Aboveground production and species richness of annuals in Chihuahuan Desert grassland and shrubland plant communities

Y. Xia*, D.I. Moore, S.L. Collins, E.H. Muldavin

Department of Biology, University of New Mexico, Albuquerque, NM 87131, United States

A B S T R A C T

Precipitation variability and shrub encroachment in response to global environmental change are likely to affect both richness and aboveground net primary production (ANPP) of annual plants in arid and semi-arid ecosystems in the northern Chihuahuan Desert, especially given the grazing history and desertification potential of this aridland region. Using a nine-year dataset (1999–2007), we examined the spatial and temporal variation in annual plant communities in grass- and shrub-dominated vegetation, and evaluated the relationships between species richness and ANPP with seasonal and annual precipitation and soil moisture. We found that species richness and ANPP varied among seasons and between years in both grass- and shrub-dominated areas. *Cryptantha crassisepala*, *Plantago patagonica*, and *Phacelia integrifolia* were the most common species found in both communities in both seasons, and *Chamaesyce serrula*, *C. serpyllifolia*, and *Kallstroemia parviflora* were more common in summer only.

We found that species richness in summer was significantly correlated with summer precipitation and summer soil moisture in both communities, but summer ANPP was significantly correlated with summer precipitation and soil moisture only in shrubland. However, richness and ANPP of winter annuals were significantly correlated with winter precipitation and winter soil moisture in shrubland and grassland. Our results demonstrate that temporal variation in rainfall can be as important as annual total amounts for plant performance, and that response to temporal dynamics varies among species but not between grass- and shrub-dominated communities. We conclude that desert annuals provide a highly dynamic system for understanding the processes that influence plant species composition and abundance, and that desert annual systems will likely be highly impacted by shrub encroachment along with increases in precipitation variability as a consequence of anthropogenic climate change.

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1. Introduction

Recent models predict that southwestern North America is likely to get warmer and drier as a consequence of increased precipitation variability and more prolonged droughts in response to anthropogenic climate change (Diffenbaugh et al., 2008; IPCC, 2007; Seager et al., 2007). In addition, shrub encroachment is occurring globally in response to multiple environmental drivers (Van Auken, 2000). Understanding how net primary productivity and biodiversity respond under current climate variability and shrub encroachment in these pulse driven aridland ecosystems is thus of critical importance to predict how these systems will respond to future environmental change (Collins et al., 2008;

Knapp and Smith, 2001; Knapp et al., 2008; Sala et al., 2000; Schimel et al., 2000; Yang et al., 2008).

The Chihuahuan Desert in southwestern North America is an ideal system for examining dynamic responses of annual plants to seasonal and annual variation in precipitation, soil moisture and temperature. In the northern Chihuahuan Desert, two relatively distinct temporally separated annual plant communities occur – one in spring that is related to winter precipitation and soil moisture, and one in summer related to summer precipitation and soil moisture. Summer annuals usually germinate in spring or summer and complete their life cycle by early autumn, whereas winter annuals mostly germinate in fall, winter or early spring, and complete their life cycles during spring when rainfall and ambient temperature are favorable (Beatley, 1967; Bowers, 1987; Freas and Kemp, 1983; Mulroy and Rundel, 1977). In addition, summer annuals have a shorter life cycle but a greater overlap of phenological phases than winter annuals. Most summer annuals are C_4 species, whereas most winter annuals are C_3 species. Both summer

and winter annuals occur in two of the major terrestrial habitat types in the Chihuahuan Desert – C_4-dominated perennial grassland and C_3-dominated creosotebush shrubland.

Much progress has been made towards understanding the structure, primary production, species richness and ecological significance of annual plants in aridland ecosystems during the last decade (Boeken et al., 1998; Cox et al., 2006; Guo et al., 2002; Muldavin et al., 2008; Yin et al., 2005). Although it is well known that rainfall is the main factor controlling germination, growth and productivity of annuals in many desert ecosystems (Beatley, 1974; Bestelmeyer et al., 2003; Gutierrez and Whitford, 1987; Knapp and Smith, 2001; Paruelo et al., 1999; Went, 1949; Yahdjian and Sala, 2006), the relationship between interannual variability in precipitation and temporal variability in annual plant production at a given site is often weak (Bai et al., 2008). This weak relationship suggests that other factors, such as interspecific competition, seed predation (Brown and Heske, 1990), or soil moisture rather than total precipitation (Beatley, 1967, 1974; Bowers, 1987; Reynolds et al., 2004; Whisenant, 1999), may control species richness and abundance in aridland plant communities. In addition, much of southwestern North America is undergoing rapid shrub encroachment where woody species, such as *Prosopis glandulosa* and *Larrea tridentata*, are invading formerly C_4-dominated grassland (Knapp et al., 2008; Peter et al., 2006, and Van Auken, 2000). One consequence of shrub encroachment is a decrease in species richness and higher temporal variability in species composition in shrubland compared to grassland (Baez and Collins, 2008). Thus, understanding how variation in the timing and amount of precipitation affects the relative richness, productivity and variability of annual species, a key component of species diversity in desert ecosystems, is needed in these relatively recent shrub-dominated areas.

