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Seed Germination Biology of Intermountain Populations of Fourwing Saltbush (*Atriplex canescens*: Chenopodiaceae)

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Abstract: Fourwing saltbush (*Atriplex canescens*) is a widely distributed shrub of semiarid western North America. We studied viability and germinability of fourwing saltbush seeds over 10 years for collections from 23 Intermountain populations. Fruit fill averaged 53 percent, and 96 percent of filled fruits contained viable seeds even after 6 years of laboratory storage. Seed collections were generally dormant to some degree at harvest and lost dormancy via two processes, moist chilling and after-ripening in dry storage. Prolonged chilling (24 wks) substituted for dry after-ripening, resulted in germination percentages similar to those obtained without chilling after 2 years of storage. Collections from warm desert habitats were generally least dormant, while collections from pinyon-juniper and mountain brush habitats were highly dormant. But these trends were not very strong. Seeds of the diploid population from Jericho Dunes were essentially nondormant at harvest, while those from a population near Page, Arizona, were essentially completely dormant. Unchilled seeds did not germinate to any degree until tested after 10 years of storage. Patterns of dormancy loss suggest that this species is opportunistic and generally able to establish in response to either winter or summer precipitation. In addition, its seeds probably form persistent seed banks in the field.

Introduction

Fourwing saltbush (*Atriplex canescens*) is one of the shrub species most widely seeded for reclamation, revegetation, and habitat improvement throughout the semiarid western United States (McArthur and Monsen 2004). It has proven to be relatively easy to establish from direct seeding, even on harsh disturbances, and it provides valuable forage for all classes of livestock as well as wild ungulates. Its seeds are easily collected in large quantities and readily cleaned and planted with commercial equipment. Perhaps because of this ease of use, the species has received relatively little study in terms of germination and establishment ecology (reviewed in Meyer on line). The classic work of Springfield (1970) remains the most detailed study of fourwing saltbush germination biology to date. He worked primarily with southwestern collections from summer rainfall areas and perhaps for this reason, recognized the role of dry after-ripening, but not moist chilling, in alleviating seed dormancy.

Fourwing saltbush is a fall to early winter ripening species, with fruits maturing earlier at higher elevations and later at lower elevations. The fruits often over-winter on the plants and are thus unavailable for germination the first spring after production. Whether they germinate soon after dispersal in spring, in response to summer rains, in response to winter chilling, or in later years depends on post-dispersal dormancy status and its interaction with the local environment.

In this study, our goal was to examine variation in the dormancy status of freshly harvested fourwing saltbush seed collections to determine the relative impact of moist chilling and dry after-ripening on dormancy status and to relate any differences in primary dormancy and patterns of dormancy loss to habitat at the site of seed origin. We also wanted to look for differences in initial viability and in patterns of viability loss among seed collections. Our collections were made in the primarily winter precipitation regions of the Great Basin, Snake River Plains, Uinta Basin, Colorado Plateau, and Mojave Desert (table 1).

Methods

Seed collections were made in the fall of 1988. A total of 27 collections were made, but four collections were subsequently dropped from the study because of very low fruit fill (< 20 percent). Seed collections were obtained from four states and from the full range of habitat types where fourwing saltbush occurs (table 1). Fruits of each collection were de-winged on a rubbing board and cleaned by screening and fanning prior to the initiation of experiments. As a rough estimate of initial viability, we performed a cut test on 200 randomly selected fruits from each lot.

Experiments with seeds designated as recently harvested were begun in January of 1989, within 3 to 8 weeks of the harvest date, depending on individual collection dates. For each treatment, eight replications of 25 fruits were included. For each replication, fruits were placed in 100 mm plastic Petri dishes between two blue germination blotters (Anchor Paper, St. Paul MN) and moistened with tap water initially and as needed during the course of the experiment. The treatments were: no chilling, 4 weeks of chilling, and 24 weeks of chilling. Chilling took place in the dark (in boxes) in a walk-in cold room at 2°C, while post-chilling incubation, also in the dark, was carried out for 4 wks at 15°C. Germination was

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Table 1. Collection locations and habitat types for 23 *Atriplex canescens* seed collections included in the study. Collection locations are approximate.

Collection location	State	Habitat type
Littlefield	Arizona	Creosote bush shrubland
Glendale	Nevada	Creosote bush shrubland
Kingman	Arizona	Creosote bush shrubland
Snow's Canyon	Utah	Blackbrush shrubland
Santa Clara	Utah	Blackbrush shrubland
Page	Arizona	Blackbrush shrubland
Torrey	Utah	Salt desert shrubland
Caineville	Utah	Salt desert shrubland
Roosevelt	Utah	Salt desert shrubland
Nampa	Idaho	Sagebrush steppe
Jordan Valley	Idaho	Sagebrush steppe
Niagra Springs	Idaho	Sagebrush steppe
Burley	Idaho	Sagebrush steppe
Ephraim	Utah	Sagebrush steppe
Wales	Utah	Sagebrush steppe
Elberta	Utah	Sagebrush steppe
Jericho Dunes	Utah	Sagebrush steppe
Cedar Canyon	Utah	Pinyon-juniper/mountain brush
Beaver Canyón	Utah	Pinyon-juniper/mountain brush
Starvation	Utah	Pinyon-juniper/mountain brush
Gay Mine	Idaho	Pinyon-juniper/mountain brush
Book Cliffs	Utah	Pinyon-juniper/mountain brush
Winnemucca	Nevada	Pinyon-juniper/mountain brush

recorded weekly in the 24-wk chilling treatment and during post-chilling incubation for all treatments. Seeds were considered germinated when the radicle visibly protruded from the tip of the fruit. At the end of the incubation period, remaining fruits in each dish were subjected to a cut test to determine their viability. Germination proportion for each treatment and replication was calculated based on the total number of viable seeds in the dish.

