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# Big sagebrush germination patterns: Subspecies and population differences

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## Abstract

**Habitat-correlated differences in laboratory germination response under autumn (15° C) and winter (1° C) temperature regimes were examined for 69 big sagebrush (*Artemisia tridentata* Nutt., Asteraceae) seed collections from a range of habitats in 7 western states. Mountain big sagebrush (ssp. *vaseyana*) exhibited the widest variation in dormant seed percentage and germination rate at 15° C. Collections from severe winter sites had larger dormant seed fractions and slower germination rates than collections from mild winter sites. Basin big sagebrush (ssp. *tridentata*) and Wyoming big sagebrush (ssp. *wyomingensis*) collections were largely nondormant and germinated quickly at 15° C regardless of collection site winter climate. At 1° C, number of days to 50% of total germination was negatively correlated with collections site mean January temperature for all 3 subspecies. Collections from severe winter sites required up to 113 days to germinate to 50% at 1° C, while collections from mild winter sites required as few as 6 days. Habitat-correlated variation in germination response appears to be of adaptive significance. Dormancy and slow germination at 15° C may prevent germination during autumn storms in the mountains, while delayed germination at continuous 1° C may prevent precocious germination under snowpack. In contrast, at mild winter sites, winter germination is promoted and probably affords the best chance for seedling survival. Between-population variation in germination strategy should be considered when artificially seeding this species.**

**Key Words: *Artemisia tridentata,* establishment ecology, intraspecific variation, seed**

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Big sagebrush (*Artemisia tridentata* Nutt., Asteraceae) is the regionally dominant shrub species over large areas of the Intermountain West (McArthur et al. 1979). The species has been studied intensively, especially from the viewpoint of control (Harniss et al. 1981). Germination behavior of the species as a whole has been well characterized (Weldon et al. 1959; McDonough and Harniss 1974a,b). The object of the present investigation was to examine variation in seed germination traits of a large number of big sagebrush collections from a wide range of habitats as a function of collection site winter temperature.

Based on our work with rubber rabbitbrush (*Chrysothamnus nauseosus* (Pall.) Britt., Asteraceae), another widely distributed autumn-flowering shrub, we hypothesized that big sagebrush seed collections from cold winter habitats would be more dormant and germinate more slowly under autumn temperature regimes, and would germinate more slowly under conditions simulating snow-

**Table 1. Location, germination response, and viability information for 24 basin big sagebrush seed collections used in germination experiments, ranked by mean January temperature.**

| Collection site | | | Seed characteristics | | | |
|---|---|---|---|---|---|---|
| | | | | | Days to 50% germination | |
| Location | State | Mean January temperature | Viability | Dormant seed | 15° C | 1° C |
| | | (C) | (%) | (%) | ——Days—— | |
| Albert Creek | WY | -9.4 | 99 | 0 | 4.5 | 96 |
| Dinosaur | UT | -8.9 | 100 | 0 | 1.0 | 68 |
| Daniel | WY | -8.3 | 94 | 12 | 5.0 | 112 |
| Stone (bench) | ID | -5.6 | 95 | 0 | 3.5 | 88 |
| Stone (bottom) | ID | -5.6 | 91 | 8 | 4.5 | 98 |
| Hatch | UT | -5.6 | 97 | 0 | 2.5 | 49 |
| Hailstone Jct. | UT | -5.6 | 99 | 8 | 6.0 | 95 |
| Emery | UT | -4.4 | 96 | 0 | 2.5 | 49 |
| Ely | NV | -4.4 | 100 | 0 | 2.5 | 68 |
| Huntington, Cyn. | UT | -3.9 | 91 | 0 | 3.5 | 51 |
| Sevier Sink | UT | -3.9 | 72 | 0 | 3.5 | 77 |
| Reynolds Crk. | ID | -3.0 | 100 | 0 | 2.5 | 45 |
| Mokee Dugway | UT | -2.2 | 96 | 0 | 3.5 | 38 |
| Salina | UT | -2.2 | 100 | 0 | 4.0 | 65 |
| Boise | ID | -2.2 | 81 | 0 | 5.0 | 70 |
| Nephi | UT | -1.7 | 95 | 0 | 6.0 | 80 |
| Kirch Refuge | NV | -1.1 | 100 | 0 | 2.5 | 40 |
| Oak City | UT | -1.1 | 95 | 0 | 2.0 | 32 |
| Moab | UT | -1.1 | 100 | 0 | 1.5 | 49 |
| Tahoe Jct. | NV | -1.1 | 99 | 0 | 3.0 | 25 |
| Dayton | NV | 0 | 98 | 0 | 2.5 | 27 |
| Hite | UT | 0 | 93 | 0 | 3.0 | 35 |
| Stagecoach | NV | 0 | 100 | 0 | 1.5 | 17 |
| Big Pine | CA | 3.9 | 100 | 0 | 1.0 | 6 |

