

Germination Rate at Low Temperature: Rubber Rabbitbrush Population Differences

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Abstract

The concept that low-temperature germination response is a population rather than a species characteristic has implications for range seeding. The success of a seeding could depend on the ability of the seed source to associate the appropriate degree of risk with germination in the cold at a particular site. Germination rate at 3° C was determined for 27 seed collections of rubber rabbitbrush (*Chrysothamnus nauseosus* [Pall.] Britt) belonging to 9 subspecies and collected in 5 states. Marked differences in low-temperature germination rate were observed. Relative percentage of germination at 14 days varied from 0.4 to 100, while the period required to reach 50% relative germination varied from 5 to 96 days. Germination rate was negatively correlated with a climatic index of winter frost risk to seedlings at the site and seed origin. Warm desert collections germinated fastest, while montane and high latitude collections germinated slowest. Many collections from mid-elevation sites showed the bet-hedging strategy of asynchronous germination in the cold. Germination rate was not correlated with subspecific identity. Subspecies of wide ecological amplitude showed nearly the whole range of germination rate response. The possibility that other important range species might show similar patterns of variation in low-temperature germination response merits investigation.

Key Words: *Chrysothamnus nauseosus*, establishment, seed, seedling

The importance of seed origin in the success of seeding efforts is acknowledged by most range managers. Yet studies of the seed germination characteristics of range plants have emphasized qualitative patterns at the species or subspecies level rather than concentrating on differences between populations. The objective of the present research was to determine whether between-population differences in a germination trait could be correlated with habitat differences at the site of seed origin. Evaluation of germination behavior might then be used to predict the probability of estab-

lishment success for a given seed source when seeded artificially onto a particular site type. Seed population differences have only rarely been related to the ecology of the site of seed origin (e.g., Young and Evans 1981).

We selected germination rate at temperatures slightly above freezing as a possible indicator of conditions at the site of seed collection, based on the following model. The adaptive significance of the set of responses that make up the germination syndrome of a seed population is that it controls germination timing so that the probability of seedling survival is enhanced. A species as a whole is under genetic constraints with regard to its germination syndrome options, but if local selective pressures are strong enough, we can expect either ecotypic differentiation or a genetically regulated plastic response to local factors (Thompson 1981, Silvertown 1984). On rangeland in the western United States, principal threats to seedling survival include frost and drought. Different habitats present these 2 threats to different degrees, and the risk associated with germinating at temperatures slightly above freezing varies accordingly. In habitats with mild winters but dry springs, rapid germination in the cold is clearly advantageous because frost risk is minimal for rapid germinators, while slow germinators face increased probability of death by drought. In habitats with severe winters but moist springs, rapid cold-temperature germinators face extreme frost risk, while slow germinators face little drought risk. If, as is the case on much western rangeland, both risks are substantial and unpredictable from year to year, the best strategy (from the point of view of the fitness of the mother plant) is to produce seeds that vary in their germination response at low temperature, so that some seedlings survive regardless of the vagaries of spring weather.

We used rubber rabbitbrush (*Chrysothamnus nauseosus*) to test the above model. It is a species of wide ecological amplitude that produces abundant, easily collected seed. Many races rely on regular establishment from seed to invade recently opened sites. This characteristic, combined with a relatively rapid growth rate, has made it useful in stabilizing severely disturbed sites and in restoring wildlife winter range (Frischknecht 1963, Hanks et al. 1975, McArthur et al. 1979). There is also renewed interest in rabbitbrush as a source of rubber and other industrial chemicals (Weber et al. 1985, Ostler et al. 1986). Few studies of rubber rabbitbrush germination have been reported (Kay et al. 1977, Sabo et al. 1979, Stevens et al.

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Methods

Rubber rabbitbrush seed collections were made in the autumn of 1984 at 27 sites in 5 states (Table 1). Representatives of 9 subspecies were included. The collections were stored at room temperature (ca. 22° C) until the start of the experiment in mid-February 1985.

Table 1. Location and altitude for 27 rubber rabbitbrush seed collection sites.

