DIFFERENCES IN SEED BIOLOGY OF ANNUAL PLANTS IN ARID LANDS: A KEY INGREDIENT OF THE STORAGE EFFECT

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Abstract. We used a combination of field studies and laboratory experiments to characterize key ecological aspects of the seed biology and soil seed bank dynamics of annual plant communities in chenopod shrublands of South Australia. A sequential study of the soil seed bank demonstrated seasonal and between-year variability in numbers and composition of the soil seed bank. Soil samples incubated under different temperature and watering regimes produced different communities, indicating that species respond differentially to various environmental combinations. Emergence was extremely low at low water availability and at high temperatures, even in trays with ample water. A high percentage of seeds of four out of five species buried in the field remained viable for two years, while the fifth, *Carrichtera annua*, showed a sharp decline in seed viability, reaching nearly zero survivorship. Our results indicate that, in this system, annual plant communities result from germination of a fraction of seeds present in the soil seed bank, when autumn or winter rainfalls occur. Because different species have different responses to various combinations of environmental conditions, the community composition varies from year to year. This variability is likely to be a component of coexistence through the storage effect.

Key words: Australia; deserts; environmental variability; seed banks; species coexistence; storage effect.

INTRODUCTION

In spite of their contribution to the biodiversity and function of arid systems, the ecology of annual plants and the factors that structure their communities are not well understood. Species-specific sensitivity of germination to environmental factors coupled with year-to-year variation in these factors produces the year-to-year variability in species composition commonly observed in these systems (Guo and Brown 1996, Pake and Venable 1996). These effects, when coupled with high persistence of ungerminated seed in the soil seed bank, have been hypothesized to be a major contributor to species coexistence by a mechanism called the storage effect (Chesson and Huntly 1989, Chesson et al. 2004). Storage effect theory defines the conditions necessary for temporal partitioning to promote species coexistence. Three factors are involved. First, there must be species-specific responses to the physical environment. Second, a positive response to the physical environment should lead to more competition (covariance between environment and competition). Third, some factor in the life history must buffer population growth against unfavorable periods.

Specific germination requirements can provide fine temporal niche partitioning, because germination requirements are often far more restrictive than requirements for vegetative growth and reproduction (Bazzaz 1996). Moreover, differences between species in germination responses to the physical environment is one of the simplest ways in which temporal partitioning can occur consistently with requirement of covariance between environment and competition. This is because the number of seeds germinating determines the density of competing seedlings and hence the intensity of competition for a given supply of resources. Thus, a detailed understanding of seedling emergence and seed bank persistence for the various species in a community of annual plants is critical to assess the possibility of coexistence by temporal partitioning, according to storage effect theory. However, with the exception of Adondakis and Venable (2004) there has been little previous attention to differences in germination behavior that would promote coexistence by the storage effect (Pake and Venable 1996).

Several studies report on the ecophysiology of germination of desert annual plants (Elberse and Breman 1989, 1990, Briede and McKell 1992, Gutterman 2000). Overall, desert annuals require relatively high water availability (Mott 1972; but see Briede and McKell 1992) and have adaptations that allow them to time their germination to the most favorable, and often more predictable, part of the year (Baskin et al. 1993, Clauss and Venable 2000). The tuning of emergence

to environmental conditions, achieved through dormancy with a physiological basis, is prevalent (Baskin et al. 1993, Gutterman 2000). In addition to responding to water, temperature, and light, seeds of some desert annuals undergo dormancy cycles controlled by the preceding temperature conditions (Baskin et al. 1993). This mechanism may prevent germination during brief periods of high water availability within the seasons when post-germination mortality risk is high (Pake and Venable 1996). The longevity of the seeds and the germination fraction of the different species are also important determinants of the system's dynamics since they influence the ability of the species to persist through a series of unfavorable years, not an uncommon event in arid lands.

In this paper we report results from a series of studies and experiments aimed to answer the following questions for the annual plant community of a chenopod shrubland of South Australia. (1) What is the composition of the soil seed bank of the system, and how does it change over two years? (2) How long do seeds of some key species remain viable in the soil? (3) How do temperature regime and water availability affect the emergence of species from the soil seed bank?

