

Demographic mechanisms in the coexistence of two closely related perennials in a fluctuating environment

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Abstract The demographic variability and life history differentiation of two closely related shrubs (*Atriplex canescens* and *A. acanthocarpa*) were investigated in the Chihuahuan Desert, and the results were interpreted in the context of theories of coexistence in fluctuating environments. Demographic information was recorded during three annual intervals and analyzed employing matrix projection models. *A. canescens* had lower λ (finite rate of population increase), higher longevity and generation time and slower convergence to a stable population structure than *A. acanthocarpa*. In favorable years for recruitment (those when, for both species, $\lambda > 1$), the λ of *A. acanthocarpa* was higher than that of *A. canescens*; in unfavorable years (when $\lambda < 1$), the reverse was true. Regardless of conditions (year), *A. acanthocarpa* had a type 2 survivorship

curve (constant rate of mortality with age), while *A. canescens* had a type 3 survivorship curve (declining mortality with age). Elasticity analyses highlighted the larger influence that fecundity and growth would have in modifying the λ of *A. acanthocarpa* in comparison to that of *A. canescens*. In contrast, survival would have a larger influence on the λ of *A. canescens*. *Atriplex acanthocarpa* behaved as an opportunistic species that benefitted from sporadic favorable conditions and declined rapidly when conditions deteriorated. In contrast, *A. canescens* behaved as a tolerant species able to withstand years when conditions were poor, but which could not gain any advantage over *A. acanthocarpa* when conditions improved. By each having a relative advantage over the other on opposite ends of the contrasting climatic conditions experienced in the Chihuahuan Desert, they are able to coexist. Their contrasting life histories agreed with the theoretical predictions for the operation of the two mechanisms of species coexistence in fluctuating environments: the storage effect and the relative non-linearity of competition. Based on these results, we conclude by speculating on the nature of succession in arid communities.

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Introduction

Fluctuating environments provide opportunities for the coexistence of potentially competing species (“niche time-sharing”; Hutchinson 1961; May and MacArthur 1972; see also Chesson et al. 2001). Desert ecosystems offer the opportunity to test the importance of resource fluctuations on coexistence (Chesson et al. 2004) because the most

limiting resource, water, occurs in pulses (Noy-Meir 1973), leading to a two-phase resource dynamics of abundance (pulse) and scarcity (interpulse) (Goldberg and Novoplanski 1997). Surviving the interpulse period becomes critical, and this is done through a variety of morphological, physiological and phenological adaptations. Thus, for example, seed dormancy is recognized as an important buffering mechanism in annual plants (Pake and Venable 1995; Venable 2007). Similarly, the differences in the temporal and spatial patterns of water use, as well as in water use efficiency, by perennial plants, which reflect species-specific responses to changes in resource abundance, are crucial to the maintenance of species diversity in arid ecosystems (Schuster et al. 1992; Schwinning and Ehleringer 2001). Whatever the specific adaptations and functional mechanisms involved, the species' response to environmental fluctuations must be expressed through differential survival and reproduction. These have been quantified for short-lived organisms with a dormant life cycle stage (desert annuals: Pake and Venable 1996; Facelli et al. 2005; *Daphnia*: Cáceres 1998), but not for perennial organisms whose buffering stage may be the adult (Chesson et al. 2004). The few long-term studies of perennial plants in arid zones record variations in plant density or cover (McAuliffe 1988; Ralphs and Sanders 2002). There are, however, no detailed records of how demographic processes change with environmental variation in perennial plants of arid zones.

A fair amount of theoretical work has been produced on the specific mechanisms expected to promote coexistence in fluctuating environments (Armstrong and McGehee 1980; Schmidha and Ellner 1984; Warner and Chesson 1985; Ellner 1987; Chesson and Huntly 1988, 1997; Chesson 1994, 2000a, b). In particular, two mechanisms are deemed to provide the conditions required for coexistence: the storage effect and the relative non-linearity of competition (Chesson 2000a). To date, empirical support for the operation of these mechanisms has been lacking, particularly for perennial organisms.

Here we explore the variation in the demographic response of two sympatric perennial shrubs over a 3-year period in the Chihuahuan Desert and provide the first demographic evidence for the occurrence of these two mechanisms advanced by theory in the context of the coexistence of two perennial species. The study species are *Atriplex canescens* (Pursh) Nuttall ("four-winged salt-bush") and *A. acanthocarpa* (Torrey) Watson ("tuberled salt-bush"). They are common in mixed shrub-grass formations in *playas* (saline flat areas, slope < 0.5%, at the bottom of endorheic basins) of the Chihuahuan Desert (Montaña, 1990). Our preliminary observations revealed that *A. acanthocarpa* tends to occur in dense patches containing thousands of small (<1 m in height) plants. Many of these populations had a high proportion of dead individuals, suggesting an ability to colonize available areas rapidly, but an uncertain and possibly short life cycle. In contrast, the larger (up to 2.5 m in height) *A. canescens* has

lower population densities, and the populations showed no signs of concentrated death (in either time or space), suggesting slower recruitment and, possibly, also a longer life cycle than that of *A. acanthocarpa*. Based on these observations, we anticipated that *A. canescens* would be better able to survive interulses of rain than *A. acanthocarpa*, but that this higher survival would be accomplished at the expense of its efficiency to convert pulses of rain into abundant growth and reproduction. *Atriplex acanthocarpa*, on the other hand, would be more likely to die during interpulse periods and must compensate this lower physiological tolerance to drought by taking advantage of sporadic favorable rain pulses. The coexistence of these two species over the large areas where they co-occur side by side must therefore arise from contrasting demographic responses to changes in resource abundance (rain). We investigated these demographic differences over three successive annual periods (1995–1998), making use of matrix population models. We addressed three questions:

1. What is the demographic response of each species to year-to-year climatic variation?
2. How do these demographic differences translate into their life histories?
3. Do these differences provide evidence for the operation of the coexistence mechanisms suggested by theory?

