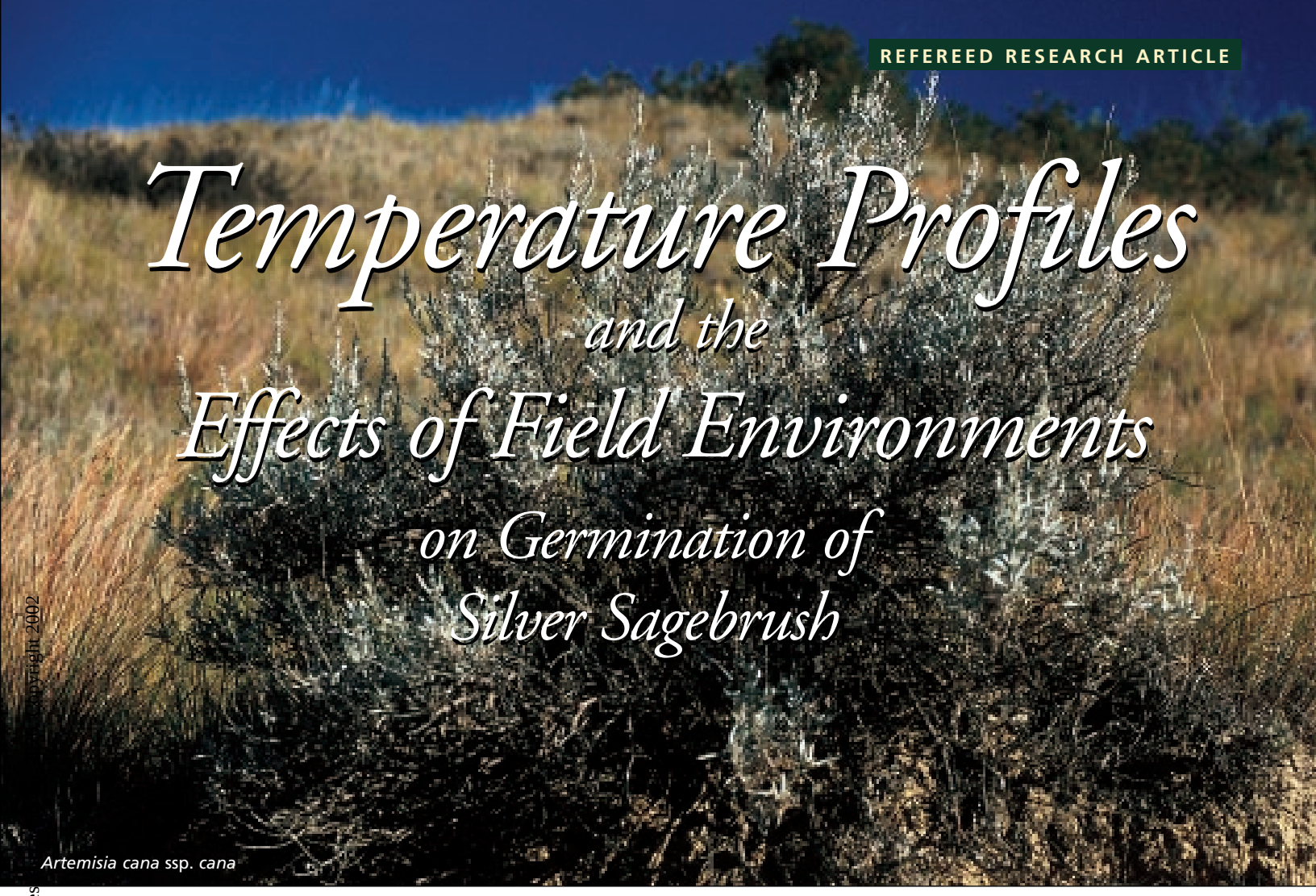
# Temperature Profiles and the Effects of Field Environments on Germination of Silver Sagebrush



*Artemisia cana* ssp. *cana*

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## ABSTRACT

In the laboratory, silver sagebrush (*Artemisia cana* Pursh ssp. *cana* [Asteraceae]) seeds germinated with increasing temperatures similar to those of spring and early summer or with cooling temperatures that occur in late summer or autumn. However, exposing seeds to similar temperatures under field environments reduced germination, with greater reductions occurring when seeds were put in the field in autumn (–36% to –81%) compared to spring (–18% to –24%). Germination of seeds placed in the field in autumn declined abruptly as daily temperatures rose in early spring, however, a gradual decline in germination was noted for seeds put in the field in spring. Nearly all non-germinating seeds were infected with fungi and were non-viable, indicating that recruitment of seedlings may be limited by loss of viability of seeds in the soil. Despite the fact that viability of seeds declined with exposure to field environments, 19% to 82% of the seeds remained viable, with greater viability in spring- than autumn-placed seeds. Seeding silver sagebrush in spring is recommended to maintain viability and high germination of seeds.