METHODS

Study site

The study was carried out at Middleback Field Centre, 16 km northwest from Whyalla, South Australia (32°57′ S, 137°24′ E). Details of the study site are described in Facelli and Brock (2000) and Facelli and Temby (2002). The area is characterized by hot summers and mild winters. The mean yearly rainfall is 223 mm (1923–2002), but between-year variability is large (from 92 to 623 mm in the same period). The winter rains are relatively predictable (CV for June–August = 85.51%), typically falling as a series of small and medium-sized rainfall events. Summer rainfall is far more variable (CV December–February = 145.23%) and tends to fall in few, large rainfall events.

The typical vegetation is an open *Acacia papyrocarpa* woodland with a sparse understory dominated by chenopod shrubs on brown calcareous soils with clay-loam (Facelli and Brock 2000). A large number of annual plants are found in the system (Facelli and Temby 2002), mostly growing during winter–spring in open spaces between shrubs. Currently the dominant species is *Carrichtera annua*, introduced from the Middle East (Gutterman and Shem-Tov 1997). For plant nomenclature we follow Jessop and Toelken (1986).

Temporal variability in soil seed bank composition

To assess changes in abundances in the soil seed bank over time, we conducted repeated seasonal sampling of the same area over two years. We established the sampling site (20 × 20 m) in an area representative of the annual plant vegetation, free of tree cover, but including several shrubs (mostly *Atriplex vesicaria* and *Maireana sedifolia*). Samples were collected in 1993 and 1994 in autumn (April) before any large emergence event, late winter (August), late spring (November) after seed dispersal, and late summer (February). At each time 20 replicated samples were collected from random points in a grid using 50-cm intervals. Each point was sampled only once, and the holes produced during sampling were filled to prevent them from acting as seed traps. Samples were always collected at least 50 cm away from the canopy of any shrub (see Facelli and Temby [2002] for a discussion of differences in the seed banks under shrubs and in open spaces). The block of soil (20 × 20 × 3 cm) was excavated and placed in a plastic bag. A preliminary study showed that the first 2 cm contain 90% of all seeds (see also Kemp 1989).

We assessed soil seed bank composition by seed extraction, to assess the total seed density, following the procedure used by Malone (1967). Once extracted, the viability of all seeds was tested by squeezing the seed to assess the presence of endosperm. Testing viability using tetrazolium was not possible as most seeds were too small for location of stained embryos. Seeds were identified using a key prepared beforehand to this effect and the seed reference collection for the Middleback area (maintained by J. M. Facelli). Some seeds that could not thus be identified were sown and the plants grown in a greenhouse until they were identified. Only 7% of all seeds remained unidentified.

Seed persistence

We assessed the ability of seeds of five species (*Carrichtera annua*, *Stipa nitida*, *Vittadinia cuneata*, *Daucus glochidiatus*, and *Brachycome lineariloba*) to persist in the soil. These species were selected because of their high abundance in the study system. Although *Crassula colorata* is very abundant in the site, the small size of its seeds (diameter 0.3 mm) make its use for persistence studies impractical.