Material and methods

Study plants

Atriplex acanthocarpa and *A. canescens* are two closely related evergreen halophyte fodder shrubs characteristic of mixed shrub-grass formations on the extended saline playas of the Chihuahuan Desert (Montaña 1990). The two species have similar life cycles and phenological patterns. *Atriplex acanthocarpa* is an erect suffrutescent plant, up to 1 m in height, freely branched from the base. *Atriplex canescens* is an erect shrub, woody throughout, loosely to densely branched, up to 2.5 m tall (Hall and Clemens 1923). Although both species are described as dioecious, in our study we found a small proportion of cosexual plants. Flower spikes are formed after the first spring/summer rains. Female flowers are wind pollinated, and their seeds ripen in the summer while still on the mother plant. Seeds have non-assisted primary dispersion either from strong winds or abundant rain. *Atriplex acanthocarpa* is able to withstand a higher soil salt concentration than *A. canescens* and is therefore more abundant on the more saline soils. However, *A. canescens* is also able to coexist with mesquites (*Prosopis glandulosa* var. *torreyana*) and creosote bush (*Larrea tridentata*) in less saline ground (Montaña 1990).

Despite these differences, the two species coexist over large areas of the Chihuahuan Desert, providing the opportunity to investigate the mechanisms responsible for their coexistence in these areas.

Study site

Fieldwork was conducted at the Mapimí Biosphere Reserve (MBR; southern Chihuahuan Desert, 26°N, 103°W; 1100 m a.s.l.) in the Mexican state of Durango. Data from the MBR meteorological station recorded an annual rainfall of 270.5 ± 14.0 mm (mean \pm SE; 1958–2005 records), concentrated in the summer (Montaña, unpublished). The MBR meteorological station is located 20 km from the study site. At this distance, the spatial variability of individual rain events is such that the recorded rain at the MBR station may not always reflect what is actually occurring at the study site. Nonetheless, the long-term data from MBR most likely reflects the average climatic conditions over a large area around it. The study period (1995–1998) was amidst a sequence of dry years (206.3 ± 16.7 mm; 1992–2002) in which average annual precipitation was 199.0 ± 11.6 mm. Despite differences in mean precipitation calculated from these three nested intervals, they were similarly variable, as judged by their standard errors. Thus, the study period was not exceptionally more or less variable than the long-term average for the zone.

Study populations

Populations were sampled at the San José del Centro site, 26°39'N–103°56'W at an altitude of 1170 m. This site is located halfway along the salinity (and sodicity) gradient between the northern (more saline) and southern (less saline) playas of the area known as the Mapimí Bolsón (Montaña and Breimer 1988). A playa is characterized by a very flat topography (<0.5%) and, locally, a somewhat irregular micro-relief due to gully erosion. The vegetation of the area has an open-grassland physiognomy with a variable shrub cover (Montaña 1990).

In 1995, five plots with similar topographic and soil conditions were established within an area of approximately 10 km² in the San José del Centro locality. These five plots were intended to cover some of the small-scale environmental variation. In all plots, *A. acanthocarpa* and *A. canescens* accounted for more than 90% of the total vegetation cover. Other shrubs were *Prosopis glandulosa* var. *torreyana* and, more rarely, *Ziziphus obtusifolia*. Perennial grass cover, mainly by *Hilaria mutica*, was very low. Grazing and browsing by large mammals was prevented by fencing off each plot. One plot (at the more specific locality of El Centro) covered 1.125 ha (125 \times 90 m), and the other four (two at La Calavera and two at La Flor) were 0.25 ha each (50 \times 50 m).

While all *A. canescens* within the enclosures were individually tagged, subplots were used for the more abundant *A. acanthocarpa*: a 100 \times 10-m subplot in the larger enclosure, and 20 \times 20-m subplots in each of the other four enclosures.

Field data collection

The location and size of each plant, including seedlings, was noted each spring (March or April) from 1995 to 1998. Over the 4-year period, a total of 5408 plants of *A. acanthocarpa* (2392 at El Centro, 1393 at La Calavera and 1623 at La Flor) and 4343 plants of *A. canescens* (3303 at El Centro, 645 at La Calavera and 395 at La Flor) were monitored.

Because of their relatively cylindrical shape and dense branch architecture, the size of each plant was calculated as the volume (V) of an elliptical cylinder with height h and radiuses r_1 (major) and r_2 (orthogonal to r_1): $V = \pi r_1 r_2 h$. Size ranged from 0.79 cm³ for a seedling 0.5 \times 0.5 \times 1 cm to approximately 8.5 m³ for an unusually large *A. canescens* (120 \times 100 \times 225 cm).

The number and length of flower spikes produced by reproductive individuals was recorded in September–October each year, and the total spike length of each adult was calculated. A sample of spikes from 50 individuals from outside the plots, and spanning the whole range of spike sizes, was collected in the summer of 1995 and their number of (one-seeded) fruits counted. Linear regression between fruit number and spike length was employed to estimate seed production of individual plants in the plots. Because cosexuals fulfill the female role of fruit production, we treated them as females. Doing this, the overall, 4-year male-to-female sex ratio of *A. acanthocarpa* was 0.44 and that of *A. canescens* 0.41. In order to simplify the analyses, we decided to treat these data as though the sex ratio were 1:1 and distributed the values of fecundity and recruitment equally between males and females (females plus cosexuals).

Matrix construction and projection

Using this field data, we constructed six (two species \times 3 years) five-stage (see below) time-invariant matrix projection models. Because both the La Flor and La Calavera sites had relatively small sample sizes, which produced variable population structures, we pooled together the data for each species from all five plots. The matrix model had the form $\mathbf{n}_{t+1} = \mathbf{A}\mathbf{n}_t$, where \mathbf{n} is a 5-cell vector recording the number of plants in each of five stage classes at two successive times, t and $t + 1$, and \mathbf{A} is a 5-by-5 matrix summarizing the contribution from each class to each and every class in a unit-time interval (Caswell 2001). We arrived at the recognition of five classes in a two-step process. Firstly, we employed

Moloney's (1986) algorithm with various subsets of our data (combinations of years and sites for each species), and these results suggested a low number of size classes for both non-reproductive (two to three) and reproductive (two to five) plants. Secondly, given the variability of the results from population to population and the convenience of employing the same number of classes for both species in all 3 years, we decided to define two juvenile and three adult classes (small, medium and big). Apart from their reproductive status, these classes were defined by the following size limits (in cm^3): $J_1 \leq 2500 < J_2$, $A_1 \leq 25,000 < A_2 \leq 75,000 < A_3$, for *A. acanthocarpa*, and $J_1 \leq 50,000 < J_2$, $A_1 \leq 100,000 < A_2 \leq 250,000 < A_3$, for *A. canescens*.