**KEY WORDS:** *Artemisia cana* ssp. *cana*, ecological restoration, seed deterioration, seed germination, seedbed ecology

**NOMENCLATURE:** Looman and Best (1979)

Shrubs are important in many aspects of the structure and functioning of ecosystems (Miller 1987; Allen 1988; Call and Roundy 1991; Pyke and Archer 1991). For these reasons, restoration specialists are interested in planting silver sagebrush (*Artemisia cana* Pursh. ssp. *cana* [Asteraceae]) on drastically disturbed sites in the Northern Mixed Prairie. Northern Mixed Prairie lays in the northern portion of the Great Plains from southeastern Wyoming and northwestern Nebraska through the Dakotas and Montana to southern Alberta, Saskatchewan, and southwestern Manitoba (Launenroth and Milchunas 1992). The Northern Great Plains encompasses the region between the foothills of the Rocky Mountains in

**TABLE 1**

*Storage locations (seed treatment), the time of the year when silver sagebrush seeds were placed in the field, and the number of seed groups in 3 y of study*

| | Storage location (seed treatment) | | |
|---|---|---|---|
| | Laboratory | Field | |
| | Time of placement | | |
| Years of study | Autumn | Autumn | Spring |
| | (Number of seed groups) | | |
| 1994—1995 | 60 | 60 | 60 |
| 1995—1996 | 60 | 60 | 60 |
| 1998—1999 | 80 | 80 | – |

the west, approximately the 100th meridian on the east, the North Platte River in Wyoming and Nebraska in the south, and southern Alberta, Saskatchewan, and Manitoba in the north (Barker and Whitman 1988). Northern Mixed Prairie is characterized by a number of mid- and short-grasses (Barker and Whitman 1988; Coupland 1992) of the genera *Agropyron*, *Stipa*, *Koeleria*, and *Bouteloua* (Coupland 1992).

With the exception of some outlying populations, distribution of silver sagebrush largely corresponds with the Northern Mixed Prairie and the Northern Great Plains (Harvey 1981). This long-lived, rhizomatous shrub occupies early to late successional communities on a variety of soils over about 14 million ha (35 million acres) (Beetle 1960). In Canada, silver sagebrush is most abundant in the *Bouteloua-Stipa* faciation, and is less common in *Stipa-Bouteloua*, *Stipa-Bouteloua-Agropyron*, *Bouteloua-Agropyron*, and *Stipa-Agropyron* faciations (Coupland 1950, 1961). Silver sagebrush can be scattered throughout the grassland matrix (Rowe and Coupland 1984) or it can be a dominant in sandhill prairies (Hulett and others 1966), coulees (Lawrence and Romo 1994), or on flats that are periodically flooded in valleys and along streams (Hanson and Whitman 1938).

Silver sagebrush establishes primarily by sprouting from rhizomes (Wambolt and others 1990) and establishment of plants from seeding is generally limited (Eddleman 1980; Walton 1984; Romo and Grilz 2001). Burial of seeds too deep in the soil (Walton 1984), predation on seeds (Romo and Grilz 2001), very specific safe site requirements for germination (Romo and Grilz 2001), soil water limitations (Walton 1984), competition from surrounding vegetation (Walton 1984; Romo and Grilz 2001), death of seedlings caused by freezing temperatures (Hou and Romo 1998b), poorly adapted ecotypes (Meyer and Monsen 1992), and adverse environmental conditions (Walton 1984) may limit establishment of silver sagebrush from seeds.

Schuman and others (1998) speculated that seeds of Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis* Beetle & Young) may enter dormancy and may remain viable in the soil. Fringed sagebrush (*Artemisia frigida* Willd), a suffrutescent commonly associated with silver sagebrush, develops a persistent seedbank (Bai and Romo 1997) and shows no seasonal pattern of seed dormancy (Bai and Romo 1994). Exposing seeds to –23 °C (–9 °F) for 30 d has no affect on germination of silver sagebrush (Walton 1984). Silver sagebrush seeds are not known to exhibit dormancy (Walton 1984) and other sagebrush species germinate over a wide range of temperatures (Harniss and McDonough 1976; Young and others 1991; Bai and others 1995).