In this study, we used a nine-year data set to examine precipitation and soil moisture effects on aboveground net primary production (ANPP) and species richness of summer and winter annuals in two representative grass- and shrub-dominated communities at the Sevilleta LTER site in central New Mexico, USA. Our study addresses the following questions: 1) How does ANPP and richness of winter and summer annuals vary from year to year? 2) Does ANPP and richness of winter and summer annuals vary with precipitation and soil moisture? 3) Does ANPP and richness of winter and summer annuals differ between grassland and shrubland communities? We hypothesized that seasonal and annual variation in ANPP and richness of annuals would be high in response to seasonal and annual rainfall variability, but that variability will be greater in shrubland than in grassland because of higher turnover rates in shrubland. Because winter moisture accumulates whereas summer moisture is pulse driven, we hypothesized that relationships between precipitation, soil moisture, ANPP and richness will be stronger for summer than winter annuals. Finally, because total ANPP in grassland was similar to that in shrubland, (Muldavin et al., 2008), we hypothesized that seasonal ANPP of annuals will be similar in grassland and shrubland communities.

2. Methods

2.1. Study area

This study was conducted at the Sevilleta National Wildlife Refuge (SNWR), located at latitude 34°20′N and longitude 106°43′W in Socorro County, central New Mexico, USA. Two common plant community-types occur in the SNWR – *L. tridentata*-dominated shrubland and *Bouteloua eriopoda*-dominated grassland that are representative of northern Chihuahan Desert. In the *Larrea* communities, the understory was characterized by scattered

perennial grasses and forbs (e.g., *Erioneuron pulchellum*, *Muhlenbergia porteri*, *Cryptantha crassicarpa*). The *B. eriopoda* grasslands had an assortment of characteristic shrubs or subshrubs (e.g., *Yucca elata* and *Ephedra* torreyana), as well as a mix of other grasses and forbs (e.g., *Bouteloua. gracilis*, *Pleuraphis jamesii*, *Sporobolus* spp., *Melampodium leucanthum*, *Sphaeralcea* spp) (Muldavin et al., 2008). Soils were classified as sandy loams with approximately 68% sand, 22% silt and 10% clay (Muldavin et al., 2008). The shrubland soils were well drained with surface texture consisting of aeolian loamy fine sands or fine sands. Water holding capacity of shrubland soil is very low and soils are highly erodible when vegetation and organic residues are removed, such as following fire (Ravi et al., 2007).

Precipitation and soil moisture data from winter of 1998 through fall of 2007 were recorded daily at the Five Points Sevilleta LTER climate station (Fig. 1), located less than 1-km from our grassland and shrubland study areas. Measurements included precipitation (event scale via tipping bucket) and soil moisture content (0–30 cm) using time domain reflectometry at 1-hr intervals. For this study values of soil moisture were calculated as daily means. The average annual precipitation in the area from winter of 1998 through fall of 2007 was 255 mm, and typically more than half (140 mm) of the precipitation occurred during the summer monsoon that extends from June through September. Remaining precipitation comes as a mixture of snow and rain during fall, winter and spring (115 mm). Thunderstorms during the monsoon season provide significant local rainfall, and monthly and daily rainfall extremes typically occur during this period. Average annual temperature is 13.2 °C (average daily temperature is 1.6 °C in January and 25.1 °C in July). Mean daily maximum/minimum temperatures varied from 34/14 °C in summer to 10/−7 °C in winter.

