

## Factors affecting seed germination and seedling establishment of a long-lived desert shrub (*Coleogyne ramosissima*: Rosaceae)

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Received 28 November 2003; accepted in revised form 24 August 2004

**Key words:** Blackbrush, Colorado Plateau, Ecotype, Episodic recruitment, Mojave Desert, Seed predation

### Abstract

Long-lived desert shrubs exhibit infrequent, episodic recruitment from seed. In spite of this long time scale, selection on life history attributes that affect seedling recruitment should be strong. We studied factors affecting germination phenology and seedling establishment for *Coleogyne ramosissima*, a dominant shrub species in the ecotone between warm and cold deserts in western North America. We also examined ecotypic differentiation in establishment strategy in response to selection regimes in two contrasting habitats. We followed patterns of dormancy loss, germination, emergence, and survival in reciprocal field experiments at warm winter Mojave Desert and cold winter Colorado Plateau study sites. Seed germination took place in late winter, under winter rain conditions at the warm desert site and under snow at the cold desert site. Distinctive germination phenologies for the two seed populations at contrasting field sites followed predictions based on laboratory germination experiments. There was no seed bank carryover across years. Seedling survival at the end of three growing seasons was remarkably high (mean survival 54%). Most seedling mortality was due to sprout predation by rodents early the first spring in unprotected caches. Emergence and establishment at each site were significantly higher for seeds from the local population, supporting the idea of ecotypic differentiation in establishment strategy. Establishment success was an order of magnitude greater overall at the Colorado Plateau site, which represents the leading edge of an upward elevational shift in distribution for this species under the current climatic regime. The Mojave Desert site is on the trailing edge of this shift, and recruitment there is apparently a much less frequent occurrence.

### Introduction

Regeneration from seed is an essential feature of the life cycle of most desert shrubs, yet there are few studies that document successful seedling recruitment for these species, especially under natural conditions (Shreve 1917; Shreve and Hinckley 1937; Sheps 1973; Friedman and Orshan

1975). There are several reasons for this. Most desert shrub species are relatively long-lived, and probably do not depend upon frequent recruitment from seed for population persistence (Goldberg and Turner 1986; Bowers et al. 1995). Favorable weather sequences may be necessary for seed production as well as for establishment from seed, and such sequences may occur infrequently

in deserts (Hunter 1989; Bowers 1997). Mature stands of desert shrubs may effectively prevent recruitment of their own offspring through superior competitive ability, so that favorable weather sequences must be coupled with some form of disturbance for natural recruitment to occur (Sheps 1973; Hunter 1989; Owens and Norton 1989; Mauchamp et al. 1993). And the seeds of shrubs may be a primary source of food for at least one of several guilds of desert granivores, including ants, rodents, and birds, so that 'mast' years of exceptionally high seed production may be necessary for seeds to escape predation and enter the seed bank (Brown et al. 1979; Kelly 1994; Herrera et al. 1998). Shrub recruitment in deserts is therefore expected to be episodic as well as patchy in nature and not often observed.

*Coleogyne ramosissima* Torr. is a rosaceous shrub that is often the dominant species on shallow soils in the transition zone between North American warm and cold deserts (Bowns and West 1976). It is known to be slow-growing and exceptionally long-lived for a non-clonal desert plant, with individuals reaching ages of several hundred years (Christensen and Brown 1963; Webb and Wilshire 1980; Webb et al. 1987). Our observations over a 12-year-period suggest that *C. ramosissima* is a mast-seeding species, producing abundant seed crops at intervals of a few to several years, even when years of favorable winter moisture and consequent vegetative growth occur at more frequent intervals (Pendleton et al. 1995; Pendleton and Meyer, unpublished data). We have also observed that juvenile plants indicative of past recruitment events most commonly occur on local-scale disturbances such as abandoned roads and pipeline corridors rather than in established stands of *C. ramosissima*, suggesting that recruitment into mature stands may be difficult. In the years that we have been observing *C. ramosissima* (1990–2003), the natural recruitment episode in 1992, which coincided with the study we report here, was the only successful recruitment observed.

*Coleogyne ramosissima* seeds are relatively large (mean mass 17 mg, mean length 6 mm). This is apparently too large for predation by ants, but the seeds are a preferred food of the heteromyid rodents that are also their primary dispersers (J. Auger, University of Nevada, Reno, unpublished data). The seeds are cached in surface scatter-hoards which are later retrieved as seeds or are

grazed as succulent young sprouts soon after emergence. In most years, even after the production of a reasonable seed crop, all the seeds are apparently consumed. Little or no emergence of seedlings is seen following years of average seed production, even under favorable weather conditions. It is only in mast years that any seeds pass through this rodent 'sieve' and have an opportunity to establish.

Because *C. ramosissima* is an ecotonal species that occupies a relatively narrow band between North American warm and cold deserts, we would expect it to exhibit elevational and latitudinal shifts in distribution in response to changing climate scenarios. Such elevational shifts in *C. ramosissima* distribution are known to have occurred in response to climate change in the past (Cole and Webb 1985; Hunter and McAuliffe 1994). Evidence for such a shift would include frequent recruitment from seed at the leading edge of the shift coupled with frequent recruitment failure at the trailing edge. Under a long term climatic trend toward warmer winters, we would predict higher *C. ramosissima* recruitment success in habitats at higher elevations and higher latitudes throughout its range.

We took advantage of an exceptional mast year in 1991 to initiate our long-term investigation of blackbrush regeneration biology in the field. Our objective was to examine factors affecting *C. ramosissima* seed germination and seedling emergence and survival under field conditions. In a related study, we discovered that the seeds of *C. ramosissima* exhibit habitat-correlated variation in germination response to chilling and in germination rate during chilling in the laboratory (Pendleton and Meyer, 2004). A major goal of this field study was to test whether these apparent ecotypic differences are truly of adaptive significance, i.e., whether establishment success in contrasting warm and cold desert habitats is higher for seeds of *C. ramosissima* ecotypes from local habitats, and whether any differences in establishment success are attributable to differences in germination response.

We also wanted to test two related hypotheses with regard to rodent predation. We hypothesized that post-dispersal predation by rodents would have major impact on establishment success, and that *C. ramosissima* seeds would fail to form a persistent seed bank even when protected from

rodent predation. The presence of only a transient seed bank could represent a response to long-term selection for germination immediately following the mast year, when predation risk to individual seeds would be expected to be reduced.

To address this set of hypotheses, we used a reciprocal design with two study sites and two seed populations, and we included a rodent exclusion treatment. The design included a seed retrieval experiment as well as a seedling establishment experiment at each site. The study sites represented contrasting *C. ramosissima* habitats: a Mojave Desert site (warm desert, near Hurricane, Utah) and a Colorado Plateau site (cold desert, Arches National Park, Utah; Table 1).

To help us understand changes in *C. ramosissima* seed dormancy status likely to be observed in the field, we supplemented our original laboratory germination experiments on the chilling requirements of recently harvested seeds (Pendleton and Meyer, 2004) with studies on the effects of various seed treatments on dormancy status and chilling response. We used seed collections from a series of *C. ramosissima* populations, including those populations used in the field establishment study. The laboratory storage experiment was

designed to tell us whether *C. ramosissima* seeds lose dormancy under dry conditions (i.e., after-ripen), and whether the rate of dormancy loss varies as a function of temperature or seed origin (Bauer et al. 1998; Meyer et al. 2000). In the factorial experiment, we tested the hypothesis that seeds would integrate sequences of time spent at different temperatures and water contents in a way that would tend to be normalizing, so that the ability to germinate at the time when probability of survival for the resulting seedlings is greatest would not be compromised.

