Annual seed dormancy cycles in two desert winter annuals

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Summary

1 Freshly matured seeds of *Eriogonum abertianum* Torr. and *Eriastrum diffusum* (Gray) Mason and those of both species exhumed after various periods of burial in the Chihuahuan Desert in Arizona, USA, were tested for germination in light and darkness at five thermoperiods.

2 Seeds of *Eriogonum* were nondormant (ND) at maturity in autumn 1988, and thus 87% of them germinated in light at 15/6 and at 20/10°C. Seeds entered conditional dormancy (CD) in winter; germination at 20/10°C decreased to 6% in light. However, a high percentage of the seeds were again ND by autumn 1990. Thus, like seeds of facultative winter annuals in humid, temperate regions, those of *Eriogonum* have an annual CD/ND cycle, which is characteristic of annuals in unpredictable habitats.

3 Seeds of *Eriastrum* were dormant (D) at maturity in May 1989. A portion of the seeds after-ripened during summer, and in October 65 and 38% of them germinated in light at 15/6 and 20/10°C, respectively. Most of the ND seeds re-entered dormancy during winter, but by the following October 92% of them were ND. Thus, like seeds of obligate winter annuals in humid, temperate regions, those of *Eriastrum* exhibit an annual D/ND cycle, which is characteristic of annuals in predictable habitats.

4 This is the first report of dormancy cycles in seeds of desert winter annuals.

Keywords: buried seeds, desert annuals, germination, dormancy cycles, seed dormancy

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Introduction

For an annual plant species to persist at a site, even if it has a long-lived seed bank, environmental conditions must at least occasionally be favourable for germination and completion of the life cycle. In some habitats, this favourable period is unpredictable, while in others it is highly predictable. Studies on germination responses of seeds exhumed after various periods of burial under natural temperature conditions in humid, temperate climates have shown that annual species in unpredictable vs. predictable habitats differ in their germination characteristics. The primary difference is that seeds of annuals in unpredictable habitats are nondormant (i.e. are capable of germinating over a wide range of conditions) or conditionally dormant (i.e. can germinate over a narrow range of conditions) throughout the year (e.g. Baskin & Baskin 1981, 1983a, 1984a; Roberts & Neilson 1982a,b), while those in predictable habitats exhibit annual dormancy/nondormancy cycles (e.g. Baskin & Baskin 1983b, 1984b). Dormant seeds do not germinate under any conditions. Thus, in habitats that become favourable for germination and completion of the life cycle at unpredictable times, seeds can germinate throughout the growing season for a species, but in predictable habitats germination is most likely to occur at the start of the favourable season – usually in either autumn or spring.

The high variability in amount and timing of yearly precipitation in desert ecosystems in the south-western United States (MacMahon 1988) means that habitat favourability for seed germination and completion of the life cycle of annual species is unpredictable. This unpredictability raises questions concerning germination characteristics of the seeds. Winter annuals are of particular interest because they germinate during the cool season of the year (which is predictable) but only after a significant rainfall event (which is unpredictable). Thus, do seeds of desert winter annuals undergo an annual dormancy/nondormancy cycle, as expected in a seasonally predictable habitat, or are they nondormant or conditionally dormant throughout the year, as expected in an unpredictable habitat?

Although numerous papers have been published on germination of desert plants (e.g. Barton 1936; Hammouda & Bakr 1969; Mott 1972; Gutterman 1983; Ismail & El-Ghazaly 1990), no one has buried seeds under natural conditions to determine if they do, or do not, undergo annual cycles in their germination responses. Thus, the purpose of our study was to ascertain the germination requirements throughout the year of seeds of the winter annuals *Eriogonum abertianum* Torr. (Polygonaceae) and *Eriastrum diffusum* (Gray) Mason (Polemoniaceae) collected and buried in the Chihuahuan desert near Portal, Arizona, USA.

Eriogonum abertianum grows in sandy plains, washes and granitic hills from western Texas to southern Arizona and south into northern Sonora and Chihuahua, Mexico (Shreve & Wiggins 1964; Correll & Johnston 1970). Thus, the species occurs in both the Sonoran and Chihuahuan deserts (Fox 1990). Seeds (achenes) germinate in late autumn or early winter after the soil has been moistened by cold frontal rainstorms (Fox 1989). Plants overwinter as rosettes and may flower the following spring (Fox 1989) and/or autumn (Davidson *et al.* 1985; Fox 1989).