Reductions in germination for seeds with high water content have been noted for many species (Hegarty 1978; Roos 1986). At 20 °C, reduced seed viability was observed at 60 d when water content was around 5% in Wyoming big sagebrush and 7% in mountain big sagebrush (*Artemisia tridentata* Nutt. ssp. *vaseyana* [Rydb.] Beetle) (Welch 1996). By comparison, germination of Wyoming sagebrush was unaffected by maintaining seeds for up to 15 d at water contents of 40% to 60% at temperatures of 2 to 15 °C (Bai and others 1997). Viability of mountain big sagebrush seeds declines faster when stored in widely fluctuating temperatures than at a constant, low temperature (Welch and others 1996). Seeds of fringed sagebrush remain viable for at least 3.5 to 5 y in the field (Bai and Romo 1994). The effects on germination of exposing silver sagebrush seeds to varying temperature and moisture conditions have not, however, been determined. It is possible that silver sagebrush seeds enter dormancy, lose viability, or are unaffected when exposed to environmental conditions in the field.

Our study objectives were to determine: 1) effects of exposing seeds to environmental conditions in the field on germination and viability of seeds of silver sagebrush, and 2) germination of seeds under constant and alternating temperatures in the laboratory. Basic requirements and characteristics of germination must be determined to increase establishment of silver sagebrush during restoration. Such information will aid restoration specialists in selecting times for seeding silver sagebrush to produce the most consistent success in establishing this shrub on drastically disturbed sites.

## MATERIALS AND METHODS

### Seed Source

Silver sagebrush seeds (achenes) were collected in mid-October 1994, 1995, and 1998 near Outlook, Saskatchewan (Lat 51° 29'N, Long 107° 03'W,

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elevation 518 m [567 ft]). The collection site, a naturally vegetated roadcut, was dominated by silver sagebrush, western wheatgrass (*Agropyron smithii* Rydb. [Poaceae]), and needle-and-thread (*Stipa comata* Trin. & Rupr. [Poaceae]). Inflorescences of silver sagebrush were cut from plants, placed in large paper bags, and air-dried in a laboratory at room temperature for about 5 d. Inflorescences were rubbed by hand to remove seeds, and seeds were cleaned with a Clipper desktop thresher (Seedburo Equipment Company, Chicago, Illinois). Cleaned seeds were stored in paper envelopes in darkness at 5 °C (41 °F) until use.

### Exposure of Seeds to Field Conditions

In 1994, 1995, and 1998, groups of 50 seeds were counted and put in paper envelopes wherein seeds could be exposed to ambient temperature and moisture conditions in the field. Seeds were stored in darkness at 5 °C (41 °F) until placed in the field. Seed-containing envelopes were put in the field at the University of Saskatchewan, Kernen Research Farm 1 km (0.6 miles) east of Saskatoon on 18 November 1994, 2 April 1995, 7 November 1995, 10 April 1996, and 17 November 1998 (Table 1). In 1994–1995, autumn–placed seeds were in the field for a total of 199 d while spring-placed seeds were exposed to the field environment for 64 d. Seeds were in the field for 211 and 57 d for autumn- and spring-placed seeds, respectively, in 1995–1996. Seeds were in the field for 216 d in 1998–1999. Envelopes were placed in two 50 by 80-cm (19.7 by 31.5-in) nylon, mesh bags and bags were secured to the ground with spikes. Envelopes were spread flat on the soil surface within the bags.

From 2 April to 5 June 1995, 10 April through 6 June 1996, and 23 January 1999 to 21 June 1999, 8 paper envelopes containing seeds placed in the field in autumn or spring were taken from the field at about 2- to 4-wk intervals. Eight replicates of seeds stored at 5 °C (41 °F) in the laboratory were processed at the same times. Water content of seeds, expressed on a fresh weight basis, was determined for 4 replicates per treatment by weighing seeds after blotting dry with tissue paper, drying at 80 °C (176 °F) for 48 h, and re-weighing. For laboratory-stored seeds the weight per 50 seeds on a fresh weight basis averaged 36 mg ($s_{\bar{x}} = \pm 1$) in 1994, 34 mg ($s_{\bar{x}} = \pm 1$) in 1995, and 31 mg ($s_{\bar{x}} = \pm 1$) in 1998. Another 4 replicates of each treatment were prepared for testing germination by placing seeds in Petri dishes containing 1 layer of #4 Whatman filter paper moistened with distilled water. Closed Petri dishes were enclosed in clear plastic bags and incubated for 20 d at 10 °C (50 °F) with 12 h darkness and 12 h light (220 µmol/(m² • s). Previous trials in our laboratory indicated complete germination of silver sagebrush seeds when incubated under these conditions. Germinated seeds were counted and removed at 4-d intervals; distilled water was added to the filter paper if needed. In 1998–1999, the number of seeds that did not germinate but were infected with fungi was recorded. A seed was considered infected if fungi could be observed on it with the naked eye. Since it was not known whether these seeds were dormant or non-viable, they were transferred to a new Petri dish and soaked in a 2% solution of tetrazolium chloride for 48 h (Grabe 1972). Seeds were dissected and deemed viable if the cotyledons and radicle were stained dark red-purple by the tetrazolium chloride.