Seeds were collected from mature plants in October 1995 (late spring), cleaned in the laboratory of all extraneous material, and placed in plastic mesh bags (5 × 5 cm). Each bag was filled with sterile soil from the study site mixed with 100 seeds of a single species. In November 1995 the bags were buried along a 1.5 cm deep trench in the field site. Each bag was properly identified to allow retrieval at the corresponding time. At the end of each season during 1996 and 1997, we collected, for each species, 10 randomly selected bags. They were taken directly to the laboratory and their contents inspected. After carefully separating the soil from the seeds, the seed condition was assessed: all empty seeds or seeds that were crushed by gentle pressure with a pair of tweezers were discarded. The remaining, seemingly viable, seeds were counted and kept for germination trials (J. M. Facelli, P. L. Chesson,
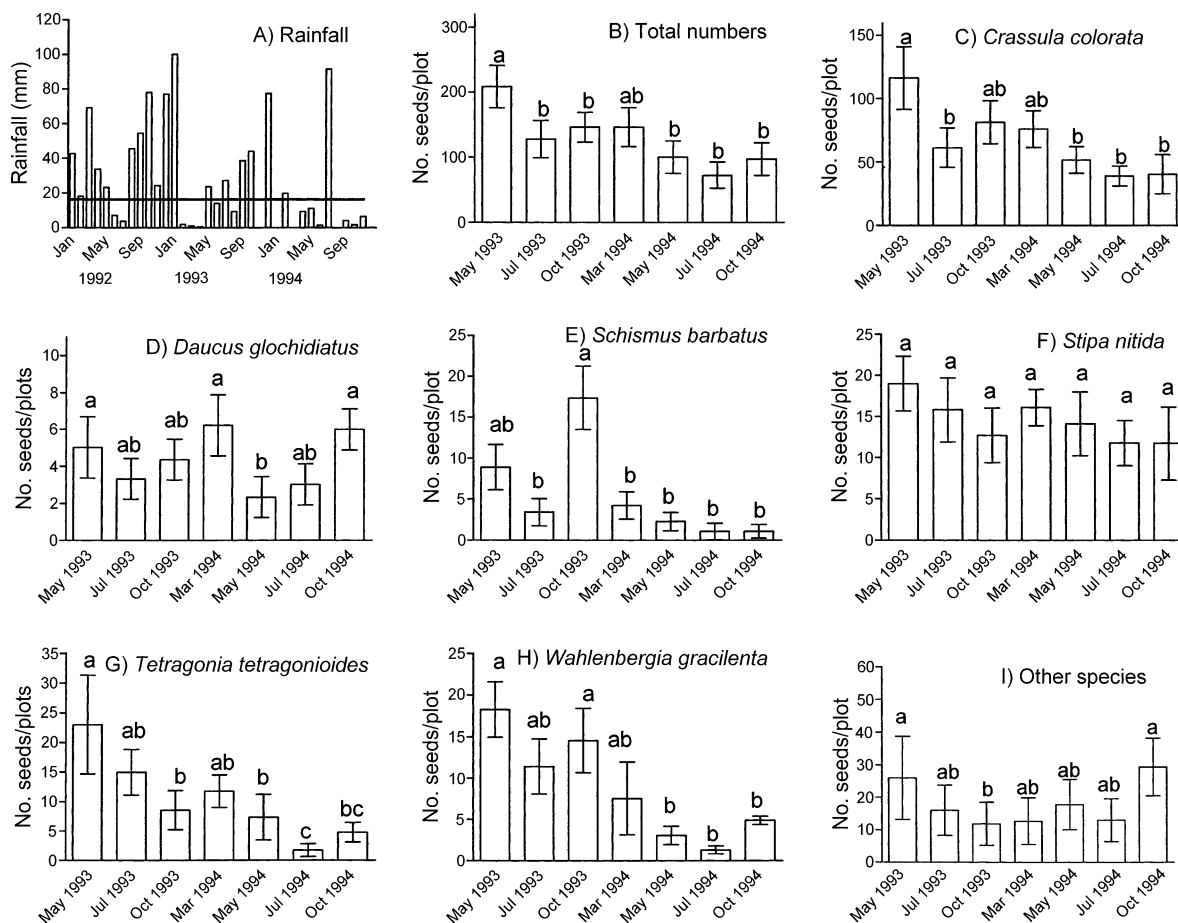
FIG. 1. (A) Monthly rainfall in the previous year and the two years of the study and (B–I) changes in abundance of seeds in the soil seed bank over the two years (means ± SD). Different letters within each graph indicate significant difference in the abundance of seeds over time (randomization $P < 0.01$). Species recorded in lower numbers (65 species across all samples) are not listed. The study was conducted at the Middleback Field Centre, 16 km northwest from Whyalla, South Australia, Australia.

and D. Bigham, *unpublished manuscript*). Because only one species (*Carrichtera annua*) did germinate in numbers large enough for analyses, the results are not reported here.

Effect of water and temperature on seedling emergence

We collected soil samples in April 1993 from a site with similar environmental and floristic characteristics and 500 m away from the site used for the soil seed bank dynamics study. We collected 15 soil samples from random points along a 150-m transect, avoiding sites under trees or shrubs. We collected, and added to the soil, the seeds of *Carrichtera annua* retained on fruits on dead plants, since this is the common form in which seeds persist from year to year (Gutterman and Shem-Tov 1997). The soil samples were air-dried, sieved through a 5-mm sieve to eliminate rocks and large organic debris, pooled, and thoroughly mixed to minimize differences in emergence due to variation in

soil type or seed bank. A constant volume (260 cm^3) of soil was placed in each of 81 aluminum foil trays. Each tray was randomly assigned to a particular temperature and water-availability treatment in growth cabinets with controlled environments. The three temperature regimes were chosen to represent summer (28° day/18°C night), spring/autumn (20°/10°C), and winter (12°/4°C) conditions. Three watering regimes (80 g/tray, 50 g/tray, and 25 g/tray, corresponding roughly to 100%, 66%, and 33% field water capacity) were incorporated in a two-way factorial. After water was added at the beginning of the experiment the trays were covered with plastic wrap to minimize evaporative loses. Emergence (i.e., appearance of cotyledons or first leaves through the soil crust) was recorded every 2 d for 4 wk. Because only three growth cabinets were available, the study used three runs, randomizing the chambers each time for temperature regime, each receiving three replicates of each water regime. Soil samples waiting to be used were kept dry at 15°C.