Eriastrum diffusum is found in desert plains from western Texas to southern California south to northern Chihuahua, Sonora and Baja California, Mexico (Shreve & Wiggins 1964; Correll & Johnston 1970). Thus, this species also occurs in both the Chihuahuan and Sonoran deserts. Seeds germinate in autumn or early winter when soil moisture becomes nonlimiting (Chesson & Huntly unpublished data), and plants flower the following spring (Kearney & Peebles 1951; Shreve & Wiggins 1964; Correll & Johnston 1970).

Methods

Seeds of *Eriogonum* and *Eriastrum* were collected at a study site 8 km west of Portal, Arizona (Cochise Co.) in a small portion of the Chihuahuan Desert that extends into south-eastern Arizona (MacMahon & Wagner 1985). Freshly matured seeds and those exhumed after various periods of burial at a depth of 2 cm on nearly flat ground in the Chihuahuan desert study site were tested for germination. For burial, seeds were placed in fine-mesh nylon bags. Seed processing and testing were done at the University of Kentucky, and seeds were sent from, to and from the Chihuahuan desert by express mail. Seeds of *Eriogonum* were collected on 28 October 1988, and 12 bags containing approximately 3000 seeds each were buried on 24 December 1988. Seeds of *Eriastrum* were collected on 19 May 1989, and 24 bags containing about 1000 seeds each were buried on 6 June 1989. After burial, one randomly chosen bag of *Eriogonum* and three of *Eriastrum* seeds were exhumed on about the first day of each month (see Figs 1 and 2 for exceptions) for 14 and 16 months, respectively.

Germination tests were initiated on seeds of both species the day they arrived from Arizona. Seeds were placed in five incubators in light (= 14-h daily photoperiod (*c.* 20 μmol m^{-2} s^{-1}, 400–700 nm of cool white fluorescent light) and in darkness (= continuous darkness for duration of germination test). The incubators were set on 12/12 h daily thermoperiods of 15/6, 20/10, 25/15, 30/15 and 35/20°C. At each thermoperiod, the photoperiod extended from 1 h before the high temperature period began to 1 h after it ended. Seeds were incubated in 5.5-cm Petri dishes on white quartz sand moistened with distilled water. Three replicates of 50 seeds each were used for each treatment. The three replicates of *Eriogonum* seeds at each of the 10 test conditions came from the same bag, while each of the three replicates of *Eriastrum* seeds at each test condition came from a different bag. Dishes containing seeds to be incubated in light were wrapped individually with plastic film and placed on an incubator shelf. Dishes incubated in darkness were wrapped with plastic film and then with two layers of aluminium foil. Final germination percentages were determined after 15 days, and protrusion of the radicle was the criterion for germination.

Daily soil temperature and precipitation data were recorded at the study site from July 1989 through December 1990. A probe was buried at a depth of about 2 cm in bare soil, and the temperature was recorded every 30 s throughout each 24-h period. The records from 07.00 to 19.00 hours each day were averaged to obtain the daytime temperature, and those from 19.00 to 07.00 hours were averaged to obtain the night-time temperature.

Analysis

The data were analysed by analysis of variance. Arcsin transformation was found to stabilize the variances, and thus it was used throughout. A three-way analysis was used for the *Eriogonum* data, with the three factors being light/dark, temperature and date. The *Eriastrum* study differed slightly in design, because three randomly chosen bags were collected on each date. This allowed for a test of the possibility that peculiarities of an individual bag of seeds could influence germination. For example, such bag effects might result from spatial variation in the microenvironments to which bags were exposed in the field, even though every effort was made to keep the microenvironment uniform. Included in this could be variation in microbial or fungal activity. If such variation were present, and bags were not replicated, a false impression of temporal changes in germination might result.

The design of the *Eriastrum* germination trial for each date was in effect a randomized block experi-

ment with bags corresponding to blocks. A test for the block effect, in a randomized block analysis for each date, revealed no suggestion of a bag effect ($P > 0.3$) until the last two dates in the study, when the P-values for a bag effect were both less than 0.05. While these results suggest that a bag effect may develop, given enough time, an inspection of the data shows that the effect is nevertheless weak compared with the treatment effects. Moreover, a combined test over all dates for a bag effect, obtained by summing the sum of squares for each date, was not significant ($P = 0.1$). Thus, for analysis of treatment effects, bag differences were ignored, and the data were analysed by a three-way analysis identical to that used for the *Eriogonum*.