## Methods

Seeds (actually one-seeded achenes) for the laboratory germination and field seed retrieval and establishment experiments were collected in late June and early July 1991 by beating ripe achenes into a hopper. Collections were cleaned using a series of screens to remove debris. Achenes retained within the calyx were removed using a rubbing board prior to screening. Only intact, mature achenes were used in the experiments. Achenes were generally free of insect damage and

Table 1. Location and habitat characteristics of the two study sites where seed retrieval and emergence experiments were conducted.

	Study site	
	Hurricane (Mojave)	Arches (Colorado Plateau)
Location	37°09'N, 113°17'W	38°43'N, 109°32'W
Elevation (m)	976	1463
Climate		
Mean annual precipitation (mm)	279	227
Mean annual snowfall (mm)	94	157
Mean January temperature (°C)	5.2	-0.4
Mean July temperature (°C)	28.0	28.2
Soil type	Aeolian sand over basalt	Aeolian sand over sandstone
Adjacent plant communities	Creosote bush shrubland	Pinyon-juniper woodland, desert grassland
Seed-eating rodents <sup>a</sup>		
<i>Ammospermophilus leucurus</i>	Present	Present
<i>Dipodomys merriami</i>	Present	Absent
<i>Dipodomys microps</i>	Present	Absent
<i>Dipodomys ordii</i>	Absent	Present
<i>Perognathus flavescens</i>	Absent	Present
<i>Perognathus longimembris</i>	Present	Absent
<i>Peromyscus maniculatus</i>	Absent	Present
<i>Peromyscus truei</i>	Absent	Present

<sup>a</sup> Rodent diversity data are based on three trapping nights per site in summer 1996.

Climate data for the Hurricane Study Site are from the LaVerkin Utah weather station, while data for the Arches Study Site are from the Arches National Park Headquarters Utah weather station (data from [www.wrcc.dri.edu](http://www.wrcc.dri.edu)).

of high viability (>85%). Each experiment used seedlots also included in chilling experiments with recently harvested seeds, and data from certain treatments in the earlier experiments served as baseline data in some of the analyses reported here (Pendleton and Meyer, 2004).

#### *Laboratory storage experiment*

The laboratory storage experiment included seedlots from Arches National Park, Hite Turnoff, Toquerville Exit, and Hurricane (Table 2). Recently harvested seeds were placed in small glass vials with screw cap lids to maintain them at a constant moisture content (sealed) in all but one storage treatment. Seeds were stored airdry (9–11% water content) for 4 and 10 months under each of five regimes: in an ultra freezer (–80 °C), in a cold room (2 °C), in laboratory room storage (20 °C), sealed in a warm incubator (35 °C) and unsealed (in paper coin envelopes) in a warm incubator (35 °C). We included the unsealed high temperature treatment to better simulate field conditions in the summer.

Following storage, the seeds were either placed directly into incubation at the optimum temperature regime of 5/15 °C (12 h:12 h) for 4 weeks or moist-chilled at 2 °C for 2 weeks prior to incubation at 5/15 °C. Two replications of 25 seeds were included per treatment. Seeds were placed in 100-mm plastic Petri dishes between two moistened germination blotters and incubated in the dark. Blotters were moistened as needed with tap water during the course of the experiment. Dishes

Table 2. Locations for *C. ramosissima* populations where seed collections were made.

Population	State	Elevation (m)	Latitude/longitude
Mojave Desert			
Hurricane	UT	976	37°09'N 113°17'W
LeGrande Heights	UT	976	37°09'N 113°18'W
Toquerville Exit	UT	1159	37°16'N 113°17'W
Red Rocks Overlook	NV	1189	36°09'N 115°25'W
Colorado Plateau			
Hite Turnoff	UT	1280	37°48'N 110°18'W
Gemini Bridges Turnoff	UT	1341	38°34'N 109°35'W
Arches National Park	UT	1463	38°43'N 109°32'W
White Mesa	UT	1524	37°30'N 109°29'W
Little Rockies	UT	1646	37°47'N 110°39'W
Island in the Sky	UT	1866	38°35'N 109°47'W

were scored weekly and germinated seeds were removed. Seeds were scored as germinated when the radicle reached 5 mm or exhibited geotropic bending. At the end of the incubation period, remaining seeds were scored for viability using a cut test. Germination percentage values were corrected for seed viability.

#### *Laboratory factorial experiment*

The factorial experiment included seeds from 10 populations (Table 2). The experiment was initiated after approximately 6 months of laboratory storage (9–11% moisture content, 20 °C). Treatment sequences were chosen to imitate sequences of events that seeds might actually encounter in the field. Because weather conditions are extremely variable in blackbrush habitat, seeds probably frequently dry out after spending time imbibed at hot summer, optimal autumn, or chilling or freezing winter temperatures, and abrupt temperature transitions from hot to cold could be encountered. We wanted to determine how these kinds of experiences would affect dormancy status of the seeds and subsequent response to chilling. The treatments included moist incubation at the superoptimum (summer) temperature of 15/25 °C (12 h:12 h) for 2 weeks, moist incubation at –5 °C (freezing) for 2 weeks, drying at 5/15 °C (by removing the lids of the Petri dishes) for 2 weeks, and moist chilling at 2 °C for 2 or 4 weeks. At the end of each treatment sequence, seeds were subjected to moist incubation at the optimum temperature of 5/15 °C for 4 weeks. We included eight treatment sequences for unchilled seeds, eight sequences for seeds subjected to a 2-week chill, and four sequences for seeds subjected to a 4-week chill.

For unchilled seeds, the sequences were: no pretreatment (directly into incubation at optimum temperature), summer, summer followed by drying, freezing, freezing followed by drying, summer followed by freezing, summer followed by drying and freezing, and summer followed by freezing and drying.

For seeds chilled 2 weeks, the sequences were: chilling (no additional treatment), chilling followed by drying, summer followed by chilling, summer followed by drying and chilling, summer followed by chilling and drying, chilling followed

by freezing, chilling followed by freezing and drying, and chilling followed by drying and freezing.

For seeds chilled 4 weeks, the sequences were: chilling (no additional treatment), chilling followed by drying, chilling followed by freezing, and chilling followed by freezing and drying.

The factorial experiment used a protocol similar to the storage experiment protocol (see above), except that four replications of 25 seeds were included for each treatment combination.

#### *Field seed retrieval experiment*

As mentioned above, the field seed retrieval and establishment studies utilized a reciprocal design with two contrasting study sites, Hurricane in the Mojave Desert and Arches National Park on the Colorado Plateau (Table 1, Figure 1). The field experiments utilized seeds from Arches National Park and LeGrande Heights. Seeds from the LeGrande Heights population, 5 km west of the Hurricane Study Site, were used in the field experiments rather than Hurricane seeds for two reasons. First, the LeGrande Heights site was also used for monitoring emergence and survival of natural caches, and it was desirable to use the same seeds in both natural and artificial cache studies. Second, the LeGrande Heights population was much larger and it was possible to obtain more seeds. We chose to carry out the experimental study at Hurricane rather than LeGrande Heights for security reasons. In the data presentation, we refer to the LeGrande Heights seed population as 'Hurricane' for the sake of clarity in describing the reciprocal experiment; in fact, the two seed populations showed similar germination patterns as recently harvested seeds (Pendleton and Meyer, 2004) and in the factorial experiment reported here.