pack, than collections from habitats with mild winters (McArthur et al. 1987, Meyer et al. 1989). More detailed work with 5 collections of each major big sagebrush subspecies (Meyer et al. 1990) and with 15 mountain big sagebrush collections (Meyer and Monsen 1991) confirmed the existence of habitat-correlated variation in big sagebrush germination patterns, but the role of subspecific identity remained unclear. Variability in patterns of germination response at the subspecies level were studied by comparing at least 20 collections for each of the 3 major subspecies (ssp. *vaseyana*, spp. *wyomingensis*, and ssp. *tridentata;* mountain, Wyoming, and basin big sagebrush, respectively).

**Table 2. Location, germination response, and viability information for 21 Wyoming big sagebrush seed collections used in germination experiments, ranked by mean January temperature.**

| Collection site | | | Seed characteristics | | | |
|---|---|---|---|---|---|---|
| | | | | | Days to 50% germination | |
| Location | State | Mean January temperature | Viability | Dormant seed | 15° C | 1° C |
| | | (C) | (%) | (%) | ——Days—— | |
| Warren | MT | -9.4 | 98 | 0 | 2.5 | 91 |
| Dinosaur | UT | -8.9 | 98 | 1 | 3.5 | 74 |
| Kemmerer | WY | -8.9 | 86 | 4 | 5.5 | 96 |
| Daniel | WY | -8.3 | 95 | 0 | 4.5 | 91 |
| Brown's Park | UT | -7.8 | 98 | 0 | 3.5 | 63 |
| Stone | ID | -5.6 | 74 | 5 | 6.5 | 74 |
| Cedar Valley | UT | -5.6 | 95 | 0 | 5.5 | 65 |
| Reynolds Creek | ID | -4.4 | 98 | 0 | 3.0 | 60 |
| Oasis | NV | -4.4 | 100 | 0 | 2.5 | 90 |
| Snake Valley | UT | -3.9 | 69 | 0 | 5.5 | 40 |
| Crowsnest | ID | -3.9 | 99 | 0 | 3.0 | 74 |
| Three Creek Well | ID | -3.9 | 81 | 4 | 4.5 | 98 |
| Mayfield | UT | -3.9 | 98 | 0 | 4.5 | 43 |
| Golconda Summit | NV | -3.3 | 98 | 1 | 2.5 | 50 |
| Blanding | UT | -2.8 | 99 | 0 | 2.5 | 30 |
| Glenn's Ferry | ID | -2.2 | 92 | 11 | 6.5 | 100 |
| Big Rock Cdy. Mt. | UT | -2.2 | 97 | 0 | 4.5 | 33 |
| Gardinerville | NV | -1.1 | 100 | 2 | 4.0 | 43 |
| Caliente | NV | -1.1 | 97 | 0 | 2.5 | 18 |
| Parowan Gap | UT | -1.1 | 99 | 0 | 2.5 | 45 |
| Veyo Road | UT | 1.1 | 92 | 0 | 3.5 | 29 |

## Materials and Methods

Seeds were collected from 69 wildland big sagebrush stands in autumn 1986 (Table 1,2,3). Collection sites were selected to represent a maximum range of climate variation for each subspecies. The collections were air-dried, cleaned to approximately 50% purity by screening and blowing, and stored in paper envelopes under laboratory conditions (20° C, 8% moisture content, oven-dry weight basis) until test initiation in early February 1987. Due to differences in harvest date, post-harvest storage period varied from 2 to 3 months.