Results

Figure 1 shows the percentage of germination for both species at various times. The three-way analyses of variance for both species gave highly significant effects of the treatments and all interactions ($P < 0.0001$). The highly significant main effects mean that each of the separate factors (time, temperature and light/dark) was sufficiently strong that its effect was still apparent when averaged over other treatments in the study. The significant interactions, however, mean that the actual pattern of response to each factor depends on the levels of the other factors. In particular, the significant two-way interactions between temperature and time mean that the germination response to temperature changes with time, as is strikingly apparent from Fig. 1. The significant three-way interaction means that this pattern of change with time in germination response to temperature depends on whether the seeds were germinated in the light or the dark. The most biologically significant features of these patterns are as follows.

When seeds of *Eriogonum* were first tested (22 November 1988), they germinated to 87% in light at both 15/6 and 20/10°C, but to only 0–5% at all other test conditions (Fig. 1). During the study, germination at 15/6°C in light ranged from 61 to 94%, while germination at 20/10°C in light ranged from 6 to 87%, with the lowest percentages occurring in late winter and spring 1989. Germination at 25/15, 30/15 and 35/20°C in light and at 20/10, 25/15, 30/15 and 35/20°C in darkness ranged from 0 to 3% over the 16-month period. Germination at 15/6°C in darkness peaked at 37 and 74% during the winters of 1989 and 1990, respectively, and dropped to 0–3% during summer 1989.

When seeds of *Eriastrum* were first tested (27 May 1989), they germinated to 1% in light at 15/6°C, 1% in darkness at 20/10°C and to 0% at all other test conditions (Fig. 1). Some of the seeds after-ripened (came out of dormancy) during summer and early autumn of 1989, and by October (test started on 29 September) seeds germinated to 65 and 38% in light at 15/6 and 20/10°C, respectively; only 0–14% of the seeds germinated at the other test conditions. During late autumn and winter, a high percentage of the seeds re-entered dormancy (secondary dormancy), and by March 1990 seeds germinated to only 1–8% over the range of test conditions. Seeds after-ripened during summer and early autumn, and by October 1990 they germinated to 92 and 58% in light and to 63 and 42% in darkness at 15/6 and 20/10°C, respectively; 0–12% of the seeds germinated at the other test conditions.

Discussion

In winter annuals of humid, temperate regions, seasonal temperature shifts cause changes in the dormancy state of seeds. Summer temperatures (30, 25/15, 30/15, 35/20°C) promote after-ripening of
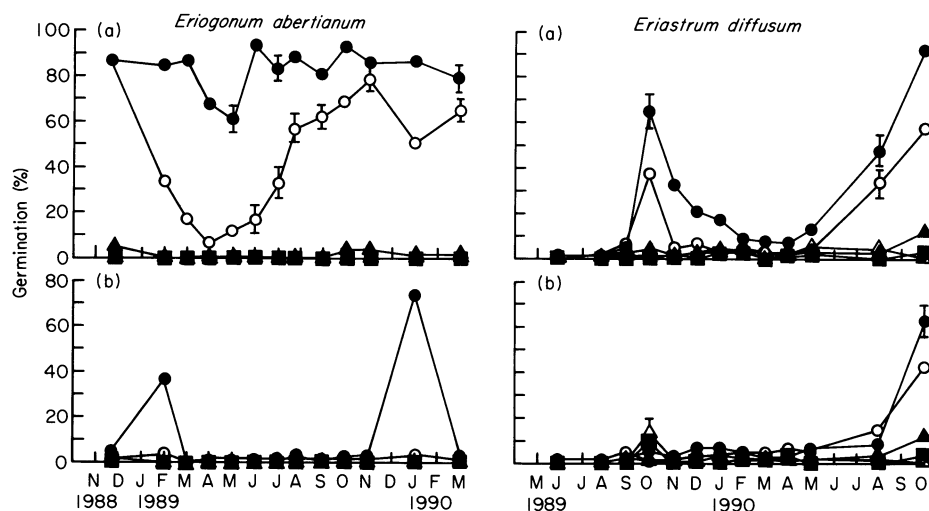

Fig. 1 Germination percentages (mean ± SE, if ≥ 5%) of *Eriogonum abertianum* and *Eriastrum diffusum* seeds incubated (a) at a 14-h daily photoperiod, or (b) in continuous darkness, for 15 days at 15/6°C (●), 20/10°C (○), 25/15°C (▲), 30/15°C (△) and 35/20°C (■) following 0–16 months of burial in the Chihuahuan desert in Arizona, USA.

