# The influence of seasonal precipitation and grass competition on 20 years of forb dynamics in northern Chihuahuan Desert grassland

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## Abstract

**Aims:** In arid grasslands forbs represent a large component of species diversity and provide a key resource for pollinators and consumers. However, low abundances and high temporal variability make it challenging to successfully predict forb presence and abundance from 1 yr to the next. In this study we: (1) characterize patterns of semi-arid forb diversity and abundance over time; (2) determine the relative importance of direct vs indirect (via grass competition) effects of precipitation on forb richness and abundance; and (3) separate the effect of precipitation timing on forb community composition from the effects of precipitation amount and season.

**Location:** Semi-arid grassland, Sevilleta National Wildlife Refuge, Socorro County, central New Mexico, USA.

**Methods:** We analysed forb dynamics along two 400-m long line-intercept transects in response to inter-annual and seasonal precipitation variability and abundance of perennial grasses using a unique 20-yr species composition data set from ungrazed native grassland in the northern Chihuahuan Desert.

**Results:** Forb richness and cover were significantly positively associated with precipitation across seasons. Total richness was high across the time series but substantially lower within any given year. A direct, positive effect of precipitation overrode any potential negative, indirect effect via grass competition. Although aggregate forb responses were strongly linked with precipitation, individual species responses were highly variable and generally not linked with either precipitation timing or season.

**Conclusions:** In the hotter, drier climate predicted by meteorological models for the US southwest, forbs may be negatively impacted if winter moisture decreases and monsoon precipitation becomes more variable. On the other hand, the flexibility exhibited by forbs in germination and establishment throughout the growing season may help buffer some common species to increased inter-annual precipitation variability.

## Introduction

Although grasses contribute the majority of biomass in semi-arid grasslands, subordinate forbs provide most of the diversity (e.g. Glenn & Collins 1990). To date, most ecological research in semi-arid systems has focused on understanding the dynamics of productive grass species and shrubs (Alward et al. 1999; Peters et al. 2006, 2012), but there is growing recognition that subordinate forbs may have a disproportionately large effect on grassland ecosystem function (Mariotte 2014). In the southwest US, for example, forbs constitute a major portion of the spring and summer forage of pronghorn (*Antilocapra americana*) (Yoakum & O'Gara 2000) and are important food resources for small mammals and other consumers (Shalaway & Slobodchikoff 1988; Hope & Parmenter 2007; Warne et al. 2010). Pollinators also rely on forbs, and stochastic fluctuations in pollinator communities, particularly in semi-arid systems, can be linked to the unpredictability of these flowering resources (McLaughlin et al. 2002; Wright et al.

2015). Increased recognition of the importance of forbs for semi-arid grassland diversity and function has fueled interest in understanding their dynamics; however, low abundances, limited dispersal and germination, and high temporal variability have made it challenging to successfully predict forb presence and abundance over time (Venable & Lawlor 1980; Schwinning & Kelly 2013).

Precipitation is a primary driver of vegetation dynamics in semi-arid grasslands (Went 1948; Webb et al. 1978; Sala et al. 1988; Yan et al. 2015) and may affect forb dynamics by altering germination, overall resource availability and competitive interactions. In particular, semi-arid grasses are highly responsive to precipitation (Collins et al. 2008; Collins & Xia 2015), and removal experiments indicate that interspecific competition is the strongest relationship between dominant grasses and forbs in semi-arid systems (Sasaki & Lauenroth 2011; Peters & Yao 2012). Yet because semi-arid grasses are adapted to an environment with low average precipitation, physiology could constrain their ability to fully utilize the water available in high precipitation years (Dalgleish & Hartnett 2006; Bai et al. 2008; Nippert & Holdo 2015). As a consequence, the net effect of a high precipitation year may be positive for subordinate forb species as well as dominant grasses.

Determining the relative importance of direct and indirect precipitation effects on forb communities is critical for predicting compositional shifts under directional climate change. Winter precipitation, for example, is expected to decline in the southwest US (Gutzler & Robbins 2011). If the response of forb species to rainfall is primarily indirect through subsequent competition from grasses, a reduction in rainfall may result in an increase in forb abundance due to competitive release. However, if precipitation directly controls forb as well as grass species, reduced rainfall may lead to a decline in both functional groups.