For each experiment, 4 replications of 25 intact achenes (hereafter referred to as seeds) were hand-selected from each of the 69 collections. The seeds were placed on the surface of 2 germination blotters saturated with tapwater inside plastic 100 × 15 mm petri dishes. The petri dishes were randomized and stacked into plastic bags closed with rubber bands to retard water loss. Each stack was topped with a blank dish (blotters but no seeds) so that all dishes would receive light only through their sides. The dishes were placed in controlled-environment chambers under cool-white fluorescent lights with a 12-hour photoperiod. Light intensity at seed level averaged $25\mu$ E $m^{-2}$ $sec^{-1}$ PAR.

For the first experiment, seeds were incubated at a continuous temperature of 15° ± 1° C for 4 weeks. Germinated seeds were counted and removed at 1-day intervals for the first 4 days and at weekly intervals starting on the seventh day. Radicle protrustion to 1 mm was the criterion for germination. At the end of the incubation period, remaining seeds were tested for viability by tetrazolium staining (Grabe 1972), and remaining viable seeds were classed as dormant.

For the second experiment, seeds were incubated at a continuous 1° ± 0.5° C for 20 weeks. Germinated seeds were counted and removed at weekly intervals as above. At the end of the incubation period, dishes were transferred to the 15° C chamber for 1 week, and germinated seeds were counted and removed. Remaining seeds were tested for viability as described above.

All data were converted to the proportion of viable seed prior to analysis. Dormant seed proportion was calculated for each replication as the number of viable seeds left ungerminated at the end of the incubation period divided by the total number of viable seeds. Number of days to 50% of total cumulative germination was interpolated from rate curves constructed for each collection in each of the 2 experiments.

Mean January temperature was used as an index of winter severity at the seed collection sites. Due to the remoteness of many of the collection sites, it was sometimes necessary to interpolate this information from isotherm maps (Water Information Center 1974). Corroboration using data from comparable nearby weather stations was obtained when possible.

The relationships between subspecies identity, collection site mean January temperature and germination parameters were examined using analysis of covariance with subspecies as the treatment variable and collection site mean January temperature as the covariate.

## Results

Analysis of covariance for dormant seed percentage showed a significant interaction ($p<0.0001$) between subspecies identity and collection site mean January temperature, indicating differences among subspecies in the slope of the regression line relating dormant seed percentage to collection site mean January temperature (Table 1). Basin big sagebrush (Table 2) and Wyoming big sagebrush (Table 3)collections were largely nondormant at 15° C in the light regardless of collection site mean January temperature (Fig. 1). Maximum dormant seed percentage was 12% for basin big sagebrush and 11% for Wyoming big sagebrush. In contrast, mountain big sagebrush collections varied in dormant seed percentage from 0 to 58% (Table 4). The most dormant collections were

**Table 3. Location, germination response, and viability information for 24 mountain big sagebrush seed collections used in germination experiments, ranked by mean January temperature.**

| Collection site | | Seed characteristics | | | | |
|---|---|---|---|---|---|---|
| | | | | | Days to 50% germination | |
| Location | State | Mean January temperature | Viability | Dormant seed | 15° C | 1° C |
| | | (C) | (%) | (%) | ———Days——— | |
| Kemmerer | WY | -8.9 | 97 | 45 | 10.0 | 107 |
| Nebo Overlook | UT | -8.9 | 92 | 30 | 8.0 | 103 |
| Huntsville | UT | -8.3 | 96 | 13 | 10.0 | 90 |
| Scow's Hollow | UT | -8.3 | 88 | 58 | 15.0 | 112 |
| Daniel | WY | -8.3 | 94 | 27 | 8.0 | 113 |
| Reynolds Creek | ID | -7.8 | 90 | 58 | 14.0 | 108 |
| Maple Cyn. | UT | -7.8 | 91 | 60 | 11.0 | 110 |
| Mirror Lake Rd. | UT | -6.7 | 90 | 36 | 11.0 | 100 |
| Park City | UT | -6.1 | 88 | 31 | 7.5 | 98 |
| Thorn Crk. Jct. | ID | -6.1 | 89 | 1 | 8.5 | 50 |
| Hailstone Jct. | UT | -5.6 | 97 | 9 | 7.5 | 88 |
| Squaw Butte | OR | -4.4 | 95 | 3 | 8.0 | 54 |
| Lucky Peak | ID | -3.9 | 84 | 8 | 9.0 | 54 |
| Wheeler Gd. Sta. | CA | -3.3 | 92 | 0 | 6.0 | 60 |
| Lee Vining | CA | -3.3 | 98 | 3 | 5.0 | 41 |
| Hiko | NV | -2.8 | 95 | 0 | 2.0 | 26 |
| Pine Valley | UT | -2.2 | 98 | 0 | 4.0 | 52 |
| Bootleg Cpgrd. | CA | -2.2 | 93 | 0 | 5.5 | 40 |
| Nephi | UT | -1.7 | 98 | 0 | 3.5 | 45 |
| Gardinerville | NV | -1.1 | 95 | 0 | 4.5 | 34 |
| Browse Offramp | UT | -0.2 | 96 | 0 | 6.0 | 44 |
| Upper Kyle Cyn. | NV | 1.1 | 89 | 0 | 5.5 | 32 |
| Lower Kyle Cyn. | NV | 2.6 | 97 | 0 | 5.0 | 16 |
| Utah Hill | UT | 2.8 | 97 | 0 | 3.0 | 30 |