dormant seeds, while winter temperatures (4, 5, 15/6°C) fully or partially inhibit after-ripening (Baskin & Baskin 1972, 1976, 1984a,b, 1986, 1990a; Roberts & Neilson 1982a,b). Further, low temperatures induce nondormant seeds of obligate winter annuals into secondary dormancy (Baskin & Baskin 1973, 1984b, 1990a), and they cause seeds of facultative winter annuals to enter conditional dormancy (Baskin & Baskin 1984a, Roberts & Neilson 1982a). Seeds that enter conditional dormancy lose the ability to germinate at high (35/20, 30/15, 25/15) but not at low (15/6, 20/10°C) temperatures (Baskin & Baskin 1981, 1983a,c, 1984a; Roberts & Lockett 1978; Roberts & Neilson 1982b). Thus, seeds of obligate winter annuals are dormant in spring (Baskin & Baskin 1983b, 1984b, 1990a,b), while those of facultative winter annuals are conditionally dormant and can germinate at spring temperatures (15/6, 20/10°C) in spring (Baskin *et al.* 1986).

Seasonal temperature shifts apparently cause the same kinds of changes in the dormancy states of seeds of desert winter annuals as they do in those of winter annuals in humid, temperate regions. Seeds of *Eriastrum* respond like those of obligate winter annuals, with a high percentage of the seeds after-ripening in summer. Furthermore, most of the seeds that fail to germinate in autumn enter secondary dormancy in winter, and this dormancy is broken the following summer. Thus, the majority of the seeds exhibit an annual dormancy/nondormancy cycle. It should be noted, however, that in the first summer of burial 35% of the seeds did not after-ripen, and in the second summer 8% did not after-ripen. The reason why all seeds of *Eriastrum* do not come out of dormancy each summer is unknown, but this also happens in some years in winter annuals of humid, temperate regions (Baskin & Baskin 1983b, 1990a,b).

Buried seeds of *Eriogonum* respond like those of facultative winter annuals, with nondormant seeds entering conditional dormancy in winter. Like facultative winter annuals of humid, temperate regions, when seeds of *Eriogonum* enter conditional dormancy they lose the ability to germinate to high percentages at high temperatures, which for *Eriogonum* is 20/10°C. Conditional dormancy was broken during summer, so this species has an annual conditional dormancy/nondormancy cycle.

Because a broad range of high temperatures break dormancy in seeds of winter annuals and a fairly wide range of low temperatures induces nondormant seeds into dormancy, year-to-year variations in temperature probably have little, or no, effect on the annual changes in dormancy state. Also, it is unlikely that yearly variations in precipitation have a large effect, if any, on annual changes in dormancy states. Seeds of winter annuals do not have to be imbibed to after-ripen; they will lose dormancy during dry storage on the laboratory

shelf (Baskin & Baskin 1971). Seeds of the winter annual *Draba verna* L. stored for 6 months at 0, 10 and 20% relative humidity (*RH*) failed to after-ripen but remained viable, at 30 and 40% *RH* they after-ripened to a low percentage, at 50 and 60% they after-ripened to a high percentage and at 70, 80, 90 and 100% *RH* the seeds died (Baskin & Baskin 1979). Although daytime *RH* in South-western deserts may be less than 30% (Wallis 1977), seeds on the soil surface would be exposed to increased *RH* at night. Further, buried seeds would be exposed to a higher *RH* than that of the air above the soil surface. The *RH* in soil is normally in the range of 95–100%, and only extremely dry, dusty soil will have *RH* <95% (Rawlins & Campbell 1986). Moisture requirements for induction of secondary dormancy have not been determined. However, even if they are relatively high, some precipitation is normal in the Chihuahuan desert in winter, and consequently seeds would have high moisture contents at least part of the time when they are exposed to low winter temperatures. Seeds of *Eriogonum* given wet/dry treatments for a 2-month period at 40 and 20°C germinated to higher percentages after they were kept continuously wet than those kept dry for 2 months (P. L. Chesson, unpublished data).

The time of rainfall is important for germination of seeds of *Eriogonum* and *Eriastrum*. In the autumn germination tests, both species germinated to higher percentages at 15/6°C than at any other thermoperiod, but these temperatures do not occur in the habitat until November and December (Fig. 2a). Although the Chihuahuan desert has a rainy season in July–September and another one from November–March (Davidson *et al.* 1985), only precipitation in autumn and winter would promote germination of seeds of *Eriogonum* and *Eriastrum* (Chesson personal observations). Actual precipitation at the study site is shown in Fig. 2(b). Temperatures during the summer rainy season are too high to permit germination of these winter annuals (Fig. 2a).