2.2. Field measurements

Two long-term study sites approximately 0.5 km apart were established in 1999. One site was in *Larrea*-dominated shrubland and the other was in *Bouteloua*-dominated grassland. In 1999, five circular, 200-m-diameter sampling webs, approximately 0.3 km apart were established to measure small mammal composition and abundance. To quantify ANPP, plant species richness and plant community composition, eight permanent 1-m^2 vegetation quadrats were located near each web for a total of 40 quadrats at each site. Data on plant species composition and ANPP were collected from 1999 to 2007 at each site. Winter annuals were measured in April or May, after the spring growing season. Summer annuals were measured in late September or early October when they had
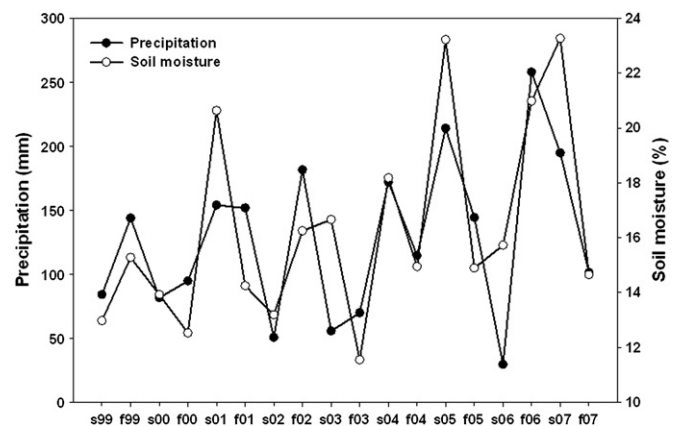

Fig. 1. Seasonal average rainfall and soil moisture from 1999 to 2007 at the Sevilleta National Wildlife Refuge, central New Mexico, USA.

reached peak biomass. All species within each quadrat were measured for density, cover, and height. ANPP of each species was derived from biomass to volume regressions developed from samples harvested nearby (Huenneke et al., 2001, Muldavin et al., 2008).

At each study site, plant density, cover, and species richness were measured in each quadrat two times each year from spring 1999 to fall 2007. Density of annuals was determined by counting individuals of all species, and species richness was the total number of species found in each quadrat. Cover for each species in each quadrat was estimated using a gridded quadrat frame. Height (cm) was measured from the base of each plant to the top of the inflorescence if present. Otherwise, measurements were taken to the top of the green foliage. For each species a range of size classes was harvested outside the measuring quadrats and these were sorted by living and dead; and then dried at 55 °C before weighing (Muldavin et al., 2008).

2.3. Data analysis

We used volumetric to weight regressions to calculate ANPP for each individual of each species in each quadrat (Huenneke et al., 2001; Muldavin et al., 2008), and then used repeated measures ANOVA to determine how annual plant performance varied seasonally and between community types over nine years. Simple linear regressions based on the nine seasonal averages per type were used to quantify the relationships between seasonal precipitation, soil moisture, and plant community structure. We used two-way analysis of variance to test if ANPP of annuals in grassland and shrubland varied from one season to the next within years as well as within seasons among years. The dependent variables were year, season and site, and the independent variables were ANPP and species richness.

For all analyses, species cover and richness were averaged over the eight quadrats on each sampling web, and sampling webs (n = 5) were treated as replicates in each community-type, We used correlation and simple linear regression to determine if ANPP and richness of annuals in the current season or year were related to ANPP or richness the previous season or year as well as the relationship between ANPP and richness in the same season or year. We used correlation analysis and simple linear regression to quantify the relationship between total and seasonal precipitation, and soil water content with plant community structure (richness, ANPP) within communities over time.

3. Results

3.1. Temporal variation of species richness

A total of thirty nine annual species was found over the nine-year study period, thirty one species in the shrubland and twenty seven species in the grassland. *Cryptantha crassisepala*, *Plantago patagonica*, and *Phacelia integrifolia* were the most common species in both communities in all seasons. Species richness varied from a low of zero per 8 m^2 in 2000 to a high of 11 per 8 m^2 in 2005 and 2006 (Fig. 2). Species richness of winter annuals generally increased from 1999 to 2007. However, species richness per quadrat was slightly higher in grassland (3.6 m^{-2}) than in shrubland (3.06 m^{-2}). Richness of summer annuals was significantly higher in grassland (3.9 m^{-2}) than in shrubland (2.8 m^{-2}). Total species richness had similar temporal dynamic patterns as richness of annuals indicating that community dynamics are driven primarily by annuals (Fig. 2).

