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Interactions between winter and summer annuals in the Chihuahuan Desert

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Abstract Using 18 years of census data from permanent quadrats, we examined the interactions between spatially coexisting but temporally segregated winter and summer ephemeral plant communities in the Chihuahuan Desert. The ability of winter and summer annuals to achieve nearly complete temporal segregation by partitioning the bimodal annual rainfall permits the coexistence of a diverse flora of annual (and perennial) plants in this unproductive arid environment. Despite the differences in their biogeographical affinities and temporal segregation, long-term data indicated that at the scales of both the entire 20-ha study site and small 0.25-m^2 sample quadrats, abundances of plants were never high in two successive growing seasons, suggesting a negative interaction between winter and summer annuals. We evaluate alternative hypotheses for this phenomenon.

Key words Chihuahuan Desert · Competition · Ephemeral plants · Long-term study · Spatial-temporal interactions

Introduction

It has long been recognized that in warm deserts, such as those of southwestern United States and northern Mexico, there are two distinct, temporally separated communities of ephemeral plants, usually referred to as winter and summer annuals (Mulroy and Rundel 1977; Davidson et al. 1985; Gutierrez and Whitford 1987a, b). Studies of desert annuals and other kinds of desert organisms have revealed specialized morphologies, physiologies, and life histories that have been interpreted as adaptations to stressful abiotic conditions, such as prolonged, unpredictable droughts and high temperatures (Went 1949; Beatley 1967; Mulroy and Rundel 1977; Venable and Lawlor 1980; Kemp 1983; Gutierrez and Whitford 1987a; Fox 1989; Ehleringer 1994; Rundel and Gibson 1995). Many individual species of winter or summer annuals have been studied with respect to ecological characteristics, such as germination (Juhren et al. 1956; Tevis 1958; Inouye 1980; Inouye et al. 1980), survival (Juhren et al. 1956; Beatley 1967), and seed banks (Freas and Kemp 1983; Philippi 1993). Previous studies of either winter or summer desert annuals have also called attention to dramatic year-to-year fluctuations in abundance, productivity, and diversity that reflect interactions between their short life cycles and the large, largely unpredictable climatic variation in arid regions (Inouye 1991; Guo and Brown 1996).

Even though desert plants have been the subject of many ecological studies in recent years, due to the limitations of data availability there has been little attempt to investigate the relationships between winter and summer annuals at population and community levels. Even though the two sets of species to coexist in the same environment with essentially no temporal overlap by specializing to be active at different seasons, there are reasons to suspect direct or indirect interactions between them. Work on such cross-season interactions is critical for understanding the dynamics of desert plant communities.

Here we use data collected in permanent quadrats at our long-term field study site in the Chihuahuan Desert of southeastern Arizona. The site receives a distinctly bimodal distribution of annual precipitation and supports diverse communities of both winter and summer annuals. On the one hand, these communities are distinct: except for a few biseasonal species, there is no overlap in species composition and no temporal overlap in their vegetative life cycles. On the other hand, the two communities occur together in the same macroenvironment and overlap ex-

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tensively in the soil seed bank, where they are exposed to similar abiotic conditions and seed consumers. Here we present evidence for important spatial-temporal interactions between the two communities despite the temporal segregation of their life cycles, and develop hypotheses on the underlying mechanisms that might have caused such cross-season interactions.

Methods

The field work was carried out on a 20-ha long-term experimental study site established in 1977 near Portal, Arizona (Brown and Munger 1985). The soil is a fairly homogeneous mixture of small alluvial boulders mixed with and overlaid by finer particles, but there is considerable micro-scale heterogeneity related to soil structure, shrub cover, animal disturbance, and other factors (Guo 1994). The vegetation is primarily upper elevation Chihuahuan Desert scrub, but the habitat varies from open grassy areas to stands of widely-spaced shrubs (Brown and Munger 1985). Livestock have been excluded from the site since 1977.