Because we did not have information on age-specific survival of seeds and, if a seed bank exists, on the age structure of the seed bank, we did not include a seed bank in the model. Individual average fecundity for each adult class was calculated as the total number of seedlings recruited in each annual interval divided by the adult population, weighted by the proportional contribution of an average individual of each size class to the total fruit set in the preceding summer (the anonymous reproduction of Caswell 2001, p 173). Therefore, when referring to fecundity, we mean the individual adult contribution to seedling recruitment. In the year when no recruitment of *A. canescens* occurred (1996–1997), and in order to close the life cycle graph and calculate the corresponding age-related life table, a figure of 0.001 was inserted in the fecundity cell of the last stage class (A_3) of the matrix model.

The reason we projected annual individual matrices (and their average) and not their product (e.g. employing stochastic or periodic models) was because we wanted to use the annual projections as measures of the overall effect that the climate experienced in a particular year would have on the demography of the two species under study, were it to remain constant. Thus, we used these time-invariant projections as “instantaneous” evaluations of their demography (see Caswell 2001, pp 29–31).

Variability of population growth rate

To investigate whether the species' demography varied significantly, we investigated differences in the projected population growth rate employing randomization tests (Caswell 2001, pp 335–345) implemented in MATLAB (MathWorks 1998). These tests assessed: (1) differences between the two species in each of the 3 years of the study, and (2) differences among years within each of the two species. In both series of tests, individual plants were randomized among treatments (for between-species comparisons, either species for each of the 3 years of study; for between-years comparisons, years within each individual species), thereby preserving the original number of

observations in each treatment level. In each case, a series of 5000 randomized matrices was obtained. For the species comparison, the statistic $\theta_i = \lambda_{a,t} - \lambda_{c,t}$ (where $\lambda_{i,t}$ is the value of the asymptotic growth rate, the largest eigenvalue of the matrix, of species *i* in year *t*) was computed for each of the 3 years of study and compared to the corresponding distribution obtained from the respective 5000 randomizations. For the equivalent, within-species, temporal comparison, the species-specific statistic $\theta_i = \text{SD}(\lambda_i)$ resulting from the 3 years of data was calculated and compared to the distribution of θ_i obtained by randomly interchanging individual plants between years (see Caswell 2001, pp 335–345).

Population parameters

Population parameters, including age-related ones, were obtained with the program STAGECOACH (Cochran and Ellner 1992). These parameters were the intrinsic rate of population increase (*r*, the natural logarithm of the largest eigenvalue, λ_1 or simply λ , of the matrix), the net reproductive rate (R_0 , Cochran and Ellner's Eq. 18), the maximum lifespan (*L*, the expected age of death conditional on passing through stage J_1 ; Cochran and Ellner's Eq. 26), the age at sexual maturity (α , Cochran and Ellner's Eq. 15) and two measures of generation time: the mean age of parents of offspring produced at stable stage distribution (\tilde{A} ; Cochran and Ellner's Eq. 26) and the mean age at which members of a cohort reproduce (μ ; Cochran and Ellner's Eq. 27). Employing the eigenvalue spectrum of the matrix, we also calculated two measures of convergence to stability: the damping ratio (ρ , Caswell 2001, Eq. 4.90) and the period of oscillation (P_t , Caswell's 2001, Eq. 4.99). The age-related life-tables produced by STAGECOACH were used to compare the projected patterns of survival and fecundity of the two species.

Elasticity of vital rates

In order to evaluate the relative influence that changes in the processes of survival (σ), growth (γ , including negative growth/retrogression ρ) and fecundity (ϕ) embedded in the matrix coefficients (not of the matrix coefficients themselves) would have in each species and year, the elasticity of population growth rate (λ) to changes in these parameters was calculated for each species in each of the 3 years of study and for their average matrices, employing the formulas provided by Zuidema and Franco (2001) and Franco and Silvertown (2004). These elasticities were standardized to add up to one (see Franco and Silvertown 2004) and summed up for each of these three processes across the entire matrix (E_σ , E_γ and E_ϕ , respectively).

Results

Population density

Both species showed the same population trends over time (Fig. 1). Density (as both number of individuals and population volume) peaked after a pulse of recruitment in the late winter of 1995–1996. It then declined during the next 2 years, as little recruitment occurred, and many of the 1996 recruits died. By 1998, densities were similar to the ones found at the beginning of the study period. Throughout the study, the number of plants of *A. acanthocarpa* was an order of magnitude higher than that of *A. canescens* (Fig. 1a). The volume occupied by the populations (the sum of the volumes of all plants) of *A. acanthocarpa* (expressed as m^3/ha) was lower than that of *A. canescens* in the first and final years of study and similar in the intermediate years (Fig. 1b). The combined volume of the two populations, an indirect measure of the demand that leaves make of water, approached a limit of 154 l m^{-2} in productive years (Fig. 1c).

Sex ratio and reproductive output

Male-to-female proportions were female biased in both species (H_0 : male:female ratio = 1:1; *A. canescens* $\chi_1^2 = 62.3$, $P < 0.001$; *A. acanthocarpa* $\chi_1^2 = 35.5$, $P < 0.001$) tending towards 40/60 and 45/55 (*A. canescens* H_0 : male:female ratio = 40:60, $\chi_1^2 = 0.06$, $P > 0.8$; *A. acanthocarpa* H_0 : male:female ratio = 45:55, $\chi_1^2 = 1.25$, $P > 0.25$). On average, an adult of *A. acanthocarpa* produced 3534 fruits (± 431 SE), while one adult of *A. canescens* produced 27,719 fruits ($\pm 2,069$ SE). Most *A. acanthocarpa* fruits contained a seed, whereas 60–65% of the fruits of *A. canescens* were empty. This made the effective reproductive output of an *A. canescens* adult about 2.5-fold higher than that of *A. acanthocarpa*. This is slightly smaller than their 3:1–4:1 size difference (see classification of plant sizes in section [Matrix construction and projection](#)).