TABLE 1. ANOVA on numbers of viable seeds retrieved over two years from mesh bags containing seeds of five species placed in the field.

Source	df	ss	F	P
Species	4	52 370	280.7	0.001
Retrieval	8	45 600	122.2	0.001
Interaction	32	29 070	19.48	0.001
Residual	225	10 500		

Note: The experiment was conducted at the Middleback Field Centre, 16 km northwest from Whyalla, South Australia, Australia.

Data analyses

We tested whether the composition of the soil seed bank samples collected at different times were different using multi-response permutation procedures (MRPP) in PCOrd (McCune and Mefford 1999, McCune and Grace 2002). We used NPFact (May et al. 1993) to test for differences in the abundances of the five most abundant species. Because of the multiple comparisons we set the alpha value at $P = 0.01$ (Quinn and Keough 2002).

We used two-way analysis of variance (with species and sampling times as factors) to test for differences in the proportion of seeds (arcsine transformed) that persisted at the different retrieval times and the Tukey test for pairwise comparisons.

We tested whether the composition of the emergent community under the different environmental conditions using the multi-response permutation procedure (McCune and Grace 2002) in PCOrd (McCune and Mefford 1999) using time as a blocking variable. We also used PCOrd to produce an ordination of the experimental units using nonmetric multidimensional scaling, set to "autopilot slow and thorough." Individual analyses using NPFact (May et al. 1993) were used for the three most abundant species, and for the abundance of all other species pooled together, the alpha value set at $P = 0.01$ was used to reduce the probability of Type II errors.

RESULTS

Temporal variability in the soil seed bank

The composition of the soil seed bank varied seasonally and from year to year (MRPP, $A = 0.052$, $P < 0.01$), possibly as a result of yearly variation in rainfall. The total number of seeds and the number of seeds of most species peaked before the autumn rains and at the end of the spring and bottomed during the winter, after the main flux of germination (Fig. 1). The only departure from this seasonal pattern was observed in *Schismus barbatus*, a grass with a spring–summer cycle. There was also a discernible reduction in the total number of seeds retrieved along the sampling period, probably reflecting the poor recruitment into the seed bank as a consequence of dry conditions (Fig. 1A). Importantly, the most abundant species, *Carrichtera annua*,

was almost completely absent from the soil seed bank. While some species (e.g., *Stipa nitida*) did not show any significant change in abundance, others (*Schismus barbatus*, *Daucus glochidiatus*) showed large variation in the seed densities (Fig. 1).

Seed persistence

There was a clear difference between the number of seeds retrieved from bags for *C. annua* and all other species over time (Table 1, Fig. 2). Linear regression fitted the data adequately (Fig. 2), showing a significantly steeper slope for *C. annua*. While roughly 70–90% of the seeds of *Stipa nitida*, *Vittadinia cuneata*, *D. glochidiatus*, and *Brachycome lineariloba* were still intact in the bags at the last retrieval time, the number of remaining seeds of *C. annua* was not significantly different from zero (*t* test, $P = 0.349$). It must be noted that the data indicate steeper slopes between the summer and the spring retrieval, corresponding roughly to the times of peak emergence.

Seed emergence from soil samples

The total number of seedlings recorded at the end of the experiment was controlled by the interaction between temperature and watering treatment (ANOVA, interaction term $P < 0.01$). Overall, medium temperatures with high to medium water additions produced the highest emergence, while high temperatures, independently of the water treatment, and all the treatments with low water addition level produced the lowest emergence (Fig. 3).