3.2. Temporal variation in ANPP

ANPP of annuals varied with respect to year, season and community type (Fig. 3). In *Larrea* shrublands, biomass of winter annuals varied significantly only in 2005 and 2007, while summer annuals were most abundant in 2006 and 2007. *B. eriopoda* grasslands were even more variable e.g., significant winter annual ANPP in 2001, 2004, 2005, and 2007 while summer production peaks were greatest in 2002, 2005, and 2006. In most years, ANPP of winter annuals in both grassland (mean = 4.5 g m^{-2}) and shrubland (mean = 1.2 g m^{-2}) was significantly higher than summer annual production (grassland 1.93 g m^{-2}; shrubland 0.96 g m^{-2}).

We found no correlation between ANPP and species richness of either winter or summer annuals in either community, nor was total ANPP of annuals correlated with total community ANPP in either grassland or shrubland communities. Total ANPP in shrubland was lower overall and varied less from year to year (mean = 65.5, CV = 33.2) than total ANPP in grassland (mean = 82.3, CV = 68.7), which increased in recent years particularly during the summer season (Fig. 3).

3.3. Species richness and environmental variables

Species richness of summer annuals was significantly correlated with summer precipitation in grassland (r^2 = 0.85, F = 40.55, P = 0.004) and shrubland (r^2 = 0.90, F = 61.54, P < 0.0001). We also found that species richness of summer annuals was significantly correlated with summer soil moisture in grassland (r^2 = 0.75, F = 21.4, P = 0.0024) and shrubland (r^2 = 0.81, F = 30.32, P = 0.0009). Species richness of winter annuals was also significantly correlated with winter precipitation in grassland (r^2 = 0.54, F = 8.09, P = 0.0249) and shrubland (r^2 = 0.60, F = 10.61, P = 0.0139). We also found a significant correlation between winter species richness and winter soil moisture in both grassland (r^2 = 0.75, F = 20.09, P = 0.0029) and shrubland (r^2 = 0.77, F = 23.3, P = 0.0019) communities.

3.4. ANPP and environmental variables

We found no correlation between ANPP of summer annuals and summer precipitation or summer soil moisture in grassland or shrubland communities. In contrast we found that ANPP of winter annuals was significantly correlated with winter precipitation and winter soil moisture in grassland (precip r^2 = 0.81, F = 34.33, P = 0.0006; soil moisture r^2 = 0.88, F = 58.97, P < 0.0001) and shrubland (precip r^2 = 0.59, F = 12.71, P = 0.0092; soil moisture r^2 = 0.68, F = 18.46, P = 0.0036).

3.5. Yearly variation of common annuals

C. crassisepala, *P. patagonica*, and *P. integrifolia* were the most common species in spring in both communities and they occasionally occurred in summer as well. These three species accounted for 56% of total ANPP of annual species. ANPP of these species varied more in grassland than in shrubland from one year to the next. Some other species, such as *Chamaesyce serrula*, *C. serpyllifolia*, and *Kallstroemia parviflora* accounted for 7.5% of total annual ANPP, were more common in summer than in spring (Fig. 4).