Population parameters

There was a high degree of variability in the population parameters calculated from the 3 years of data (Fig. 2; Table 1). The intrinsic rate of increase (Fig. 2a) and the net reproductive rate (Fig. 2b) varied more in the smaller, shorter-living *A. acanthocarpa* than in the larger, longer-living *A. canescens* (Fig. 2e). Damping ratio, longevity and generation time μ (Fig. 2c, e, f) had a lower variability in *A. acanthocarpa* than in *A. canescens*. There was a substantial amount of variation in the predicted period of oscillation for *A. acanthocarpa* (Fig. 2d). However, because of zero or very low recruitment in the second and

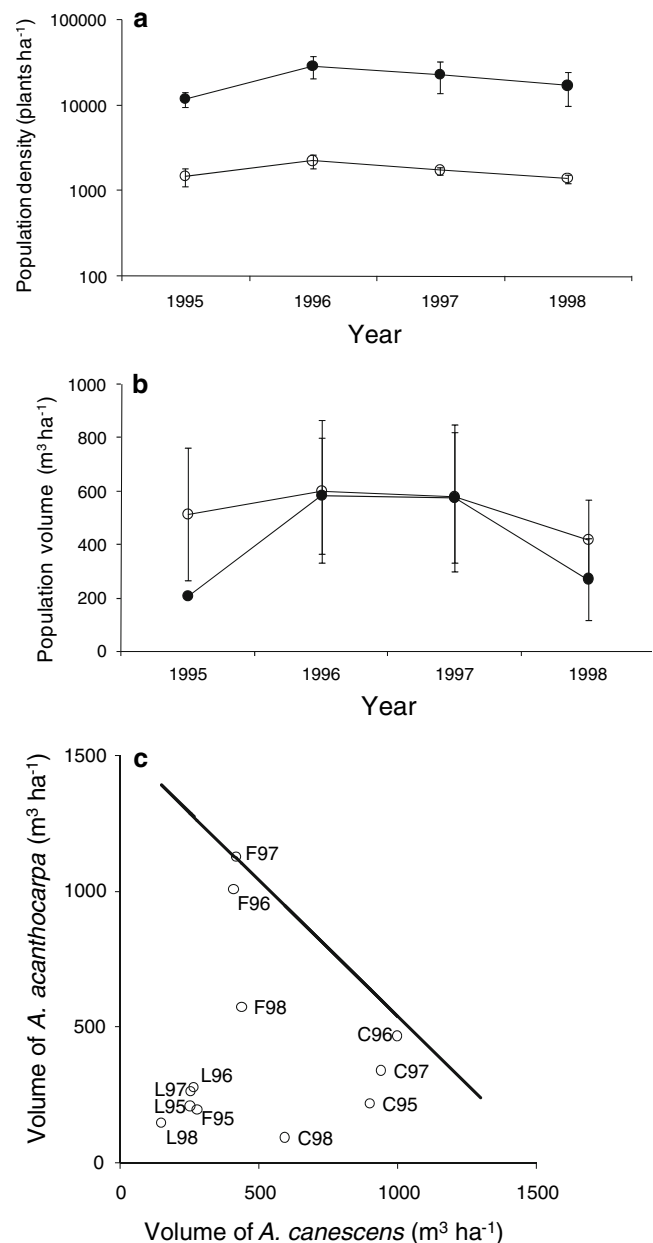
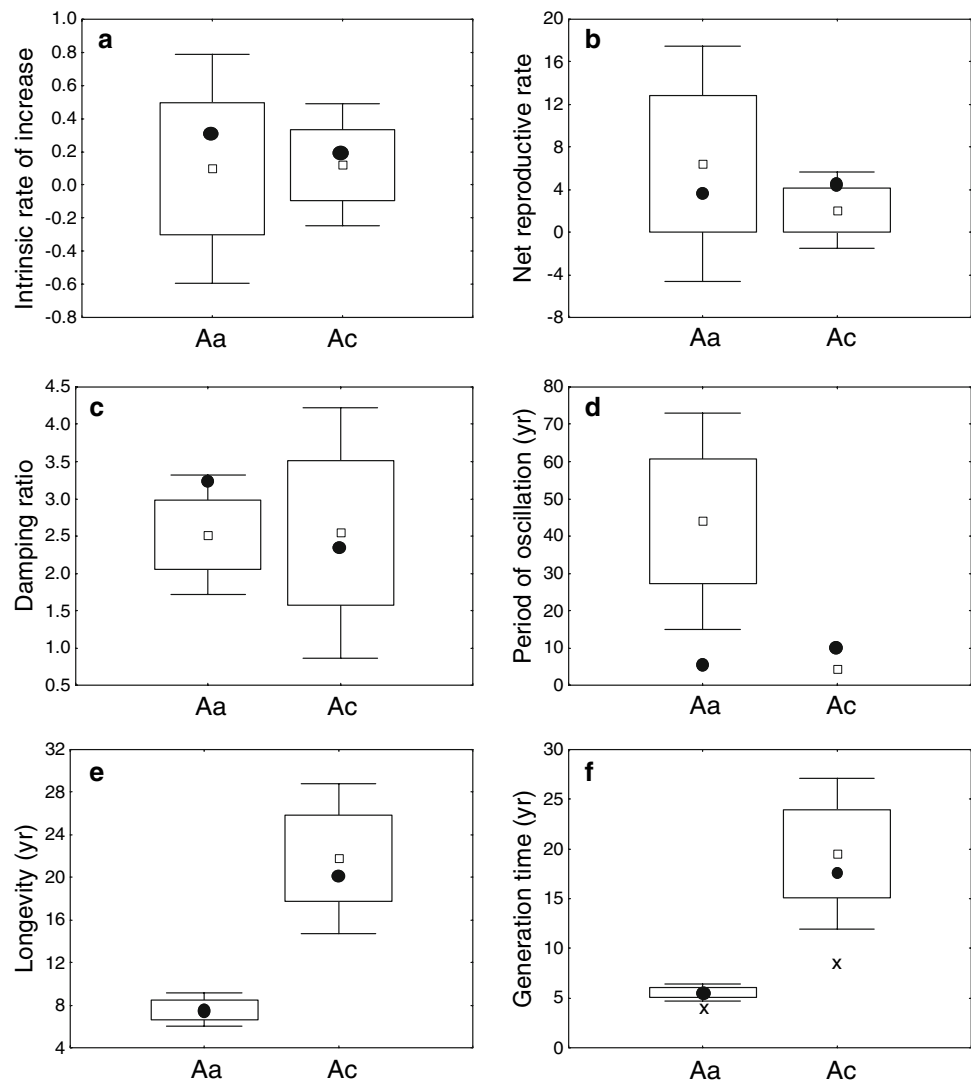