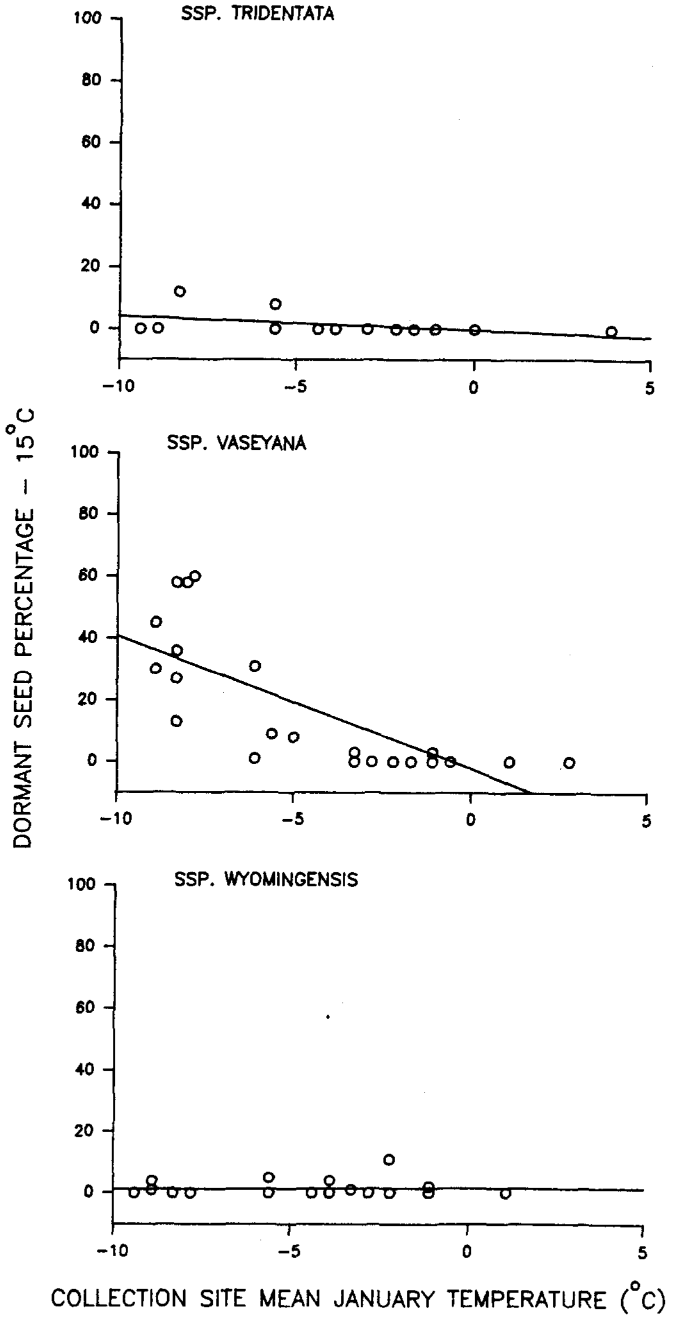


**Fig. 1. Relationship between dormant seed percentage after incubation at 15° C in the light for 28 days and collection site mean January temperature for the 3 major subspecies of big sagebrush ($R^2$=0.176, $p$<0.05 for ssp. *tridentata;* $R^2$=0.578, $p$<0.001 for ssp. *vaseyana;* $R^2$=0.001, n.s. for ssp. *wyomingensis*).**

