

Long-term dynamics of winter and summer annual communities in the Chihuahuan Desert

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Abstract. Winter and summer annuals in the Chihuahuan Desert have been intensively studied in recent years but little is known about the similarities and differences in the dynamics between these two communities. Using 15 yr of census data from permanent quadrats, this paper compared the characteristics and temporal dynamics of these two distinct, spatially co-existent but temporally segregated communities. Although the total number of summer annual species recorded during our 15 yr of observation was higher than winter annuals, the mean number of species observed each year was higher in the winter community. The winter community exhibited lower temporal variation in total plant abundance and populations of individual species, lower species turnover rate and higher evenness than the summer community. The rank abundances of species in winter were significantly positively correlated for a period of up to 7 yr while in summer significant positive correlations in rank abundance disappeared after 2 to 3 yr. The higher seasonal species diversity (i.e. number of species observed in each season) in winter rather than the overall species pool (over 15 yr) may be responsible for the greater community stability of winter annuals. The difference in long-term community dynamics between the two communities of annual plants are likely due to the differences in total species pool, life history traits (e.g. seed size), and seasonal climatic regimes.

Keywords: Climate; Life history; Seed size; Species pool.

Nomenclature: Kearney & Peebles (1960).

Introduction

In the southwestern United States and northern Mexico, there are two distinct, spatially overlapping, but temporally separated communities of ephemeral plants, usually referred to as winter and summer annuals (Mulroy & Rundel 1977; Davidson et al. 1985; Gutierrez & Whitford 1987). These two communities occur together in the same habitat and co-exist in the soil seed bank, where they are exposed to similar physical conditions and seed predators. Studies of these desert annuals have been extensive, and many individual species of winter or summer annuals have been studied with respect to ecological characteristics, such as germination (Inouye 1980), survival (Juhren et al. 1956; Beatley 1967; Fox 1989) and seed banks (Freas & Kemp 1983).

The special nature of the spatial co-existence of winter and summer annuals has stimulated comparative studies between the two communities. Such studies have compared features of the two annual plant groups in a broad sense, including morphology and physiology (e.g. Mulroy & Rundel 1977), the different responses to experimental manipulations and disturbances (e.g. Samson et al. 1992; Heske et al. 1993; Valone & Kelt 1999), distribution and abundance (Guo et al. 2000a, b) and the spatial-temporal interactions between the two groups (Guo & Brown 1997). All of these studies have called attention to dramatic year-to-year fluctuations in abundance, productivity and diversity that reflect interactions between their short life cycles and the largely unpredictable climatic variation in arid regions; see review by Inouye (1991 and literature therein).

While desert plants have been the subject of many ecological studies in recent years, there has been little systematic attempt to compare temporal dynamics in community structure (e.g. species turnover over time) between the two communities, especially when plant life history characteristics and the climatic regimes in which they occur are considered. However, if the two

communities differ in diversity then such a comparison, based on long-term data, can allow examination of the effect of diversity on community stability. The relationship between diversity and stability has long been debated in ecology (e.g. Elton 1958; May 1972; Goodman 1975; Pimm 1984; Tilman 1996). Numerous theoretical treatments have yielded conflicting predictions (May 1972; Goodman 1975; Pimm 1984; Doak et al. 1998) and recent empirical tests have been controversial (Givnish 1994; Tilman & Downing 1994; Tilman 1996; Huston 1997).

Here, we use long-term (15 yr) census data from permanent quadrats to quantitatively describe the winter and summer annual plant communities at one site and compare their temporal dynamics. Comparisons between the two communities enable us to examine the interrelationships between community diversity, dynamics, life history traits (e.g. seed size) and climatic regimes. Specifically, we address the following questions: 1. What are the similarities and differences in community structure and life history characteristics between the two communities? 2. How is community stability related to community diversity (species richness)? 3. To what extent can climatic factors (i.e. precipitation and temperature) explain the similarities and differences in the dynamics of the two communities? Finally, how are the community structure and dynamics of the two communities related to life history characteristics (e.g. seed size, life-span) of the component species?

Methods

The field data were collected from a 20-ha long-term experimental study site near Portal, Arizona. Livestock have been excluded from the site since 1977. The soil conditions are relatively homogeneous but there is remarkable small-scale heterogeneity due to microtopography, shrub spacing, and animal disturbance (Guo 1998). The vegetation consists of scattered shrubs (common genera include *Acacia*, *Ephedra*, *Flourensia* and *Prosopis*), semi-shrubs (e.g. *Gutierrezia sarothrae*, *Haplopappus tenuisectus* and *Zinnia* spp.) and perennial grasses (e.g. *Eragrostis* spp., *Aristida* spp. and *Muhlenbergia porteri*).

The site is characterized by a distinctly bimodal distribution of annual precipitation and supports diverse winter and summer annual plants. Compared to summer rains (May–September), winter rains (October–April) are lower in magnitude (118 vs 219 cm), but more variable from year to year ($CV = 42.7$ vs 35.3) and dispersed over a longer season. The first winter annuals typically germinate in response to the first autumn rains in October or November but there tends to be a large

phenological variation among the winter annual species in timing of germination and initial growth. The 28 most common winter species are found in five families: *Asteraceae* (11 species), *Fabaceae* (5), *Poaceae* (4), *Boraginaceae* (4) and *Brassicaceae* (4). In contrast, nearly all germination of summer annuals typically occurs within a few days immediately following the first summer rain, which usually falls in late June or early July but sometimes occurs several weeks earlier or later (Kemp 1983; Fox 1989). The 26 most common summer species are found in the following four families: *Poaceae* (11), *Asteraceae* (9), *Euphorbiaceae* (3) and *Aizoaceae* (3).