At each site the location selected for installation of experiments was a local-scale disturbance within a matrix of more or less intact *C. ramosissima* vegetation. At Arches, a several-year-old disturbance along a natural gas pipeline corridor was selected, while at Hurricane, the study was installed in a field that had been cleared of *C. ramosissima*, possibly by burning, at some unknown earlier date.

For the seed retrieval study, seeds were weighed into groups of approximately 100 and placed in 5 × 5 cm flat packets made of nylon mesh (mosquito netting), which were then folded over and stapled on the open end. The seeds were returned to the field in mid-July 1991, within 2 weeks of harvest, at each site. The packets were placed flat in shallow excavations and buried side by side (one packet from each seed population) at a depth of 15–20 mm. The buried packets were then covered with hardware cloth cones (10 mm mesh, 20-cm diameter, 20-cm height) that were held in place with two u-staples pushed through their edges and into the ground, to protect the packets from rodent predation or other disturbance. At each of the two study sites, the cone-covered packet pairs were arrayed in groups of 12, to allow for a maximum of twelve retrieval dates. Five groups (blocks) of 12 packet pairs were laid out at each site.

Starting in October 1991, seeds from each block at each study site were retrieved at intervals during the year following installation of the experiment, for a total of six retrieval dates. At the end of the first year, no viable seeds remained in the packets at Arches and the Hurricane retrieval experiment was vandalized. Consequently, retrievals were discontinued at that time.

On each retrieval date, seed packets were taken back to the laboratory in ziplock bags in an insulated box to maintain field moisture and temperature status, and were processed the same day. For each packet, germinated seeds were counted and removed, and the remaining seeds were incubated at optimum temperature (5/15 °C) for 4 weeks as described above. Seeds that germinated during this period were scored as germinable (i.e., non-dormant). Seeds remaining ungerminated at the end of the incubation period were then evaluated for viability as described above, and viable seeds were scored as dormant.

#### *Field seedling establishment study*

For the seedling establishment study, seeds were counted into groups of approximately 20 viable seeds. Minor differences in viability between the two seed populations (92% for LeGrande Heights vs. 97% for Arches) were taken into account, so that the total mean seed number for the Arches lot was 20.5 for the Arches lot and 22 for the

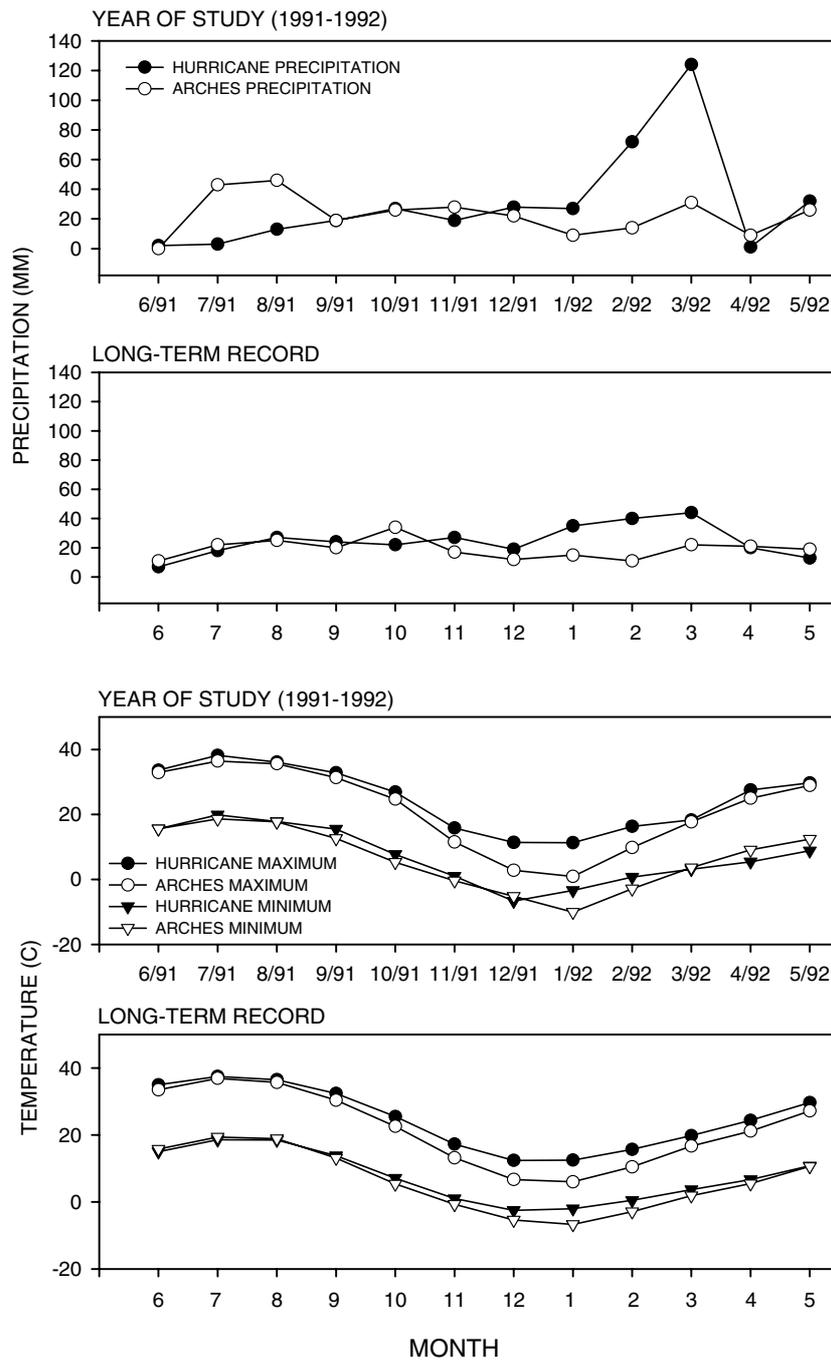


Figure 1. Monthly precipitation during the year of the study, long term mean monthly precipitation, mean monthly maximum and minimum temperatures during the year of the study, and long term mean monthly maximum and minimum temperatures for the Hurricane and Arches Study Sites, represented by data from the LaVerkin Utah and the Arches National Park Headquarters Utah National Aeronautic and Oceanic Administration reporting stations (data from Western Regional Climate Center: www.wrcc.dri.edu).

lower-viability Hurricane lot. Each group of seeds was planted at a depth of 15–20 mm to simulate a surface cache that a scatter-hoarding rodent would

deposit (VanderWall 1993). At each site, 10 blocks of artificial caches were laid out at the same time the retrieval experiments were installed, i.e., in

mid-July 1991. Within each block, six artificial caches were planted for each seed population for a total of 12. For each seed population, half of these caches were covered with hardware cloth cones as described above to prevent rodent predation, while the remaining caches were marked with nails but left unprotected. The artificial cache experiments were scored by counting the number of seedlings in each cache on 10 occasions during the period from October 1991 through September 1994.