Fruits of each of the 23 collections were stored unsealed under laboratory conditions (20 to 22°C, ca. 30 to 35 percent relative humidity) for 10 years following the initial germination experiment. Germination tests were carried out after 1, 2, 6, and 10 years of storage. The experiments at 1 and 2 years were similar in design to those for recently harvested seeds, except that 4 replications of 50 seeds were included for each treatment and collection. After 6 years, the 23 collections were subjected to the no chilling treatment only. At the end of the incubation treatment, these seeds were evaluated for viability using tetrazolium chloride in addition to a simple cut test, that is, fruits whose seeds appeared filled were stained to determine seed viability. After 10 years, four replications of 25 seeds for each collection were subjected to the no chilling and 4-week chilling treatments. These seeds were not subjected to a post-incubation cut test. We used initial viability values in the calculation of germination percentages for the 10-year data.

We analyzed our data using analysis of covariance for completely randomized designs with seed collection as the class variable and seed age (storage period) and chilling duration as continuous variables. Two analyses were performed. The first was a complete factorial using the data for recently harvested, 1-year-old, and 2-year-old seeds. These were the experiments that included all three chilling durations. The second analysis was for the no chilling treatment only and included data for recently harvested seeds and seeds 1, 2, 6, and 10 years old. This approach gave two balanced designs. We did not analyze the 4-wk chilling data for the 10-year-old seeds beyond calculation of means and standard errors because it became apparent that the effects of dormancy loss and vigor loss were confounded in this treatment. Germination proportions were arcsine-transformed to improve homogeneity of variance prior to analysis.

Simple *t*-tests were used to compare means obtained from different measures of viability, that is, initial cut test, post-germination cut tests at 1 and 6 years, and tetrazolium viability evaluation at 6 years.

Principal components analysis (PCA) was performed using germination percentages from each of the 12 treatment combinations for each of the 23 seed collections as variables. The goal was to detect groups of collections with similar germination responses and to examine whether these groups could be interpreted ecologically. Because all the variables were in the same units, we performed PCA on the non-standardized correlation matrix. Scores from the first two principal components were plotted for each collection, and eigenvector loadings on these two principal components were used in the interpretation of the resulting scattergram.

Results

Viability Evaluation

Initial viability as estimated by fruit fill varied from 35 to 75 percent across collections, with a mean of 52.3 percent (table 2). This value was closely matched by the viability estimate based on germinated seeds plus filled seeds remaining from experiments with recently harvested seeds (52.0 percent mean). Viability percentages based on post-germination cut tests from the experiment with 6-year-old seeds were similar (54.3 percent mean). More importantly, the viability percentage based on tetrazolium staining at 6 years was also very close

Table 2. Mean percentage of viable seeds for 23 *Atriplex canescens* collections included in the study, as determined by initial cut test to determine fruit fill, post-germination cut tests on recently harvested and 6-year-old fruits, and post-germination tetrazolium staining for 6-year-old fruits.

	Viability percentage		
Viability measure	Mean	Standard error	Range
Initial fill estimate	52.3	2.25	35-75
Post-test fill estimate - recently harvested seeds	52.0	2.73	27-72
Post-test fill estimate - 6-year-old seeds	54.3	2.81	31-74
Tetrazolium viability - 6 year old seeds	52.0	2.69	30-72
Tetrazolium viability as percentage of filled fruits	95.8		

to these values (52 percent). The four viability estimates are not significantly different from each other. This means that the cut test is an excellent estimate of viability for fourwing saltbush seeds from 1 to 6 years of age, and that seeds in this study did not lose any significant viability overall during this period. Tetrazolium viability at 6 years averaged 96 percent of viability estimated by cut test.

Viability at 10 years was not explicitly measured, but decreases in germination percentage relative to the 6-year data suggest that seeds of some lots were beginning to lose vigor. This interpretation is supported by the fact that in many of these collections, a 4-wk chilling treatment actually resulted in a substantial decline in germination percentage relative to the no chilling treatment. This effect was rarely seen in earlier experiments.

Germination Experiments

Both moist chilling and dry after-ripening resulted in increases in germination percentage overall (fig. 1). In the factorial experiment with seeds up to 2 years old, both chilling and seed age main effects were highly significant, as was their interaction (table 3). Longer chilling periods were especially effective in breaking the dormancy of recently harvested collections. After a year in storage, germination in both the no chill and 4-wk chill treatments increased substantially, while the increase in response to 24-wk chilling was smaller. After an additional year in storage, there was little further change in response to no chill and 4-wk chill treatments, while the response to a 24-wk chill increased.