Of the 12 species recorded (*Carrichtera annua*, *Crassula colorata*, *Tetragonia tetragonioides*, *Danthonia caespitosa*, *Vittadinia cuneata*, *Medicago* sp., *Calotis hispidula*, *Daucus glochidiatus*, *Brachycome lineariloba*, *Senecio glossanthus*, *Wahlenbergia gra-*
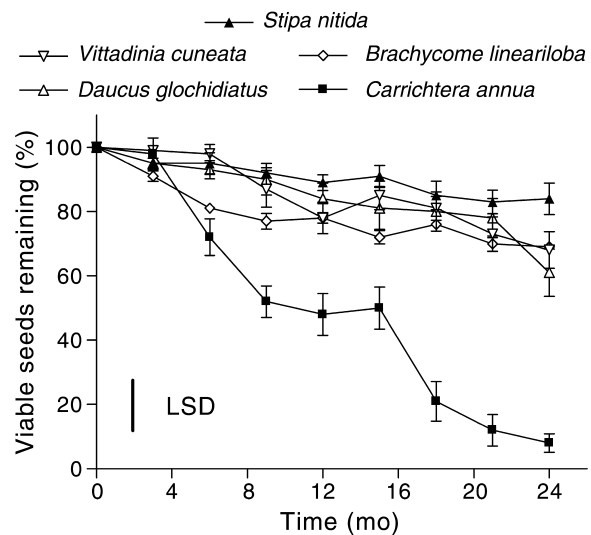
FIG. 2. Persistence of seeds of five annual species over two years in bags buried in the field (means ± SD).
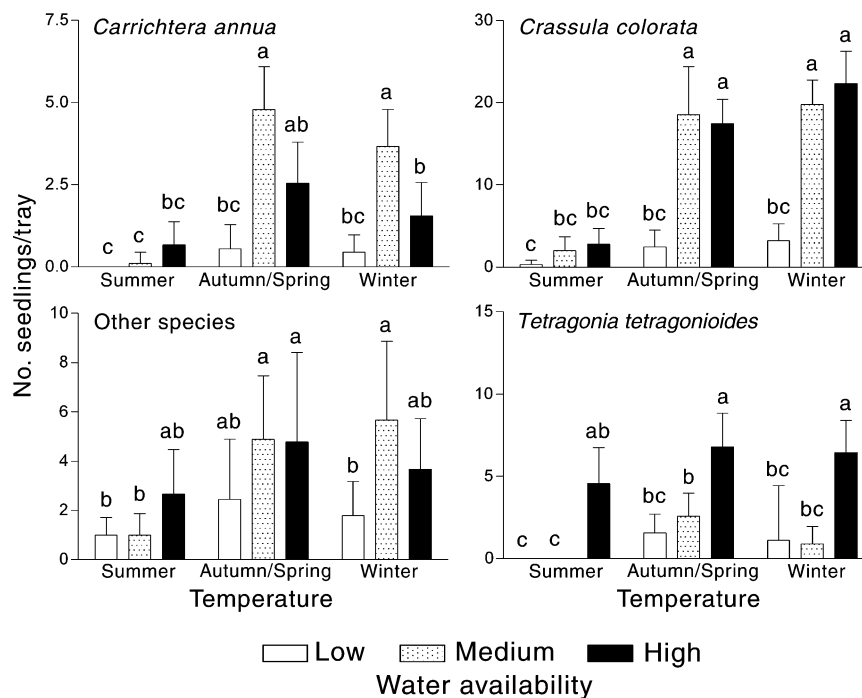
FIG. 3. Emergence of seedlings of selected species of annual plants from soil samples incubated at different temperatures and water availabilities (means + SD). The three temperature regimes were chosen to represent summer (28° day/18°C night), spring/autumn (20°/10°C), and winter (12°/4°C) conditions. Other species recorded include *Danthonia caespitose*, *Vittadinia cuneata*, *Medicago* sp., *Calotis hispidula*, *Daucus glochidiatus*, *Brachycome lineariloba*, *Senecio glossanthus*, *Wahlenbergia gracilenta*, and *Schismus barbatus*.

cilenta, and *Schismus barbatus*) only the first six were abundant enough to attempt individual statistical analyses. We detected significant differences only for the first three of them (NPFact permutations, $P < 0.01$) and for all other species lumped together.

In all cases except for *T. tetragonioides*, the effects of water and temperature were interdependent (Table 2, Fig. 3). The emergence of *Carrichtera annua* was higher in intermediate temperatures, followed by low temperatures, and the lowest emergences were recorded at higher temperatures. Emergence was higher in the intermediate water availability than at lower water content. Higher water availability was intermediate between them. The lowest number of seedlings of *Cras-*

TABLE 2. *P* values from an ANOVA on total number of seedlings and randomization tests (NPFact; May et al. 1993) for seedlings of the most abundant species emerging from trays of soil incubated under different temperatures and water availabilities.