### *Statistical analyses*

Preliminary analysis of data from the seed storage experiment showed that the ultra-freezer and cold room storage treatments were not significantly different, nor were the sealed and unsealed high temperature storage treatments. Data from these two sets of treatments were therefore combined for analysis of covariance (ANCOVA) with storage temperature, chilling treatment, and population as the class variables, storage duration as the continuous variable, and germination percentage as the dependent variable. Germination data from an earlier experiment with recently harvested seeds of these lots (Pendleton and Meyer, 2004) were used as the data for the storage duration zero weeks. Percentage (proportional) data were arcsine-transformed to decrease heterogeneity of variance prior to analysis. Examination of a graphical portrayal of the resulting sets of regression lines suggested that storage at 35 °C for 10 months had a negative impact on seed vigor as measured after chilling, and the analysis was repeated without this treatment combination. Both versions of the analysis are presented in the ANOVA results. Slopes of the regression lines for the three temperature treatments were then regressed on storage temperature to test the hypothesis that dormancy loss rate would increase as a function of temperature in this species (Bauer et al. 1998). The storage temperature for the combined low temperature treatments was considered to be 0 °C for this analysis, on the rationale that the slow rate of change below freezing would not be a function of the extremely low temperature used, as there was no significant difference in the rates of change at -80 and 2 °C. Data used for calculating the slope for 35 °C

storage used in this analysis did not include the anomalous result discussed above.

The factorial experiment was analyzed using fixed effects analysis of variance (ANOVA) for a completely randomized design, with each treatment sequence handled as a separate treatment for the treatment main effect, and with seed population as the other main effect. Arcsine-transformed germination percentage (proportion) was the response variable. Means separations for the treatment main effect were generated using the Student–Newman–Keuls criterion. Treatment means are also presented for the two seed populations used in the field studies.

The seed retrieval experiment was analyzed using partially nested ANOVA (Quinn and Keough 2002) with study site, seed population, and retrieval date as fixed main effects and block nested within site as a random effect. Arcsine-transformed percentages of field-germinated, germinable, and dormant seeds were the response variables.

The emergence study was also analyzed using partially nested ANOVA with study site, seed population, and protection (caged or uncaged) as fixed main effects. Block (position) nested within site was considered a random effect. Response variables were maximum number of seedlings emerged and number of seedlings surviving at 12 and 30 months after emergence.

## **Results**

### *Laboratory storage experiment*

*Coleogyne ramosissima* seedlots became less dormant during dry storage, both in terms of their ability to germinate at optimum temperature without chilling and in terms of their response to a 2-week chill (Table 3, significant storage duration main effect; Figure 2). The storage temperature by storage duration interaction was also significant; the reason for this significant interaction was faster dormancy loss and therefore a steeper slope at higher storage temperatures. The significant chilling treatment main effect showed that a 2-week chill was effective in removing dormancy regardless of the stage of after-ripening of the seeds (which did not become completely non-dormant without chilling during the storage intervals used

Table 3. ANCOVA results for the seed storage experiment, conducted with and without the anomalous data from the 10-month high temperature storage chilling treatment (see text for explanation).

Main effect/interaction	With anomalous data			Without anomalous data		
	df	F-value	p-value	df	F-value	p-value
Seed population	3, 160	21.69	0.0001	3, 152	21.75	0.0001
Chilling treatment	1, 160	201.59	0.0001	1, 152	198.37	0.0001
Storage duration	1, 160	103.29	0.0001	1, 152	100.40	0.0001
Storage temperature × storage duration	2, 160	4.86	0.0089	2, 152	5.12	0.0070

The continuous variable was storage duration, the class variables were seed population, chilling treatment (with and without a 2-week chill), and storage temperature, and the response variable was the arcsine-transformed germination fraction after 4 weeks at 5/15 °C. Only significant ( $p < 0.05$ ) effects are included in the table.

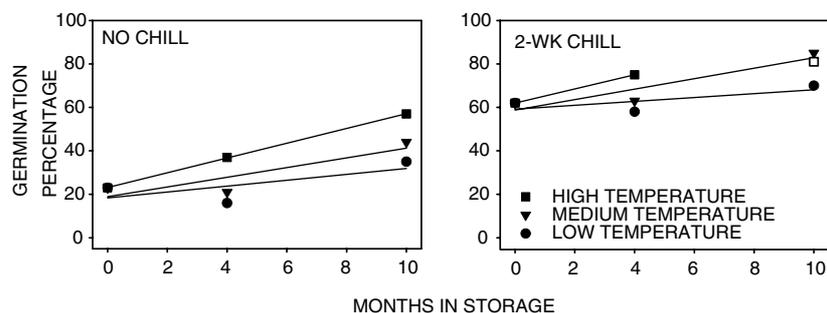


Figure 2. Mean germination percentages for seeds from four blackbrush populations stored for 0, 4, and 10 months under three temperature regimes: low (0 °C), medium (20 °C), and high (35 °C), then incubated at 5/15 °C for 4 weeks with and without a prior 2-week chilling treatment at 2 °C. The plotted regression lines are from ANCOVA (see Table 3). The open box symbol for 10 months of storage at high temperature followed by a 2-week chill was not included in the calculation of the slope for the high temperature treatment (see text for explanation).

in this experiment). The slopes of change in dormancy at the different storage temperatures did not change as a consequence of chilling, only the intercept, as indicated by the lack of any significant chilling interactions. The slopes plotted in Figure 2 reflect this fact, as they are identical for chilled and unchilled seeds at each storage temperature. Similarly, while the seed population main effect was significant, indicating different levels of initial dormancy among the four seed populations, there were no significant population interactions. These four populations responded similarly to both dry storage and chilling, so that there was no net change in their relative dormancy rankings as a result of these treatments (data not shown).

When the slopes of the lines representing rate of dormancy loss at each temperature were plotted as a function of temperature, a linear relationship was obtained (after-ripening rate (months<sup>-1</sup>) = 0.0000522 (storage temperature) +

0.0136,  $df = 1$ ,  $R^2 = 0.989$ ,  $p < 0.10$ ), lending support to the hypothesis that dormancy loss rate increases as a function of temperature for *C. ramosissima* seeds, as it does for seeds of other species (Bauer et al. 1998; Meyer et al. 2000).

#### Laboratory factorial experiment

When *C. ramosissima* seeds were subjected to a series of treatment sequences with or without chilling prior to incubation, both the treatment and population main effects were highly significant, as was the treatment by population interaction, indicating that seed populations responded differently or at least to different degrees as a consequence of these treatments (Table 4).

Subsequent germination of unchilled seeds at optimum temperature was negatively affected by incubation at high summer temperature, i.e., this treatment induced some degree of secondary

Table 4. ANOVA results for the germination experiment with 10 seed populations and 20 combinations of superoptimal-temperature incubation, chilling, drying, and freezing treatments.

Effect	df	F-value	p-value
Seed population	9, 600	19.53	0.0001
Treatment	19, 600	119.95	0.0001
Population × treatment	171, 600	2.32	0.0001

The response variable was arcsine-transformed germination fraction after 4 weeks at 5/15 °C.

dormancy (Figure 3). This secondary dormancy was alleviated, however, if the seeds were dried after high temperature incubation, then rehydrated for

incubation at the optimum. Treatment sequences that included freezing tended to decrease dormancy in unchilled seeds, i.e., freezing substituted for chilling in this case. High summer temperature incubation prior to freezing and drying after freezing actually enhanced the dormancy-breaking effect of freezing, while combining all three treatments gave an effect similar to freezing alone. Thus all treatments that included freezing increased germination in unchilled seeds, and only high temperature incubation followed immediately by incubation at optimum temperature resulted in a decrease.