Subspecies/collection site	Lat(N)	Long(W)	Alt(Meters)
<i>Ssp. albicaulis</i> Walker River, CA	38°28'	119°30'	2,000
<i>Ssp. consimilis</i> Quinn River, NV	41°32'	118°23'	1,260
Chester, UT	39°27'	111°33'	1,690
Big Rock Candy Mtn., UT	38°37'	112°20'	1,880
Gerlach, NV	40°39'	119°21'	1,220
Black Rock Desert, NV	40°43'	119°11'	1,230
<i>Ssp. graveolens</i> Salina Canyon, UT	38°45'	111°35'	2,280
Leeds, UT	37°20'	113°35'	1,140
Colorado City, AZ	36°59'	112°58'	1,540
Point of Rocks, AZ	36°49'	112°40'	1,400
Paragonah, UT	37°54'	112°50'	1,750
<i>Ssp. hololeucus</i> Nephi Canyon, UT	39°42'	111°43'	1,780
Marysville, UT	38°34'	112°20'	1,850
Bottle Creek, NV	41°19'	118°16'	1,310
Cove Fort, UT	38°30'	112°40'	1,850
Cuyuma, CA	34°57'	119°41'	610
<i>Ssp. mojavenis</i> Lancaster, CA	34°41'	118°07'	730
<i>Ssp. nauseosus</i> Terry, MT	46°47'	105°18'	740
<i>Ssp. salicifolius</i> Ephraim Canyon, UT	39°20'	111°25'	2,520
<i>Ssp. turbinatus</i> Black Rock, UT	38°35'	112°58'	1,450
<i>Ssp. viridulus</i> Victorville, CA	34°36'	117°20'	830
Palmetto, NV	37°26'	117°40'	1,940
Benton, CA	37°54'	118°38'	2,050
Palmdale, CA	34°37'	118°07'	820
Leevining, CA	37°56'	119°05'	2,090
Barstow, CA	34°53'	117°04'	680
Rosamond, CA	34°52'	118°10'	720

Four replications of 50 filled seeds were used for each source. The seeds were placed in folded germination toweling that had been moistened with tapwater. The folded towels containing the seeds were stacked, wrapped in plastic, and placed in a controlled-environment chamber at 3° C. Stevens et al. (1981) showed that this germination method gave reliable viability estimates for a variety of western range plants. A seed was considered germinated when its radicle protruded at least 2 mm. Germinated seedlings were counted and removed at approximately biweekly intervals during the experiment, which lasted 120 days. To facilitate rate comparisons between sources, germination percentages were converted to a relative basis (i.e., percent of final absolute percentage). These relative percentages were calculated for each count day and used to plot the time course of germination over 120 days for each source. The number of days required to reach 50% of final germination was extrapolated from each time course plot.

Regression analysis was used to test the hypothesis that germination rate at temperatures slightly above freezing is inversely correlated with frost risk at the site of seed origin (Snedecor and Cochran 1980). Mean January temperature was used as an index of frost risk. Values for each collection site were interpolated from isotherm maps (Water Information Center 1974) using data from

nearby weather stations at comparable elevations for corroboration when available. Because of the remoteness of many of the collection sites, accurate and detailed climatic data are not available. Mean January temperature, a factor that can be interpolated from isotherm maps, may not be the best climatic index to use in this context, but it is itself probably correlated with more appropriate factors such as the probability of late spring frosts.

Results

Most of the seed collections achieved almost 100% germination by the end of the test period, but a few sources were of poorer quality (Table 2). Only one source showed more than 2% viable ungerminated seed (as evaluated by cut test) at the end of this period.

Table 2. Germination parameters for 27 seed collections of rubber rabbitbrush germinated at constant 3° C for 120 days.

	Abs. final % germ. (mean±SE)	Rel. % germ-14 days (mean±SE)	Days to 50% RG
<i>Ssp. albicaulis</i> Walker River, CA	99±1	40±4	17
<i>Ssp. consimilis</i> Quinn River, NV	57±2	38±4	29
Chester, UT	76±2	14±3	63
Big Rocky Candy Mtn., UT	99±1	12±2	42
Gerlach, NV	100±0	45±3	18
Black Rock Desert, NV	99±1	27±3	38
<i>Ssp. graveolens</i> Salina Canyon, UT	82±3	1±0	96
Leeds, UT	100±1	30±1	19
Colorado City, AZ	100±0	10±4	43
Point of Rocks, AZ	98±1	31±3	22
Paragonah, UT	95±2	1±3	72
<i>Ssp. hololeucus</i> Nephi Canyon, UT	96±2	35±2	28
Marysville, UT	88±2	5±2	70
Bottle Creek, NV	42±4	35±3	19
Cove Fort, UT	45±3	75±2	10
Cuyuma, CA	95±1	98±1	7
<i>Ssp. mojavenis</i> Lancaster, CA	94±3	91±2	8
<i>Ssp. nauseosus</i> Terry, MT	46±4	1±0	46
<i>Ssp. salicifolius</i> Ephraim Canyon, UT	94±1	7±1	60
<i>Ssp. turbinatus</i> Black Rock, UT	85±2	20±5	33
<i>Ssp. viridulus</i> Victorville, CA	96±2	96±2	6
Palmetto, NV	100±0	38±3	40
Benton, CA	99±1	83±2	8
Palmdale, CA	98±1	99±1	5
Leevining, CA	91±5	35±2	29
Barstow, CA	100±1	100±1	5
Rosamond, CA	54±4	93±1	6