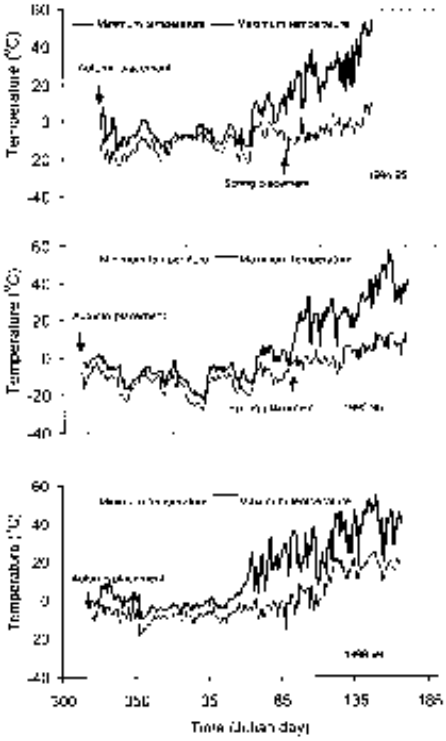


*Figure 1 • Daily maximum and minimum temperatures to which seeds of silver sagebrush were exposed when put in the field on 18 November 1994 or 2 April 1995, 7 November 1995 or 10 April 1996, and 17 November 1998.*

A Campbell Scientific 21X data logger (Campbell Scientific Canada Corporation, Edmonton, AB) with temperature sensors was placed in the field at the same time seeds were put out in autumn. Two temperature sensors were placed in paper envelopes and daily minimum and maximum temperatures were recorded through the duration of the experiments. Precipitation was recorded continuously at the Kernen Research Farm weather station about 100 m (109 ft) from where seeds were placed.

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**TABLE 2**

*Water content of seeds and total germination for silver sagebrush during the seed retrieval test in 1994–1995*

| Seed treatment (location and time of placement) | Date of retrieval in 1994—1995 | | | | | | |
|---|---|---|---|---|---|---|---|
| | 18 Nov | 2 Apr | 15 Apr | 27 Apr | 8 May | 23 May | 5 Jun |
| | Water content of seeds (% fresh weight) | | | | | | |
| Laboratory | 23 | 13 | 11 | 9 | 9 | 6 | 11 |
| Field—Autumn | 19 | 36 | 40 | 23 | 37 | 16 | 36 |
| Field—Spring | 12 | 9 | 40 | 19 | 28 | 11 | 23 |
| Standard error (date of germination X time of placement interaction) | | | | | | | 2.4 |
| | Total germination (%) | | | | | | |
| Laboratory | 95 | 89 | 94 | 87 | 91 | 94 | 96 |
| Field—Autumn | 92 | 83 | 75 | 68 | 63 | 55 | 59 |
| Field—Spring | 98 | 95 | 92 | 98 | 91 | 88 | 80 |
| Standard error (date of germination X time of placement interaction) | | | | | | | 3.9 |

In 1994–1995, seeds placed in the field in autumn were exposed to temperatures ranging from –23 to 54 °C (–9 to 129 °F) while seeds put out in spring experienced temperatures between –20 and 54 °C (–4 to 129 °F) (Figure 1). Diurnal variation in temperatures ranged from 1 to 51 °C (34 to 124 °F) for seeds put in the field in autumn, and from 6 to 51 °C (43 to 124 °F) for seeds put in the field in spring. Seeds were covered by snow (77 mm [3.0 in] of precipitation) after being put in the field in November 1994 through March 1995. In 1995, 34 mm (1.3 in) of precipitation were received in April, and 15 mm (0.6 in) were received in May.

During 1995–1996, seeds placed in the field were exposed to temperatures between –28 and 43 °C (–18 to 109 °F) in autumn and –9 to 43 °C (16 to 109 °F) in spring (Figure 1). Diurnal variation ranged from about 1 to 43 °C (34 to 109 °F) in autumn and 6 to 43 °C (43 to 109 °F) in spring. Seeds were covered by snow from November 1995 through late March 1996, which provided 76 mm (3.0 in) precipitation. Monthly precipitation totaled 30 mm (1.2 in) in April, 59 mm (2.3 in) in May, and 101 mm (4.0 in) in June.