Drying seeds after a 2-week chill decreased subsequent germination at the optimum (induced

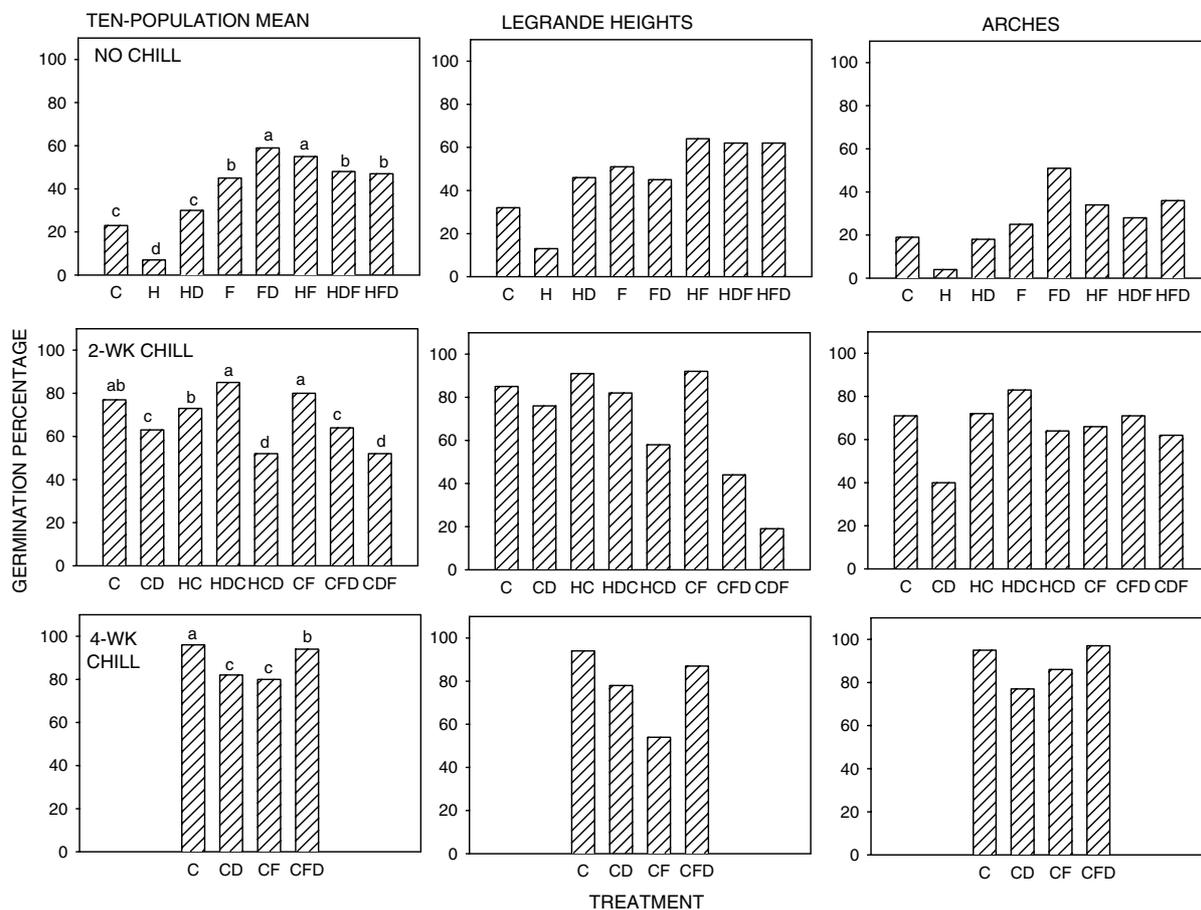


Figure 3. Mean germination percentages for seeds from 10 blackbrush populations, and from the LeGrande and Arches populations considered individually, after chilling for 0, 2 or 4 weeks in combination with a series of pretreatments and post-treatments, followed by a 4-week incubation at 5/15 °C. For each chilling duration, C = chilling treatment (control in the case of no chill), H = pre-incubation at high (superoptimal) temperature, F = post-treatment freezing, and D = post-treatment drying. The sequence of symbols indicates the sequence of treatments. For 10-population means within each chilling duration, treatments with columns headed by the same letter are not significantly different at the  $p < 0.05$  level (Student–Newman–Keuls means separation criterion).

Table 5. ANOVA results for the seed retrieval experiment.

Effect	Effect df	Error df	Field-germinated fraction		Germinable fraction		Dormant fraction	
			F-value	p-value	F-value	p-value	F-value	p-value
Seed population	1	2	0.60	n.s.	0.22	n.s.	2.65	n.s.
Study site	1	2	2.93	n.s.	2.52	n.s.	0.67	n.s.
Date	5	10	270.0	0.0001	48.25	0.0001	2.28	n.s.
Population × site	1	2	62.48	0.0001	0.26	n.s.	0.57	n.s.
Population × date	5	10	1.61	n.s.	1.55	n.s.	1.65	n.s.
Site × date	5	10	23.3	0.0001	5.67	0.0098	2.35	n.s.
Population × site × date	5	10	4.73	0.0178	0.85	n.s.	4.50	0.0208

The experiment was analyzed as a partially nested mixed model ANOVA. Data were arcsine-transformed for analysis. Block main effect and interactions were not significant (not shown).

secondary dormancy), whereas high temperature incubation treatment before chilling, with or without subsequent drying, had no significant effect (Table 4, Figure 3). But if the seeds were dried after the high temperature-chilling treatment sequence, germination decreased relative to chilling followed by drying alone. Freezing had no effect alone, but when freezing was combined with drying following chilling, germination percentages decreased. Only treatments that included drying after chilling induced secondary dormancy in seeds chilled for 2 weeks. When seeds were chilled for 4 weeks, subsequent freezing or drying reduced germination percentages.

In summary, drying after chilling almost always had a negative effect regardless of the chill duration. Freezing had a positive, chill-substituting effect on germination of unchilled seeds, little effect on seeds chilled for 2 weeks, and a negative effect on seeds chilled for 4 weeks. These interactions between freezing, chilling, and drying would tend to have a normalizing effect on germination phenology in the field. Drying tends to reset the chilling clock and prevent precocious germination, whereas freezing substitutes for chilling under scenarios where chilling might be inadequate but is not additive with chilling when chilling periods are longer.

A comparison of the responses of two contrasting seed populations to the set of treatment sequences shows that the treatment by population interaction was due mainly to differences in degree of response (Figure 3). In the treatment set for unchilled seeds, the patterns of these two populations were very similar to the 10-population mean pattern, but the Arches population was more

dormant overall than the Hurricane (LeGrande) population. For seeds chilled 2 weeks, the Arches seeds were more sensitive to drying after chilling than the Hurricane seeds, but this effect was alleviated by freezing, whereas for the Hurricane seeds, treatments that included freezing and drying after chilling resulted in decreased germination percentages relative to chilling and drying alone. After 4 weeks of chilling, the Hurricane seeds were more adversely affected by freezing than the Arches seeds, but their responses were otherwise similar.