Species	Water	Tempera-ture	Interaction
Total number of seedlings	0.01	0.01	0.03
Carrichtera annua	0.01	0.01	0.01
Crassula colorata	0.01	0.01	0.01
Tetragonia tetragonioides	0.01	0.08	0.24
Danthonia caespitosa	0.26	0.45	0.71
Vittadinia cuneata	0.56	0.18	0.28
Medicago sp.	0.09	0.17	0.69

sula colorata occurred in the trays with low water content and in the trays with medium water content and high temperatures (Fig. 3). The highest emergence was recorded at intermediate temperatures and high and intermediate water availability. The emergence of *T. tetragonioides* was controlled purely by water availability, with the greater emergence occurring at the highest water availability (Fig. 3).

Overall, the different combinations of water and temperature treatments triggered the emergence of different assemblages of annual plants (MRPP, $A = 0.264$, $P < 0.01$). The MDS ordination (Fig. 4) shows a clear distinction along the first axis between all treatments with low water and/or high temperature and the treatments subject to more benign conditions. Amongst the former, the low-water, high-temperature treatment shows a clear grouping. The latter present a clear patterning, with the trays with medium water and either low or medium temperature forming a group, medium temperature and high water another, and the third formed by trays subject to low temperatures and high water availability.

DISCUSSION

We found evidence of a large and diverse seed bank, subject to seasonal and interannual variation. Of the five species trialed, four had long persistence in the soil, and only *Carrichtera annua*, an exotic, had only
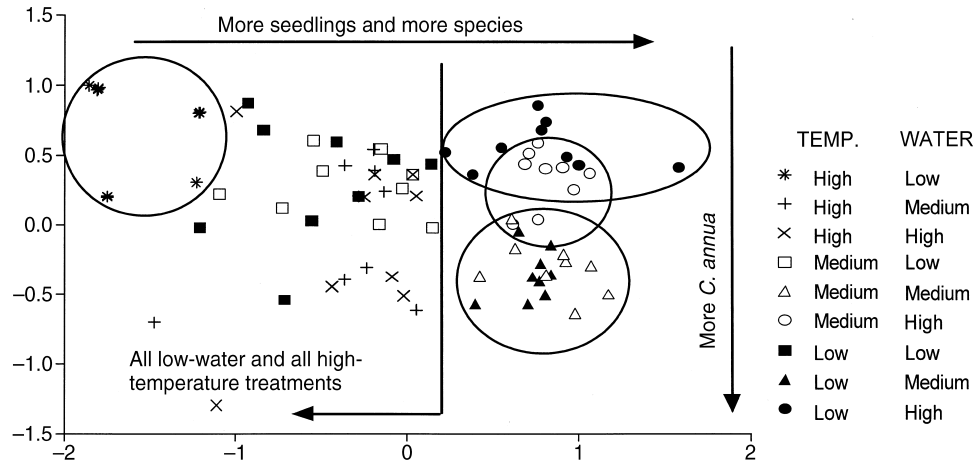
Fig. 4. Nonmetrical dimensional scaling ordination of the seedlings emerged from soil samples incubated in trays under different environmental conditions according to their species composition. The ordination was obtained after 50 iterations and has final stress = 10.956 and final instability = 0.0148. The lines and envelopes indicate groups that were detected to be significantly different by the multi-response permutation procedure ($P < 0.01$), after correcting for multiple comparisons.

short seed storage ability. Species differ in their responses to environmental conditions. *Carrichtera annua*, the most abundant species in the guild (Facelli and Temby 2002, Harris and Facelli 2003), was conspicuously infrequent in the soil seed bank, as a consequence of both its main storage occurring in stems of dead plants (Gutterman and Shem-Tov 1997) and the low ability of the seeds to persist for more than a couple of years. In another study, seeds of this species showed a complex response to time since storage, temperature, and water availability (J. M. Facelli, P. Chesson, and D. Bigham, *unpublished manuscript*). Overall, the various species in the soil seed bank seem to have contrasting strategies, which potentially can promote coexistence by the storage effect.

Temporal variability

As is the case in most other arid lands studied (Kemp 1989, Pake and Venable 1996, Guo et al. 1999), our results indicate the presence of a soil seed bank composed mostly of annual species. The only perennial components of any significance are two species of *Sclerolaena*, a short-lived suffrutescent chenopod. (Note, however, that although *Stipa nitida* and *Danthonia caespitosa* can behave as perennials, in this system almost always their cycles end at the onset of the summer.)