There was also a significant increase in the fraction of seeds that could germinate without chilling as the storage period increased (seed age main effect highly significant; table 4). After 6 years of storage, germination of unchilled seeds was almost as high as the germination percentage after 24 weeks of chilling for 2-year-old seeds (fig. 1). These results show that chilling can be an important mechanism of dormancy removal for recently dispersed seeds, but that dry after-ripening will eventually render most of these seeds germinable without chilling. Chilling thus serves as a substitute for dry after-ripening in recently dispersed seeds. The net effect of these processes is to ensure a nondormant seed fraction available for germination in response to both winter and summer germination-triggering precipitation events. It also ensures

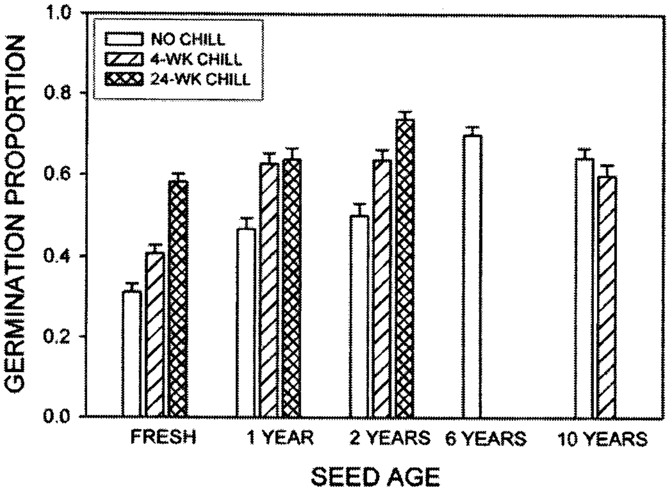

Figure 1. Mean germination proportions (averaged across 23 collections of *Atriplex canescens*) for 12 combinations of seed age and chilling duration. For each treatment combination, seeds were incubated for 4 weeks at 15°C following the seed storage and chilling treatments. Germination data are expressed as proportion of viable seeds. Standard error bars are shown for each mean.

Table 3. Analysis of covariance based on a completely randomized design for germination experiments with 23 collections of *Atriplex canescens* in which seeds of each collection were tested when recently harvested and after 1 and 2 years of laboratory storage. For each seed age, three chilling durations were included: no chilling, 4 weeks of chilling, and 24 weeks of chilling.

Source of Variance	d.f.	Mean square	F-value	P-value
Seed collection	22	1.4679	33.23	<0.0001
Seed age	1	9.3949	212.70	<0.0001
Chilling duration	1	10.7489	243.36	<0.0001
Seed collection x seed age	22	0.1943	4.40	<0.0001
Seed collection x chilling duration	22	0.3031	6.86	<0.0001
Seed age x chilling duration	1	0.5075	11.49	0.0007
Seed collection x seed age x chilling duration	22	0.0831	1.88	0.0083
Error	1012	0.0442		

Seeds were incubated at 15°C for 4 weeks after each treatment sequence, and germination proportion was scored as a fraction of viable seeds. Data were arcsine transformed for analysis. Seed age and chilling duration are treated as continuous independent variables in the analysis, while seed collection is considered a class variable.

Table 4. Analysis of covariance based on a completely randomized design for germination experiments with 23 collections of *Atriplex canescens* in which seeds were tested when recently harvested and after 1, 2, 6 , and 10 years of storage. Seeds were incubated for 4 weeks at 15°C.

Source of Variance	d.f.	Mean square	F-value	P-value
Seed collection	22	0.7771	24.39	<0.0001
Seed age	1	8.6748	272.31	<0.0001
Seed collection x seed age	22	0.0969	3.04	<0.0001
Error	506	0.0319		

Germination data are based on viable seed proportion determined at the end of each test with one exception. For the 10-year data, germination is based on the proportion of fruits initially viable as determined by an *a priori* cut test on recently harvested seeds. Data were arcsine transformed for analysis. Seed age was treated as a continuous independent variable in the analysis, while seed collection was considered a class variable.

that not all seeds in a cohort will germinate in response to the same triggering event. Instead, germination may be spread across seasons and probably even across years.

The trend toward increasing germination percentages with increasing seed age did not hold for the 10-year data. Instead, percentages dropped slightly, and there was a trend for decreased germination after chilling. These effects are probably an indication of decreasing seed viability and vigor in 10-year-old lots.

There was tremendous variation among seed collections in terms of dormancy status at harvest and response to dormancy breaking treatments (highly significant seed collection main effects and interactions; tables 3, 4). We chose to group the collections in terms of their habitat of origin, then look for common patterns that could be interpreted ecologically. Such patterns were only sometimes in evidence, but examining collection responses by habitat enabled us to extract some meaningful generalizations from this complex data set.

Fourwing saltbush seed collections made in warm desert creosote bush (*Larrea tridentata*) habitats were relatively nondormant at harvest (51 to 77 percent without chilling; fig. 2). They generally changed very little in dry storage over 2 years, but after 6 years achieved germination from 76 to 95 percent without chilling. They showed little viability loss after 10 years.