In the southwest US, plant growth occurs during two discrete seasonal periods: in the spring following winter precipitation, and during the summer monsoon (Muldavin et al. 2008; Notaro et al. 2010). Early, short-term studies indicated that there are two sets of non-overlapping forb species: those that appear following winter rains and those following the summer monsoon (Went 1948). Yet rainfall can be highly variable within seasons and, consequently, short-term studies that detect seasonal differences in composition may be confounded through precipitation effects. Long-term records can help to disentangle a direct effect of season from precipitation, with important implications for predicting the effects of climate change on forbs and the consumer resources they provide. For instance, if forb communities are comprised of species that can grow in either season but have different precipitation responses, it is more likely that overall forb abundances will be maintained despite shifts in seasonal precipitation patterns.

Here we analysed a unique, continuous 20-yr data set of forb composition (Collins 2015) in relation to precipitation patterns and grass cover in the semi-arid northern Chihuahuan Desert. We had three goals: (1) to characterize patterns of semi-arid forb diversity and abundance over time; (2) to test the relative importance of direct vs indirect (via grass competition) effects of precipitation on forb richness and abundance; and (3) to separate the effect of precipitation timing on forb community composition from the effects of precipitation amount and season. In combination, addressing these goals would fill a critical knowledge gap for a system in which the focus has primarily been on dynamics of the dominant grasses.

## Methods

### Study area

Our study was conducted at the Sevilleta National Wildlife Refuge (SNWR; 34°20′ N, 106°43′ W) in Socorro County, central New Mexico, USA. Much of the SNWR was grazed by domestic livestock from the mid-1930s until 1973, when domestic grazers were permanently removed from the site (USFWS 2011). We focused on northern Chihuahuan Desert grassland within the SNWR, which is dominated by the perennial bunchgrass *Bouteloua eriopoda*. Other abundant grasses are *B. gracilis*, *Sporobolus* spp., *Aristida* spp. and *Muhlenbergia arenicola* (Muldavin 2002). Common forbs include a mixture of perennial and annual species, such as *Sphaeralcea* spp., *Machaeranthera* spp., *Chamaesyce* spp. and *Astragalus* spp.

The climate of the region is mid-elevation continental, with relatively hot summers and cold winters. Average annual temperature in the SNWR is 13.9 °C, with means in Dec and Jul of 2.4 and 25.3 °C, respectively. The average daily minimum in Dec is −5.2 °C and the average daily maximum in Jul is 33.3 °C. The SNWR averages ~250 mm of precipitation annually, with 60% falling from Jul through Sept during the summer monsoon; the rest occurs largely with winter frontal systems (Gosz et al. 1995; Pennington & Collins 2007; Notaro et al. 2010).

### Vegetation sampling

In 1989, two permanently marked 400-m line intercept transects, known hereafter as Deep Well (DW) and Five Points (FP), were established approximately 2 km apart along a north–south orientation in undisturbed Chihuahuan Desert grassland. Transects were sampled each spring (late April to early June) and fall through 2008 when the site was burned by a lightning-caused wildfire. The fall data were initially collected in late July or early August (1989–1993) but subsequently shifted to late September through early November to prevent sampling

prior to or during the monsoon. Sampling was done by recording the starting and stopping distances and identifying each plant species or non-vegetated substrate type (i.e. soil, litter or rock) intersecting the transect at 1-cm resolution; multiple species could be recorded in a given cm (See: Collins & Xia 2015). Fourteen species were difficult to distinguish in the field and combined at the generic level for analysis (*Astragalus* – two spp., *Chamaesyce* – six spp., *Machaeranthera* – two spp., *Sphaeralcea* – four spp).