Seeds placed in the field in 1998–1999 were exposed to temperatures ranging from –19 to 51 °C (–2 to 124 °F), with diurnal variation from 0 to 38 °C (32 to 100 °F) (Figure 1). Seeds were covered with snow from December through late March, which contained 58 mm (2.3 in) precipitation. Precipitation totaled 15 mm (0.6 in) in April, 144 mm (5.7 in) in May, and 59 mm (2.3 in) in June.

In the 1994–1995 and 1995–1996 experiments, the experimental design was a randomized-complete-block with placement of seeds (seed treatment) in the field in autumn and spring and laboratory storage, and dates of germination applied factorially (Snedecor and Cochran 1980). Main effects and their interactions on water content of seeds and total germination were tested with analysis of variance (Snedecor and Cochran 1980). Linear, quadratic, and cubic contrasts were performed on means of total germination (Petersen 1985). These contrasts compared mean germination over time for seeds stored in the laboratory with that of seeds put in the field in autumn and spring, and for seeds placed in the field in autumn versus placement in the spring. Data from each year were analyzed separately because of different and an unequal number of sample dates. In the 1998–1999 experiment, the seed treatments were factorially applied in combination with dates of germination in randomized-complete-block design. Main effects and their interacting effects on water content of seeds, total germination, percentage of seeds infected with fungi, and seeds staining with tetrazolium chloride were tested with analysis of variance. In all cases statistical significance was presumed at $P < 0.05$.

### Germination of Seeds Under Constant and Alternate Temperatures in the Laboratory

Seeds were sent to the USDA Agriculture Research Service Laboratory in Reno, Nevada, in 1994, 1995, and 1998, where germination was investigated in 55 constant and alternating temperatures (Evans and others 1982) about 3 mo after collection. A randomized-complete-block-design with 25 seeds in each of 4 replicates was used. Seeds were incubated in dark germinators in closed Petri dishes on 1-mm thick germination paper that was kept moist with water. Constant temperature regimes were 0, 2, 5, and 5 °C (32, 36, 41 and 9 °F) incre-

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ments through 40 °C (104 °F). Alternating temperature regimes consisted of a 16-h cold period and an 8-h warm period, at all possible higher temperatures each 24-h interval. For example, a 2 °C (36 °F) cold period was alternated with 5, 10, 15, 20, 25, 30, 35, or 40 °C (41, 50, 59, 68, 77, 86, 95, 104 °F) warm period, whereas a 30 °C (86 °F) cold period was alternated with a warm period of 35 or 40 °C (95 or 104 °F). Germination of seeds was recorded after 4 wk of incubation. Four wk of incubation of wildland species is standard protocol in this laboratory, thus it was used in these germination tests. Response surfaces were developed for germination of each collection using multiple regression analysis (Evans and others 1982).

## RESULTS

### Exposure of Seeds to Laboratory and Field Environments

#### *1994–1995 and 1995–1996*

In both years the interacting effects of seed treatment and the date of germination affected water content of seeds and total germination ($P = 0.000$ to 0.002). Water content of seeds varied widely among dates, and it averaged 30% for autumn-placed seeds, 20% for spring-placed seeds, and 12% for seeds stored in the laboratory in 1994–1995 (Table 2). In 1995–1996, water content of seeds in the field averaged 23% and 18% when put out in autumn and spring, respectively, while that of laboratory-stored seeds averaged 10% (Table 3).

More seeds germinated when stored in the laboratory than if exposed to field environments, and germination was greater for seeds placed in the field in spring compared to those put out in autumn (Tables 2 and 3). Contrasts of means indicated total germination changed through time in unique ways for laboratory-stored seeds versus seeds placed in the field (Table 4). The field environment affected total germination of autumn- and spring-placed seeds differently as indicated by changes in germination over time (Table 4). From the first to the last date, germination declined 36% for autumn-placed seeds in 1994–1995 and 41% in 1995–1996. Over the same period, an 18% reduction occurred for total germination in 1994–1995 and 24% in 1995–1996 for seeds put in the field in spring. In both years the decline in germination in April for seeds placed in the field in autumn corresponded with a rapid increase in temperatures and several freeze-thaw events (Figure 1), in comparison to a steady decline in germination for seeds put in the field in spring. In 1994–1995, germination of laboratory-stored seeds was up to 38% greater than seeds placed in the field, and germination of seeds placed in the field in spring was 7% to 61% greater than that of seeds put in the field in autumn. Germination of laboratory seeds was up to 95% greater than for seeds placed in the field in 1995–1996; seeds exposed to the spring environment germinated greater than ones also exposed to winter environments.