Fig. 1 Population density of *Atriplex acanthocarpa* (closed symbols) and *A. canescens* (open symbols) in the southern Chihuahuan Desert at the beginning of four annual intervals (means \pm SE from three sample areas—El Centro, La Calavera and La Flor—for each species). Density is expressed as number of plants per hectare (a) and volume occupied per hectare, the sum of all individual volumes of *A. acanthocarpa* and *A. canescens* at each of three study sites over 4-years (1995–1998) are represented by letters that denote the study sites (F Flor, C Centro, L Calavera) and numbers that denoted the years (1996–1998). In c, the maximum combined volume approached 154 l m^{-2} (continuous line)

last year of study, which produced no complex eigenvalues for the corresponding matrices, the period of oscillation of *A. canescens* could only be calculated for the 1995–1996

Fig. 2 Variation in population parameters (*open square* arithmetic mean, *boxes* standard error, *whiskers* standard deviation) estimated from three annual matrix projections for *A. acanthocarpa* (Aa) and *A. canescens* (Ac) in the Chihuahuan Desert. *Filled points* represent the projections from the corresponding 3-year average matrix. In **f**, the measure of generation time employed is μ , the mean age at which members of a cohort reproduce; *crosses* represent the 3-year average-matrix measure of generation time \bar{A} , the mean age of parents at stable stage distribution. Because of low recruitment in 2 of 3 years, the period of oscillation (**d**) could only be calculated for one annual matrix of *A. canescens*, and only this value (*open square*) and that obtained from the average matrix (*filled dot*) are shown (see [Material and Methods](#))



interval and for the average 3-year matrix (open square and filled dot on right-hand side of Fig. 2d, respectively). Low recruitment and a large proportion of plants retrogressing to smaller size classes produced absurd values of the mean age of parents of offspring produced at stable stage distribution (\bar{A}). Therefore, only its projected value for the average matrices is shown (crosses in Fig. 2f). The lower value of \bar{A} relative to mean μ in both species indicates that (in the growing average populations) the stable age distribution is skewed towards younger ages relative to the survival curve of a cohort (Caswell 2001, p 130).

Employing the average 3-year matrices, on the other hand (filled points in Fig. 2), *A. acanthocarpa* was projected to have a slightly higher intrinsic rate of increase and a lower net reproductive rate than *A. canescens* ($r = 0.297$ vs. $r = 0.126$, and $R_0 = 3.69$ vs. $R_0 = 4.12$, respectively; Fig. 2a, b). These average matrices predicted a faster convergence to the stable population structure for

A. acanthocarpa (i.e. higher damping ratio and lower period of oscillation) than for *A. canescens* (Fig. 2c, d). They also yielded a shorter longevity and generation time (both μ and \bar{A}) in *A. acanthocarpa* than in *A. canescens*. The projected lifespan from their average matrices was 7 and 20 years, respectively, and these values were set as the limit for their life tables.

Life tables

The life tables generated by STAGECOACH from the projection of each of the 3 years of data produced clear differences in survival and fecundity patterns with age (Fig. 3). *Atriplex canescens* was predicted to have a type 3 survivorship curve with a high initial mortality that decreased with age, while *A. acanthocarpa* would have a type 2 survivorship curve with a fairly constant mortality (Fig. 3a). Although these patterns were consistent from

Table 1 Projection matrices of *Atriplex acanthocarpa* and *A. canescens* employed in this study, showing survival in each stage class (σ_I) and the projected finite rate of population increase (λ)

	<i>A. acanthocarpa</i>					<i>A. canescens</i>				
	J ₁	J ₂	A ₁	A ₂	A ₃	J ₁	J ₂	A ₁	A ₂	A ₃
1995–1996										
J ₁	0.045	0.002	0.860	4.468	17.82	0.361	0.056	0.150	0.477	5.489
J ₂	0.093	0.041	0	0	0	0.177	0.191	0	0	0
A ₁	0.160	0.102	0.119	0.062	0.012	0.130	0.145	0.481	0.163	0.013
A ₂	0.140	0.204	0.309	0.175	0.093	0.044	0.193	0.342	0.418	0.044
A ₃	0.142	0.347	0.257	0.500	0.538	0.109	0.344	0.051	0.397	0.900
σ_I	0.579	0.696	0.684	0.737	0.642	0.821	0.929	0.873	0.979	0.957
λ	2.45					1.72				
1996–1997										
J ₁	0.321	0	0.002	0.011	0.035	0.546	0.043	0	0	(0.001)
J ₂	0.147	0.050	0	0	0	0.027	0.362	0	0	0
A ₁	0.042	0.177	0.245	0.112	0.033	0.005	0.052	0.469	0.132	0.011
A ₂	0.011	0.311	0.196	0.266	0.124	0.003	0.147	0.259	0.395	0.066
A ₃	0.006	0.210	0.082	0.319	0.599	0.002	0.267	0.074	0.380	0.883
σ_I	0.526	0.748	0.522	0.698	0.756	0.582	0.871	0.803	0.907	0.960
λ	0.73					0.95				
1997–1998										
J ₁	0.461	0.045	0.028	0.088	0.223	0.020	0.010	0.001	0.002	0.007
J ₂	0.042	0.061	0	0	0	0.043	0.361	0	0	0
A ₁	0.226	0.595	0.566	0.204	0.071	0.012	0.103	0.556	0.222	0.049
A ₂	0.002	0.156	0.131	0.298	0.155	0.004	0.124	0.099	0.403	0.088
A ₃	0	0.034	0.021	0.123	0.353	0.001	0.237	0.062	0.255	0.796
σ_I	0.732	0.892	0.719	0.625	0.579	0.080	0.835	0.716	0.879	0.933
λ	0.75					0.88				
Average										
J ₁	0.276	0.016	0.297	1.522	6.026	0.309	0.036	0.050	0.160	1.832
J ₂	0.094	0.051	0	0	0	0.082	0.305	0	0	0
A ₁	0.143	0.291	0.310	0.126	0.039	0.049	0.100	0.502	0.172	0.024
A ₂	0.051	0.224	0.212	0.247	0.124	0.017	0.155	0.233	0.406	0.066
A ₃	0.049	0.197	0.120	0.314	0.496	0.037	0.283	0.062	0.344	0.860
σ_I	0.612	0.779	0.642	0.686	0.659	0.494	0.878	0.797	0.922	0.950
λ	1.35					1.13				