Fourwing saltbush seed collections made in warm desert fringe blackbrush (*Coleogyne ramosissima*) habitats were extremely variable in their germination responses (fig. 3). They were generally more dormant at harvest than collections from creosote bush habitats, but showed sharply contrasting responses to chilling. The Santa Clara collection achieved germination of 86 percent after chilling when recently harvested, while at the other extreme the collection from Page, Arizona, germinated to only 4 percent when recently harvested regardless of chilling regime. The Page collection did not acquire any substantial ability to germinate without chilling until after 10 years of storage, and by that time was losing vigor, as indicated by the precipitous drop in germination after a 4-wk chill. The other two collections behaved more like collections from the creosote bush habitat, with generally small and inconsistent change in dormancy status and chilling responsiveness over the first 2 years, then a jump

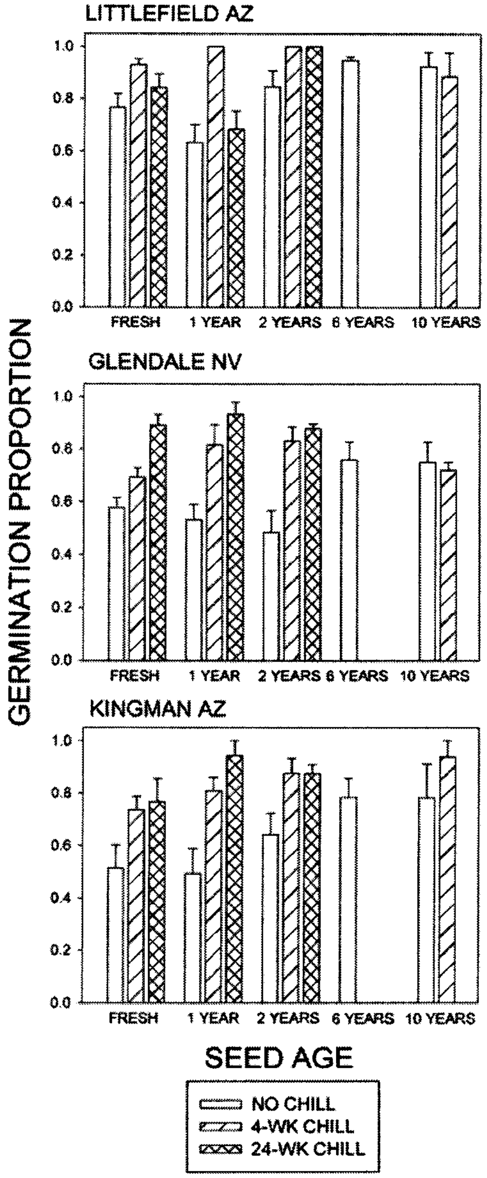

Figure 2. Germination proportions for three *Atriplex canescens* seed collections from the creosote bush shrubland habitat type following 12 combinations of seed age and chilling duration. For each treatment combination, seeds were incubated for 4 weeks at 15°C following the seed storage and chilling treatments. Germination data are expressed as proportion of viable seeds. Standard error bars are shown for each mean.

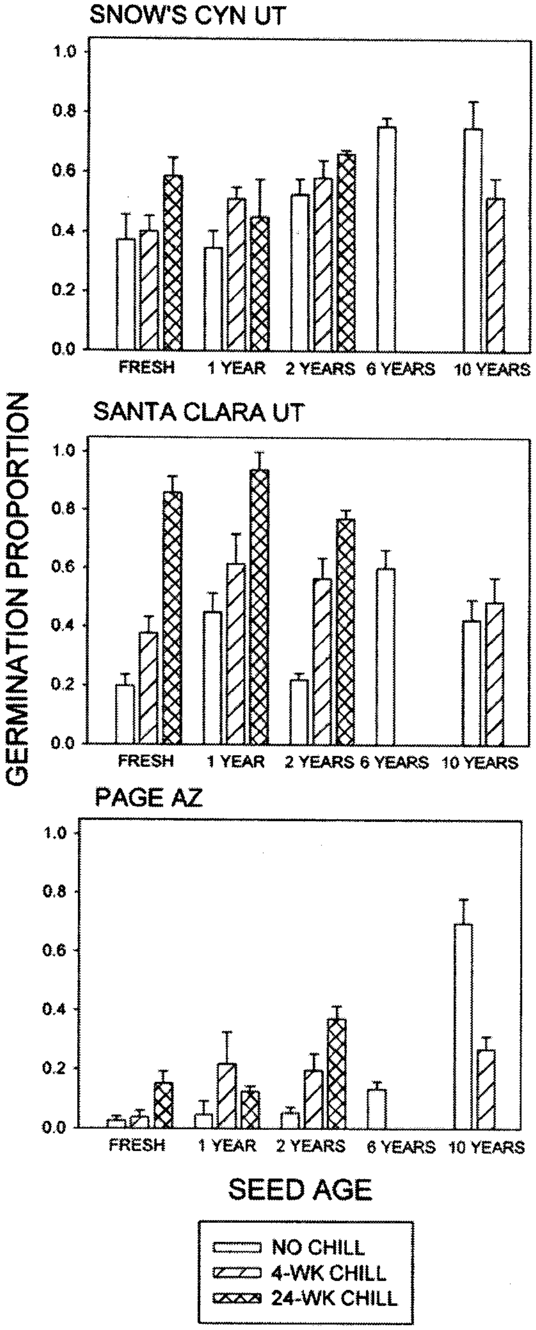

Figure 3. Germination proportions for three *Atriplex canescens* seed collections from the blackbrush shrubland habitat type following 12 combinations of seed age and chilling duration. For each treatment combination, seeds were incubated for 4 weeks at 15°C following the seed storage and chilling treatments. Germination data are expressed as proportion of viable seeds. Standard error bars are shown for each mean.