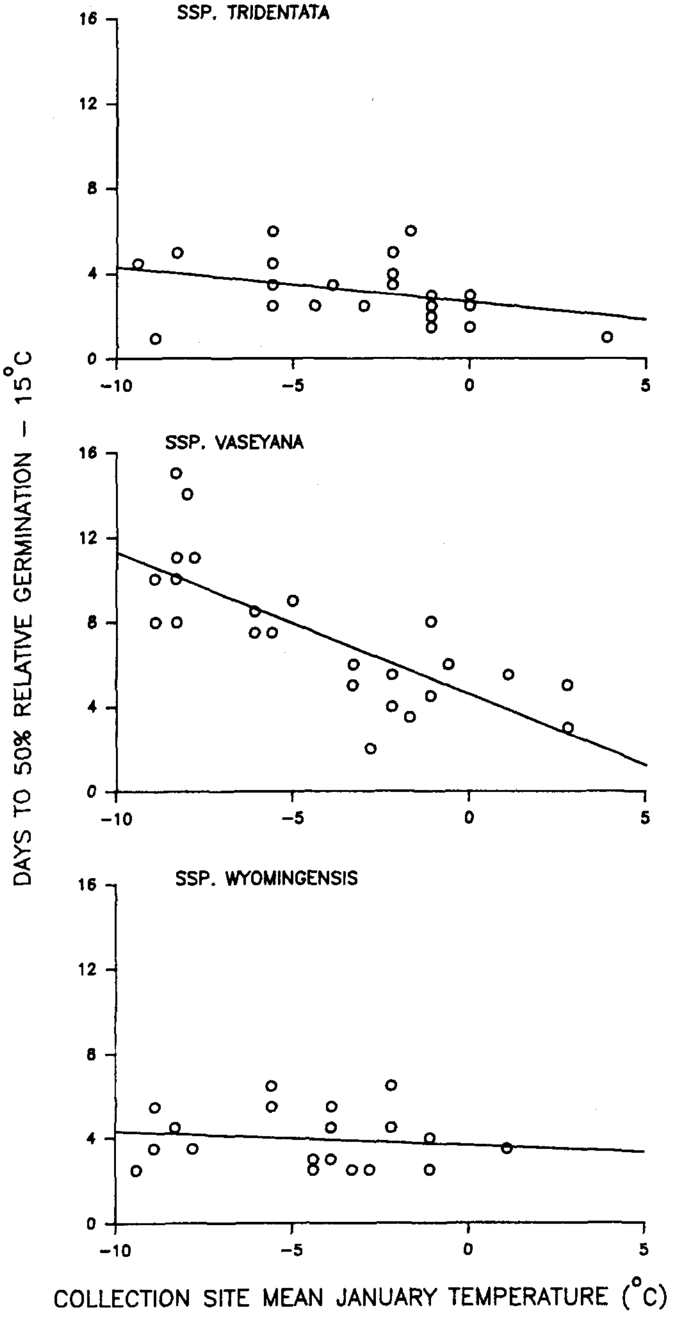


**Fig. 2. Relationship between germination rate expressed as number of days to 50% of total germination at 15° C in the light and collection site mean January temperature for the 3 major subspecies of big sagebrush ($R^2$=0.130, n.s. for ssp. *tridentata* $R^2$=0.578, $p$<0.01 for ssp. *vaseyana* $R^2$=0.020, n.s. for ssp. *wyomingensis*).**

from colder winter sites, although not all cold winter collections had high dormant seed percentages (Fig. 1). Mountain big sagebrush collections from sites with mean January temperatures above -5° C were essentially nondormant at 15° C in the light.

Slopes for the relationship between days to 50% of total germination at 15° C and collection site mean January temperature also differed significantly among subspecies ($p$<0.0003). Germination rate at 15° C in the light was not correlated with collection site mean January temperature for basin and Wyoming big sagebrush collections (Fig. 2). All collections germinated to 50% in less than 7 days. For mountain big sagebrush, germination rate at 15° C and collection site mean January temperature were negatively correlated (Fig. 2). Collections from sites with mean January temperatures of -5° C or less required more than 7 days to germinate to 50% at 15° C.

