ECOSYSTEMS

Seasonal Rainfall, Shrub Cover and Soil Properties Drive Production of Winter Annuals in the Northern Sonoran Desert

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ABSTRACT

Winter annual plants play an important role in arid and semiarid ecosystems because of their rapid response to resource pulses, which drive primary production that provides resources for herbivores and pollinators. Understanding the factors that control annual plant growth is key to predicting how arid and semiarid ecosystems will respond to changes in climate and resource availability from anthropogenic activities. We used a long-term nutrient enrichment experiment that spanned precipitation and urbanization gradients in central Arizona, USA, to examine the effects of climate, surface soil properties, soil nutrient availability and shrub cover on winter annual plant growth. At a landscape scale, aboveground net primary production (ANPP) of winter annual plants had a positive, nonlinear relationship to the amount of precipitation received from October through March of the current growing season. We found evidence for sequential resource limitation of ANPP initially from water then nitrogen and phosphorus. The resource limitation cascade was modified by surface soil properties and location relative to shrubs (under or between shrubs), highlighting the effect of small-scale factors on large-scale processes. Specifically, gravel cover had a negative effect on ANPP, and the effect of shrub cover on ANPP depended on nitrogen and current season rainfall. Our study emphasizes how small-scale factors, such as gravel cover, nutrient availability and presence of shrubs, can interact with large-scale drivers, such as seasonal precipitation, to affect interannual variation in winter annual plant production in the northern Sonoran Desert.

GRAPHICAL ABSTRACT

Sonoran Desert landscape showing production of winter annuals363 x 241mm (300 x 300 DPI)

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HIGHLIGHTS

- Across sites, winter annual production had a nonlinear relationship to seasonal precipitation
- Winter annual production was limited first by water then by nitrogen and phosphorus
- Large- and small-scale factors interacted to affect production of Sonoran Desert winter annuals

INTRODUCTION

Seasonal ephemeral plants play an important role in ecosystems. These species supply resources for herbivores and pollinators, increase diversity and provide a temporary sink for nutrients (Tessier and Raynal 2003; Chen and others 2007, 2009). For example, in temperate systems, winter ephemeral plants and their soil microbial communities can act as vernal dams (temporary nutrient sinks) that reduce runoff and leaching losses of soil nutrients through their rapid rates of growth after snowmelt (Muller and Bormann 1976; Rothstein 2000; Eisenhut and others 2022). Similarly, rapid recovery of herbaceous plants and microbial communities following fire increases nitrogen retention in Mediterranean ecosystems (Goodridge and others 2018). Although less studied, annual plants in arid and semiarid ecosystems play a similar role due to their substantial contribution to annual primary production and their quick response to rainfall pulses that characterize dry regions (Chen and others 2009; Xia and others 2010; Huang and others 2016; Wilcox and others 2020). However, understanding the drivers of annual plant production in drylands is complicated, in part, due to the difficulty in quantifying ecological relationships across spatially and temporally heterogeneous patterns of resource availability (Collins and Xia 2015; Petrie and others 2015; Arredondo and others 2016; Liu and others 2016).

Mean annual precipitation (MAP) is strongly related to aboveground net primary production (ANPP) at large spatial scales in drylands (Sala and others 2012; Maurer and others 2020), but its impact on local plant production is constrained by numerous factors that influence water availability and growth (Yahdjian and others 2011; Sala and others 2012). For example, germination and production of dryland plants often depend on legacy effects of litter, seed or meristem production, which, in turn, depend on rainfall (Sala and others 2012; Dudney and others 2017, Qian and others 2023). Additionally, soil properties, such as texture and gravel cover, are important drivers of ANPP at smaller scales as they may regulate water and nutrient availability for plants under intermittent rainfall regimes (Hamerlynck and others 2002; Cable and others 2008; Hall and others 2011). Moreover, the relative importance of various resources for plant production can change depending on characteristics of the rainfall regime or patch type, which further controls biotic interactions. For example, at the local scale, the relationship between perennial shrubs and annual plants can shift from facilitative or neutral to competitive depending on rainfall amount (Tielborger and Kadmon 1997; O'Brien and others 2017). Similarly, low to medium cover of surface rocks can facilitate plant growth by providing favorable microenvironments (Nobel and others 1992; Pérez 1998; Xiaoyan and others 2000; Peters and others 2008), but high rock cover can create 'pavements' that limit water infiltration (Young and others 2004).