The study site contains 24 long-term experimental plots, each 0.25 ha in area, subjected to various experimental manipulations (Brown & Munger 1985). From 1977–1987 there were two control plots. In 1988 two new control plots were initiated. Within each plot are 16 permanent, regularly spaced 0.25-m² quadrats. All plants were counted individually by species in each quadrat. Corresponding to the bimodal precipitation, we censused the quadrats twice each year, during April–May and August–September, beginning in April 1978. Each census was conducted during a 1–3 wk period of peak flowering and maximum biomass (for details, see Samson et al. 1992). From winter 1978 to winter 1981 data were not complete (only common species were recorded), therefore, in all analyses we used data censused from summer 1981 to winter 1995. To exclude any potential experimental treatment effects, all analyses are restricted to the quadrats from the control plots.

To compare characteristics of the winter and summer annual plant communities, we compiled the following information for each species: photosynthetic type (C_3 or C_4), life history, leaf size, plant height, seed size and geographic distribution using herbaria specimens, published materials (e.g. Kearney & Peebles 1960; Mulroy & Rundel 1977; Ehleringer 1985; Martin & Hutchins 1980–1981) and data collected from the site. The differences in plant height, leaf area, and seed size between winter and summer annuals were tested using unpaired *t*-tests. The three biseasonal species (i.e. *Eriogonum abertianum*, *Haplopappus gracilis* and *Baileya multiradiata*) were included as both winter and summer annuals, because they are important members of both communities.

To examine the temporal changes in community structure of the plant communities, we examined the rank abundance patterns of species of both winter and summer annuals over a 5-yr period (1989–1994) using the four control plots (64 quadrats). To illustrate comparisons in rank abundance patterns more clearly between the communities, we plotted the rank abundance data for consecutive censuses starting with the summer 1989–winter 1990 pair of censuses.

To examine the consistency of each community over

Table 1. Differences in seasonal precipitation and winter and summer annual community structure and population dynamics at the study site. All measures (including CVs over time) were based on our 15-yr records.

	Winter	Summer	<i>t</i>	df	<i>P</i>
Precipitation (mm)	117.5 (CV = 42.7)	218.8 (CV = 35.3)			
Total number of species*	37	45			
Mean seasonal richness	27.64 (CV = 0.21)	21.73 (CV = 0.37)	2.11	26	0.028
β-diversity (over 15 yr)	0.23	0.93			
Evenness (see Results, Fig. 2)	higher	lower			
CV of whole community	1.20	2.11			
Mean CV of all species	2.09	2.59	-2.90	78	0.002

* Including three typical biseasonal annuals

time, we computed the Spearman rank correlation coefficient of the rank abundances of species in pairs of years separated by different time lags from 1981 to 1995 using quadrats from the two original control plots only. For the most common 28 winter annuals from 1982 to 1995 and the most common 25 summer annuals from 1981 to 1994 (the rest of the species were extremely rare), we calculated the Spearman rank correlation coefficients of the rank abundances of species on the two control plots for all pairs of years separated by a lag time of 1, 2, 3, ..., 13 yr. In other words, we calculated the Spearman rank correlation for all pairs of consecutive years, pairs of years separated by 2 yr, pairs of years 3 yr apart and so forth.

The species turnover rates for both winter and summer annual communities were calculated using Whittaker's (1960) β-diversity index:

$$\beta = \gamma/\alpha - 1 \tag{1}$$

where β represents species turnover rate over time, γ is total species richness observed over 15 yr of the study and α is the mean species richness in each season.

Regression methods were used to examine possible relationships between climatic variables such as annual or seasonal precipitation and temperature on plant densities of winter and summer annuals.

Results

Community structure and characteristics

Over the duration of the study, we recorded a total of 34 species of winter annuals, 42 of summer annuals and three biseasonal annuals (species which germinate in winter but flower and set seeds in summer; Table 1). Except for the biseasonal species, there was little overlap in species composition between the winter and summer communities, presumably reflecting their non-overlapping phenologies and their requirements for different abiotic conditions. Compared with summer annuals, winter annuals all used C₃ photosynthetic pathways whereas ca. 50% of the summer annuals used C₄ photosynthetic pathways. Although there was no difference in leaf area (*t* = -0.65, *df* = 42, *P* = 0.25), winter annuals tended to have larger seeds (*t* = 1.94, *df* = 42, *P* = 0.029; see also Davidson et al. 1985, Samson et al. 1992), smaller plant height (*t* = -2.15, *df* = 78, *P* = 0.017) and a rosette growth form rather than cauline (Table 2). Supplemental data from the literature would suggest that winter annuals had more extensive root systems that extend to greater depths in the soil (Mulroy & Rundel 1977; Ehleringer 1985).

There were consistent differences in the degree of dominance between the winter and summer annual communities. Regardless of overall species richness, within

Table 2. Differences in life history traits between winter and summer annuals at the study site near Portal, Arizona.