At times corresponding to the bimodal precipitation, we censused winter and summer annual plants, as well as biseasonal species and perennials twice each year, during April–May and August–September, beginning in 1978. The data were most complete after 1989, when we were confident that even the rarest species were identified correctly and counted accurately. Each census was conducted during a 1- to 3-week period of peak flowering and maximum biomass (for details, see Davidson et al. 1985; Samson et al. 1992). All plants were counted individually by species in 384 permanent quadrats, each 0.25 m^2 in area (0.5 × 0.5 m). There were 16 quadrats placed at regular intervals within each of 24 plots, 0.25 ha in area (50 × 50 m).

Several measures of performance are useful for understanding the population and community ecology of annual plants. These include post-germination and end-of-season density, survivorship, plant size, and survival and carry over of seeds in the soil seed bank. In this study we analyze only data on density at the end of the growing season. This is the only measure of performance that we have for the same quadrats over many years. R. Inouye (personal communication) found that when standing dead plants were clipped and removed for weighing at the end of a growing season, the densities of the next cohort was reduced by a factor of approximately 2, apparently because of removal of seeds that would contribute to the local seed bank or possibly because of removal of nutrients that would be recycled to contribute to plant growth and survival. Other methods of trying to estimate plant size or biomass nondestructively either had very large error variances (reflectometry) or were impractical to do each year on 384 quadrats (measuring height of individual stems).

The 24 experimental plots were subjected to replicated experimental manipulations that involved primarily removal of some or all species of rodents or ants (see Brown and Munger 1985; Heske et al. 1993). Effects of these treatments on abundance and species composition of the annuals were sometimes substantial, and have been documented in other publications (Davidson et al. 1985; Brown et al. 1986; Samson et al. 1992; Guo et al. 1995). In analyzing the data, the three common biseasonal species (see below) were included as both winter and summer annuals, because they are important members in both communities.

Results

Biogeography, phenology, and relations with climate

During the 18 years of this study, we recorded 34 species of winter annuals, 42 of summer annuals, and 3 of biseasonal annuals. The geographic ranges of the winter species tended to extend westward, into the Sonoran and even the Mojave Desert. In contrast, ranges of summer annuals tended to extend eastward, into the Chihuahuan Desert and the Great Plains. This distributional patterns are reflected in the large proportion of winter species that are listed in the flora of California, and the large proportion of summer annuals in the Texas flora (Table 1). Presumably, these geographic affinities reflect the association of winter annuals with predominantly winter rains from the Pacific Ocean and Baja California and of summer annuals with summer rainfall from the Gulf of Mexico (Mulroy and Rundel 1977).

Table 1 Geographical affinities of winter and summer annuals at the study site as indicated by the number of species falling into each distributional category

	California	Texas	Both CA and TX	Neither
Winter annuals	14	4	14	5
Summer annuals	1	15	24	5

The first winter annuals typically germinated in response to the first autumn rains, in October or November. The early-germinating species formed rosettes and grew relatively slowly during the cold midwinter months. Additional pulses of germination often occurred in response to subsequent rains, with some species germinating as late as March in certain years. There tended to be considerable phenological variation among the winter annual species in timing of germination and initial growth, but all species overlapped substantially in flowering, seed production, and death, which occurred when the soil dried out in late spring (March to May, depending on the timing of the last rains; see Fox 1989). In contrast to this pattern, nearly all germination of summer annuals typically occurred within a few days immediately following the first summer rain, which usually fell in early July but sometimes came as late as mid-August. The plants grew rapidly as long as soil moisture was available. Rains typically ceased in late August or early September, and this resulted in a period of relatively synchronized flowering, seed production, and death as the soil moisture was rapidly depleted (Heske et al. 1993; Guo and Brown 1996).

The three biseasonal species (*Eriogonum abertianum*, *Haplopappus gracilis*, and *Baileya multiradiata*), germinated in fall and winter, but unlike the winter annuals, individuals survived through the spring droughts (Fig. 1). Although mortality during this period was often severe (sometimes > 95%) and the surviving rosettes lost their outer leaves, the surviving plants grew rapidly in response to the first summer rains. In years when mortality during the spring drought was relatively low, the surviving plants, because of their size advantage and well established root system, were often able to dominate the summer annual plant community in terms of both individual plant size and total species biomass (Kemp 1983; Inouye 1991).