#### *Field seed retrieval experiment*

In the field seed retrieval experiment, ANOVA's for dormant seed percentage, germinable seed percentage, and field-germinated seed percentage showed significant second and third order interactions among study site, seed population, and retrieval date main effects, indicating that the traits of the two seed populations interacted with contrasting environments at the two study sites to produce distinctive phenological patterns of dormancy loss and field germination (Table 5). The pattern of decreasing dormancy through the summer and fall was similar at the two sites (Figure 4). The Hurricane seed population was less dormant initially than the Arches population, and the two seed populations lost dormancy at a similar rate under the relatively dry conditions of summer and fall, so that the Hurricane seed population showed lower dormancy in October. Seeds from both populations were completely non-dormant at both study sites by mid-January, and

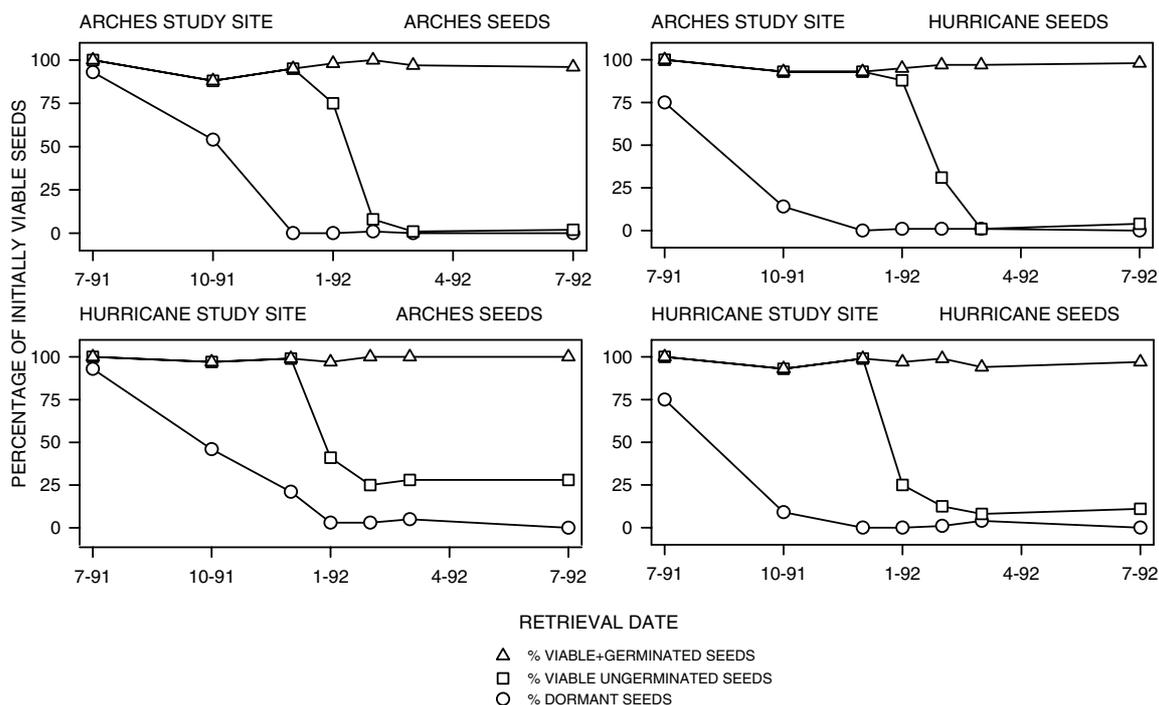


Figure 4. Dormant seed percentage, viable ungerminated seed percentage, and viable plus germinated seed percentage for seeds collected from the Arches and Hurricane Study Sites, placed into retrieval experiments at the two study sites in a reciprocal design in July 1991, and retrieved at intervals during the following year. The viable ungerminated seed percentage represents the dormant seed percentage plus the non-dormant (germinable) seed percentage. The viable plus germinated seed percentage represents the sum of the dormant seed percentage, the germinable seed percentage, and the field-germinated seed percentage. See Table 5 for statistical analysis.

only the Arches seed population at the Hurricane study site showed dormancy (21%) in mid-December. There was no evidence for the induction of secondary dormancy. Under field conditions encountered by the seeds and at the temporal scale of sampling we used, the trend toward lower dormancy through time was unidirectional in all cases.

The size of the germinable fraction at first increased through time as seeds became less dormant, then decreased as seeds germinated (Figure 4). At Hurricane, under mild conditions with winter rain (Figure 1), field germination began in mid-January and was essentially complete by mid-February. Not all the seeds germinable by laboratory standards succeeded in germinating in the field. The size of the germinable fraction at the end of spring at Hurricane was much larger for the Arches seed population (30%) than for the Hurricane seed population (<10%), suggesting that these seeds were still

functionally dormant under field conditions, though able to germinate in the laboratory after 4 weeks of continuously optimal conditions. This failure to germinate later in the spring was not due to a lack of spring moisture, which was well above average that year at the Hurricane study site (Figure 1).

At Arches, the winter was exceptionally cold (Figure 1), and the seeds were snow-covered through most of January and February. Under these conditions, seeds of the Arches population germinated more quickly than those of the Hurricane population. Germination began in mid-January for the Arches population and was largely complete by mid-February, whereas the germination of the Hurricane seed population did not really start until mid-February and was not complete until mid-March. Arches seeds were able to germinate more quickly beneath the snow than Hurricane seeds. Seeds of both populations germinated to near 100% in the field at Arches.

Table 6. ANOVA results for the field emergence study.

Effect	Effect df	Error df	Maximum seedling number		Twelve-month survival		Thirty-month survival	
			F-value	p-value	F-value	p-value	F-value	p-value
Population	1	18 (16)*	1.18	n.s.	7.15	0.0155	5.29	0.0352
Site	1	18 (16)*	97.7	0.0001	83.4	0.0001	52.8	0.0001
Protection	1	18 (16)*	52.8	0.0001	144.3	0.0001	70.4	0.0001
Population × site	1	18 (16)*	7.87	0.0117	9.92	0.0055	9.67	0.0067
Population × protection	1	18 (16)*	0	n.s.	0.15	n.s.	0.10	n.s.
Protection × site	1	18 (16)*	0.63	n.s.	60.6	0.0001	43.1	0.0001
Population × protection × site	1	18 (16)*	1.09	n.s.	0.54	n.s.	0.75	n.s.
Block (site)	18 (16)*	160 (144)*	1.71	0.0417	3.10	0.0001	4.16	0.0001
Protection × block (site)	18 (16)*	160 (144)*	2.50	0.0013	–	–	1.94	0.0213

\*Degrees of freedom equal 16 and 144 for these effects and error terms for the variable 30-month survival because of loss of two blocks at the Hurricane Study Site.

The experiment was analyzed as a partially nested mixed model ANOVA (Quinn and Keough 2002). Block interactions that were not significant are not listed. Dependent variables were maximum number of seedlings emerged and number of seedlings surviving 12 and 30 months after emergence.