Germination rate at 1° C was significantly correlated with collection site mean January temperature for all 3 subspecies, and analysis of covariance indicated no significant differences among subspecies for the slope or y-intercept of the relationship (Table 4, Fig. 3). Collections from colder sites germinated much more slowly at 1° C than collections from warmer sites. Collections from colder sites required up to 113 days to germinate to 50%, while those from warmer sites required as few as 6 days. Only 1 collection (Reynolds

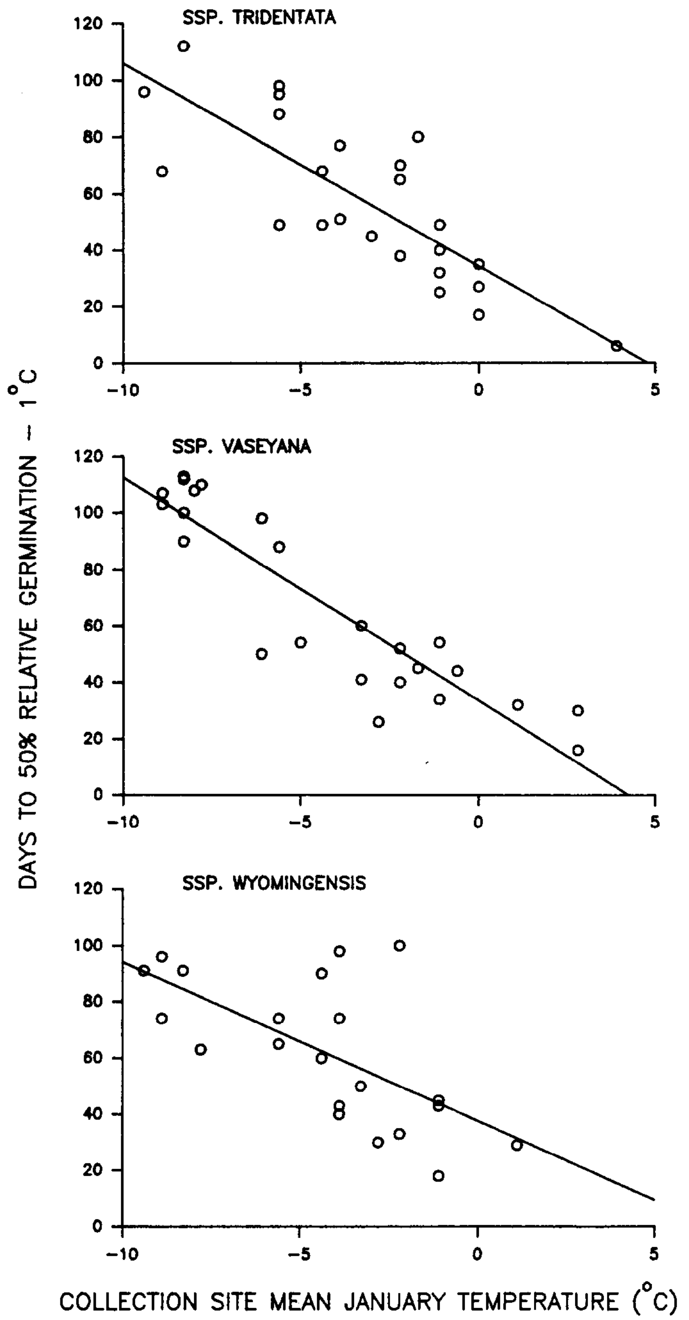


**Fig. 3. Relationship between germination rate expressed as number of days to 50% of total germination at 1° C in the light and collection site mean January temperature for the 3 major subspecies of big sagebrush ($R^2$=0.640, $p$<0.001 for ssp. *tridentata;* $R^2$=0.810, $p$<0.001 for ssp. *vaseyana;* $R^2$=0.500, $p$<0.01 for ssp. *wyomingensis*).**