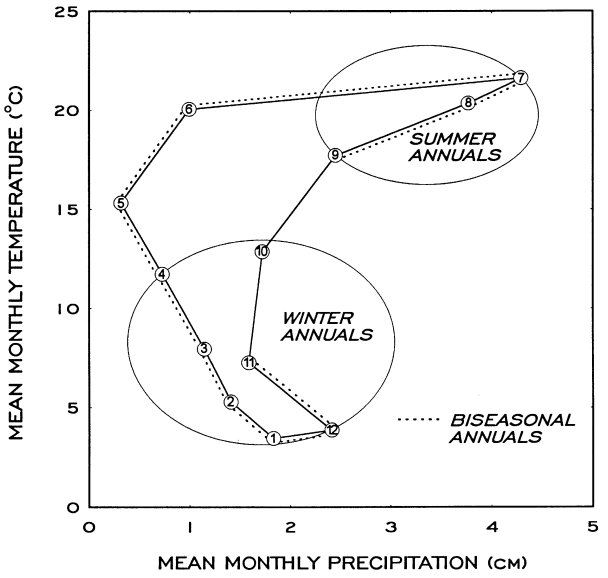

Fig. 1 Monthly temperature and precipitation (± SE; *above*) and a composite climograph (*below*) of the study site, which permits comparison of two seasonal climate regimes in which winter and summer annuals occur. Monthly means of temperature and rainfall have been plotted against each other and the months were connected by lines. *Numbers in open circles* represent individual months. Data from the weather station of Southwest Research Station at Portal, Arizona, about 17 km from the study site

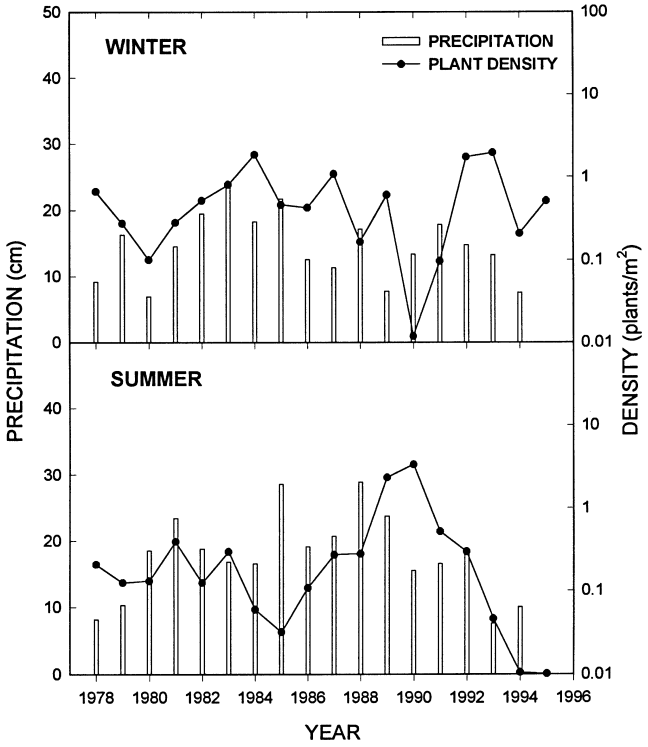

Fig. 2 Temporal variation in seasonal precipitation and winter (October–April; *above*) and summer (May–September; *below*) annual plant density over the 18–year study

The annual precipitation regime was distinctly bimodal (Fig. 1). Compared to the summer rains (May–September), the winter rains (October–April) were on average lower in magnitude (141 vs. 187 mm), but more variable from year to year (CV = 36.88 vs. 29.2) and dispersed over a longer season. The annual pattern of average temperature is also shown in Fig. 1, as is the generalized phenology of the winter, summer, and biseasonal annuals. The long lifespans and "climate spaces" of the biseasonal species overlap with the much narrower ones of the winter and summer annuals.

Despite the necessary dependence of desert annuals on moist soil for a sufficient period to complete their vegetative life cycles, we did not observe the expected positive relationship between precipitation and abundance (Fig. 2). There was no correlation between total precipitation during the growing season and density of individual plants at the end of that season for either winter or summer annuals ($r^2 = 0.073$, $P = 0.29$; $r^2 = 0.002$, $P = 0.86$, respectively). Further, the range of variation as reflected by the coefficient of variation, was greater for summer annual density than for winter annual density (CV = 94 vs. 54, respectively), even though the variation in winter precipitation was slightly greater than summer precipitation.