To allow convergence of the matrix of *A. canescens* in 1996–1997, we used an artificial fecundity value of 0.001 in its projection. This did not affect the projected value of λ , but allowed the calculation of other parameters

For definition of size classes in each species, see text

year to year, the variability of the projected survival was higher in *A. canescens* than in *A. acanthocarpa*. This difference, however, is concentrated in early ages: older, “established” individuals of *A. canescens* have lower mortality rates than similarly aged individuals of *A. acanthocarpa* (Fig. 3b). *Atriplex canescens* had lower individual fecundity than *A. acanthocarpa* in all three years (Fig. 3c). As a consequence of failed and low recruitment in two out of three annual intervals (1996–1997 and 1997–1998), the variability of fecundity of *A. acanthocarpa* was projected to be wider than that of *A. canescens* (Fig. 3c). The logarithmic scale on the y-axis of this figure can be visually misleading in this respect, but it allows us to see the extremely low projected age-related fecundity values (see also top rows of matrices in Table 1) in the years 1996–1997 and 1997–1998.

Variability of population growth rate and elasticity of vital rates

The projected population growth rate differed between the two species in all 3 years (Fig. 4) and among years within each species (Fig. 5). *Atriplex acanthocarpa* was projected to grow faster (1995–1996) and to decline more rapidly (1996–1997 and 1997–1998) than *A. canescens* (Fig. 4; λ values in Table 1). Both species were projected to have a higher variability of population growth rate among years than would be expected by chance (i.e. by randomly interchanging individual plants between years; Fig. 5). The variability of λ of *A. acanthocarpa* (and the spread of this variability from the randomization tests) was higher than that of *A. canescens* (Fig. 5).

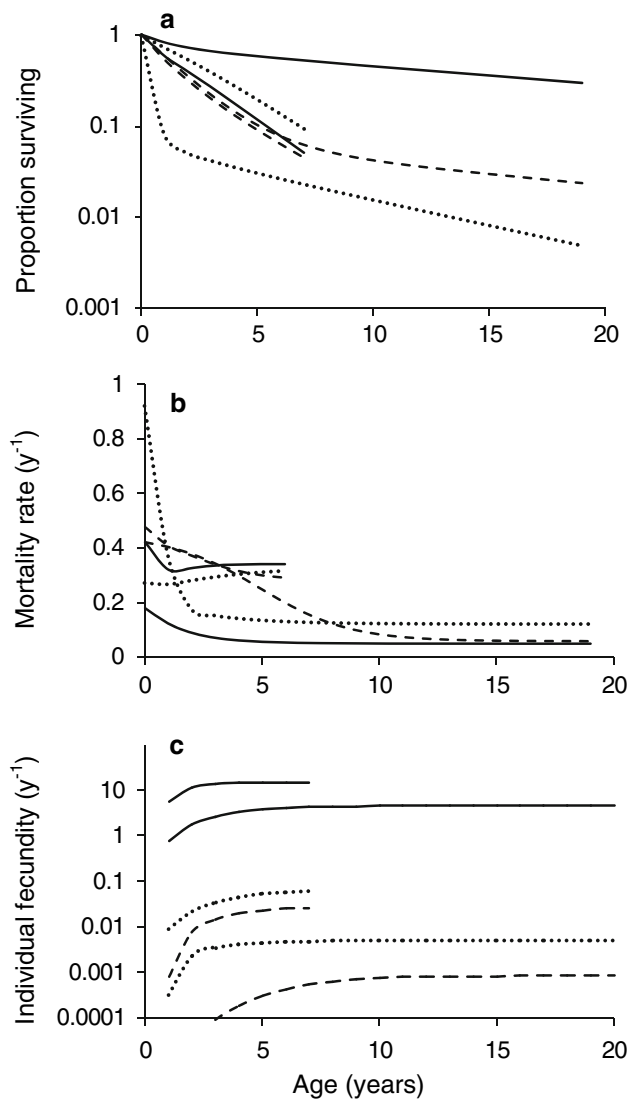


Fig. 3 Projected survivorship (a), mortality (b) and fecundity over the lifespan (c) of *A. acanthocarpa* (longevity 7 years) and *A. canescens* (longevity 20 years) in three annual intervals (continuous lines 1995–1996, dashed lines 1996–1997, dotted lines 1997–1998)

Demographic variability was also reflected in the relative contribution that the elasticities of survival, growth and fecundity made to λ in each of the six annual projections (Franco and Silvertown 2004). These elasticities indicated that changes in fecundity and growth would have a larger influence on the population growth rate of the faster-growing *A. acanthocarpa* (elasticities of fecundity, growth and survival calculated from the average matrix: $E_\phi = 0.17$, $E_\gamma = 0.20$, $E_\sigma = 0.63$), while changes in survival would have a larger effect on the population growth of *A. canescens* ($E_\phi = 0.10$, $E_\gamma = 0.14$, $E_\sigma = 0.76$). With some variability, the elasticities calculated for each individual year (not shown) followed the same trend.