We found substantial changes in the total number of seeds, both between seasons and between years, such as reported in Kemp (1989). Overall the changes in seeds in the soil seem smaller than those reported for other systems. Since this should be a function of both current environmental conditions and the adaptations of the species, we interpret this as a sign of overall smaller germination fractions. This is consistent with the high persistence of seeds in the field we documented. Under the far more variable environmental

conditions of Australian arid lands, germination fractions should be smaller, hence resulting in less fluctuation in seed bank size (Cohen 1966, Ellner 1985). A different strategy seems to be present in *Carrichtera annua*, the species with far the largest biomass in the system (Facelli and Temby 2002, Harris and Facelli 2003). While almost completely absent from the soil seed bank, it stores seeds in unopened fruits attached to the dead plants for up to two years (Gutterman 2000). There was a correspondence between the ability of seeds to persist in the soil and the temporal variability in abundance: of the native species studied *Stipa nitida* had the highest seed persistence and the least variation, while *Daucus glochidiatus*, the species with the lowest persistence, showed substantial temporal variability.

Seed persistence

Species differed in their degree of seed persistence. Amongst the native species *S. nitida* was the one with the highest persistence rates, while *B. lineariloba* was the one with the lowest. The most remarkable contrast, however, was that between the persistence of seeds of *C. annua* and all other species. This suggests a large difference between *C. annua* and the native species' strategies promoting persistence. The relatively large size of *C. annua* seeds may reduce the risk of post-germination mortality through rapid establishment following germination. As a consequence, variance in reproduction per germinated seed would be reduced (Venable and Brown 1988, Pake and Venable 1996). Alternatively, the species may persist even during the worse years in small depressions or other spatial refugia from which it reinvades the system during favorable periods.

Seed emergence from soil samples

The emergence of different assemblages of species in the trays subject to different environmental combi-

nations indicates a combined control of temperature and water on seed germination. Emergence was very low in all high-temperature treatments, irrespective of water treatment. Only one species, *T. tetragonioides*, was insensitive to high temperatures, and another, *Schismus barbatus*, established better at high temperatures, but only when water was at the highest availability. This indicates that most species in the system are obligate winter annuals (Baskin and Baskin 1989) and have mechanisms that prevent germination during the hotter months even when water is plentiful (Baskin et al. 1993), a strategy that avoids inherent risk of dessication after summer rainfall events when water may evaporate too quickly for survival and effective annual plant growth.

The different floristic composition of trays subject to different environments is an indication that species-specific responses to environmental variability may result in different assemblages of growing plants in different years, according to specific patterns of rainfall.

Putting it all together

Storage effect theory identifies the conditions under which temporal partitioning can be effective in promoting diversity (Chesson and Huntly 1989, 1997, Chesson et al. 2004). These conditions are: (1) Responses to temporally varying physical environmental conditions must differ between species. For example, as shown here, different species may have different germination responses to physical conditions. (2) There must be covariance between environment and competition. For example, if physical conditions lead to higher germination of a species, then that higher germination should lead to higher competition for limiting resources (Chesson et al. 2004). (3) There must be some life-history attribute that buffers a population against catastrophic decline when conditions for its growth are unfavorable. For example, a persistent seed bank means that even though conditions may be unfavorable for germination or seed production following germination, the population can still persist as an underground seed store, which builds up during times that are favorable for germination and seed production.

The above three features define the conditions necessary for temporal niches to promote diversity (Chesson et al. 2001). Fundamentally, condition 1 means that covariance between environment and competition must weaken for a species as it drops to low density, reducing the tendency of competition to limit population growth during times when the physical environment favors that species (Chesson et al. 2004) and allowing robust increase during those times. Buffered population growth means that particularly favorable times have much more effect on long-term population growth than particularly unfavorable times, which will also occur. The net result is that when a species is reduced to low density, it has a strong tendency to recover in the long run. Species loss is thus inhibited, and diversity is promoted.

We documented several characteristics of the study system that suggest that these conditions are met. (1) We found a large persistent soil seed bank, where most species were found, providing buffered population growth. (2) The dynamics of the seed bank over the two years studied suggest that several species may have had quite different germination fractions in these two years. Changes in the proportion of species present in the seed bank are indicators that different species responded to the same environmental conditions with different combinations of germination, mortality, and reproductive output. (3) The emergence of different assemblages of species under different simulated environments further indicates time partitioning. Different combinations of water and temperature produced different species composition arising from the same soil seed bank supporting the perception that the variability in floristic composition of the annual plant community is produced by the timing of rainfall events that trigger emergence.