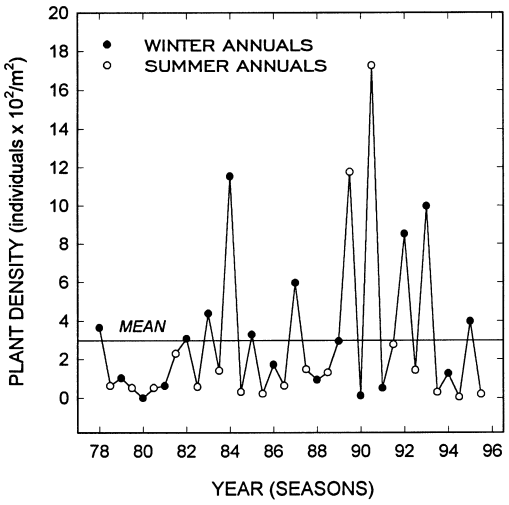

Fig. 3 Fluctuation in total densities of annual plants over seasons and years. Densities were measured as total plant abundance in 384 permanent 0.25-m^2 quadrats. The mean value is also shown

Interactions between winter and summer annuals

Figure 3 shows that there were ten occasions (i.e., W78, W83, W84, W85, W87, S89, S90, W92, W93, W95) when the abundance of either winter or summer annuals equaled or exceeded the long-term average (high), and in every case the abundance in the following season was below the average (low). The abundances are right-skewed rather than normally distributed, making parametric statistics problematic. The probability of obtaining the above pattern by chance can be estimated

nonparametrically as follows. The null hypothesis is that the abundances in successive seasons are independent events. There were 35 transitions between seasons (winter to summer or vice versa), so the probability of 10 highs each being followed by a low is $(25/35)^{10}$ or $P = 0.034$). The tenth highest abundance (W82) was nearly exactly equal to the long-term average, and if this is called a high, the abundance the following season was again low. The probability of this by chance is $(24/35)^{11}$ or $P = 0.023$. After this the consistency of the pattern diminishes, since the 11th highest abundance (W89) is followed by a high in the next season. The above probability estimates should be taken with caution, but they suggest that very high densities in one season tend to be followed by low densities in the following season. This cannot be attributed to the pattern of precipitation, because there was no relationship between high and low rainfall in successive seasons (i.e. the seasonal fluctuation of precipitation did not show the pattern of highs followed by lows observed for the plants; Fig. 4). There were 20 seasons with above-average precipitation, and 13 of these were followed by another season with above-average rainfall. Furthermore, as reported above, there was no relationship between total seasonal precipitation and density of annuals in that season. Therefore, variation in precipitation between successive seasons cannot account in any single way for patterns seen in the annual plants. There is no doubt that abundance and other measures of annual plant performance are affected by precipitation. However, such effects may be very complex, because factors including total rainfall, timing and frequency of precipitation events, runoff and infiltration, and buildup and depletion of soil moisture, and temperature and photoperiod regimes all influence germination, growth, and survival of plants (Inouye 1991; Ehleringer 1994).

The same pattern of high density in one season being followed by low density in the following season was also observed at the scale of individual quadrats over the 18 years. Two examples from 1991–1992 are shown in Fig. 5. We selected these data because species richness and abundance were relatively high in these three adjacent seasons. When the density during one season was plotted as a function of the density during the previous season, all of the points fell within a triangular space. Thus, when a quadrant had a low density of annuals, it could have either a high or a low density in the following season. When the density was very high, however, the density in the following season was always low. The probability of obtaining such triangular distributions of data points by chance can be estimated by computer simulations in which the values for one season (on the X axis) are paired at random with the values for the following season (on the Y axis), and the number of simulated data points falling outside the triangular space are tallied and compared with the observed distribution (see Enquist et al. 1995 for details). Based on 1,000 simulations, both the distributions of data points in Fig. 5