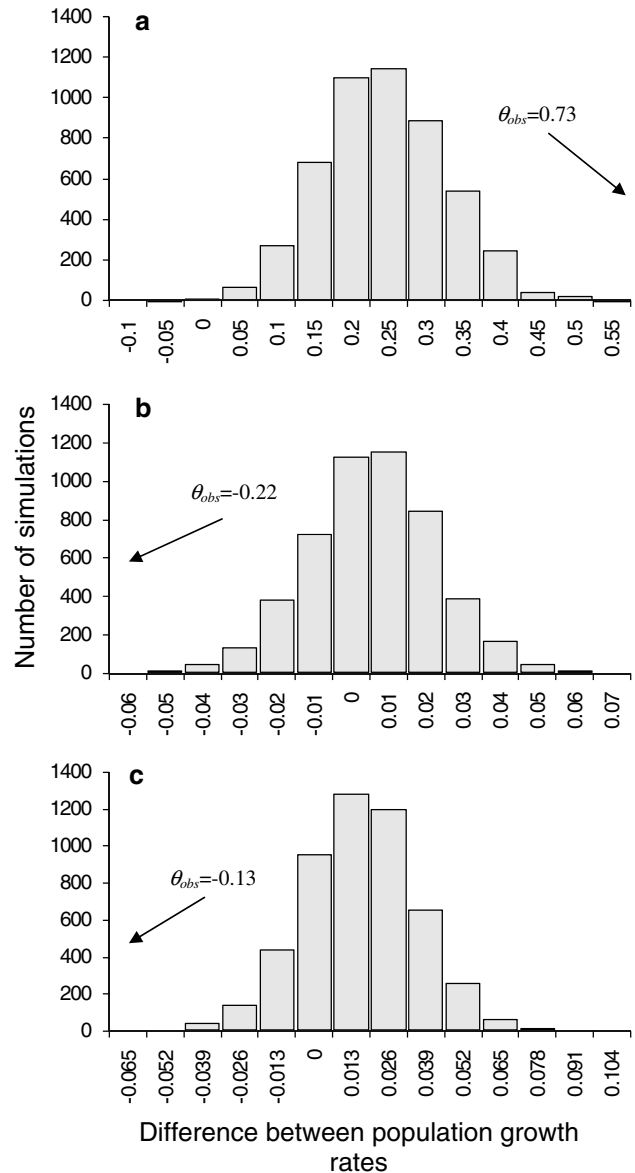


Fig. 4 Frequency distributions from 5000 randomizations of the difference between the projected finite rate of population growth of *A. acanthocarpa* (λ_a) and that of *A. canescens* (λ_c) in three annual periods (a 1995–1996, b 1996–1997, c 1997–1998). In all 3 years, the observed difference (θ_{obs}) was well outside the distribution obtained from 5000 randomizations, and this is indicated by the arrows pointing away from the respective distribution

Discussion

Clear differences in the life history of the two sympatric *Atriplex* species were found. *Atriplex canescens* had a lower population density (number of plants per hectare) and fecundity (number of recruits per adult), a longer lifespan and generation time, and more stable dynamics (lower asymptotic population growth rate of the average matrix and lower variability of its population growth rate in

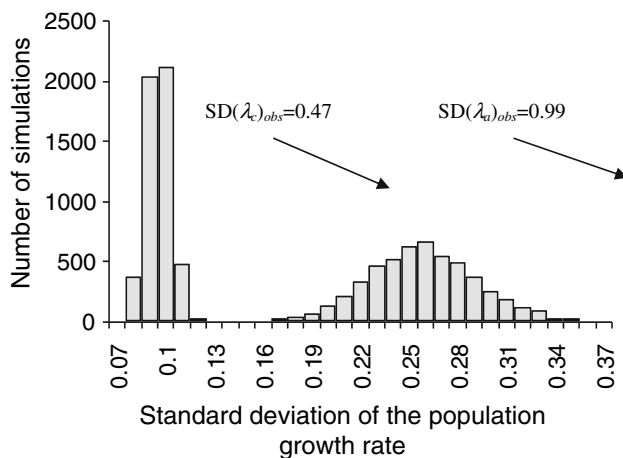


Fig. 5 Frequency distributions from 5000 randomizations of the standard deviation of the projected finite rate of population growth of *A. acanthocarpa* [$SD(\lambda_a)$; right-hand side] and that of *A. canescens* [$SD(\lambda_c)$; left-hand side] calculated from three annual periods (1995–1996, 1996–1997 and 1997–1998). In both species, the observed standard deviation of λ (SD_{obs}) was substantially higher than that of all 5000 randomizations (indicated by the arrow)

the year-to-year matrices) than *A. acanthocarpa* (Figs. 1a, 2, 3). When the size of the plants (volume occupied) was taken into account, however, both species had similar abundances in years of plenty (1996 and 1997), but *A. canescens* dominated in years of scarcity (1995 and 1998) (Fig. 1b). These population volumes were particularly high in the more productive years, 1996 and 1997. The biomass packed into such volumes is substantial for a semiarid ecosystem and is likely to lead to increased competition for water as the pulse period fades.

The species also differed markedly in their patterns of mortality and fecundity (Fig. 3). *Atriplex acanthocarpa* had near constant mortality with age irrespective of year, while *A. canescens* mortality vary widely from year to year at early ages, but declined with age and was fairly low in the adult stages. These patterns indicate an ability of established individuals of *A. canescens* (though not of their seedlings and saplings) to survive interpulse periods and an ability of *A. acanthocarpa* to reproduce and recruit abundantly in pulse periods.

The overall population responses, as measured by their projected population growth rates, differed between the two species in each of the three study years (Fig. 4) and within each species among years (Fig. 5). Both species performed better in the period 1995–1996, when abundant recruitment occurred: population growth rate was projected to be positive for both species and was higher for *A. acanthocarpa*. In contrast, in years when recruitment was either nil or low (1996–1997 and 1997–1998), resulting in $\lambda < 1$ ($r_0 = \ln \lambda < 0$), the projected population growth rate of *A. acanthocarpa* was lower than that of

A. canescens. Thus, *A. acanthocarpa* behaved as a fugitive species that was able to benefit more than *A. canescens* from episodes of favorable conditions. However, in years when conditions deteriorated, it declined faster than *A. canescens*. In contrast, *A. canescens* seemed better able to tolerate years when conditions were poor (it had higher survival and population growth rate) but was unable to take full advantage in terms of growth and reproduction in years when conditions improved.

Despite the relative short duration of the study, it is clear that the two species differ in their demographic response to temporal environmental variation (resource availability) and suggests that these differences have resulted in contrasting life histories. Our results are also the first empirical evidence of the operation of the mechanisms of coexistence in perennial species in a fluctuating environment and confirm that the mechanisms of coexistence in structured populations are the same in both structured and unstructured populations (Dewi and Chesson 2003).

As suggested by Chesson (2003), evidence that one or both of the mechanisms of coexistence predicted by theory are operating in a system would be provided by the relatively large difference in the variances of the logarithms of recruitment weighted by adult survival of the two species. Thus, while variance of the natural logarithm of recruitment was 9.55 for *A. acanthocarpa* and 12.83 for *A. canescens*, their average adult survival was 0.66 and 0.89, respectively (calculated from data in Table 1). This gives a difference of 5.08 between the two species, which is meant to be proportional to the overall stabilizing effect of both the storage effect and the relative non-linearity of competition (Chesson 2003).