## Precipitation monitoring

Precipitation was recorded at the event scale via tipping bucket rain gauges at two climate stations between 600 m and 3 km from the transects. The station at DW provided a continuous record for the duration of the study. In 1999, the second station was installed 1 km closer to FP. This second station also provided volumetric percentage soil water content from 0–30 cm at 1-h intervals using time-domain reflectometry (Campbell Scientific CS615; Logan, UT, US). To determine if rainfall was a good surrogate for available soil moisture, we used linear regression to test the relationship between total precipitation and mean percentage soil moisture within each season. We compared differences in non-monsoon, monsoon, and yearly total precipitation between sites with a *t*-test.

## Analysis

We characterized forb community composition by calculating richness and abundance (i.e. number of cm occupied by a forb species along each transect) within each season and year. To understand if richness and abundance patterns captured shifts in species identity over time, we additionally described species composition using a rank frequency distribution (i.e. the proportion of years a species occurred) within each season. To compare whether the same species were common between seasons, we characterized species composition using a rank abundance distribution (i.e. the mean rank of species by mean abundance) within each season. All analyses were conducted in R v 3.2.2 (R Foundation for Statistical Computing, Vienna, AT).

To separate the direct effect of precipitation on forb richness and abundance from its indirect effect (via grass cover) we utilized structural equation modeling (SEM). Richness and abundance were tightly correlated (Pearson correlation coefficient = 0.82, $P < 0.001$ with abundance on a log scale). Consequently, we used a single SEM model that focused on forb richness and linked it directly to previous season richness, growth form (annual or perennial), season and total seasonal precipitation, and indirectly to precipitation via grass cover. To assess if pathways differed

for each growth form, we additionally conducted separate SEMs for annual vs perennial species (the same model structure, but omitting growth form as an explanatory variable). Because these models were similar to the full model we did not present them below (but see Appendix S1, Figs S2 and S3). We fitted the model using maximum likelihood via library 'lavaan' in R.

To test the importance of precipitation timing as well as amount on the identity and abundance of different forb species, we utilized RDA using the rda() function 'vegan'. To explain spring community composition we included total seasonal precipitation (mm), mean number of days between precipitation events, and mean number of days between events ≥5 mm, with site as a conditioning variable. To explain fall community composition we considered the above variables, as well as maximum number of summer (Jul and Aug) days without rain, and number of days from 15 Jun before 5-mm and 10-mm events. The 5-mm event was selected as a minimum rainfall amount because it is a known threshold at which a physiological response is triggered in arid-land grasses (Sala & Lauenroth 1982; Thomey et al. 2011). Prior to inclusion in each RDA, we tested variables for collinearity and chose a single proxy for any pair of variables that had a Pearson correlation coefficient > |0.8|. We compared full and nested RDA models using step-wise AIC comparisons (using the function ordistep() in 'vegan'. Because total forb abundance can be quite low and varied greatly over time, we used absolute rather than relative abundances and only included species that occurred at least six times, allowing us to better detect synchronous species responses to environmental drivers.

Of the variables considered for inclusion in the RDA, total spring precipitation was closely correlated with number of spring precipitation events and number of spring precipitation events ≥5 mm; we retained total precipitation to represent these three precipitation variables for subsequent analyses. Total fall precipitation was similarly correlated with the number of fall events ≥5 mm; total fall precipitation was retained.

## Results

### Precipitation patterns

Mean annual precipitation over the course of the study (1989–2008) was 241.0 mm, occurring in a bimodal distribution with peaks in winter and during the summer monsoon. Precipitation during the non-monsoon period (October–May) averaged 98.8 mm and was a mixture of rain and snow. Average monsoon precipitation (June–September) was higher (142.2 mm) and fell mostly as rain produced by convective thunderstorms. Precipitation and percentage soil moisture, summarized as daily means,

were significantly correlated in each season (non-monsoon: $R^2 = 0.76$, $P < 0.001$; monsoon: $R^2 = 0.90$, $P < 0.001$; Appendix S1, Fig. S1). Differences in non-monsoon, monsoon and yearly total precipitation between the two meteorological stations were not significant ($t \geq -1.39$, $P \geq 0.20$).