Relative germination percentage after 2 weeks at 3° C varied markedly between seed sources (Table 2). Some sources had essentially completed germination, while others had scarcely begun. The time required to reach 50% germination varied from 5 to 96 days.

As predicted by the model, the time required to reach 50% germination in the cold was inversely correlated with mean January temperature at the site of seed origin (Fig. 1a), decreasing exponentially as frost risk decreased. The frost-risk factor accounted for almost 60% of the variation in time to 50% germination ($r = -.771, p < .0001$). Similarly, relative percentage of germination at 2 weeks in the cold showed a strong positive correlation with mean January temperature at the seed collection site ($r = +0.779, p < .0001$) (Fig. 1b).

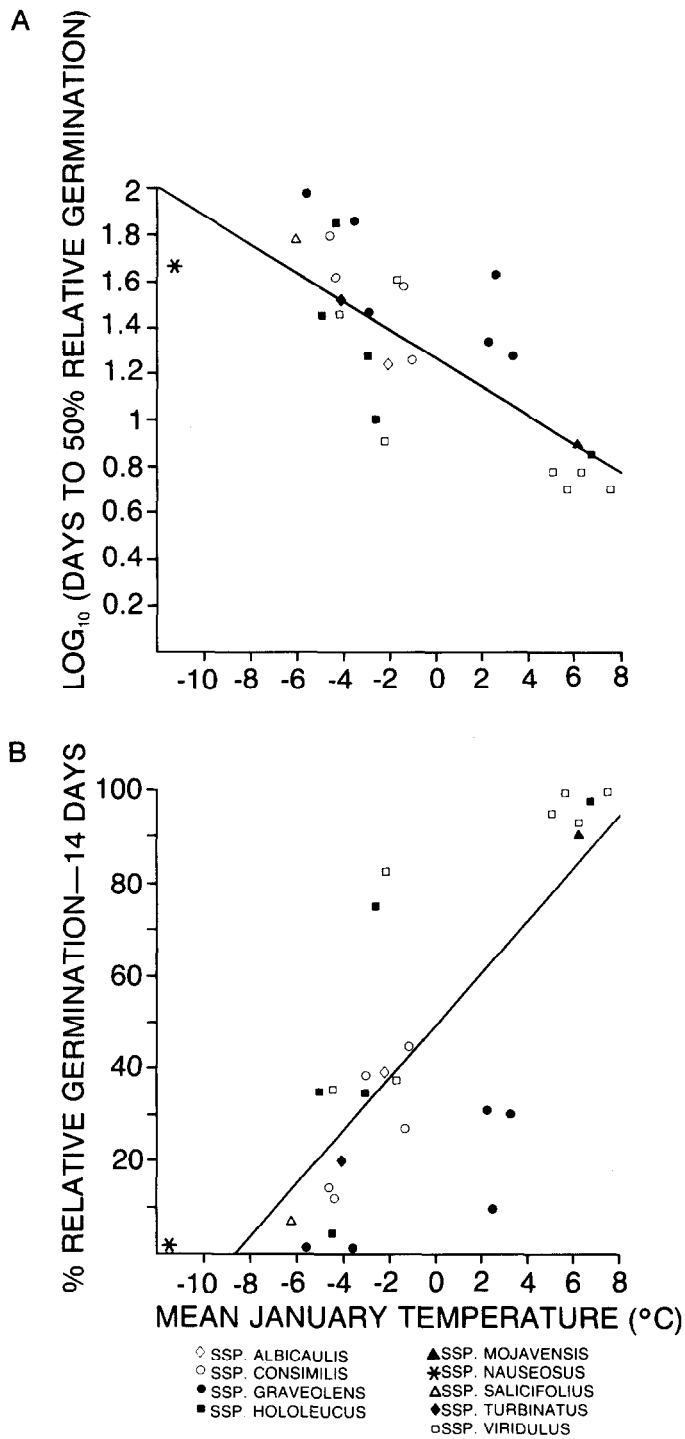


Fig. 1. (A) The relationship between the \log_{10} of the number of days required to achieve 50% relative germination at 3° C and mean January temperature at the site of seed collection for 27 collections of rubber