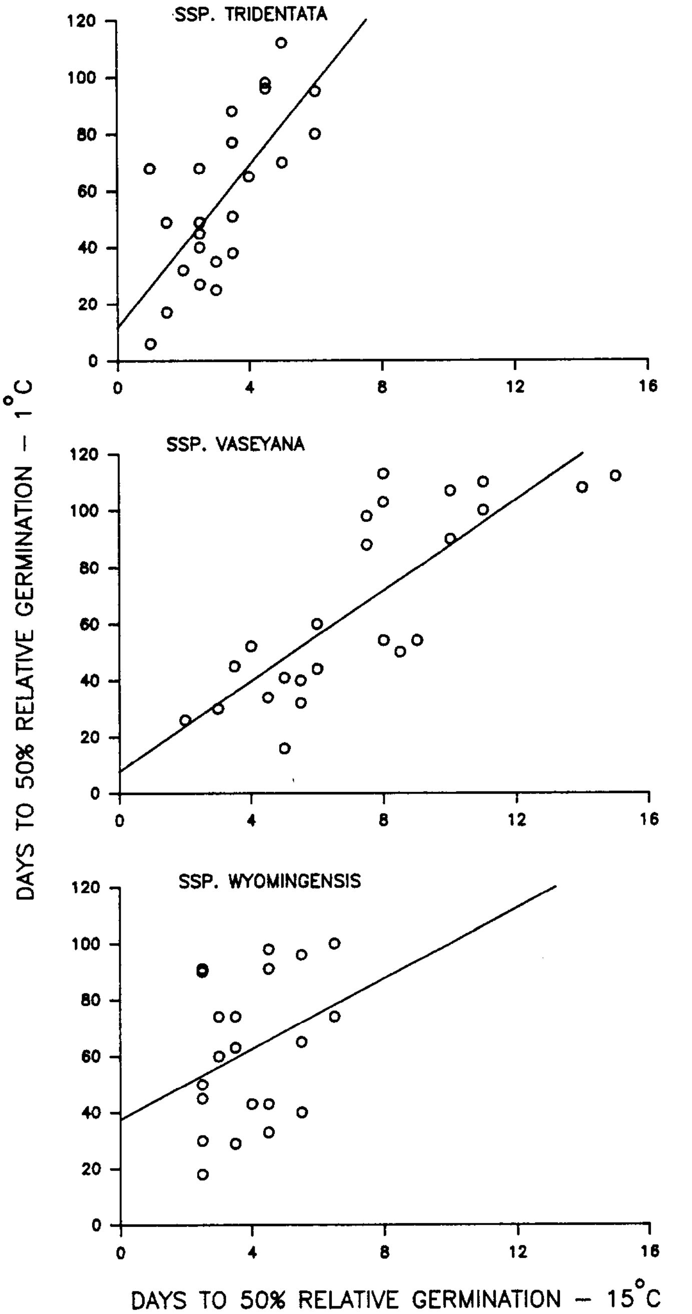


**Fig. 4. Relationship between germination rate at 15° C in the light and germination rate at 1° C in the light for the 3 major subspecies of big sagebrush ($R^2$=0.518, $p$<0.001 for ssp. *tridentata;* $R^2$=0.656, $p$<0.001 for ssp. *vaseyana;* $R^2$=0.109, n.s. for ssp. *wyomingensis*).**

Creek, Idaho, mountain big sagebrush) had a dormant seed percentage of greater than 5% after incubation for a week at 15° C following 20 weeks at 1° C.

Germination rate at 1° C was positively correlated with and predictable from germination rate at 15° C for the 3 subspecies overall, and analysis of covariance revealed no significant differences among subspecies in the slope or y-intercept of the relationship (Table 1). For all 3 subspecies, collections that were slow to germinate at 15° C also tended to be slower at 1° C (Fig. 4).

## Discussion

Habitat-correlated variation in germination pattern exists in all 3 widely distributed subspecies of big sagebrush, but each subspecies tends to exhibit a different pattern of variation. These between-subspecies differences may be related to habitat variation that is not reflected in differences in collection site mean January temperature. Many climate variables in addition to winter temperature could operate to select for specific germination responses. Duration of winter snowpack, date of last killing frost in the spring, and reliability of autumn or spring moisture are climate variables that are only loosely correlated at best with mean January temperature. For example, mountain big sagebrush sites with low mean January temperatures tend also to be sites with ample autumn precipitation and prolonged periods of winter snowpack, whereas the colder Wyoming big sagebrush sites are often wind-