### Species richness and abundance patterns

Seventy unique forb species were identified between 1989 and 2008 (Appendix S1). Of the 56 taxa analysed at the species level, 26 were perennials, 21 annuals and nine had variable life histories. The four generic level associations included species that were either perennial (*Sphaeralcea*) or annual/perennial (*Astragalus, Chamaesyce, Machaeranthera*).

Mean species richness was similar between seasons (spring = 12 ± 6 SE, fall = 13 ± 4 SE species on a 400-m transect), but seasonal richness varied considerably across

years (from three to 22 species·transect$^{-1}$; Fig. 1). Total forb abundance, while highly variable (0.13–17.2%), was generally low and comparable between seasons (spring = 2.5 ± 2.5%, fall = 3.0 ± 3.6%; Fig. 1). The majority of species were detected in ≤50% of seasons, while only a few were found throughout the course of the study; many species were observed just once over this 20-yr period (Fig. 2). However, a number of species tended to be frequent in both seasons, including *Chaetopappa ericoides, Machaeranthera* spp., *Astragalus* spp., *Sphaeralcea* spp., *Solanum elaeagnifolium* and *Hoffmannseggia drepanocarpa*. These frequent species were often perennials, although *Machaeranthera* and *Astragalus* spp. represented annual/perennial species complexes (Fig. 2).

Sixteen taxa accumulated a mean seasonal abundance of ≥0.25% (1 m) along at least one transect, and most of these were present in both spring and fall (Fig. 3). *Chamaesyce* spp. occurred at the largest mean abundance
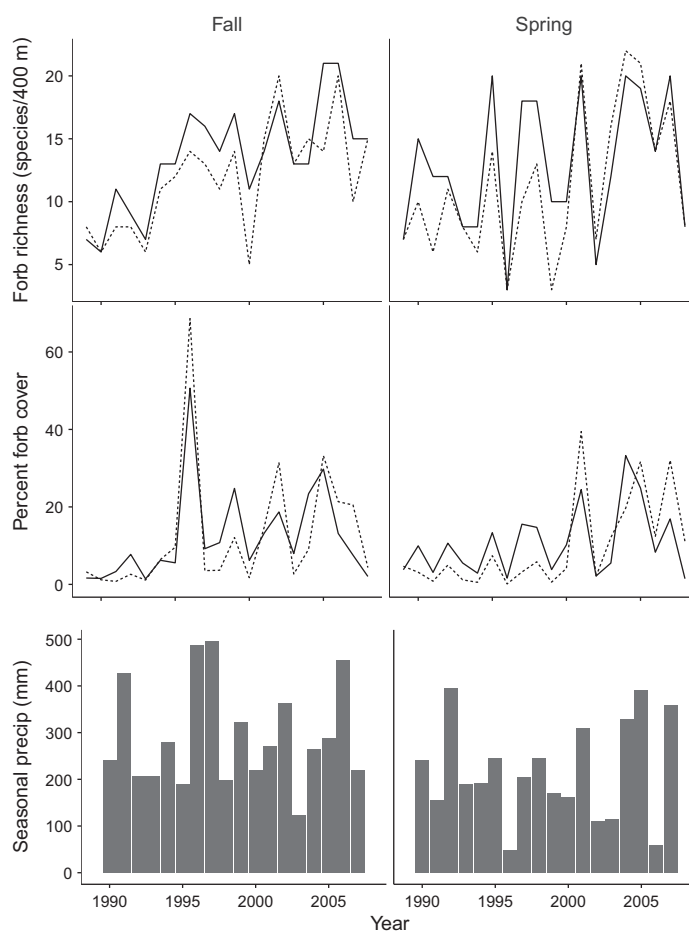