	Winter	Summer	<i>t</i>	df	<i>P</i>
Predominant growth structure	Basal rosettes (73%)	Cauline leaves (84%)			
Predominant rooting depth	Deeper	Shallower			
Vegetative life span (wk)	3-7	2-3			
Plant height (cm)	32.61 ± 17.79	41.85 ± 20.42	-2.15	78	0.017
Leaf size* (cm ² ± standard deviation)	5.89 ± 6.64	9.43 ± 27.4	-0.65	42	0.250
Seed size (mg)	0.93 ± 1.07	0.31 ± 0.50	1.94	42	0.029
Monocots (%)	8.1	24.44			
C ₃ (%)	100	41.86			

* Calculated as length × width.

a season, abundances were much more even among the winter species than among the summer species (Table 1, Fig. 1). The summer annual community tended to be dominated by one to five very common species in a given year, but the identity of these common species differed from year to year.

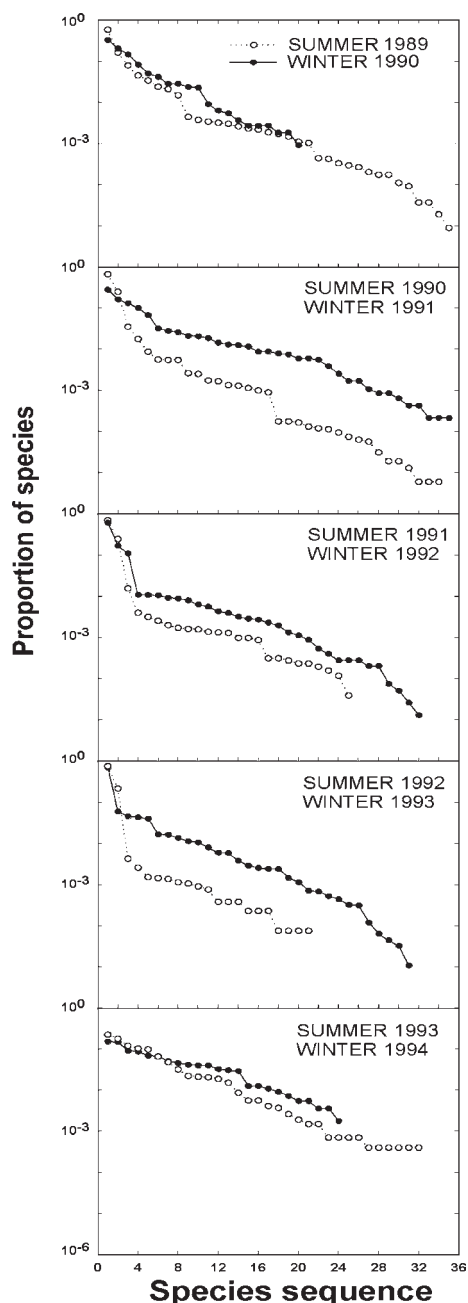


Fig. 1. Dominance-diversity curves for winter and summer annual communities during 1989-1994 at the study site. Each dot represents an individual species and is plotted as relative abundance of the species against its rank (based on its abundance) in the whole community.

Population dynamics

The population densities of most species, and all the common species, exhibited dramatic fluctuations over the course of the study (Fig. 2). Two general features are apparent in Fig. 2. First, the population dynamics of each species are complex and it is difficult to identify pairs or larger sets of species that exhibit highly similar dynamics. Second, despite the individualistic patterns, there appear to be distinct years in which many species exhibit either high or low abundance. For the winter community, 1981-1984 and 1991-1994 were periods of high abundance for many species while abundances of most species were low in the intervening periods. Likewise, many species in the summer community were very abundant in 1982-1983 and 1988-1990 but in other years (e.g. 1994) all species were rare. Regression analyses using raw density data failed to reveal any significant relationships between climatic data (precipitation and temperature) and plant densities of both winter and summer annuals (in all cases $P > 0.05$). However, using log-transformed density data, summer annual density and summer precipitation or summer temperature was marginally related (positive, $r^2 = 0.16$, $P = 0.09$ and negative, $r^2 = 0.21$, $P = 0.05$, respectively). Although the abundances of some winter and summer annuals had positive relationships with seasonal precipitation, none of these relationships were significant (results not shown). Winter annuals showed lower temporal variation in population dynamics over 15 years than summer annuals (mean CV s for all species: $CV_{winter} = 2.09$, $CV_{summer} = 2.59$; $t = -2.90$, $df = 78$, $P = 0.0024$). In both winter and summer annual communities, common species had smaller temporal variation over time than rare species (Fig. 3).

Community diversity and dynamics

Year-to-year variation in species richness was high for both communities (Fig. 4). Despite the fact that more summer than winter annual species were observed over the course of the study, the mean number of species observed per year was significantly higher in winter than in summer (winter mean = 27.64 species; summer mean = 21.73 species; $t = -2.11$, $df = 26$, $P = 0.028$; Table 1).