#### *1998–1999*

Water content of seeds, total germination, and seeds infected with fungi were affected ($P < 0.0001$) by the interacting influences of seed treatment and date of germination (Table 5). Water

**TABLE 3**

*Water content of seeds and total germination for silver sagebrush during the seed retrieval test in 1995–1996*

| Seed treatment (location and time of placement) | Date of retrieval in 1995–1996 | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | 7 Nov | 10 Apr | 22 Apr | 1 May | 13 May | 21 May | 29 May | 6 Jun |
| | Water content of seeds (% fresh weight) | | | | | | | |
| Laboratory | –[a] | 17 | 16 | 9 | 6 | 5 | 11 | 4 |
| Field—Autumn | – | 31 | 29 | 24 | 8 | 48 | 13 | 7 |
| Field—Spring | – | 18 | 33 | 25 | 9 | 19 | 13 | 8 |
| Standard error (date of germination X time of placement interaction) | | | | | | | | 4.5 |
| | Total germination (%) | | | | | | | |
| Laboratory | 79 | 82 | 71 | 81 | 83 | 74 | 82 | 84 |
| Field—Autumn | 78 | 65 | 52 | 56 | 58 | 49 | 52 | 46 |
| Field—Spring | 79 | 81 | 76 | 80 | 78 | 54 | 67 | 60 |
| Standard error (date of germination X time of placement interaction) | | | | | | | | 4.8 |

[a] Water content of seeds was not determined

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**TABLE 4**

*Levels of significance for linear, quadratic, and cubic contrasts of mean total germination over time for silver sagebrush seeds stored in the laboratory or placed in the field in autumn or spring on total germination*

| Year | Contrast | Linear | Quadratic | Cubic |
|---|---|---|---|---|
| 1994–1995 | Laboratory storage versus autumn and spring placement in the field | 0.002 | 0.008 | 0.046 |
| | Autumn versus spring placement in the field | 0.00 | 0.019 | 0.025 |
| 1995–1996 | Laboratory storage versus autumn and spring placement in the field | 0.006 | 0.003 | 0.049 |
| | Autumn versus spring placement in the field | 0.805 | 0.272 | 0.041 |

content of seeds in field conditions varied considerably among dates of retrieval and averaged 34% compared to 15% for laboratory-stored seeds. Total germination of seeds stored in the laboratory varied between 82% and 94% while that of seeds placed in the field declined 81%. Germination for seeds placed in the field dropped sharply and the percentage of seeds infected with fungi increased dramatically as temperatures rose in March and many freezing and thawing events occurred (Figure 1). Of the seeds not germinating, 6% to 18% of laboratory-stored seeds were infected with fungi, but fungal infection increased from 12% to 83% in seeds exposed to field environments. The percentage of seeds (0.4%, $s_{\bar{x}} = 0.12$) that stained with tetrazolium chloride was similar among dates ($P = 0.409$), seed treatments ($P = 0.682$) and the date X treatment interaction ($P = 0.369$).

### Influence of Temperature on Germination in the Laboratory

Silver sagebrush seeds germinated over a broad range of temperatures (Figure 2). Germination was least at the extremes of the temperatures, and greatest at intermediate temperatures. Averaged over all 55-temperature combinations, total germination was 57% ($s_{\bar{x}} = 2.4$) in 1994, 45% ($s_{\bar{x}} = 2.0$) in 1995, and 53% ($s_{\bar{x}} = 1.9$) in 1998.

## DISCUSSION

Under natural situations, seeds of silver sagebrush are exposed to field environments of autumn through winter before germinating in spring and early summer (Romo and Grilz 2001). Silver sagebrush flowers from late August through early September (Budd and Campbell 1959), and most seeds mature and are dispersed in October (Romo personal observations) to early November (Wambolt and others 1989). Some seeds are maintained on mother plants into the following spring (Walton 1984; Romo personal observations). Variation in the rate of seed dispersal among individual plants of silver sagebrush (Wamboldt and others 1989) likely creates a gradient in time in which seeds are exposed to environmental conditions in the seedbed. Seeds maintained in the canopy are not exposed as long to environmental conditions in the seedbed compared to seeds that are shed quickly from mother plants. A prolonged period of seed dispersal may enable some seeds of silver sagebrush to occupy safe sites in time similar to fringed sagebrush (Bai and Romo 1994, 1997) and Wyoming big sagebrush (Schuman and others 1998). Prolonged dispersal likely also enables some seeds to avoid stressful conditions of the seedbed.