**Fig. 1.** Forb richness and species abundance (cover), and precipitation over time and by season (fall monsoon; June–September and spring; October–May) at the Sevilleta National Wildlife Refuge, central New Mexico, USA. Within the abundance and richness panels the Deep Well (DW) site is the solid line and the Five Point (FP) site is dotted.
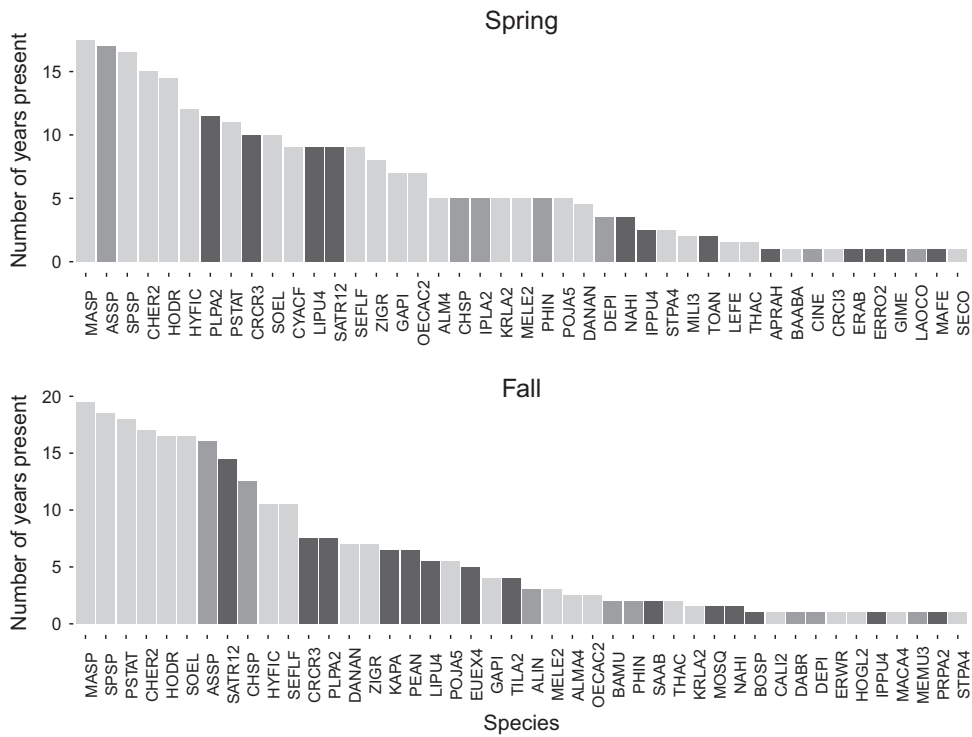
**Fig. 2.** Frequency of species occurrence from 1989 to 2008 within season and averaged across sites. Light grey indicates perennial species, dark grey indicates annual species and medium-grey indicates species with mixed annual/perennial growth forms. See Appendix S1 for species codes.
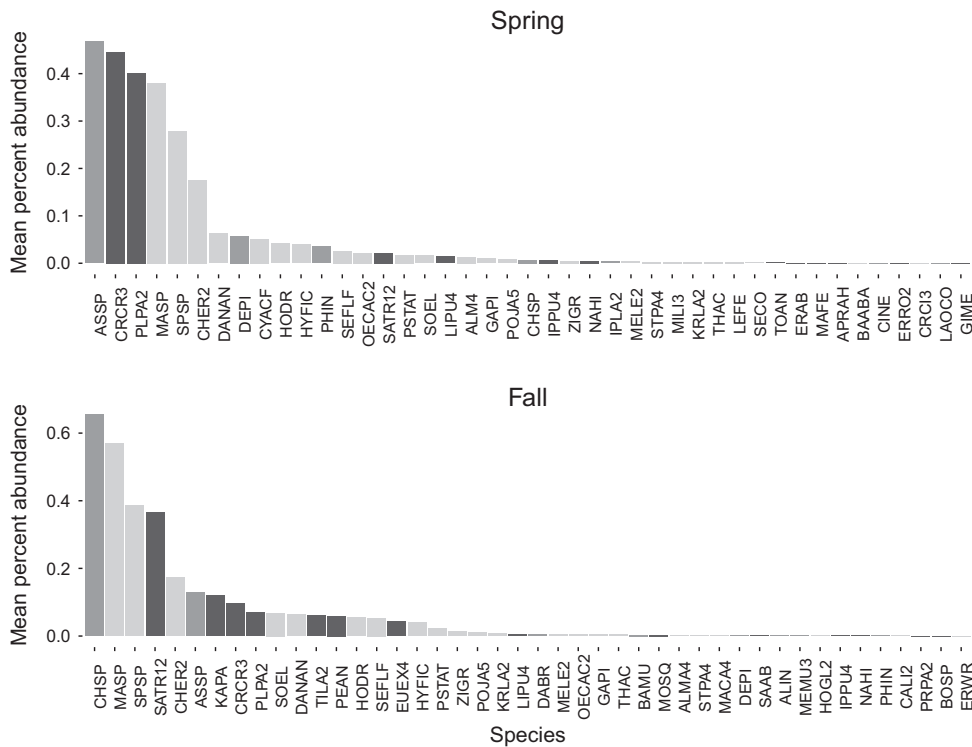