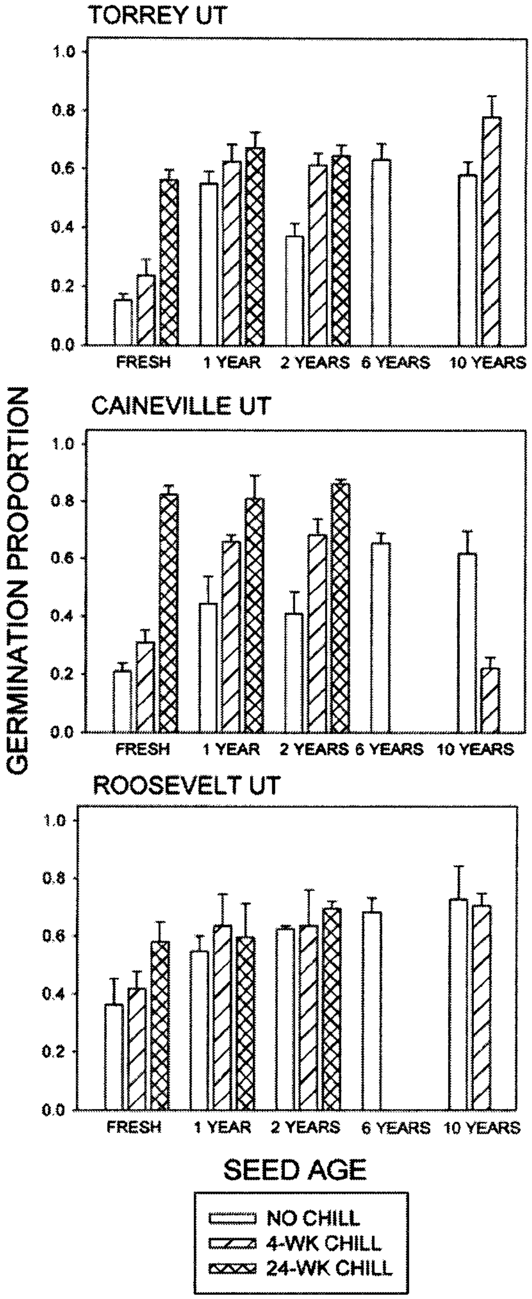

Figure 4. Germination proportions for three *Atriplex canescens* seed collections from the salt desert shrubland habitat type following 12 combinations of seed age and chilling duration. For each treatment combination, seeds were incubated for 4 weeks at 15°C following the seed storage and chilling treatments. Germination data are expressed as proportion of viable seeds. Standard error bars are shown for each mean.

at 6 years in the fraction able to germinate without chilling. Both these collections showed signs of decreasing viability after 10 years.

Fourwing saltbush collections made in salt desert habitats were generally more dormant at harvest than those from warm desert habitats (15 to 36 percent germination without chilling) and were not very responsive to short chilling (fig. 4). They varied in their response to long chilling; the Caineville collection was most responsive and the Roosevelt collection the least. Dormancy generally decreased in dry storage through 6 years, but maximum germination percentages without chilling were only moderate (63 to 68 percent) and chilling of short duration, as would be expected in this habitat, did little to increase total germination beyond these values.

Fourwing saltbush probably achieves its greatest abundance in sagebrush steppe habitats in the Intermountain West, a fact reflected in the larger number of collections we made in this habitat (table 1). Seven of the eight collections in this group followed a similar pattern (fig. 5). Their seeds were moderately dormant at harvest (16 to 50 percent germination without chilling) and lost dormancy steadily and usually quickly in dry storage (38 to 92 percent germination after 2 years). They were generally not very responsive to short chilling when recently harvested and showed variable response to long chilling. The eighth collection included in the sagebrush steppe group, from Jericho Dunes, was actually from a sand dune habitat embedded within the sagebrush type, and is also unusual in being diploid (Stutz and others 1975). It was the least dormant collection in the study, with germination from 85 to 100 percent regardless of seed age or chilling treatment (fig. 5).

Fourwing saltbush collections from foothill woodland or mountain brush habitats were uniformly dormant when recently harvested (germination without chilling 3 to 11 percent). The fraction germinable without chilling increased steadily through time but never achieved high values (54 to 62 percent). Seeds were moderately chilling-responsive when recently harvested (21 to 45 percent maximum germination after chilling). The fraction to germinate in response to chilling generally showed incremental increase through time over the first 2 years (fig. 6).