Silver sagebrush seeds are not dormant (Walton 1984) and our findings indicate autumn-dispersed seeds could potentially germinate with cooling of

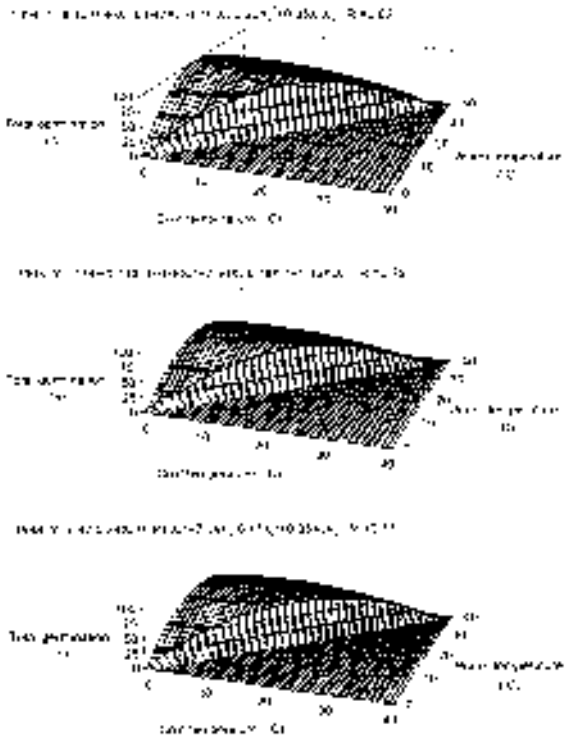

*Figure 2 • Response surfaces for total germination of silver sagebrush seeds collected in 1994, 1995, and 1998 and incubated at constant and alternating temperatures ranging from 0 to 40 ˚C (32 to 104 ˚F).*

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**TABLE 5**

*Water content of seeds, total germination, and non-germinating seeds infected with fungi when silver sagebrush seeds were exposed to laboratory or field conditions in 1998–1999*

| Seed treatment (location) | Date of retrieval in 1998—1999 | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | 17 Nov | 23 Jan | 20 Feb | 20 Mar | 31 Mar | 24 Apr | 14 May | 28 May | 21 Jun |
| | Water content of seeds (% fresh weight) | | | | | | | | |
| Laboratory | 20 | 18 | 18 | 15 | 16 | 13 | 12 | 14 | 13 |
| Field | 18 | 33 | 53 | 72 | 32 | 22 | 29 | 23 | 26 |
| Standard error (location X date of germination) | | | | | | | | | 2.7 |
| | Total germination (%) | | | | | | | | |
| Laboratory | 89 | 84 | 92 | 93 | 88 | 82 | 91 | 87 | 94 |
| Field | 89 | 79 | 78 | 32 | 35 | 44 | 40 | 18 | 17 |
| Standard error (location X date of germination) | | | | | | | | | 5.5 |
| | Non-germinating seeds infected with fungi (%) | | | | | | | | |
| Laboratory | 11 | 16 | 9 | 8 | 13 | 18 | 9 | 12 | 6 |
| Field | 12 | 20 | 22 | 68 | 65 | 56 | 60 | 82 | 83 |
| Standard error (location X date of germination) | | | | | | | | | 5.6 |

the environment. Late-autumn dispersal coupled with temperatures that are unlikely to be warm enough or of adequate duration to permit germination until the following spring reduces the probability of germination in autumn or winter to near nil. It is possible, however, that seeds could germinate in autumn if temperatures and soil water are adequate when artificially seeded in early autumn. Seedlings emerging in autumn would be predisposed to freezing temperatures of autumn and winter, with 100% mortality expected for seedlings at temperatures below –13 °C (9 °F) (Hou and Romo 1998b). Winter temperatures around –40 °C (–40 °F) are common in our study area (Environment Canada 1982).

If conditions are not conducive to germination in autumn, silver sagebrush seeds would be exposed to field environments over the winter before germinating the following spring or summer. Reduced germination and viability, with greater reductions occurring during autumn- than in spring-placed seeds indicates the field environment, particularly during the winter, is stressful to many seeds in the population studied. This reduction in germination contrasts with improved germination after exposure to field environments in shrubs with dormant seeds (Haferkamp and others 1990; Shaw and others 1994). Bewley and Black (1982) argued that seeds could be damaged by freezing temperatures if their water content is greater than about 14%. Freezing damage to seeds is probable in our studies because water content exceeded 14% in both autumn- and spring-placed seeds, and seeds were exposed to several freezing events, particularly in spring, with more occurring in the former treatment.