**Table 4. Analyses of covariance for dormant seed percentage, days to 50% of total germination at 15° C, and days to 50% of total germination at 1° C, with subspecies as the class variable and collection site mean January temperature (first 3 analyses) or days to 50% germination at 15° C (fourth analysis) as the covariate. Error degrees of freedom = 63.**

| Variance source | df | F | P |
|---|---|---|---|
| Dormant seed percentage | | | |
| Subspecies | 2 | 0.4 | .6917 |
| Mean January temperature | 1 | 22.0 | .0001 |
| Ssp × mean January temperature | 2 | 19.7 | .0001 |
| Days to 50% germination (15° C) | | | |
| Subspecies | 2 | 3.4 | .0404 |
| Mean January temperature | 1 | 20.9 | .0001 |
| Ssp × mean January temperature | 2 | 9.4 | .0003 |
| Days to 50% germination (1° C) | | | |
| Subspecies | 2 | 0.1 | .8929 |
| Mean January temperature | 1 | 108.0 | .0001 |
| Ssp × mean January temperature | 2 | 1.0 | .3858 |
| Days to 50% germination (1° C) | | | |
| Subspecies | 2 | 1.4 | .2522 |
| Days to 50% germination (15° C) | 1 | 33.2 | .0001 |
| Ssp × days to 50% germination (15° C) | 2 | 2.0 | .1515 |

swept and relatively dry in both autumn and winter in spite of their high elevation. Dormancy under the latter conditions could be a disadvantage, because the seeds might not receive sufficient chill to trigger germination the following spring. The lower risk of precocious autumn germination at these drier sites would also eliminate the chief advantage of autumn dormancy. Timing of seed production may also be a factor. Basin big sagebrush populations generally ripen seed later than mountain big sagebrush populations in the same area, and therefore run less risk of autumn germination.

Seed bank studies of big sagebrush indicate that its seed banks are transient, with little or no seed carry-over from year to year (Young and Evans 1989, Meyer 1990). Germination timing mechanisms increase the probability that germination will occur at the season most conducive to seedling survival, rather than providing seeds with the ability to remain ungerminated under optimum conditions. Early spring soon after snowmelt is the usual time for big sagebrush seedling emergence (Meyer and Monsen 1990, Monsen and Meyer 1990). Our data suggest that germination would take place in winter at mild winter sites, while at cold winter sites it would be delayed until snowmelt or shortly before.

In this study seeds were incubated at low temperature in light. This probably does not simulate conditions under snowpack very well. We have found that big sagebrush seeds will germinate in the dark during prolonged chill at 1° C, but that the period required is longer (Meyer et al. 1990). Germination rates in dark chill and light chill were strongly correlated. In a field seed retrievel experiment, big sagebrush seeds initiated germination under prolonged snowpack, but the germination rate was lower than at 1° C in the light under laboratory conditions (Meyer 1990).

Even though there were difference among subspecies in germination response, much of the variation among collections was related to climate differences, not subspecific differences. There was no 1 germination pattern that characterized the species as a whole or any 1 subspecies. Attempting to characterize the germination response of a native species that occurs over such a wide range of habitats from 1 or a few collections results in accounts that are often conflicting (e.g., Weldon et al. 1959; McDonough and Harniss 1974a,b; Harvey 1981; Evans and Young 1984). These differences appear to represent discrete samples along a more or less continuous spectrum of variation among populations in the field.

Within-population variation in germination response also affects measured values. This variation could result from genetic differences between individual bushes (Meyer and Walker unpublished data) or from differences in environmental conditions during ripening (Harniss and McDonough 1976, Gutterman 1980). Collecting seeds at the end of the season rather than during the peak period of production for the population could skew the results, as it does for rubber rabbitbrush (Meyer et al. 1989). But the clear correlation between germination pattern and collection site mean January temperature is all the more striking, given all these possible sources of lack of correlation.

Whether one is motivated by a desire to control big sagebrush or to reestablish it in areas that have been severely disturbed, a knowledge of its establishment ecology is essential. This study indicates that big sagebrush establishment ecotypes probably occur within each subspecies, though the genetic basis for the observed variation in germination response has not yet been demonstrated. Ecotypic differentiation with regard to vegetative features has long been known in big sagbrush (McArthur et al. 1979). Our findings underscore the need for using source-identified site-matched seedlots when seeding this species for wildlife habitat improvement or disturbed land rehabilitation. Nonadapted seeds may misread germination cues and germinate at inappropriate times, seedlings may fail to emerge or persist, and the result may be stand failure (Meyer and Monsen 1990).

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