rabbitbrush. The equation for the plotted regression line is: $\log_{10}(\text{days to } 50\%) = -0.063(\text{mean temperature}) + 1.28$ ($R^2 = 0.595$) (B) The relationship between 14-day relative % germination at 3° C and mean January temperature at the site of seed collection for the same 27 collections. The equation for the plotted regression line is: $14\text{-day \% rel. germ.} = 5.69(\text{mean January temperature}) + 48.4$ ($R^2 = 0.607$)

Subspecies were characterized by particular cold-temperature germination rates only to the extent that they showed the appropriate habitat restriction. Subspecies of wide ecological amplitude showed trends relative to mean January temperature that were similar to the main trends (Fig. 1a, 1b). For example, *Chryso-*

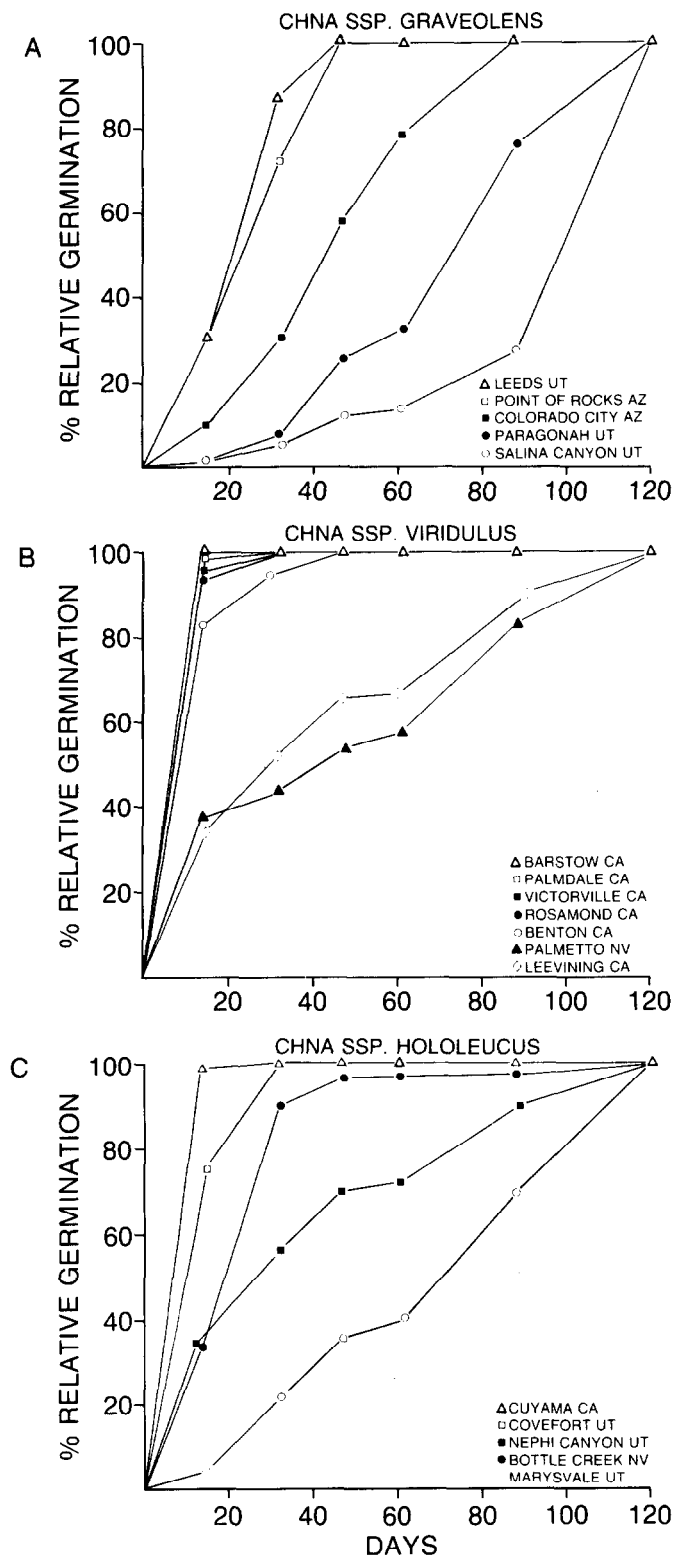


Fig. 2. Time course plots of relative percentage of germination at 3° C for different populations of (A) *Chrysothamnus nauseosus* ssp. *graveolens*, (B) *Chrysothamnus nauseosus* ssp. *viridulus*, and (C) *Chrysothamnus nauseosus* ssp. *hololeucus*.