Principal Components Analysis

The first principal component from PCA accounted for 77 percent of the total variance, and the eigenvector loadings for all 12 variables were positive and of similar magnitude. PC1 basically represents a scale of increasing overall germinability (decreasing dormancy), with the most dormant collection (Page) at the left hand extreme and the least dormant collection (Jericho Dunes) at the right hand extreme (fig. 7). In fact, scores on PC1 are highly correlated with mean germination percentages (averaged across 12 treatments), with an r-value of 0.982 (d.f.=21, p<0.0001). The high eigenvalue (77 percent) for PC1 reflects the fact that the germination variables tend to be correlated, sometimes highly correlated.

Other than the two anomalous collections (Page and Jericho Dunes), collections from different habitats form a reasonably orderly progression along PC1, with the more dormant foothill collections grouped to the left, the less dormant creosote bush shrubland collections grouped to the right, and the intermediate sagebrush steppe, salt desert shrubland, and blackbrush shrubland collections in the middle (fig. 7).

PC2 accounts for only an additional 9 percent of the total variance, so scores on this PC are less important for interpretation than scores on PC1. They do have a clear interpretation, however. The eigenvector loadings for PC2 are all either near zero or negative, except for the loadings for the three 24-week chilling response variables, which are all positive and large. This can be interpreted to mean that collections with high scores on PC2 responded more to 24-week chilling than collections with low scores. All six foothill collections were intermediate in this respect, and form a tight group on the graph (fig. 7). The remaining collections did not show any clear relationship to habitat in terms of their scores on PC2. For example, Snow's Canyon and Santa Clara, both from blackbrush shrubland, had similar germination percentages overall and similar scores on PC1. But they differed widely on PC2, because Santa Clara seeds tended to respond positively to 24 week chilling, while Snow's Canyon seeds did not (fig. 3).

Discussion

We can safely conclude that both moist chilling and dry after-ripening play important roles in seed dormancy regulation for Intermountain populations of fourwing saltbush. Chilling is especially important as a mechanism of dormancy removal for recently dispersed seeds, but most seeds eventually become nondormant through the process of dry after-ripening.

Levels of primary dormancy and patterns of change in dormancy status as a function of both chilling and dry after-ripening varied dramatically among collections. With the notable exception of the collections from Page and Jericho Dunes, there was a general pattern of increasing primary dormancy and decreasing maximum germination percentages in the progression from warm desert to foothill habitats. Most collections from creosote bush dominated sites seemed to be composed of a sizeable fraction able to germinate at the first opportunity and a smaller fraction that became germinable after short chilling or short-term after-ripening. Seed bank carry-over across years seems unlikely in this group, except that in this dry environment, wet conditions that last long enough to trigger germination of non-dormant seeds may not be encountered in any given year. Particularly in a heterogeneous seed bed, many seeds may find themselves in microenvironments that dry very rapidly at germination-conducive temperatures. A 4-week period of moist chilling may be equally unlikely. Thus the seeds may not need elaborate dormancy protections in order for a fraction to persist across years.

At the other end of the spectrum, collections from foothill pinyon-juniper and mountain brush habitats were highly dormant at dispersal and achieved relatively low germination percentages even after prolonged chilling. Chilling continued to be incrementally effective as a dormancy-breaking treatment even in seeds stored 2 years. This response pattern would tend to limit emergence to the spring in these cold winter environments, where the winter chilling period lasts much longer than 4 weeks and occasionally even as long as 24 weeks, and where frost risk to fall-emerging seedlings is high. Seed bank carryover across years is assured in these environments by virtue of the fact that there is always a chilling non-responsive fraction, even after a very long chilling period.