**Fig. 3.** Mean abundances by species from 1989 to 2008 within season and averaged across sites. Light grey indicates perennial species, dark grey indicates annual species and medium-grey indicates species with mixed annual/perennial growth forms. See Appendix S1 for species codes.

(0.78%), followed by *Machaeranthera* spp. (0.73%) and both *Astragalus* spp. and *Plantago patagonica* (0.65%; Fig. 3). The vast majority of taxa exhibited mean seasonal abundances well below 0.1%. Life forms were relatively evenly distributed, with some of the most abundant species being annuals (Fig. 3).

### Forb responses to precipitation

Structural equation modeling (SEM) indicated that total seasonal precipitation had a significant, positive effect on forb richness (Fig. 4). There was higher total precipitation
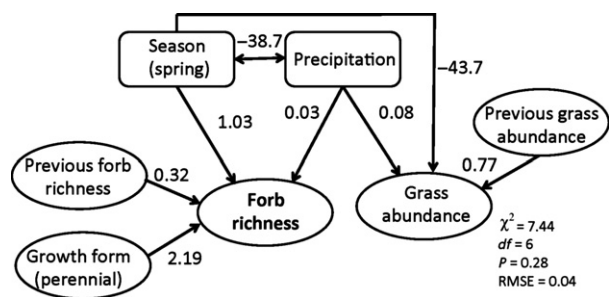


**Fig. 4.** SEM developed to relate the direct and indirect (via grass abundance) effects of precipitation and season on desert forb richness. Effect sizes are reported next to each pathway; only statistically significant pathways are drawn. Precipitation and season had direct effects on both forb richness and grass abundance, but did not indirectly affect forb richness via grass abundance.

in the fall but an independent positive association of forb richness with the spring season moderated the degree to which seasonal differences in precipitation affected total forb richness (Fig. 4). Most forb richness was due to the presence of perennial species (Fig. 4). Grass abundance was also positively associated with total precipitation and differed by season (higher abundance in the fall); however, there was no significant indirect effect of precipitation or season on forb richness via grass abundance ($P = 0.42$). Strong previous-season lag effects positively influenced both forb richness and grass abundance (Fig. 4).

The two RDAs explained 8.6% (fall) and 14% (spring) of the variance in species abundances over time. At both sites the best-fit RDA retained total spring and fall precipitation and grass cover; number of days between precipitation events was an additional explanatory variable for species composition in spring (Fig. 5).