The summer community exhibited greater temporal variation in overall density than the winter community: in summer, there were more years of very low and also very high density compared to winter (CV of total seasonal abundance: $CV_{winter} = 1.20$, $CV_{summer} = 2.11$). Concomitant with the higher variation in density, the summer annual community also exhibited significantly higher year-to-year variation in seasonal species richness

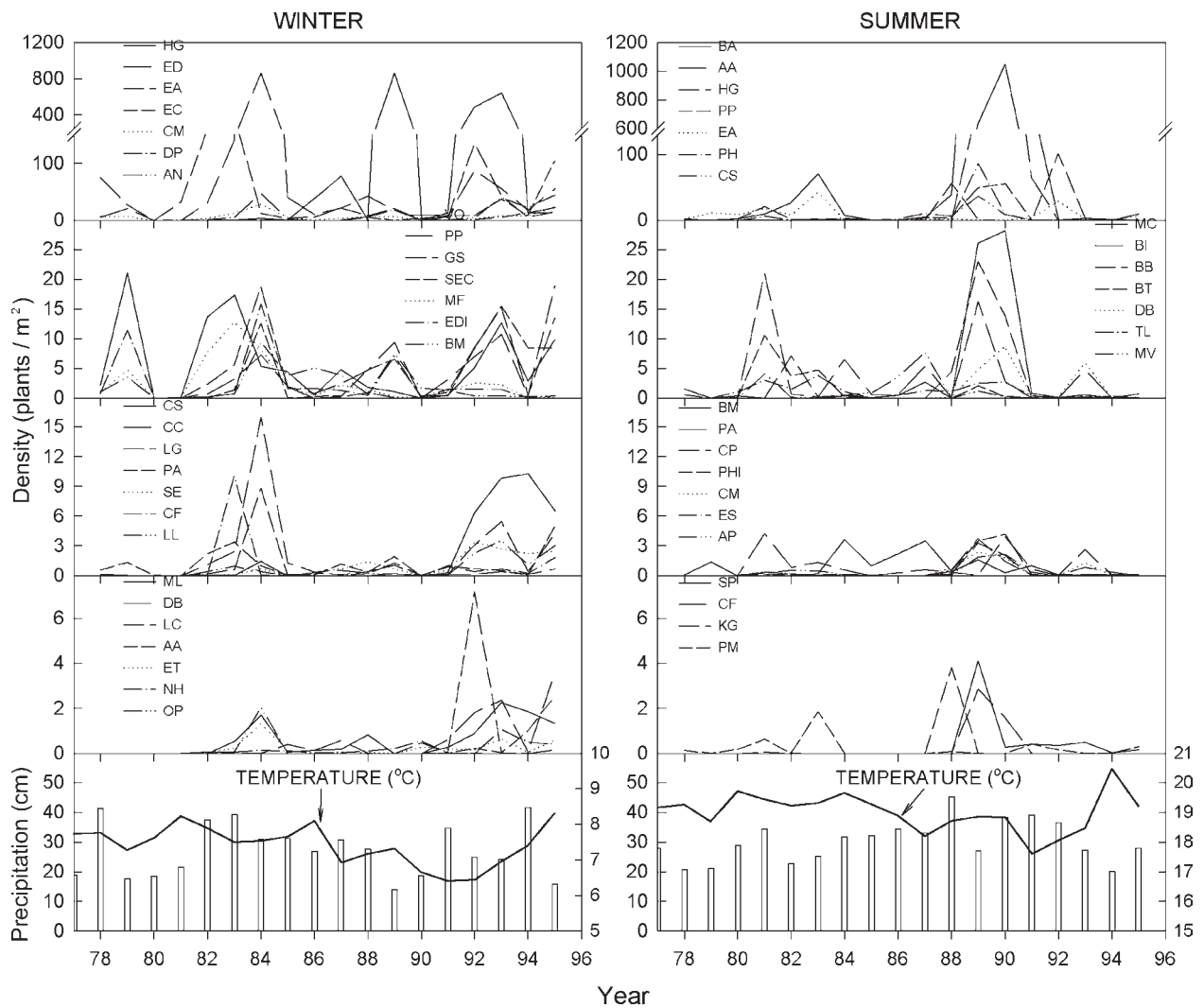


Fig. 2. Population dynamics of 28 winter annuals, 25 summer annuals and seasonal precipitation over time. Abbreviated species names are listed in Table 3. Note that data from summer 1978-winter 1981 were not complete and only a few dominant species are shown here. Precipitation data are from the weather station at Portal, Arizona.

than the winter annual community ($CV_{winter} = 0.21$, $CV_{summer} = 0.37$) and in species turnover rate over time ($\beta_{winter} = 34/27.64 - 1 = 0.23$, $\beta_{summer} = 42/21.73 - 1 = 0.93$).

Table 3 further illustrates the differences in compositional consistency between the two communities; it contains the rank abundances of the most common species in each community from 1982 to 1995 (28 winter and 25 summer species). Inspection of Table 3 reveals that most species were consistently rare, while a few exceptional species were relatively common over time (e.g. *Eriastrum diffusum* in winter, *Bouteloua aristoides* in summer). Several species, however, varied greatly in abundance over time including *Haplopappus gracilis*, which was very rare prior to 1986 but generally

abundant after 1987 and *Erodium cicutarium* and *Aristida adscensionis* which were very common in several years but extremely rare in other years.