Long-term observations across multiple scales and gradients of resource availability are needed to understand how heterogeneous drylands will respond to current and future environmental challenges across scales (Wu and others 2011; Munson and others 2016; Wilcox and others 2017). Arid and semiarid ecosystems cover 45% of Earth's land surface (Huang and others 2016) and are particularly susceptible to climate change and the effects of urban encroachment (Reynolds and others 2007; Shen and others 2008; Poulter and others 2014; Hoover and others 2020). Among the expected changes in climate, variability in the amount and timing of precipitation is likely to alter ecological processes, as both control water and nutrient availability for dryland primary producers (Wu and others 2011; Collins and others 2014; Fernandes and others 2022; Brown and others 2022). Indeed, global models predict a future characterized by increased aridity and precipitation variability in many arid and semiarid regions (Diffenbaugh and others 2008; Seager and Vecchi 2010; Polade and others 2014; Cook and others 2015).

In the Southwestern United States, regional models predict less precipitation specifically in winter and spring (Gutzler and Robbins 2011). Given the importance of soil moisture for driving dryland ecosystem processes (Collins and others 2008, 2014), reduced rainfall could alter the com-

position and production of ephemeral plant communities (Archer and Predick 2008; Gherardi and Sala 2015). Over the past 100 years, this region has become more arid and interannual variability in climate has increased (Maurer and others 2020). In addition, models predict an intensification of the North American Monsoon as well as the El Niño Southern Oscillation, which are likely to lead to increased interannual variability and more extreme winter and summer precipitation events (Liu and others 2016; Demaria and others 2019; Grothe and others 2020; Hu and others 2021).

Arid and semiarid ecosystems account for much of the global trend in urban land expansion (Seto and others 2011; Bocquier 2014, Maestre and others 2016), resulting in increased rates of atmospheric deposition leading to increased soil nutrient availability, especially nitrogen and potentially phosphorus (Kanakidou and others 2016; Cook and others 2018) and altered nutrient cycles (Williamson and Ball 2023). Nutrient enrichment in resource limited ecosystems, such as forests and grasslands, alters species composition, production and ecosystem functioning (Suding and others 2005; Elser and others 2007; Fay and others 2015; Simkin and others 2016; Komatsu and others 2019). However, the consequences of chronic resource addition in aridland systems are less clear (Hall and others 2011; Yahdjian and others 2011; Wheeler and others 2021; Keller and others 2023; Williamson and Ball 2023). For example, increased soil N availability led to higher production in some dryland ecosystems in some years, but not in others (Fisher and others 1988; Peterjohn and Schlesinger 1990; Yahdjian and others 2011; Ladwig and others 2012; Su and others 2013). A study in the Sonoran Desert found that annual plant diversity was reduced on plots enriched in both N and P, and that the effects varied among upwind, urban and downwind sites (Wheeler and others 2021). Furthermore, lag effects were evident. Current and previous growing season precipitation increased annual plant diversity in wetter years and diversity was more responsive to precipitation following a wet year. Thus, the interactive effects of long-term nutrient deposition and precipitation on dryland plant communities is temporally variable and contingent on seasonal rainfall.

In this study, we determined the independent and interactive effects of climate, nutrients, urbanization, shrub patches and surface soil properties on ANPP of winter annual plants in the northern Sonoran Desert over a decade, using a long-term nutrient enrichment experiment across gradients of urbanization and precipitation in cen-

tral Arizona, USA (Hall and others 2011). The current study is among the first to identify key long-term drivers of desert annual plant ANPP across gradients of resource availability and urbanization. Specifically, we asked: (1) How do precipitation, N and P affect ANPP of winter annuals and are these effects altered by soil properties and shrub cover? and (2) Does proximity to an urban area influence the drivers of ANPP of winter annual plants? We hypothesized that annual plant ANPP is primarily limited by water and that ANPP is only affected by nutrients when sufficient water is available (Shen and others 2008; Yahdjian and others 2011; Ladwig and others 2012). If water is primarily limiting, then we expect soil properties that enhance water availability to increase ANPP of winter annual plants. In high-rainfall years, when evaporation is less important, we expect higher cover of surface rocks to have a negative effect on soil moisture by acting as a barrier between rainfall and soil. In wet years, nutrient limitation will favor ANPP in fertile shrub islands (Schlesinger and others 1996) and in areas closer to the city where N deposition is most intense (Hall and others 2011; Cook and others 2018).