## Discussion

Total seasonal precipitation was by far the strongest predictor of forb richness and abundance patterns at our semi-arid northern Chihuahuan Desert site, suggesting that it is simply moisture that limits forbs and not the timing or magnitude of precipitation events. The positive direct correlation between precipitation and forb richness and abundance was strong and overwhelmed any potential negative relationship with grass competition. Although aggregate
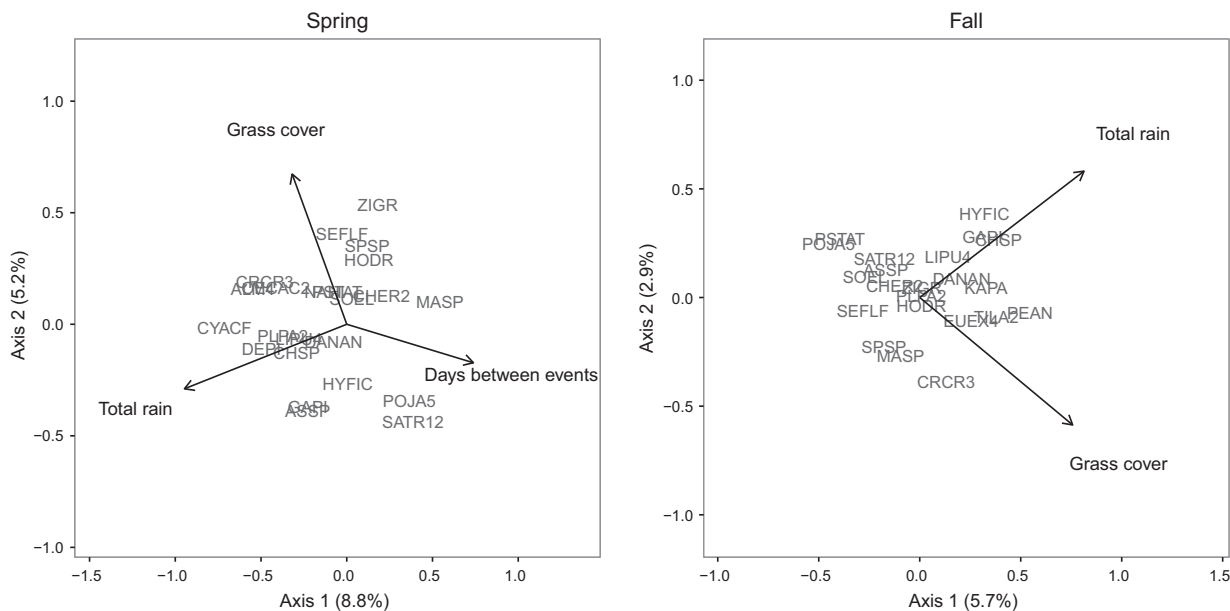


**Fig. 5.** Best-fit RDA scores for abundant species and environmental variables for spring and fall species composition by year (1989–2008). Only species recorded at least six times for a season are shown. See Appendix S1 for species codes and Fig. S4 for a visualization that additionally includes year scores.

forb responses were predictable and similar among both annual and perennial species, species identities fluctuated greatly over time, and the variance in individual species responses was weakly predicted from rainfall patterns and grass cover. Overall, the high number of forb species observed across the time series, and the fact that some species frequently occurred in both seasons, suggests that seed bank diversity (e.g. storage effect; Chesson 2000) may support varied forb responses to future climate shifts.

In contrast to mesic systems, in which precipitation effects are often mediated by competition (Mariotte et al. 2013), we did not observe a significant relationship between grass abundance and forb richness. Competitive barriers to forb establishment may be reduced or overridden in this system because the amount of available substrate is quite high; on average, 32 ± 1% of each transect was non-vegetated soil across the time series. Further, as our results suggest that both dominant grasses and subordinate forbs utilize available soil moisture following rainfall events (Muldavin et al. 2008), niche partitioning via differences in root morphology and depth may have allowed both grasses and forbs to benefit from increased precipitation. For example, perennial grasses have fibrous roots that are generally in the upper 20 cm of the soil profile (Kurc & Small 2007), whereas perennial forbs often have deeper taproot systems (Nippert & Knapp 2007). Such variable root distribution has been found to facilitate grass–forb coexistence (Nippert & Holdo 2015), particularly when moisture infiltrates deeper into the soil and remains longer following large rain events (Vargas et al. 2012). We found that available soil moisture, down to at least 30 cm, was strongly tied to precipitation events. Further, deeper moisture infiltration typically occurs following large events (Bhark & Small 2003; Pockman & Small 2010), and the tight correlation between total spring precipitation and events ≥5 mm indicates that total precipitation is likely associated with increased soil moisture across the soil profile.