thamnus nauseosus ssp. *graveolens*, showed a significant regression of time to 50% germination on mean January temperature even when considered separately ($r = 0.916$, $p < 0.05$). Time course curves for this subspecies show almost the whole range of germina-

tion responses, from synchronous rapid germination through non-synchronous germination to synchronous slow germination (i.e., a long lag period) (Fig. 2a). These responses correlated well with frost and drought risk characteristics at the site of seed origin. Subspecies *Chrysothamnus nauseosus* ssp. *viridulus* and *Chrysothamnus nauseosus* ssp. *hololeucus* showed similar trends (Fig. 2b, 2c) within the constraints of the habitats they occupy. Populations from the Mojave Desert or from a California mediterranean-type climate germinated rapidly in the cold, while populations from cold but relatively dry sites tended to show the bet-hedging strategy of spreading their germination over time.

Discussion

For rubber rabbitbrush, germination rate at low temperature appears to be a population characteristic rather than a species or subspecies characteristic. It serves as a reasonably reliable indicator of winter/spring frost risk to seedlings at the site of seed origin. A key question is whether this result can be generalized to other important range species.

Thompson (1981) reviewed the evidence for adaptive population differentiation in germination response and concluded that, while the idea of such adaptive difference is widely accepted, remarkably few studies have demonstrated its existence. His own studies with the Caryophyllaceae of Europe are among those that have (Thompson 1971, 1975). He found trends both within species and between species for populations from mediterranean climates (mild winters, dry summers) to germinate more rapidly in the cold than populations from temperate oceanic climates (mild winters, wet summers). The slowest low-temperature germination was found in populations from more continental temperate climates (cold winters). These results support the model proposed here.

There are reports in the range literature on population differences in response to temperature (e.g., Springfield 1964, Moyer and Lang 1976). In addition, many of the conflicting reports regarding germination requirements for range plants are more probably due to differences in seed source tested than to problems with technique (e.g., Young and Evans 1976 versus McHenry and Jensen 1967 on the stratification requirements of antelope bitterbrush). But systematic examination of many more species is needed before the generality of the present results can be established.

Slow germination rate in the cold does not seem to be related to true dormancy in rubber rabbitbrush. Even fresh seed germinates fully within 4 weeks at 30° C (unpublished data). Germination rate control in the cold appears to function as a substitute for true dormancy in this autumn-ripening species.

Another variable that needs evaluation is the effect of seed age and afterripening processes on germination response at low temperature. Year-old seed might show quite a different response than freshly collected seed such as that used in this experiment.

The source of interpopulation variation in germination response—i.e., whether it represents ecotypic (genetic) differentiation or phenotypic plasticity—has rarely been established (Thompson 1981). Considerable evidence shows that the germination responses of seeds vary widely (within genetic constraints) as a function of conditions (i.e., temperature, moisture stress, photoperiod, etc.) during the final stages of fruit maturation on the mother plant (Gutterman 1980, Silvertown 1984). This might explain some of the scatter on Figure 1 because germination depends on weather during ripening in a given year rather than on a long-term climatic index. As long as seed is wild-collected, it would be expected to behave aberrantly only rarely as a result of these environmental effects because on the average the weather at a site does represent its climate. But as we move into the era of commercial seed orchards for native seed production we should not ignore the possibility that seed will possess germination characteristics

that reflect conditions at the seed orchard, rather than the original collection site.

Lastly, we need to know how germination rate at a constant low temperature relates to the rate for seeds experiencing actual winter seedbed conditions, and whether the shape of the low-temperature response curve can actually predict the probability of seedling survival on different types of sites.

Low-temperature germination response has potential as an assay tool for management in the evaluation of seed for planting. If the suitability of a seed source of unknown origin could be determined in a simple test, the costly error of seeding with an inappropriate source could be avoided. Our results indicate that the idea merits further investigation.

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