4. Discussion

4.1. Temporal variation of desert annuals

Bouteloua eriopoda grassland and *L. tridentata* shrubland are two common plant communities in the northern Chihuahuan Desert
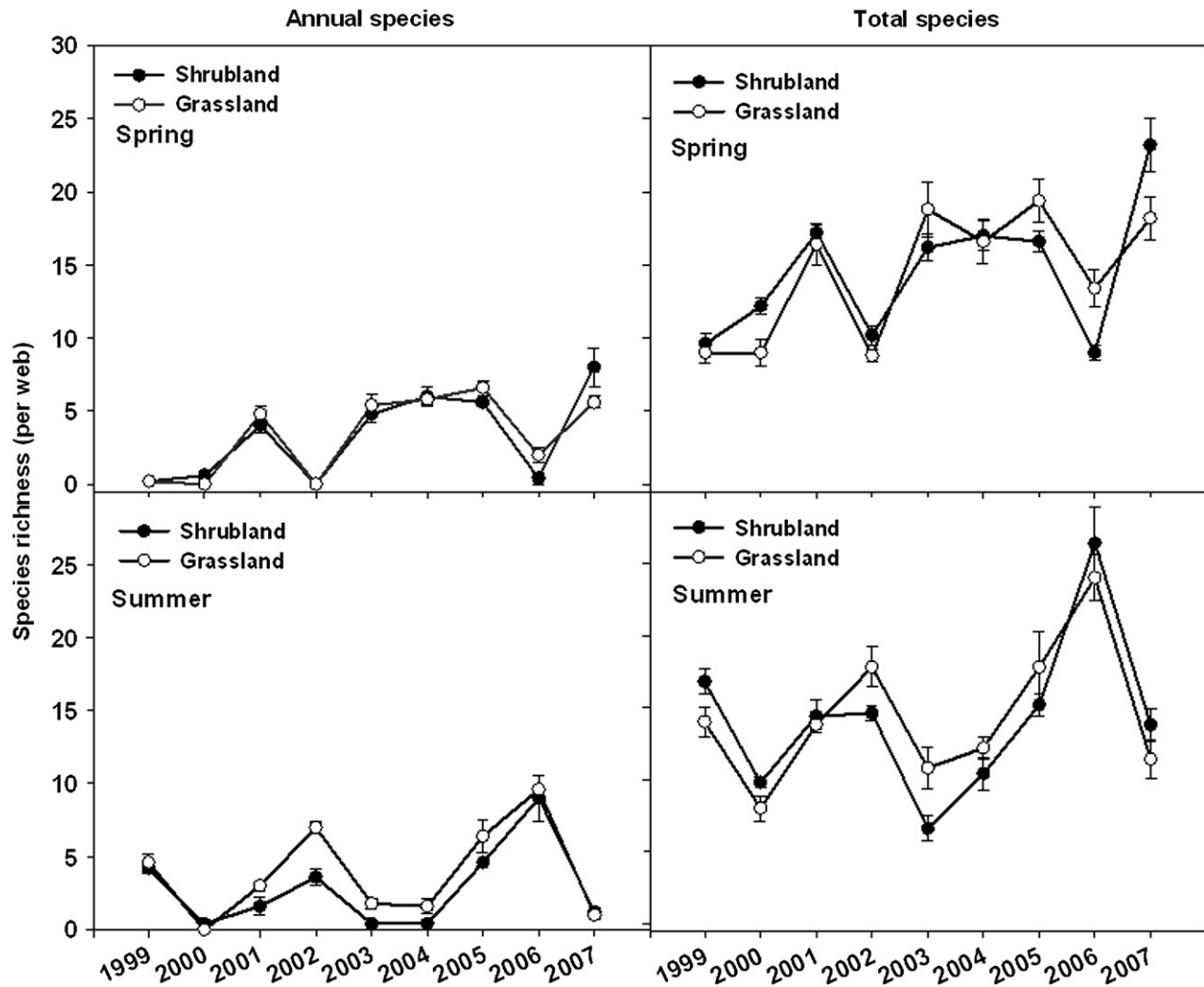
Fig. 2. Comparison of yearly variation of total species richness (8 m^{-2}, N = 5), and richness of winter and summer annuals during spring and summer in *Bouteloua*-dominated grassland and *Larrea*-dominated shrubland.

(Murtaugh and Albright, 2007). From one year to the next, annuals may play a significant role in community structure and ecosystem functioning in desert vegetation, such as enhancing species richness, increasing total net primary production, and producing seeds and foliage for consumer communities. Previous studies reported that both winter and summer desert annuals had dramatic year-to-year fluctuations in abundance, productivity, and richness that reflected interactions between their short life cycles and the largely unpredictable climatic variation that characterizes desert ecosystems (Guo and Brown, 1997; Inouye, 1991). Our results showed that both winter and summer annuals exhibited large seasonal and interannual variation in species richness and ANPP as well. We also found that species richness of summer annuals was more variable than richness of winter annuals, but that ANPP of winter annuals was more variable than ANPP of summer annuals in both grassland and shrubland communities, indicating that the relationship between species richness and productivity in desert annuals is quite complex.

Theory predicts that species richness will be highest at intermediate levels of productivity (Connell, 1978; Huston, 1994, 1999; Tilman, 1993; Tilman and Pacala, 1993). That is, at the lowest level of productivity species richness is constrained by abiotic forces whereas under high productivity species richness is limited by competition for light. In arid and semiarid communities, however,

empirical studies suggest that this productivity-richness relationship does not hold, i.e. low production desert communities can be comparatively species rich (Waide et al., 1999; Mittelbach et al., 2001). Our study area occurs at the low end of the net primary production gradient, and following the hypothesis, we would predict a positive relationship between productivity and species richness at our site. However, we found no correlation between production and species richness in either grassland or shrubland, seasonally or annually. This likely occurs because abundance of annuals is regulated by abiotic variables, such as soil moisture, and potentially competition from perennial C$_4$ grasses (Hochstrasser and Peters, 2004). Even during wet years, annuals are never so abundant that mechanisms such as aboveground competition for light can lead to local competitive exclusion.