The Spearman rank correlation coefficients of community similarity differed dramatically for different time lags (Fig. 5). For the winter community (Fig. 5A), all pairs of years exhibited positive correlations, even comparisons of years separated by more than a decade. Many pairs of years separated by less than 7 yr exhibited significant positive correlations; the mean correlation coefficient was 0.51 ($sd = 0.19$, $n = 63$). Pairs of years separated by longer time lags exhibited much lower positive correlations (mean correlation coefficient = 0.31, $sd = 0.09$, $n = 28$). For the summer community (Fig. 5B), only time

Table 3. Temporal variation in species composition in both winter and summer communities over time, shown by mean species ranks in density from 1982 to 1995. Most abundant species were listed first and very rare species were not included. If two or more species had equal abundances, they were given the same rank.

Species/(species code/family)	Year	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95
Winter																
<i>Haplopappus gracilis</i> (HG/Asteraceae)		12	16	14	12	1	1	24.5	1	4	1	1	1	4	4	
<i>Eriastrum diffusum</i> (ED/Polemoniaceae)		2	2	1	1	2	2	1	4	15	3	3	2	2	1	
<i>Eriogonum abertianum</i> (EA/Polygonaceae)		1	1	8	5	3	3	2	2	11	4	2	3	9	6	
<i>Erodium cicutarium</i> (EC/Geraniaceae)		9	8	2	10	23.5	18	3	3	2	21	19	12	3	9	
<i>Cryptantha crassisepala</i> (CC/Boraginaceae)		5	5	3	3	11	6	4	9	1	14	16	11	8	3	
<i>Descurainia pinnata</i> (PP/Plantaginaceae)		3	3	13	2	7	4	8	13	8	16	9	8	10	10	
<i>Astragalus nuttallianus</i> (AN/Fabaceae)		16	19	20	16	13	21	5	24	23	2	4	5	7	8	
<i>Vulpia octoflora</i> (VO/Poaceae)		30.5	30.5	30	27	23.5	25.5	24.5	24	23	12	11	4	1	2	
<i>Plantago purshii</i> (PP/Plantaginaceae)		26	12	7	20	14	14	6	8	7	17	6	6	6	11	
<i>Gilia sinuata</i> (GS/Polemoniaceae)		6	7	4	6	23.5	17	11	24	14	10	5	7	16	7	
<i>Spermolepis echinata</i> (SEC/Apiaceae)		10	10	12	7	6	7	7	5	11	5	8	9	15	5	
<i>Malacothrix fendleri</i> (MF/Asteraceae)		4	4	11	8	8	8	10	19	23	8	14	18	22	37	
<i>Erigeron divergens</i> (EDI/Asteraceae)		14	15	6	9	5	9	15	7	12	6	18	19	23	28	
<i>Baileya multiradiata</i> (BM/Asteraceae)		15	14	9	4	4	5	13	6	3	7	23	24	19	29	
<i>Chaenactis stevioides</i> (CS/Asteraceae)		25	24	17	27	23.5	25.5	24.5	17	23	20	9	10	5	34.5	
<i>Cryptantha crassisepala</i> (CC/Boraginaceae)		8	11	5	11	9	12	17	11	13	23	26	23	20	23	
<i>Lesquerella gordonii</i> (LG/Brassicaceae)		13	17	10	24	10	25.5	14	12	23	24	13	13	17	13	
<i>Phacelia arizonica</i> (PA/Hydrophyllaceae)		7	9	19	18	17	10	16	10	23	9	21	22	24	12	
<i>Stephanomeria exigua</i> (SE/Asteraceae)		30.5	22	21	22	12	11	9	14	16	15	12	15	11	16	
<i>Chenopodium fremontii</i> (CF/Chenopodiaceae)		18	6	28	27	23.5	25.5	24.5	24	23	11	22	20	18	17	
<i>Lepidium lasiocarpum</i> (LL/Brassicaceae)		11	13	23	23	23.5	19	18	18	23	25	15	14	13	15	
<i>Microseris linearifolia</i> (ML/Asteraceae)		30.5	18	16	17	16	16	12	24	23	19	20	17	12	18	
<i>Dalea brachystachys</i> (DB/Fabaceae)		30.5	30.5	30	27	23.5	25.5	24.5	24	6	27	7	26	27	34.5	
<i>Lupinus concinnus</i> (LC/Fabaceae)		30.5	29	30	13	15	13	24.5	24	23	13	17	16	25	14	
<i>Astragalus allochrous</i> (AA/Fabaceae)		23	20	18	14	23.5	20	20	24	10	22	25	21	21	25	
<i>Erodium texanum</i> (ET/Geraniaceae)		21	23	26	15	18	22	19	16	5	28	27.5	19	14	27	
<i>Nama hispidum</i> (NH/Hydrophyllaceae)		19	25	15	27	23.5	25.5	24.5	24	23	26	27.5	27	27	33	
<i>Oenothera primavera</i> (OP/Onagraceae)		30.5	21	25	19	23.5	15	24.5	15	17	18	24	25	27	24	
Summer																
<i>Bouteloua aristidoides</i> (BA/Poaceae)		5	1	1	1	3	4	4	2	1	1	5	3	1		
<i>Aristida adscensionis</i> (AA/Poaceae)		16	8	5	16	17.5	11	10.5	24	2	2	2	10	10	5	
<i>Haplopappus gracilis</i> (HG/Asteraceae)		24	17	10	10	17.5	18.5	18.5	1	22	26.5	18	24.5	4	7	
<i>Pectis papposa</i> (PP/Asteraceae)		1	6	8	5	7	9	5	5	4	3	7	24.5	9	13	
<i>Eriogonum abertianum</i> (EA/Polygonaceae)		3	2	2	12	5	8	8.5	7	25	24	3	2	6	2	
<i>Portulaca halimoides</i> (PH/Portulacaceae)		6	9	15	4	17.5	18.5	18.5	9	3	6	12	12	14	21.5	
<i>Chamaesyce serpyllifolia</i> (CS/Euphorbiaceae)		24	22	21	25.5	6	3	1	3	5	7	14	16	18	17	
<i>Mollugo cerviana</i> (MC/Aizoaceae)		2	10	12	2	4	5	3	24	8	11	25.5	24.5	2	21.5	
<i>Boerhaavia intermedia</i> (BI/Nyctaginaceae)		24	22	21	14	8	6	7	24	6	4	5	13	11	21.5	
<i>Bouteloua barbata</i> (BB/Poaceae)		24	3	13	13	17.5	18.5	18.5	4	7	5	25	24.5	26	9	
<i>Boerhaavia torreyana</i> (BT/Nyctaginaceae)		4	4	3	20	17.5	18.5	18.5	24	17	21	20	14	16	4	
<i>Dalea brachystachys</i> (DB/Fabaceae)		24	22	21	25.5	17.5	18.5	18.5	17	9	8	16	9	1	11	
<i>Tidestromia lanuginosa</i> (TL/Amaranthaceae)		9	5	4	7	9	7	10.5	8	15	12	13	19	13	21.5	
<i>Mollugo verticillata</i> (MV/Aizoaceae)		8	15	21	11	2	1	2	24	21	23	23	24.5	17	21.5	
<i>Baileya multiradiata</i> (BM/Asteraceae)		24	22	11	3	1	2	6	13	19	19	4	11	27	13	
<i>Panicum antidotale</i> (PA/Poaceae)		7	7	7	9	17.5	10	8.5	14	27.5	10	6	15	8	3	
<i>Crotalaria pumila</i> (CP/Fabaceae)		18	16	21	21	17.5	18.5	18.5	16	13	14	24	24.5	5	6	
<i>Panicum hirticaule</i> (PHI/Poaceae)		24	12	21	25.5	17.5	18.5	18.5	12	12	9	21	24.5	20	10	
<i>Chamaesyce micromera</i> (CM/Euphorbiaceae)		12	14	21	19	17.5	18.5	18.5	10	16	15	22	17	7	15	
<i>Euphorbia serrula</i> (ES/Euphorbiaceae)		13	13	14	15	17.5	18.5	18.5	11	11	17	17	18	15	16	
<i>Amaranthus palmeri</i> (AP/Amaranthaceae)		15	11	9	17	17.5	18.5	18.5	18	13	11	24.5	28	21.5		
<i>Sida physocalyx</i> (SP/Malvaceae)		24	22	21	25.5	17.5	18.5	18.5	24	10	18	10	4	12	12	
<i>Chenopodium fremontii</i> (CF/Chenopodiaceae)		11	22	6	25.5	17.5	18.5	18.5	19	27.5	26.5	9	8	25	21.5	
<i>Kallstroemia grandiflora</i> (KG/Zygophyllaceae)		14	18	16	25.5	17.5	18.5	18.5	20	24	20	25.5	24.5	22	21.5	
<i>Panicum miliaceum</i> (PM/Poaceae)		24	22	21	22	17.5	18.5	18.5	24	23	25	15	24.5	24	8	