Recapitulating what was stated in the Introduction, the theoretical work of Chesson and others suggests that the equilibrium mechanisms of stable coexistence under fluctuating environments are the storage effect and the relative non-linearity of competition. Each of these two mechanisms has three components. The components of the storage effect are: S1, a differential response to environmental fluctuations (e.g., resource abundance); S2, covariance between environmental variation and competition; S3, buffered population growth rate. Those of the (relative) non-linearity of the response to varying resources are: N1, the population growth rates of the species respond differently to changes in the abundance of the limiting resource (i.e. one increases faster than the other); N2, the species with the larger curvature (non-linearity) of this response has an average fitness advantage in the absence of resource fluctuations (i.e. in the absence of fluctuations, it would eliminate the other species); N3, the species with the larger curvature of the response experiences lower fluctuations in resource availability when it is an invader than when it is a resident (i.e., this species produces

large-amplitude cycles in resource availability; Armstrong and McGehee 1976, 1980).

For component S1, the population growth rates of the two species differed every year (Fig. 4) and differed also in their response to annual resource fluctuations (Fig. 5). In addition to this, and as predicted by Chesson (2000a and own references therein), Dewi and Chesson (2003) and Chesson et al. (2004), both species buffered the effect of environmental variation through the (differing degrees of) tolerance of the adults to drought (ingredient S3; for documentation of the ecological and physiological mechanisms responsible for this buffering effect in desert plants, see Comins and Noble 1985; McAuliffe 1988; Schuster et al. 1992; Schwinning and Ehleringer 2001). The S2 ingredient requires that the covariances between the responses to environmental changes and competition vary between resident and invader species; that is, that the population responses to the physical environment modify competition in such a way that intraspecific competition outweighs interspecific competition and hence acts as a stabilizing mechanism. To date, however, we lack experimental quantification of competition to assess this component.

For component N1, the projected intrinsic rate of increase for each species in each of the 3 years had a non-linear relationship with resource abundance for both species (Fig. 6), thereby showing that the two species responded differently to changes in the abundance of the limiting resource. *Atriplex acanthocarpa* increased more rapidly when water was more abundant and declined faster when water was scarce (Fig. 6). If the intrinsic rate of population growth is proportional to the amount of the limiting resource being captured by each species, Fig. 6 must mirror the functional response of these two species to

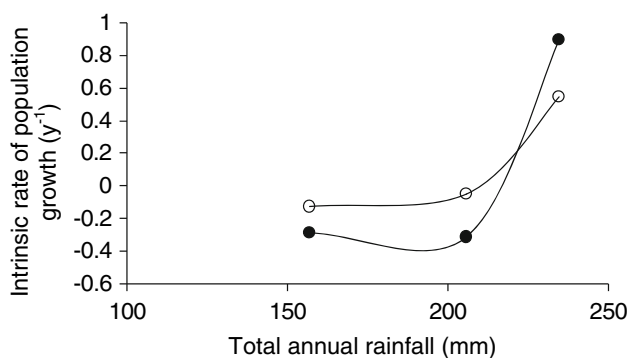


Fig. 6 The relationship between the projected intrinsic rate of population growth in three consecutive annual intervals (approx. May 1995 to approx. April 1998) and total annual precipitation (Jan–Dec) for the years 1996–1998. Filled symbols *Atriplex acanthocarpa*, open symbols *A. canescens*. Curves are only meant as visual guides and were drawn employing the cubic splines of EXCEL’s plotting option

the abundance of the resource, and the relative curvature of these responses is higher in one species (*A. acanthocarpa*) than in the other (*A. canescens*) (components N2 and N3; compare Fig. 6 with Fig. 1 of Chesson 2000a). This means that the relative advantage that one species has over the other is reversed at opposite ends of resource abundance. Although this situation should make the roles of resident and invader species reversible at opposite ends of resource abundance, their life history characteristics may not always allow them to fulfill these two roles. *Atriplex acanthocarpa* tends to act as invader when conditions improve after dry years, but it would have difficulty staying as resident indefinitely. In contrast, *A. canescens* may recover and act as invader after, for example, excessive browsing by cattle, but in the absence of browsing, it would act as resident most of the time.

In summary, the inferior capacity of *A. acanthocarpa* to survive long dry periods, relative to that of *A. canescens*, is compensated by its higher efficiency to convert resources into growth and recruitment during favorable episodes. This difference in life history, expressed through the two mechanisms of coexistence proposed by theory, accounts for their coexistence. This does not exclude the possibility that other differences in resource utilization or additional buffering from a seed bank may also contribute to these mechanisms.

The action of these mechanisms of coexistence in this system sheds light on a long-debated issue, that of whether ecological succession occurs at all in arid environments. The classic scheme where early successional (“*r*-selected”) species are favored in open spaces with abundant resources and are eventually replaced by late successional (“*K*-selected”) species in saturated areas where resources are limiting is apparently not applicable to arid zones (McAuliffe 1988). Our results suggest that, unlike communities where the limiting factor (e.g. incident light in a forest) is relatively constant over long periods of time, the fluctuating, unpredictable nature of the limiting factor in arid environments makes the climax a constantly moving target. What on broad temporal and spatial scales is perceived as eventual saturation by one or a few species in a habitat with a constant supply of the limiting resource is confounded in arid environments at every spatial and temporal scale. Although at small spatial scales there is always disturbance in a forest, and therefore different stages of succession, at the landscape level the forest always tends towards, and is perceived to be mostly at, a stable climax stage where one or a few species dominate. In arid zones, however, the carrying capacity determined by the limiting resource is not constant, but changes dramatically over a range of temporal and spatial scales. Consequently, species with contrasting life histories coexist indefinitely. There is no optimal life history capable

of maintaining positive population growth when the limiting resource fluctuates (as if it were at opposite ends of the temporal sequence of succession) over short periods of time. Thus, despite the fact that the mechanisms that drive the dynamics of each individual population are the same in both (and all) environments, succession in arid communities is an illusion because the habitat is a spatial and temporal mosaic of resource abundance (the successional mosaic hypothesis of Chesson and Huntly 1997). As a corollary, the demographic and life-history evidence provided by our study makes us agree with these authors that the differentiation between harshness, stress and disturbance employed by some authors as mechanisms that have differential effects on coexistence is artificial. What is stressful to one species is the optimal physiological condition for another. Disturbance or harshness is also only meaningful with respect to a particular life history or set of physiological adaptations. A mechanistic understanding of the effects that conditions have on the dynamics of the populations is essential to account for species coexistence and, hence, diversity.

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