Persistence over unfavorable periods is especially important for competitively inferior species that recruit sporadically. Most native species in this system satisfy this condition through high persistence in the seed bank. The absence of high persistence in the seed bank by *Carrichtera annua*, the most abundant species, is of less importance because it is numerically dominant and able to recruit consistently in most winters. It may also benefit from an alternative method of persistence over less favorable times through spatial refuges.

The high sensitivity of emergence to environmental conditions we documented is a key way in which the final important requirement, covariance between environment and competition, can arise. As discussed above, when coupled with the other requirements, this covariance should vary with the abundances of the individual species. As it is stronger for more abundant than for less abundant species, it should promote recovery of species from low density and resistance to further declines by low-density species. In these ways, we expect the features of seed bank ecology uncovered here to help maintain the diversity of this annual plant system.

With the exception of Adondakis and Venable (2004), previous work on diversity maintenance in annual plants of an arid region focused not on environmental dependence of germination, but on environmental dependence of growth and seed production of the growing plant (Pake and Venable 1996). Although it is still possible for covariance between environment and competition to arise in such circumstances (Pake and Venable 1996, Chesson et al. 2001), this key requirement for temporal partitioning to promote diversity (as revealed by storage effect theory) is not so clearly satisfied.

The storage effect is one of two general mechanisms identified by Chesson (1994, 2000*a*) able to promote coexistence in a variable environment. It has been proposed as a key diversity maintenance mechanism in a variety of systems in addition to desert annuals, including annuals in mediterranean environments (Levine and Rees 2004), aquatic macrophytes (Bonis et al. 1995), forest trees (Keller and Bowler 2002), Daphnia (Caceres 1997), and coral reef fishes (Chesson and Warner 1981, Munday 2004), as well as having a role in the maintenance of genetic diversity (Turelli et al. 2001). The second general mechanism, "relative nonlinearity of competition," involves different nonlinear responses of the species to common fluctuating competitive factors and was first identified theoretically by Armstrong and McGehee (1980). It has been suggested as applicable to phytoplankton in lakes (Huisman and Weissing 1999) and, despite some recent enthusiasm (Abrams 2004), does not appear to be a robust promoter of coexistence of many more species than limiting resources (Chesson 1994, Huisman and Weissing 2001). We do not expect that relatively nonlinear competition has a major diversity-maintaining role in this system.

Although disturbance, defined as temporally fluctuating mortality rates, is often invoked as a mechanism of diversity maintenance (Roxburgh et al. 2004), Chesson and Huntly (1997) pointed out that it cannot maintain diversity unless different species are affected differently in ecologically significant ways by disturbance. Moreover, any diversity maintenance mechanism relying on temporal variation must be a version of these two, a combination of them, or their combination with equilibrium mechanisms (Chesson 2000*a*, Roxburgh et al. 2004).

Chesson and Huntly (1997) argue that disturbance as diversity maintenance mechanism is better viewed in a spatial context in which mortality varies in space and time and involves successional processes related to competition–colonization trade-offs. Levine and Rees (2004) argue that competition–colonization trade-offs can have a role in diversity in annual plant systems only when they are associated with different responses of different species to spatial variation in the physical environment. Such differential responses of the species to spatial variation in general lead to a spatial version of the storage effect (Chesson 2000*b*, Snyder and Chesson 2004), which is just one of several spatial coexistence mechanisms with convincing theoretical support (Chesson 2000*a*, Chesson and Neuhauser 2002).

In this particular system, it is quite likely that different species have different responses to the spatially varying physical environment through germination, seedling survival, growth, and seed production, suggesting an important role for the spatial storage effect. For example, variation in species performance in open spaces and underneath shrubs has been reported by Facelli and Temby (2002). Localized dispersal would mean that an individual species would tend to build up

in spatial locations that are favorable to it. This phenomenon, called fitness–density covariance (also known as "growth–density covariance"), can promote diversity in a way similar to the spatial storage effect (Chesson 2000*b*, Snyder and Chesson 2004). Indeed, there is every reason to expect that the spatial storage effect and fitness–density covariance help maintain diversity in this system, in addition to the temporal storage effect, which is the focus of this article. Investigations of spatial mechanisms in this system are the subject of future publications.

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