#### Field seedling establishment experiment

In the seedling establishment experiment, the two independent variables that had the greatest effect on both maximum seedling number and number of seedlings surviving at 12 and 30 months were

study site and protection (caged vs. uncaged; Table 6). Emergence success was over three times higher at Arches than at Hurricane, with an average maximum of 10.3 seedlings per plot, which represents over 50% of viable seeds planted (Figure 5). At Hurricane, average maximum

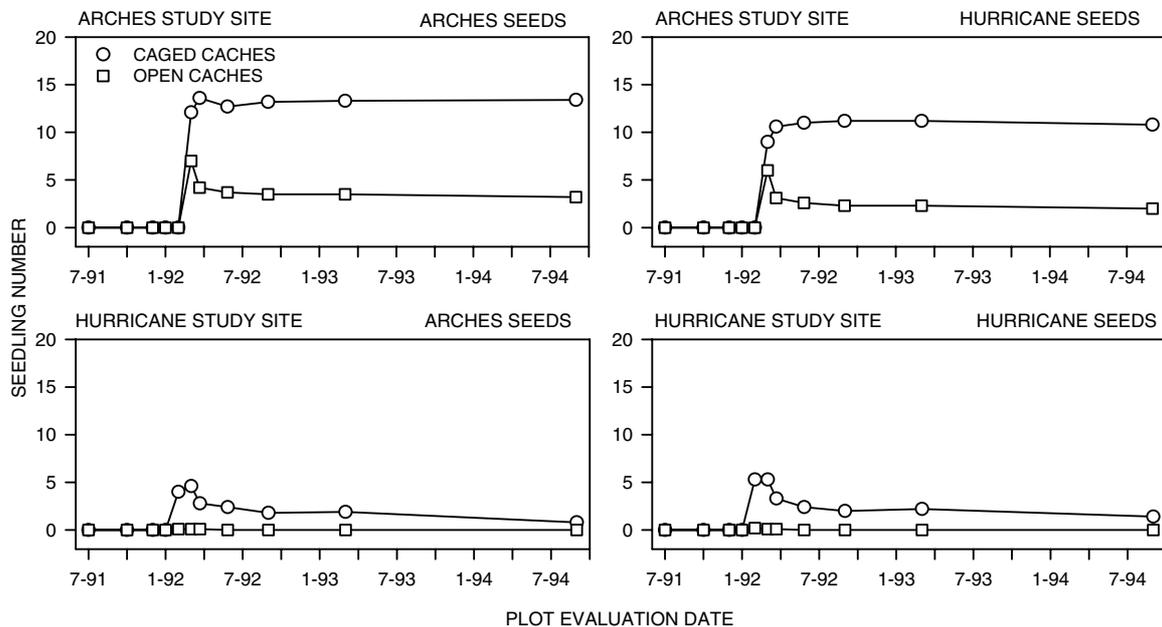


Figure 5. Number of seedlings present for seeds collected from the Arches and Hurricane Study Sites, placed into artificial cache experiments at the two study sites in a reciprocal design in July 1991, and scored at intervals through September 1994. Half the caches were caged with hardware cloth cones to protect them from rodent predation, while the other half were left unprotected in the open. See Table 6 for statistical analysis.

emergence was 3.0 seedlings per plot or 15% of viable seeds planted. There were substantially more seedlings emerging from protected (caged) caches than from unprotected caches (9.7 vs. 3.4). This difference was particularly marked at Hurricane, where mean maximum emergence in unprotected plots was only 0.2 seedlings per plot, as opposed to 5.8 seedlings per plot under cages. At Arches, protection doubled the number of successfully emerging seedlings (13.6 vs. 6.6 seedlings per plot). Numbers of seedlings surviving a year after emergence followed a similar pattern with regard to study site and protection.

Seed population *per se* had little effect on maximum emergence or number of seedlings surviving after 12 months, but in each case there was a significant interaction between seed population and study site (Table 6). These interactions were due to the fact that emergence and survival values were 20–30% higher at each study site for the seed population indigenous to that site. Maximum emergence for Arches seeds at Arches was 11.0 seedlings per plot, and number of seedlings surviving was 8.4 seedlings per plot. For Hurricane seeds at Arches, these numbers were 9.3 and 6.7. At Hurricane, maximum emergence for Hurricane seeds was 3.4 and number of seedlings surviving was 1.1. For Arches seeds at Hurricane, these values were 2.6 and 0.9.

Patterns of survival after 30 months also showed a significant site by population interaction (Table 6). After three summers at Arches, there was still an average of 8.3 seedlings per cache in Arches seed caches, while Hurricane seed caches averaged 6.4. At Hurricane, Arches caches averaged 0.4 seedlings while Hurricane caches averaged 0.7. For protected caches, these numbers were 13.4 for Arches at Arches, 10.8 for Hurricane at Arches, 0.8 for Arches at Hurricane and 1.4 for Hurricane at Hurricane.

The block (nested within site) effect was significant for all three response variables, indicating spatial heterogeneity at each site with regard to both microsite quality and rodent predation (Table 6). The significant interaction between block and protection for maximum number of seedlings emerging supports the idea that the degree of rodent predation on the seeds had a spatial component.

Seedling emergence began in mid-February at Hurricane and was largely complete by mid-

March, whereas at Arches it was initiated and peaked a month later, undoubtedly due to the colder, snowier weather (Figure 5). There was little seedling mortality in the caged treatment at Arches from the time of maximum emergence until the following spring. In the uncaged treatment there was a drop in seedling number from mid-March to mid-April due to rodent predation on sprouts, and then a levelling off, with little or no subsequent mortality during the following year. At Hurricane in the uncaged treatment, rodents finished off what few seedlings emerged, and there was no survival. Survival was also lower at Hurricane in the caged treatments, with about two-thirds of the cohort succumbing to death from unknown causes the first spring. There was little further mortality at Hurricane during the first year after emergence.

There was no further emergence from artificial caches, whether caged or not, in the subsequent spring (1993) at either Arches or Hurricane, even though 30% of the Arches seeds in the retrieval at Hurricane did not germinate the first spring. The spring of 1993 was exceptionally favorable in terms of precipitation. Seeds left ungerminated at the end of the first spring apparently were unable to function as a persistent seed bank that could generate emerged seedlings in subsequent years even under favorable conditions.

## Discussion

Our laboratory germination experiments were reasonably good predictors of *C. ramosissima* seed germination phenology in the field. *Coleogyne ramosissima* seeds from both study populations lost dormancy under mostly dry conditions in summer and early fall at similar rates, as predicted by the laboratory thermal after-ripening model, but because the Arches seed population was more dormant initially, it still retained some dormancy at the initiation of chilling. Under the colder chilling conditions under snow at Arches, the Arches seed population initiated and completed germination a month earlier than the Hurricane population. This result is in accord with our germination experiments with recently harvested seeds, which showed that seeds of Colorado Plateau populations germinate more quickly at near-freezing temperatures than seeds of Mojave Desert populations (Pendleton and Meyer, 2004). In

contrast, in response to the warmer winter rain scenario at Hurricane, the Hurricane seeds germinated to higher percentages in the field than the Arches seeds. Seed dormancy functioned to time germination during the first year after production, but not as a mechanism promoting carryover of seeds between years.

Emergence patterns for the two seed populations were similar at each site, but emergence at Hurricane took place in February, a month earlier than at Arches. Emergence phenology for *C. ramosissima* seems to be strongly weather-dependent. T. Graham (United States Geological Survey, Biological Research Division, Moab, Utah, unpublished data) reported that *C. ramosissima* seeds produced in a masting event at Arches in 1987 emerged the following November in response to heavy autumn rains, a result that agrees with our finding that the seeds lose dormancy prior to chilling in the field. Beatley (1974), on the other hand, reported *C. ramosissima* seedling emergence in response to spring rains. It appears that *C. ramosissima* seeds can germinate any time during the cooler part of the year, as soon as moisture become non-limiting. The seeds are highly dormant at summer temperatures soon after dispersal and are therefore not likely to germinate in response to summer rain (Pendleton and Meyer, 2004). Many warm desert species have a broad range of potential germination phenologies, but usually are cued to be either warm-season or cool-season germinators (Bowers 1994). *C. ramosissima* falls in the latter category.