Overall, we found that ANPP of winter and summer annuals was greater in grassland than in shrubland. This occurred despite the fact that soil fertility and organic matter content are equal to or only slightly higher in grass- compared to shrub-dominated areas at our study site (Brandel, unpublished data; Kieft et al., 1998). The small differences in soil conditions between grassland and shrubland communities are surprising given the dramatic differences in composition and structure between grass- and shrub-dominated vegetation at the Sevilleta (Hochstrasser and Peters, 2004). To some extent this may reflect the relatively recent expansion of *Larrea* into
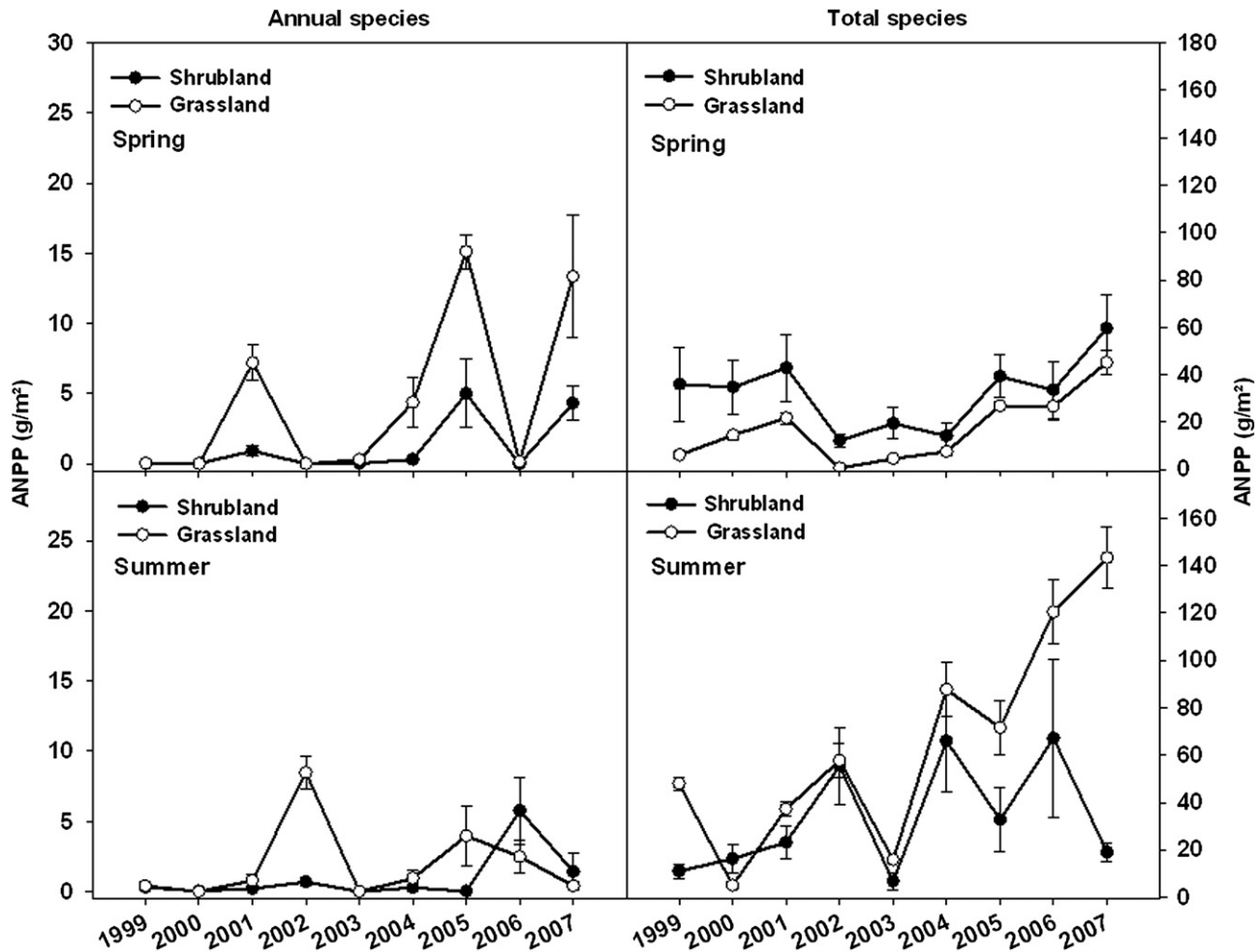
Fig. 3. Comparison of yearly variation of total ANPP (g m^{-2}), and ANPP of winter and summer annuals during spring and summer in *Bouteloua*-dominated grassland and *Larrea*-dominated shrubland.