The decline of germination as temperatures rose in spring is consistent with the prediction that aging of moist seeds increases with temperature (Ellis and Roberts 1980). Increasing temperatures, precipitation, and relative humidity reduces germination of soybean (*Glycine max* (L.) Merr. [Fabaceae]) (TeKrony and others 1980). Exposing seeds to unfavorable environmental conditions for longer periods reduces germination more than exposure for shorter periods (Roberts and Ellis 1982). Greater reduction in germination for autumn-placed seeds is attributed to longer exposure to more unfavorable environmental conditions than seeds put out in spring.

Nearly all of the seeds that failed to germinate were not viable. More than 90% of big sagebrush (*Artemisia tridentata* Nutt.) seeds lost viability within 6 mo, and 100% decomposed within 10 mo of being placed in soil (Crist and Friese 1993). Young and Evans (1989) concluded that big sagebrush (*Artemisia tridentata* Nutt. ssp. *tridentata*) does not develop a soil seed bank. Anecdotal evidence prompted Schuman and others (1998) to conclude that seeds of Wyoming big sagebrush may enter dormancy and persist in the soil. Fringed sagebrush, a common associate with silver sagebrush in the Northern Mixed Prairie (Coupland 1950), maintains a persistent soil seedbank (Bai and Romo 1994, 1996). Even though germination of silver sagebrush declined with exposure to field environments, some seeds remained viable, suggesting that a soil seedbank

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could develop for this shrub. Apparently no studies have examined the dynamics of silver sagebrush seed reserves in soil.

Seeds dispersed in autumn through spring can germinate as temperatures rise in spring and early summer. As predicted from our germination tests, most seedlings of silver sagebrush emerge in late spring and early summer (Romo and Grilz 2001). Romo and Eddleman (1995) also concluded that seeds and seedlings of silver sagebrush are adapted to germinate and grow at low temperatures. Increasing germination with warming temperatures presumably improves the probability that most seeds of silver sagebrush germinate early in the growing season, maximizing the period for seedling growth in this environment with a short growing season. Early emerging seedlings are also more vigorous than later emerging ones (Hou and Romo 1998a). Conversely, freezing temperatures or desiccation may kill seedlings emerging early in spring (Hou and Romo 1997, 1998b).

The fact that some seeds did not germinate at the lowest temperatures tested in the laboratory suggests that additional seeds could germinate as temperatures warm later in spring and summer. Stratification has no effect on germination of silver sagebrush (Walton 1984). Later-emerging seedlings might avoid freezing temperatures of early spring, however, they would face an abbreviated period for growth, especially because of soil water limitations during summer. Summer drought is a major cause of seedling death in silver sagebrush and more seedlings establish in wet than dry years (Walton 1984). Later emerging seedlings are less tolerant of freezing temperatures than early emerging ones (Hou and Romo 1998b). Therefore, although later emerging seedlings can avoid freezing temperatures in spring, they may be predisposed to summer drought or freezing damage the following winter.

## SUMMARY

Our studies were conducted on seeds from a population at the northern reaches of the distribution of silver sagebrush. Although ecotypic studies have yet to be completed for silver sagebrush, seeds of ecotypes from different environments may have adaptive germination responses that are unique as shown for big sagebrush, Wyoming big sagebrush, and mountain big sagebrush (McDonough and Harniss 1974; Meyer and others 1990; Meyer and Monsen 1991, 1992). Silver sagebrush seeds germinate over a broad range of temperatures like other species of sagebrush (Young and others 1991; Bai and others 1995). Viability in a substantial portion of the seed population declines with increasing exposure to environmental conditions in the field. Seeds put in the field in autumn experience stressful environmental conditions longer and hence germination is reduced more than spring-placed seeds. High water content and increasing temperatures over time (Ellis and Roberts 1980; Roberts and Ellis 1982) likely caused the decline in germination under field environments. Despite seed viability declining under field environments, 19% to 82% of the seeds remained viable, suggesting that silver sagebrush may develop a soil seedbank. Greater contributions to the seedbank are predicted for seeds that are naturally dispersed or artificially sown in spring versus autumn. Our studies strongly implicate loss of seed viability in the field as a primary factor limiting establishment (Eddleman 1980; Walton 1984; Romo and Grilz 2001) of this shrub from seeds. Since most seedlings of silver sagebrush emerge in spring and early summer (Romo and Grilz 2001), seeding in early spring is recommended to maintain high viability and germination of seeds in this shrub.

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