Because, in our study, buried seeds of both species lived until the second germination season following dispersal, they appear to have the potential to form persistent seed banks (*sensu* Grime 1981). A reserve of seeds would ensure persistence of the species at a population site, even if no seeds are produced in a given year(s). In a study of seed reserves in desert grassland in New Mexico (Dwyer & Aguirre 1978), *Eriogonum* failed to germinate in soil samples kept in a greenhouse from 26 March to 26 May, but germinated in the field in autumn. Because daily maximum and minimum temperatures in the glasshouse were 27–32 and 16–21°C, respectively, they were too high for germination of seeds of this species. Thus, even if seeds were present in the soil samples, they could not germinate.

The annual dormancy/nondormant cycle in seeds of *Eriastrum* means that there are times during the
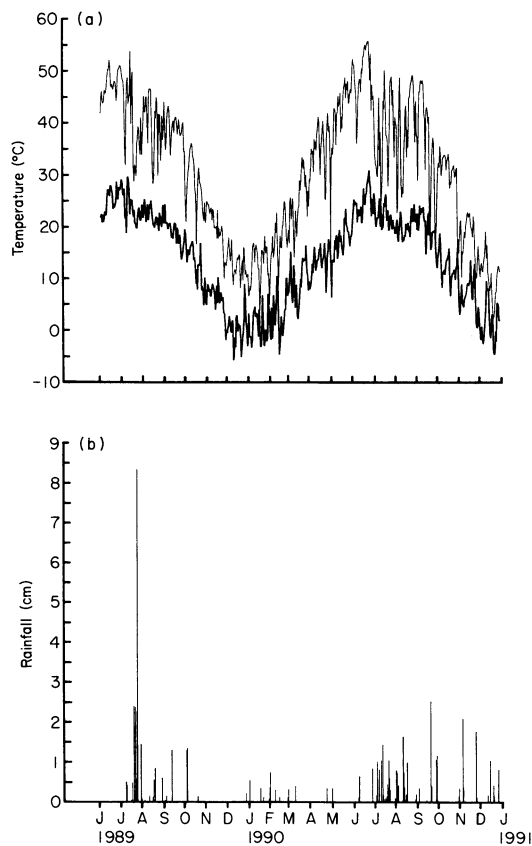
Fig. 2 (a) Mean daytime and nighttime temperatures recorded at a soil depth of 2 cm at the study site in the Chihuahuan Desert, 8 km west of Portal, Arizona. (b) Daily precipitation record.

mination of *Eriogonum* and *Eriastrum* seeds in darkness are similar to those recorded for *Lamium amplexicaule* L. which were not exposed to any light when they were exhumed (Baskin & Baskin 1984a). The implication of germination in darkness in autumn is that seeds can germinate while they are buried and that this would cause a gradual depletion of seed reserves. However, no seedlings of either *Eriogonum* or *Eriastrum* were found in the exhumed bags of seeds.

The annual conditional dormancy/nondormancy cycle in buried seeds of *Eriogonum* is characteristic of annuals living in unpredictable habitats, and the annual dormancy/nondormancy cycle in seeds of *Eriastrum* is characteristic of annuals living in predictable habitats. Thus, it appears that the Chihuahuan desert is an unpredictable habitat for *Eriogonum* and a predictable habitat for *Eriastrum*.

The often-quoted papers of F. W. Went and co-workers (e.g. Went 1949, Went & Westergaard 1949) have given the impression that precipitation (*via* leaching of germination inhibitors) and temperature are the only factors controlling germination of seeds of desert annuals. However, our research and that of others (Barton 1936; Mott 1972; Freas & Kemp 1983) show that seeds of desert winter annuals have internal dormancy control mechanisms physiologically similar to those of winter annuals of humid temperate regions. The concept of control of the timing of germination of desert winter annuals needs to be broadened.

Acknowledgements

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year when seeds of this species will not germinate regardless of environmental conditions, i.e. soil moisture and temperature can control germination only in autumn and early winter, after the seeds have lost their dormancy. However, the annual conditional dormancy/nondormancy cycle in seeds of *Eriogonum* means that temperature and soil moisture control germination throughout the year. An unanswered question is how many winter annuals in the Chihuahuan desert have dormancy–germination characteristics like those of *Eriastrum*, and how many have characteristics like those of *Eriogonum*? Obviously, more studies are needed on annual changes in dormancy states before we have a clear picture of the germination ecology of desert winter annuals.

Caution should be used in interpreting the results obtained from incubating seeds of *Eriogonum* and *Eriastrum* in darkness, because even partially imbibed seeds may be photostimulated by short exposures to light (McArthur 1978). If seeds of the two species were sufficiently hydrated to be light stimulated when they were exhumed, we would expect them to germinate to high percentages in darkness at 15/6°C. However, the autumn–winter peaks of ger-

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