areas formerly dominated by perennial C$_4$ grasses during the last century (Archer et al., 1988; Buffington and Herbel, 1965; Branson, 1985; Van Auken, 2000). Although the exact cause of shrub encroachment varies from site to site, the consequences include a dramatic decrease in plant species richness and total vegetation cover (Baez et al., 2006; Baez and Collins, 2008), along with increased surface runoff and soil erosion (Bhark and Small, 2003; Schlesinger et al., 1990; Saunders et al., 1991). In our study, although we did not find differences in species richness of annuals between the grassland and shrubland, we did find that species that occurred in both communities, such as *P. patagonica*, *C. crassisepala* and *P. integrifolia*, had greater individual biomass in grassland compared to shrubland. This may reflect slightly lower nitrogen availability in shrub- as well as the low productivity of intershrub space compared to grass-dominated areas. Seed predation by rodents may also impact species richness and primary productivity in shrubland communities where rodent populations are generally greater than in grassland (Parmenter et al., 2003). Although rodents are known to impact soil seed banks in desert ecosystems in arid regions (Brown and Heske, 1990), there is little evidence that rodents differentially affect soil seed banks in grassland and shrubland at the Sevilleta. Indeed, higher seed densities were found in shrubland compared to grassland soils in areas with and without rodents (Koontz, 2005). Thus, seed predation by rodents is not likely to be a significant driver of differences in annual abundance

and ANPP between grassland and shrubland communities at our study site.

4.2. Effects of environmental factors

Our finding that species richness was positively correlated with precipitation and soil moisture in both the grassland and shrubland communities is consistent with previous studies on factors that control plant community structure in Chihuahuan Desert ecosystems (Bestelmeyer et al., 2003; Gutierrez and Whitford, 1987; Knapp and Smith, 2001). Whisenant (1999) and Reynolds et al., (2004) reported that plant growth and species abundance in the Chihuahuan Desert responded more strongly to soil moisture than to precipitation. We also found that species richness of winter annuals was significantly correlated with either winter precipitation or winter soil moisture in both the grassland and shrubland. In our system, we believe this pattern results from the fact that spring ANPP is a function of accumulated soil moisture over a series of precipitation events during the winter dormant season, rather than total precipitation, *per se* (Muldavin et al., 2008). Once this cumulative soil moisture reaches a threshold, ANPP of winter annuals is likely to be less influence by additional precipitation and soil water content. This can also be explained by the minimum threshold water requirement for seedling germination and root growth (Wilson and Witkowski, 1998).
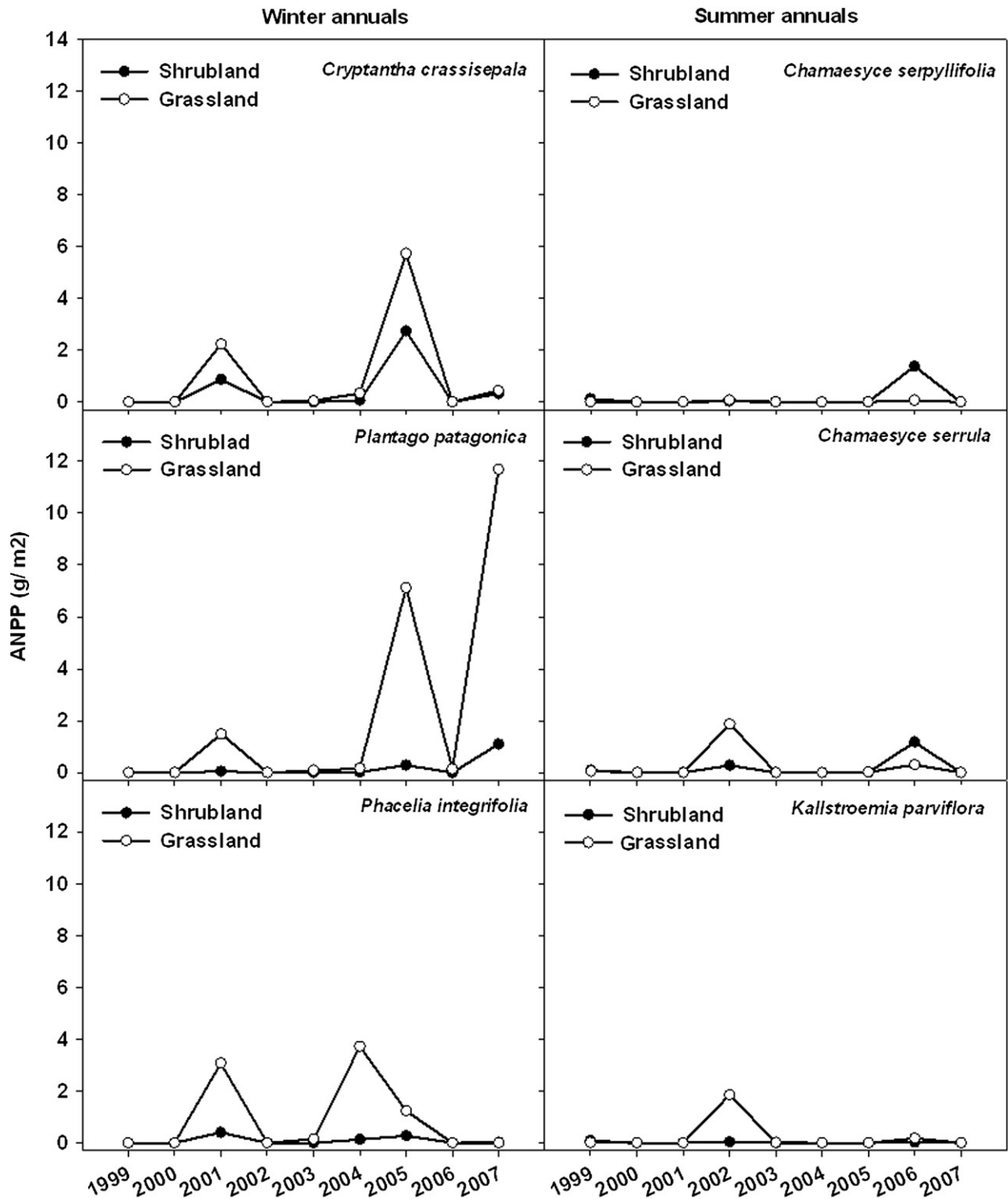
Fig. 4. ANPP of common annual forbs in *Bouteloua*-dominated grassland and *Larrea*-dominated shrubland.