lags of 1 or 2 yr exhibited consistently high positive correlations (mean coefficient = 0.43, $sd = 0.25$, $n = 25$). Pairs of years separated by ≥ 3 yr exhibited only weak positive or occasionally negative correlations in rank abundance (mean coefficient = 0.17, $sd = 0.15$, $n = 66$).

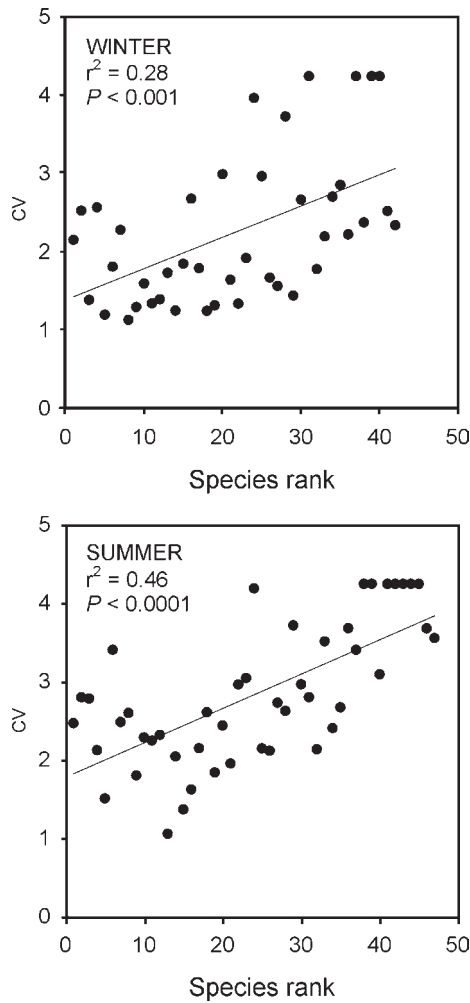


Fig. 3. Temporal variation measured as CV of density over 15 yr vs species rank. All winter (34) and summer species (42) were included.