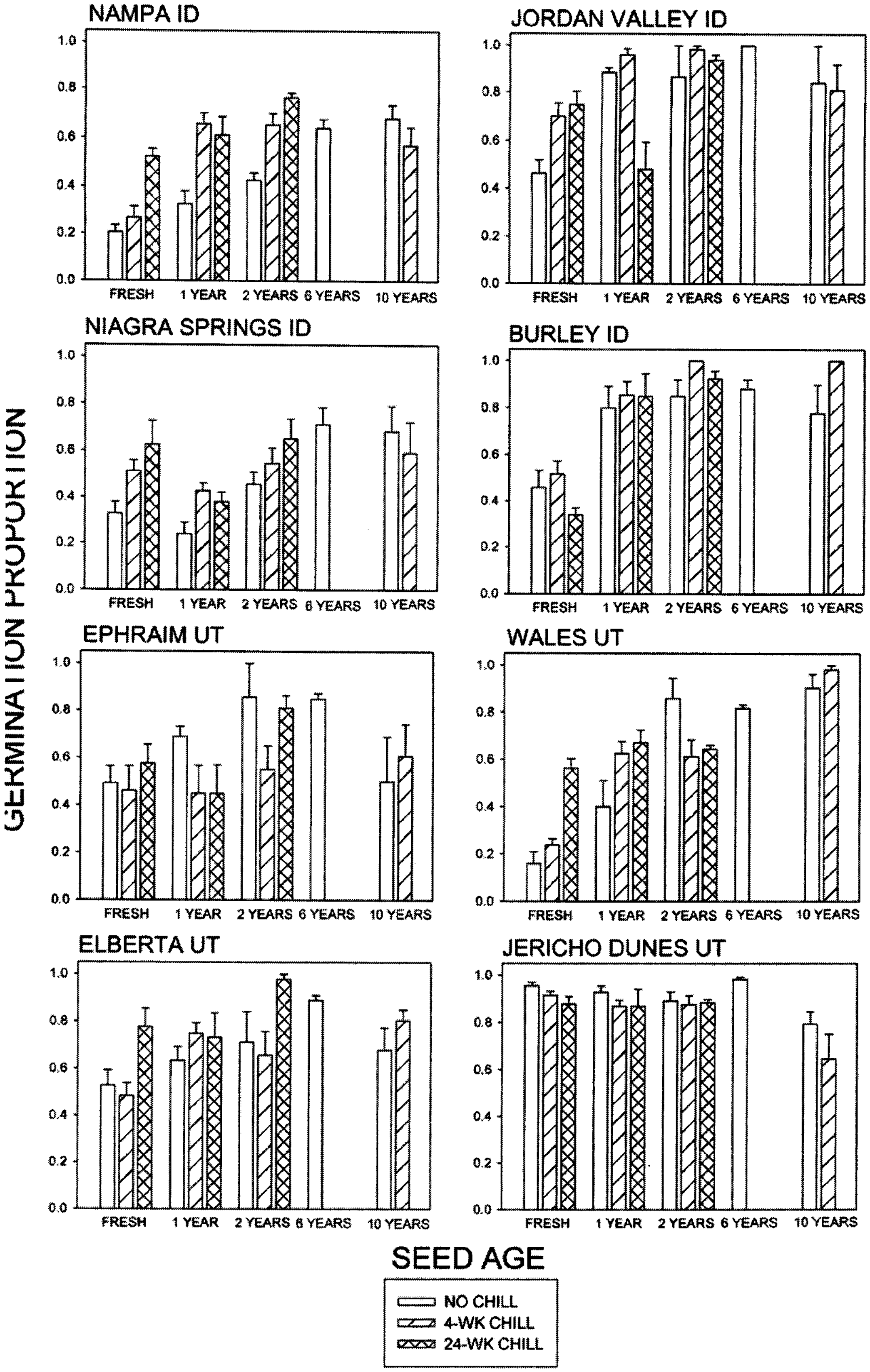

Figure 5. Germination proportions for eight *Atriplex canescens* seed collections from the sagebrush steppe habitat type following 12 combinations of seed age and chilling duration. For each treatment combination, seeds were incubated for 4 weeks at 15°C following the seed storage and chilling treatments. Germination data are expressed as proportion of viable seeds. Standard error bars are shown for each mean.