We found no correlations between ANPP of summer annuals and summer precipitation or summer soil moisture in grassland. Indeed, ANPP of annuals during the summer monsoon when peak biomass of C_4 grasses occurs is negatively affected by perennial biomass (Hochstrasser and Peters, 2004). Peters (unpublished data) found that richness and cover of forbs, including annuals, increased when the dominant perennial C_4 grasses were experimentally removed. This suggests that the weak correlation between summer annual productivity and moisture in our system may reflect

a complex interaction between the amount of rainfall, its timing, and competition with perennial grasses.

We did find a positive correlation between ANPP of winter annuals and winter soil moisture in both grassland and shrubland communities. Our finding that ANPP of winter annuals, which generally complete their life cycles prior to the main growth period of the dominant C_4 grasses, was positively correlated with precipitation also supports our contention that competition modulates production and richness of summer annuals but not winter

annuals. Guo and Brown (1997) reported that overall seasonal productivity was not correlated with seasonal precipitation at their study site in southeastern Arizona. Instead, they found a temporal pattern in which periods when density of annuals was high were generally followed by low annual density the following season. In contrast, after periods when density of annuals was low, density could be either high or low in the following season.

5. Conclusion

In general, our results supported previous findings that plant species richness and primary productivity of desert annuals were controlled by precipitation and soil moisture in arid regions. Also, we found that species richness and ANPP differed between grassland and shrubland communities, and both varied greatly between years. We found no correlation between annual species richness and ANPP; thus, ANPP of annuals is more dependent on species identity and perhaps competition with perennial grasses rather than richness *per se*. Desert ecosystems are strongly dependent on seasonal and annual rainfall, and thus are likely to be highly sensitive and responsive to anthropogenic climate change (Diffenbaugh et al., 2008). In our region, models predict both lower mean annual precipitation (Cook et al., 2004, Seager et al., 2007), along with an increase in the frequency and intensity of extreme events (IPCC, 2007). As a consequence, land management activities should incorporate the impacts of a shifting precipitation regime in sustaining annual species biodiversity and the role of annuals in arid land ecosystem functioning.

Acknowledgements

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