We recorded a remarkably high number of forb species (70 species) over 20 yr. In comparison, only 23 grass species were observed during this time. However, seasonal forb richness and abundance were often relatively low. Nearly all taxa went undetected for at least a portion of the study, illustrating the transitory nature of forb establishment in this semi-arid grassland, as well as the infrequent occurrence of germination cues for many species (e.g. Venable & Lawlor 1980; Chesson 2000). Annual forbs especially may remain dormant in the seed bank until conditions are favourable, and therefore exhibit significant fluctuations in richness and abundance (Went 1948; Inouye 1991; Guo & Brown 1997; Xia et al. 2010; Peters & Yao 2012; Yan et al. 2015). As one example, in our study *Plantago patagonica* had high peak abundance values even

though it was seen in only a few years. Species in nutrient- and water-deficient systems are often short-lived and highly variable in establishment (Glenn & Collins 1993; van der Maarel & Sykes 1993; Grime et al. 2008; Cleland et al. 2013; Wright et al. 2015). Overall, our results highlight the unpredictable nature of appearances and abundances of forb species under a highly variable precipitation regime in this native desert grassland.

Early records of forb abundance patterns in arid systems suggested that there could be two sets of non-overlapping species: those that appear following winter rains, and those following the summer monsoon (Went 1948). Our long-term analysis allows us to refine these designations. Although the identities of very rare species changed considerably between seasons, with many being observed in only a single season, several more common species were consistently observed over time. This finding indicates that the perception that there are seasonally restricted species may not always be accurate; our results suggest this impression may be attributed to high variability in species appearances across seasons and years. Unsurprisingly, many of the species that occurred frequently in both seasons were perennials, underscoring the likely importance of previous season lag effects, such as below-ground growth or seed production, on current season abundances. The high number of forb species that appeared across the time series, along with the moderate number of forb species that occurred consistently despite season and precipitation variability, indicates that forb abundance may persist despite fluctuations in richness under predicted future increases in precipitation variability. Such potential resilience has been attributed to forb species in other arid systems (Salguero-Gómez et al. 2012; Gremer et al. 2016).

Our findings closely mirror Hanski's hypothesis that within a region numerous species will be sparse and observed at relatively few sites ('satellite' species) while a smaller number of distinct taxa will be widespread ('core' species; Hanski 1982). Similar patterns have also been noted for species occurrences within semi-arid grassland over time (Collins & Glenn 1991; Glenn & Collins 1992). Several factors may lead to the ephemeral nature of the many satellite species at our site. First, it is possible that satellite species appearances were due to stochastic seed dispersal and local extinction events across the landscape. Alternatively, it could be that satellite species were present in the seed bank, but only responded to very specific environmental germination cues. This scenario may be more likely for species like *Plantago patagonica* and *Cryptantha crassisepala* that occurred infrequently but at high abundances. Annuals such as these are perhaps more subject overall to variability in the environment (Shriver 2015). Finally, frequency-dependent granivory can significantly influence plant community composition (Kuang &

Chesson 2009; Chesson & Kuang 2010) and may also generate patterns in which species exhibit high abundances but at low frequencies. However, other studies in northern Chihuahuan Desert have found that the impact of grazers and granivores on the seed bank is negligible (Koontz 2005; Báez et al. 2006), suggesting that other factors may more strongly control the apparent stochasticity of satellite species.

## Conclusion

Winter precipitation in central New Mexico is predicted to decline by about 10% over the next century (Gutzler & Robbins 2011) and, while total monsoon precipitation is not predicted to change, it is expected to become more variable. If winter moisture decreases, forb richness and abundance may be reduced. Yet forbs respond to moisture throughout the year, and the potential impact of higher precipitation variability during the monsoon appears somewhat moderated by the influence of the previous season on growth and abundance. Perhaps analogously, with no clear shift in forb composition between seasons, most species seem adapted to take advantage of moisture whenever it arrives. Similarly, Gremer et al. (2016) noted the potential benefits of delayed germination ('bet hedging') and germination plasticity in Sonoran Desert winter annuals. Alternating patterns of establishment suggest that a diversity of precipitation responses may be represented in the forb seed bank, potentially buffering ecosystem functions supported by forbs (e.g. consumer resources, belowground processes) to future increases in precipitation variability.

## Acknowledgements

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## Supporting Information

Additional Supporting Information may be found in the online version of this article:

**Appendix S1.** Taxa observed over the study period and their life forms.