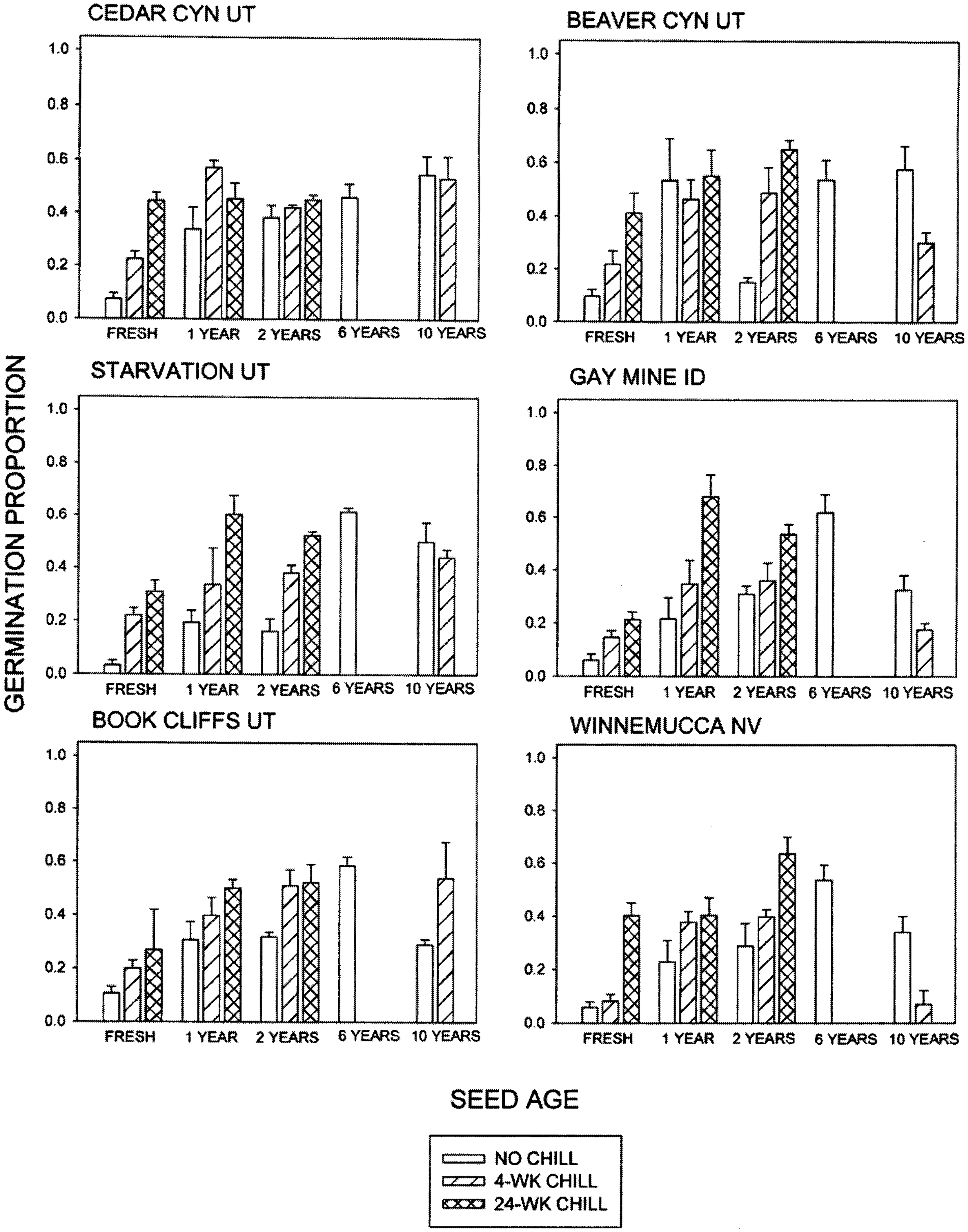

Figure 6. Germination proportions for six *Atriplex canescens* seed collections from the pinyon-juniper woodland/mountain brush habitat type following 12 combinations of seed age and chilling duration. For each treatment combination, seeds were incubated for 4 weeks at 15°C following the seed storage and chilling treatments. Germination data are expressed as proportion of viable seeds. Standard error bars are shown for each mean.

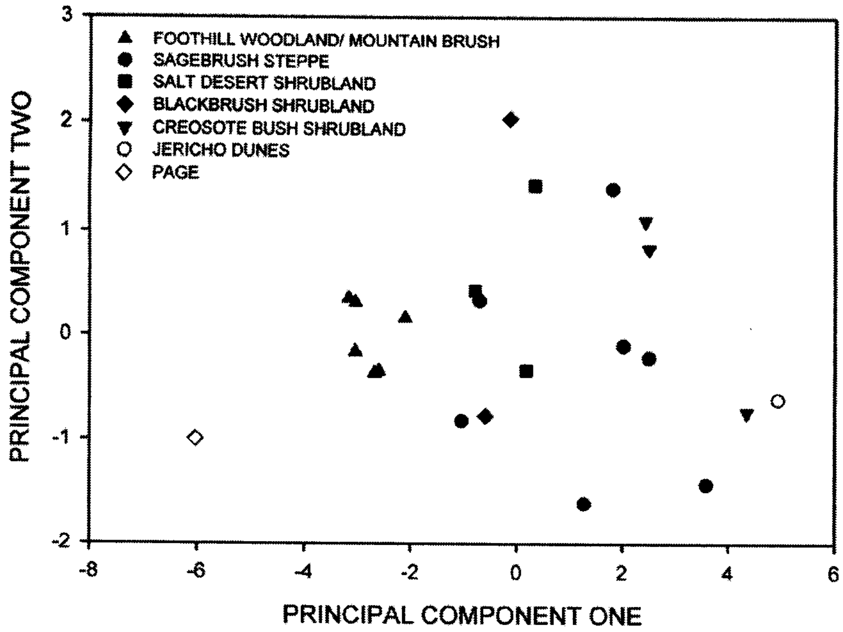

Figure 7. Principal components analysis based on *Atriplex canescens* seed germination data. Scores on the first two principal components for each of the 23 populations were used to create the plot. These two principal components accounted for 86 percent of the total variance. Symbols correspond to plant communities where the seed collections were made. Two unfilled (white) symbols correspond to populations with anomalous germination responses (see text for explanation).

Germination patterns for the numerous collections from intermediate blackbrush shrubland, salt desert shrubland and sagebrush steppe habitats were much more variable and difficult to generalize. The seeds tended to be intermediate between the warm desert and foothill groups in primary dormancy, to lose dormancy fairly rapidly in dry storage, and to reach intermediate to high final germination percentages under test conditions. An explicit ecological interpretation of these results would require much more detailed knowledge of the climate at particular collection sites, as well as additional experiments under a broader array of test conditions.

Because of the large number of collections in our study, we were limited in terms of the number of treatments we could apply, so that extrapolation of our laboratory results to the field must be done cautiously. Seeds under field conditions experience a changing temperature and moisture environment. For example, the rate at which seeds dry after-ripened in our experiment is only an index of the after-ripening speed under one uniform condition. While this index is useful in making comparisons among collections, it is almost certain that temperature will have a strong positive effect on after-ripening rate in fourwing saltbush, as it does in the related species shadscale (*Atriplex confertifolia*; Garvin and Meyer 2003). Similarly, temperature and moisture conditions during chilling are not uniform under field conditions, and this variation, as well as time spent either above or below effective stratification temperatures, undoubtedly has an effect on the pattern of change in dormancy status. This limits our ability to interpret our results in the absence of a field study to corroborate our laboratory findings. However, we were able to successfully predict germination timing and seed bank carryover for shadscale seed collections from contrasting habitats placed under field conditions, using results of experiments similar to those described here (Meyer and others 1998). The predictions were verified in a field seed retrieval experiment, an approach that would be the logical next step in understanding dormancy loss and germination phenology in fourwing saltbush.

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