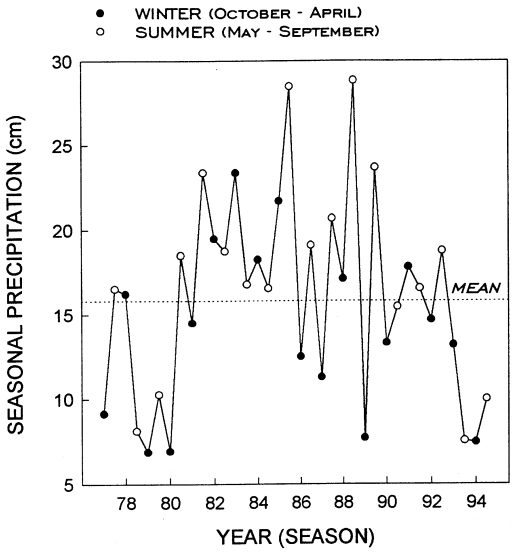

Fig. 4 Fluctuation in total seasonal (*winter* = October–April, *summer* = May–September) precipitation over seasons and years. The mean is also plotted

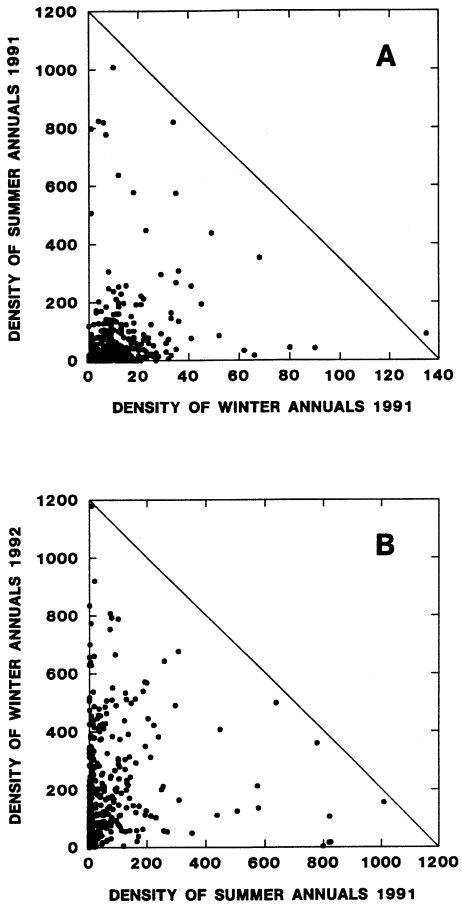

Fig. 5 The relationship between winter and summer annuals in successive seasons in 384 0.25-m^2 permanent quadrats (each *data point*). Note that all points fall within a triangular constraint envelope, such that high densities within a local patch in one season are followed by low densities in the following season

are highly significantly different from those expected by chance ($P < 0.04$ and 0.02, respectively for W91 to S91 and S91 to W92). Thus the patterns at the scale of the entire study site and individual 0.25-m^2 quadrats both suggest that very high densities of plants in one season are obligately followed by low densities in the next season. This implies some kind of strong negative interaction between winter and summer annuals, despite their nonoverlapping vegetative phenologies. In winter, *Haplopappus gracilis*, *Eriastrum diffusum*, and *Eriogonum abertianum* and in summer, *Aristida adscensioni*s, *Bouteloua aristidoide*s, and *Pectis papposa* tend to show both the highest average densities (within quadrats) and the widest distribution over the study site (among quadrats). Therefore, these account for most of cross-seasonal phenomenon reported above (details will be reported elsewhere; Q. Guo, J. Brown, and T. Valone, unpublished work).

Discussion

Given the differences in biogeographical affinities and the complete temporal separation in the vegetative and reproductive phases of their life cycles, it is surprising that our data suggested strong negative interactions between the winter and summer communities. A large number of individuals in one season appeared to inhibit germination and/or survival in the subsequent growing season, resulting in low numbers of plants. This was apparent at two spatial scales: (1) the entire 20-ha study site, where higher than average numbers of plants were never observed in successive seasons; and (2) individual 0.25-m^2 quadrats, where high numbers in one season was always followed by low numbers in the following season, resulting in a triangular constraint envelope.