METHODS

Site Description

We measured plant and soil properties in 15 protected native Sonoran Desert preserves within and surrounding the Phoenix, AZ metropolitan area as part of the Central Arizona-Phoenix Long-term Ecological Research project (CAP LTER). All sites were located on alluvial fans with gentle slopes, a common geomorphic setting across the region, and soils were primarily covered in gravel and classified as Aridisols with a sandy loam texture at 0–5 cm depth (Table 1). Perennial vegetation was dominated by creosote bush (*Larrea tridentata*) as well as bursage *(Ambrosia deltoidea* and *A. dumosa)* and several cactus species (*Carnegiea gigantea* and *Cylindropuntia spp.*). Common winter annuals included *Amsinkia menziesii, Cryptantha decipiens, Erodium spp, Pectocarya spp, Plantago spp, Schismus arabicus* and *Vuplia octoflora).* Abundances of annuals varied temporally in response to precipitation and spatially in response to shrub cover and fertilizer treatment. See Wheeler and others (2021) for more details on the spatial and temporal dynamics of winter annual composition. Although N-fixing trees are common in the Sonoran Desert (for example, *Parkinsonia* spp. and *Prosopis* spp.), care was taken when selecting the long-term nutrient

Table 1. Descriptive Variables for the 15 Sonoran Desert Sites Used in this Study

Region	Site code	Elevation (m)	MAP (mm)	MAT (°C)	Soil type	Sand %	Silt %	Clay %	Gravel %, 0.2–7.5 cm	Cobble %, 7.5–25 cm	Stone %, 26–59 cm	Boulder %, > 60 cm	Total rock cover %	WHC (% water)
West	EME	331	138	25.7	Typic Haplargids	76.1 (0.9)	7.7 (0.8)	16.2 (0.2)	61.9 (1.4)	2.1 (0.3)	0.7 (0.3)	–	64.8 (0.9)	30.5
West	EMW	382	139	24.7	Typic Haplargids	80.6 (0.6)	3.2 (0.5)	16.2 (0.2)	20.4 (1.8)	1.8 (0.3)	–	–	22.3 (2.0)	27.5
West	SNE	492	139	23.5	Typic Camborthids	74.7 (0.4)	9.0 (0.4)	16.2 (0.2)	74.8 (0.3)	0.4 (0.0)	–	–	75.2 (0.3)	29.2
West	SNW	375	164	23.5	Typic Camborthids	72.4 (0.7)	11.2 (0.7)	16.4 (0.1)	57.8 (3.0)	0.6 (0.0)	–	–	58.4 (3.0)	31.7
West	WTM	454	156	23.6	Typic Haplargids	66.9 (0.5)	14.6 (0.6)	18.5 (0.4)	33.5 (0.5)	4.0 (0.3)	–	–	37.6 (0.5)	33.2
Urban	DBG	396	184	23.7	Typic Paleorthids	48.6 (0.4)	30.2 (0.4)	21.2 (0.3)	39.0 (1.2)	7.5 (0.3)	1.3 (0.3)	9.3 (0.2)	57.2 (1.4)	40.9
Urban	MVP	397	156	19.9	Typic Haplargids	52.3 (0.6)	29.3 (0.6)	18.4 (0.2)	62.8 (2.3)	7.2 (0.4)	0.5 (0.4)	–	70.5 (2.3)	34.9
Urban	PWP	456	134	26.3	Typic Haplargids	56.0 (0.9)	24.7 (0.7)	19.3 (0.3)	44.0 (2.1)	15.3 (1.4)	0.7 (1.4)	4.6 (0.1)	64.5 (0.8)	41.5
Urban	SME	372	161	25.6	Typic Haplargids	57.4 (0.6)	23.4 (0.5)	19.2 (0.2)	24.7 (0.9)	14.1 (0.2)	3.2 (0.2)	0.6 (0.2)	42.5 (1.0)	38.8
Urban	SMW	458	155	24.6	Typic Durorthids	68.8 (0.7)	14.5 (0.7)	16.7 (0.2)	53.3 (0.9)	6.2 (0.3)	0.3 (0.3)	–	59.8 (0.9)	35.5
East	LDP	620	292	21.7	Typic Haplargids	62.8 (0.5)	18.4 (0.4)	18.8 (0.2)	73.8 (1.4)	1.6 (0.2)	0.1 (0.2)	–	75.5 (1.5)	42.8
East	MCN	476	227	23.1	Typic Calciargids	61.7 (1.4)	19.8 (1.4)	18.4 (0.2)	49.0 (2.0)	0.1 (0.0)	–	–	49.2 (2.0)	28.0
East	MCS	539	203	22.9	Typic Haplargids	52.0 (0.6)	27.5 (0.6)	20.5 (0.4)	47.2 (1.0)	3.4 (0.2)	0.5 (0.2)	–	51.0 (1.0)	42.3
East	SRR	434	274	22.9	Typic Calciargids	68.1 (0.3)	14.6 (0.2)	17.3 (0.2)	30.0 (1.4)	2.2 (0.3)	–	–	32.1 (1.3)	31.6
East	UMP	592	219	23.4	Typic Haplargids	72.1 (0.3)	10.8 (0.3)	17.1 (0.2)	64.3 (1.0)	0.02 (0.0)	–	–	64.3 (1.0)	32.5

Rock class describes surface rock cover (%) of a given diameter at each site (mean ± 1 SE). Soil types were compiled from NRCS (NRCS 2009) except for soil from the SRR site, which was classified according to USDA field and laboratory methods as reported in Hall and others (2011). Soil texture classifications are from a depth of 0–5 cm (mean ± 1 SE). Mean annual precipitation (MAP) and mean annual temperature (MAT) are 10-year averages from standardized climate sensors within 20 km of our sites (2007–2017; FCDMC 2017; Table S1).

enrichment plots to avoid inclusion of N-fixing trees within 5 m of the plot boundaries.