Discussion

Diversity and stability

We observed numerous differences between two spatially co-existing but temporally segregated annual plant communities. The two communities differed in diversity in two ways. While the total species pool of the summer community was larger than the winter community, seasonal species richness was generally higher in the winter community. The two communities differed significantly in our five measures of community stability: CV of species richness, mean CV of the abundance of all component species, mean CV of the abundances of each species, species turnover rate (β -diversity) and temporal consistency in rank abundances. For each measure, the winter community exhibited greater stability.

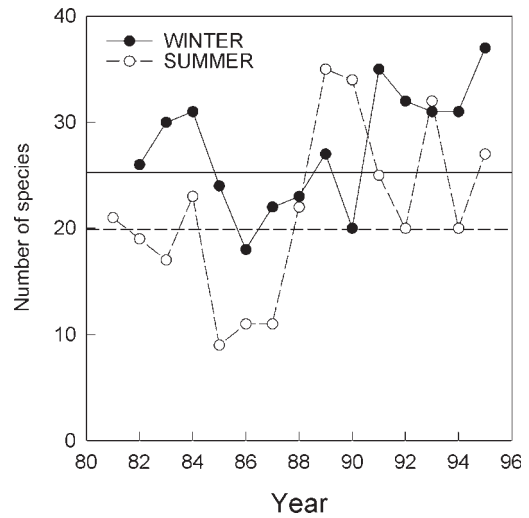


Fig. 4. Temporal variation of species richness. Lines indicate the mean values for winter (solid) and summer (dashed) annual communities.

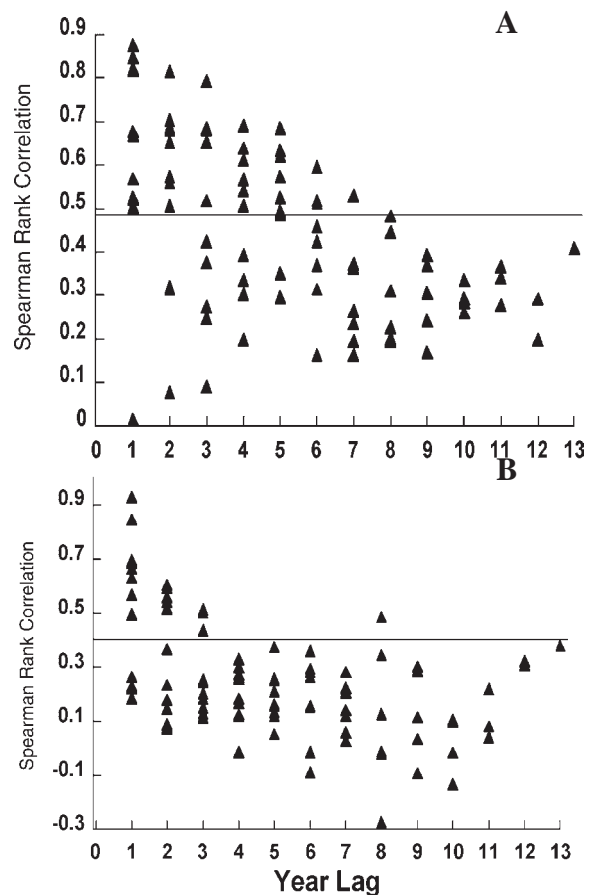


Fig. 5. Spearman rank correlation coefficients for the rank abundances of species for (A) winter and (B) summer annual communities for different time lags. Values above the solid line indicate significant positive correlations.

The differences in community richness and variability result mainly from the different fraction of each community's species pool that germinated each year. In a typical year, only 22 of the 42 (52%) summer species were observed compared to 28 of the 34 (81%) winter species. The higher species turnover rate in the summer is probably due to the smaller fraction of species that germinate each year from a relatively larger species pool in the seed bank. Thus, the larger species pool and relatively low fraction of species that germinate in summer generates much more year-to-year variation in species composition. In addition, the summer community was typically dominated by two or three species that were usually different each year whereas the winter community tended to consist of several relatively common species that differed much less over time. Although virtually all winter and summer species were variable in their rank abundances over time (Table 3), the summer community exhibited greater turnover, greater variation in abundance and greater variation in species richness than the winter community. As such, community stability was lower in the summer community.

Because annual plant communities exist both in the seed bank and as above-ground communities, and because our communities exhibited tremendous temporal variation in the above-ground community structure, the relationship between diversity and stability in this system is complex. Certainly the summer community exhibited greater variability than the winter community but because the summer community contained a larger species pool but fewer species above-ground each year, it is less clear which community is more diverse. Previous theoretical and empirical analyses of the relationship between diversity and stability consider species richness of above-ground assemblages. Indeed, all of our measures of stability involved aspects of the above-ground communities (e.g. Tilman & Downing 1994). Using that focus, the winter community would be deemed more diverse and more stable. But, our results suggest that future work on diversity-stability relationships should consider how seed bank vs above-ground diversity affect community stability.