We can suggest four mechanistic hypotheses for this cross-seasonal phenomenon. First, a direct negative interaction may be mediated through the biseasonal species, which can be important components of both communities. This was suggested by Davidson et al. (1985) and Inouye (1991). Biseasonal species might account for some effect of winter on summer annuals, because a favorable winter season with high densities of individuals could potentially result in greater survival of biseasonal species through the spring drought, and their competitive inhibition of germination and survival of seedlings of summer annuals. It cannot account, however, for the negative effect of summer annuals on winter annuals during the subsequent season, which was also observed (Figs. 3 and 5B). For some not yet understood reason, all three biseasonal species germinate in winter and reproduce in the subsequent summer (Fig. 1; see also Fox 1989).

A second hypothesis is that the negative interaction between the winter and summer annual communities is indirect, mediated by "enemies." Such an indirect effect would be an example of "apparent competition" (Holt 1977). It is easy to imagine that abundant plants in one season might lead to the increase in some kind of relatively unspecialized granivore, herbivore, parasite, or pathogen, which would then cause high mortality and low populations of plants the following season. While this mechanism is plausible, we have no evidence that it has a significant influence on population and community dynamics of desert annuals at our study site or elsewhere. For example, we know that granivorous rodents and birds have a major impact on the composition of the winter annual community by foraging selectively for large seeds and suppressing the densities of large-seeded species (Brown et al. 1986; Samson et al. 1992; Guo et al. 1995; Guo and Brown 1996), but it is hard to see how these granivores would affect the summer annuals, which do not include any large-seeded species.

A third hypothesis was suggested by R. Inouye (personal communication). Carbon dioxide is known to inhibit germination of many seeds. Inouye (1980) suggested that CO_2 produced by the roots of seedlings that had germinated in response to earlier rains accounted for the reduced germination of winter annuals after subsequent rains that he observed. It is possible that CO_2 emitted by the decomposing biomass of annuals from a previous season could have a similar inhibitory effect on germination. This would require that in the season after a high density of desert annuals there is sufficient decomposition in the superficial soil and overlying litter to raise significantly the concentration of CO_2 in the microenvironment of the germinating seeds. While this may be plausible, we have no data that would either support or refute it.

A final hypothesis is that plants growing in one season deplete some resource and immobilize it for sufficiently long to inhibit germination and/or survival in the following season. The most likely resource is nitrogen (Romney et al. 1978; Gutierrez and Whitford 1987a) or some other limiting nutrient, that is tied up in the standing dead vegetation of the previous season, and hence unavailable to support growth in the current season. Our observations suggest that most of the annual biomass produced in any one season remains either as standing dead plants or as surface litter, and decomposition does not begin until microbial and other (e.g., termites) decomposers become active during the next rainy season. Such a mechanism is very plausible. Nitrogen is known to be limiting to annual plants in desert habitats (Gutierrez and Whitford 1987a). Further, decomposition in deserts is performed by a variety of invertebrates and microbes, whose activity is dependent on soil moisture. Therefore, recycling of the nutrients in dead biomass from the previous season is unlikely to begin until after there has been sufficient precipitation to also stimulate germination (Parker et al. 1984). This mechanism could also explain, at least in part, the absence of a close correlation between precipitation and abundance of annuals within a growing season. While water may be one critical limiting resource for desert annuals, it may not be the only one (see Whitson 1975, 1976; Romney et al. 1978; Gutierrez and Whitford 1987a; Schlesinger et al. 1990).

Thus, we suspect that competition for a limiting nutrient that is immobilized in dead biomass is the most likely mechanism to account for the negative interaction between winter and summer annuals. We note, however, that the above hypothesized mechanisms are not mutually exclusive, and all could potentially contribute the observed negative influence of annuals in one season on those in the following season. We know from our data that this interaction affects the density of annuals at the end of the growing season, presumably by influencing some combination of germination and subsequent survival. It may affect other aspects of plant performance, such as growth rates and plant size, which we have not measured but which would offer additional clues to the mechanism. Even though the winter and summer annual communities are temporally segregated, almost completely non-overlapping in species composition, and different in several aspects of plant structure and function, they are not as independent as they might seem.

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