*Coleogyne ramosissima* seeds are long-lived in storage; we obtained over 80% germination after 15 years of warehouse storage for a seedlot from southwestern Utah (Pendleton and Meyer, unpublished data). But we found no clear evidence that *C. ramosissima* seeds form a persistent seed bank in the field. Seed populations indigenous to each of the two study sites germinated to near 100% during the first spring following seed production. The Arches seeds germinated to only 70% at Hurricane, and the remainder were alive at the end of the first spring, but we saw no further emergence in subsequent springs, indicating that these seeds did not effectively carry over across years, even with protection from predation. Our hypothesis that *C. ramosissima* seeds do not form persistent seed banks is thus tentatively supported.

A species whose seeds and seedlings are at high risk from rodent predation would likely not be adapted for carrying over a small fraction of mast year production, as those seeds would no longer benefit from the protection afforded by the seed surplus from the previous masting event.

Our hypothesis that rodent predation would have a major impact on *C. ramosissima* seeds and seedlings was also supported. Establishment success at each of the two study sites was a consequence of the interplay of rodent predation and abiotic factors. At Arches, where the field experiments were placed in a small opening in a large contiguous population of adult plants, the mast effect apparently lowered but did not eliminate predation on unprotected caches. Maximum emergence in protected caches averaged 68% of initially viable seeds, while only 33% emerged in unprotected caches. Assuming equivalent emergence success of remaining seeds, rodents at Arches took 51% of the seeds from unprotected caches prior to emergence. Another 15% suffered rodent-caused mortality (sprout-grazing) as seedlings for a total of 66% loss to rodents. At Hurricane, maximum emergence from protected caches was much lower, only 29%, but emergence from unprotected caches averaged only 0.2 seedlings, for an estimated pre-emergence predation of 96%. Post-emergence predation raised this value to near 100%, as no seedlings survived outside cages at Hurricane. The much higher seed predation at Hurricane may have been due to the fact that the experiment was installed on a larger disturbance with smaller adjacent *C. ramosissima* stands, so that seeds were not present at satiating levels. It is also possible that rodent population levels were higher at Hurricane, but we have no data to address this possibility. The seed-eating rodent communities at both sites are comprised of a mixture of heteromyid and non-heteromyid species and show similar levels of diversity (J. Auger, unpublished data; Table 1). Similar strongly contrasting levels of seed predation at two sites were reported for *Simmondsia chinensis* in Sonora (Castellanos and Molina 1990).

The Hurricane site also proved to be harsher in terms of presumably abiotic factors influencing emergence and survival, though it is not clear from weather data for the two sites exactly why this was so (Figure 1). In addition to reduced emergence from protected caches at Hurricane (29% vs. 68%

as mentioned above), survival was also lower at Hurricane. Only 36% of the seedlings that emerged in protected caches were alive at the end of the first year. After three summers, survival was reduced to 19%. In contrast, at Arches, there was remarkably little mortality for emerged seedlings in protected caches, with 98% surviving the first year and 89% surviving after three summers.

The reduced first-year survival at Hurricane is especially puzzling in light of above-average spring precipitation there (Figure 1). Precipitation at Arches closely tracked the average, yet survival was astonishingly high. The seedlings grew in clusters that averaged 13 plants, but there was little or no sign of self-thinning even after three summers. This suggests that *C. ramosissima* seedlings are adapted to grow in close proximity to one another (Howe 1989). Perhaps the high initial density of seedlings in caches at Arches created a local microenvironment that actually increased survival there. Such an adaptation would be advantageous in a species dependent on scatterhoarding rodents for dispersal (VanderWall 1994).

Unprotected caches at Arches showed lower survival of emerged seedlings than protected caches after 12 and 30 months (53 and 39% respectively). A substantial portion of this difference was due to rodent-grazing on the sprouts early the first spring (Figure 5). Even seedlings that survived grazing could have had lowered subsequent survival due to root damage from the extensive digging that accompanied the search for seeds in caches late in the winter. Also, it is possible that the cages protected the seedlings from other herbivores as well as shading them to some degree. The smaller number of emerging seedlings per cache may also have contributed to reduced survival, as postulated above.

While there were differences in survival at the two sites, the percentages of seedlings surviving for 30 months was much higher than seedling survival percentages generally reported for desert shrubs (Sheps 1973; Ackerman 1979; Sherbrooke 1989). Most emergence flushes in established stands of desert shrubs apparently result in little or no recruitment. The high survival in our experiment was probably largely due to the fact that we placed the artificial caches on disturbances, far from the competitive influence of mature shrubs. Hunter (1989) found drastic differences in survival and growth for *Ambrosia dumosa* on a disturbance vs.

in established stands. Survival on the disturbance averaged 65%, while it averaged less than 5% in the established stand. This suggests that the function of seed production in desert shrubs is not regular recruitment into established stands, which may effectively be 'full', but as a reservoir for recolonization in the event of stand loss, or perhaps to provide propagules to establish into gaps that result from the death of mature individuals, resulting in slow but measurable turnover in stable populations of mature plants (Crisp 1978; Eldridge et al. 1990; Milton 1994; Bowers et al. 1995).

There were significant differences between the two seed populations in our study in terms of germination and emergence phenology, and these resulted in contrasting patterns of survival at the two sites. The Arches seed population germinated earlier at Arches and showed higher emergence percentages than the Hurricane seed population, whereas the Hurricane seed population germinated to higher percentages than the Arches seed population at Hurricane. These differences persisted as differences in numbers of surviving individuals after 12 and 30 months, but the relative magnitude of the site by seed population interaction did not change appreciably, i.e., the proportion of emerged seedlings surviving was similar for the two seed populations at each site. Differences between the two seed populations detectable in this study were thus in traits that affected germination and emergence phenology, not seedling ecophysiological traits that would influence post-emergence survival. Under the field conditions that pertained in 1991–1992, each seed population had a significant adaptive advantage when planted at its site of origin, averaging 20–30% more seedlings emerging and 30–75% more seedlings establishing than the seed population from the contrasting site. This shows that habitat-correlated variation in germination timing regulation in *C. ramosissima* (Pendleton and Meyer, 2004) is relevant to seedling performance in the field, and supports the hypothesis of ecotypic differentiation in establishment strategy in this species.

The small but significant increases in establishment success for locally adapted seeds were overshadowed in our study by the major differences in emergence and survival at the two sites. Both seed populations showed much higher emergence and survival at the cold desert Arches study site. We have observed similar patterns in the distribution

of juvenile cohorts across a range of sites (Meyer and Pendleton, unpublished data). Successful recruitment apparently occurs much more frequently on the Colorado Plateau than in the Mojave Desert, especially in established stands, a finding that supports our hypothesis that this species may be shifting its elevational distribution upward in response to a long-term warming trend.

### Acknowledgments

We gratefully acknowledge the technical assistance of Stephanie Carlson and Bettina Schultz. We thank Janene Auger for trapping and identifying rodents at the study sites and for many fruitful discussions of heteromyid-*C. ramosissima* interactions. Jayne Belnap provided early encouragement and logistical support, and Tim Graham shared his unpublished data on *C. ramosissima* seedling establishment. Officials at the National Park Service, Southeastern Utah Group, in Moab, Utah, and at Arches National Park kindly provided us with permits for carrying out research in the park and otherwise facilitated our work. We also thank Rhean Pendleton for use of the Hurricane site.

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