Dynamics and climate

Micheli et al. (1999) recently outlined two different forms of community variability: compositional, which reflects changes in relative abundances of component species and aggregate, which reflects changes in community summary properties such as overall abundance. Different combinations of these descriptors generate four types of community based on combinations of low or high levels of the two types of variability. According to this classification system, the summer annual plant

community exhibits asynchronous variation because it exhibits high variability in both compositional and aggregate variability. The winter community is an example of synchronous variation because it has low compositional variability and high aggregate variability. These different patterns of community variability result from several mechanisms. Synchrony can result from parallel responses of component species to abiotic conditions while asynchrony can result when species respond differently to abiotic drivers (Micheli et al. 1999).

The Micheli et al. (1999) classification scheme suggests that the component species of the winter and summer communities respond differently to precipitation. Our work and previous studies suggest that the response of these two communities to abiotic variation is complex. The amount of variation in seasonal precipitation does not explain differences in community variation that exist: the 18 yr precipitation data from our site indicate that total winter precipitation is more variable than summer precipitation whereas community variability is higher in summer. While the abundances of only a few species in each community are weakly correlated with seasonal precipitation (Went 1949) overall seasonal abundances are not correlated with seasonal precipitation (Guo & Brown 1997). Using different time lags for regression analyses also failed to detect any significant relationships between plant density and precipitation. However, even if regression analysis based on time lags revealed significant relationships, satisfactory explanations would be difficult to achieve unless long-term seed bank data were also available.

We do know that summer annuals require a minimal amount of moisture to germinate and that the amount of precipitation after germination is important (Inouye 1991). However, a suite of other factors probably play important roles in affecting component species response to abiotic conditions including the intensity of precipitation, intervals between rains events (Beatley 1974), light (Mitchley 1988; Mitchley & Grubb 1986), species-specific time lags in response to precipitation, temperature and the availability of soil nitrogen at the time of germination (Goldberg & Miller 1990) and interactions with other species. Thus, it may not be surprising that total seasonal precipitation correlates poorly with overall plant abundance for these communities (Kemp 1983; Gutierrez & Whitford 1987). The marginally significant relationship between summer annual density and summer rainfall or temperature further proved our earlier findings from experimental exclusion plots that winter annuals had greater granivory effects while summer annuals had greater climatic effects (Guo & Brown 1997).

Life history

Plant life history traits can affect community dynamics in several ways (Inouye 1980; Dodd et al. 1995). For example, the range of seed sizes differs greatly between the winter and summer communities. Summer annuals all possess small seeds while many of the winter annuals possess large seeds (Davidson et al. 1985). Small seeded species exhibit both low and high yearly abundances while large seeded species never attain high abundance (Guo et al. 1998). A community of species with similar seed size (summer annuals) may respond to environmental variation in very similar ways (Harper 1977). This is also suggested by greater variation of winter precipitation but smaller variation of overall winter annual plant abundance (see Table 1; R. Inouye pers. comm.).

The existence of both large and small seeded species in winter annuals probably facilitates co-existence of multiple species within the relatively long winter season (Baker 1972). Large seeded species tend to germinate after the first fall rains, grow rapidly to form robust rosettes, and are able to tolerate unpredictable drought, freezing, and other abiotic stresses during a prolonged growing season. Small seeded species, by contrast, tend to germinate later in the winter season, require continuously higher levels of soil moisture, have less well developed root systems, more open growth forms and are able to complete their life cycles within a shorter period of time (Inouye 1991).

Community co-existence

Chesson & Huntly (1985) have suggested that co-existence and diversity of annual plants may be facilitated by environmental differences between years, which favour different species. This hypothesis is consistent with the observed relationships among the highly variable seed sizes, growth forms and phenologies of the winter annuals. It does not seem to account so straightforwardly, however, for the co-existence of even more species of summer annuals, with less diversity of seed size, growth form and phenology within a shorter and less variable season of precipitation. We are not yet prepared to offer a cogent explanation of the ability of so many species of summer annuals to co-exist in the face of these environmental constraints and structural and functional similarities. The fact that the summer annual species do exhibit pronounced differences in abundances of many species between years, however, suggests that interannual variation may facilitate long-term co-existence.

The total flora of the Chihuahuan Desert (and other deserts with bimodal patterns of annual precipitation) is enriched because of the co-existence of temporally

segregated annual plant communities. Such co-existence depends on a delicate balance of similarities and differences between the two sets of species: enough similarities so that they can tolerate the same macro-environmental conditions and persist over many years, but enough differences so that they can respond differently to the two rainy seasons and exhibit temporally segregated life cycles. We have shown that these two communities exhibit some similarities and many differences in their temporal dynamics. While we believe that species pool (vs fraction of species germination) and plant life history (e.g. seed size) explain some of these differences, further work is required to explain the differences in the range of seed sizes between the two communities and why a smaller fraction of the summer annual species pool germinates in a typical year and to explicitly test the effects of physical factors, such as long-term climatic variations vs the biological factors, such as the spatial-temporal interactions between the two annual cohorts on temporal community consistency (Grubb et al. 1982; Turner 1990; Brown et al. 1997).

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