The climate in the Sonoran Desert is arid to semiarid. The average monthly temperature is 12.2 °C in January and 33.9 °C in July (for 1933–2016). Our study sites spanned a strong precipitation gradient, with average rainfall ranging from 138 to 156 mm in the west and 203–292 mm in the east during the study (Table 1). The long-term average annual precipitation at the Sky Harbor Airport weather station in Phoenix is 182.7 mm and follows a bimodal pattern, with approximately 42% during the summer monsoon (July–October) and 51% during the winter rains (November–March; 1933 to 2016; https://wrcc.dri.edu/cgi-bin/cliMAIN.pl?az6481).

Our study sites also spanned an urban–rural gradient, with five sites located in protected Sonoran Desert parks within the Phoenix, AZ, metropolitan area (hereafter referred to as 'Urban' sites), five sites located in protected areas to the west of the city (hereafter 'West' sites) and five sites in protected areas to the east of the city (hereafter 'East' sites) (after Hall and others 2011; Figure 1 and Table 1). N deposition in the study area is moderate relative to other cities of comparable size, at 6.5 ± 0.2 kg N ha^{-1} y^{-1} (Cook and others 2018), although Urban sites receive about 15% more inorganic N as both dry and wet deposition than sites to the east or west of the city.

Long-Term Nutrient Enrichment Experiment

At each site, four 20 m × 20 m plots were established in 2006, three of which were amended with nutrients in a factorial design, including N, phosphorus (P), and N and P together (NP). The fourth plot served as an unfertilized control (C) (Hall and others 2011). N (60 kg N ha^{-1} y^{-1} in the form of NH$_4$NO$_3$) and P fertilizers (12 kg P ha^{-1} y^{-1} in the form of triple superphosphate) were distributed by hand in pellet form twice per year after the first winter rainfall and again at the start of the summer monsoon rains. The level of fertilization for the N treatments was 8–10 times the estimated N deposition rates in the Phoenix metropolitan area (Cook and others 2018), while the P treatments were added in excess (120 kg P ha^{-1} in 2006 and 12 kg P ha^{-1} thereafter) to increase the chances of soluble P reaching the deeper-rooted shrubs (Lajtha and Bloomer 1988; Fenn and others 2003; Hall and others 2011; Cook and others 2018).

ANPP

ANPP was measured as annual herbaceous aboveground biomass during seven winter growing seasons between 2008 and 2017. Harvest dates occurred at peak production, ranging from March 1-April 2 depending on the timing of rainfall and senescence of the annual plant community.

In each year, we harvested all aboveground plant material by cutting plants at the soil surface from one quarter (0.25 m × 0.25 m) of each of four permanently established 1-m^2 subplots in each 20 m × 20 m plot. Two permanent subplots were placed in each of two patch types: underneath *Larrea tridentata* (patch type = 'under shrub') in which the subplot was centered under an individual shrub, and in the open spaces between shrubs (patch type = 'between shrubs'). The harvest was conducted on a clockwise rotation within the 1-m^2 subplot to ensure that the same quarter was not harvested more frequently than once every four years. We then dried the collected plant material at 60 °C and determined its dry mass. Biomass (as dry mass per m^2) was calculated for each subplot and then the two subplots per patch type were averaged. We used this seasonal biomass accumulation as a measure of annual ANPP of winter annual plants because they grow only in response to winter rains. ANPP data were not collected in 2011, 2012 and 2014, years in which seasonal rainfall was low and annual plants did not consistently emerge across our study area.

Precipitation, Temperature and Aridity Index

We collated total daily precipitation and temperature data for the winter growing season for each year from Flood Control District of Maricopa County (FCDMC; Figure S1) rain gauges that were closest to our study sites (FCDMC 2017; Table S1). If data from stations were only available for a subset of years, data from additional nearby stations were used, with a maximum of five stations used for one site. Stations within 10 km and 150 m elevation of the site were selected when available. Of the 59 stations used, 35 were located within 6 km of the site while the rest were located between 6 and 19 km. Most stations (62%) were located within an elevation of 50 m of the site. The remaining stations were located between 51 and 210 m elevation of the sites. We used monthly average temperature values to calculate the seasonal aridity index (seasonal precipitation/seasonal
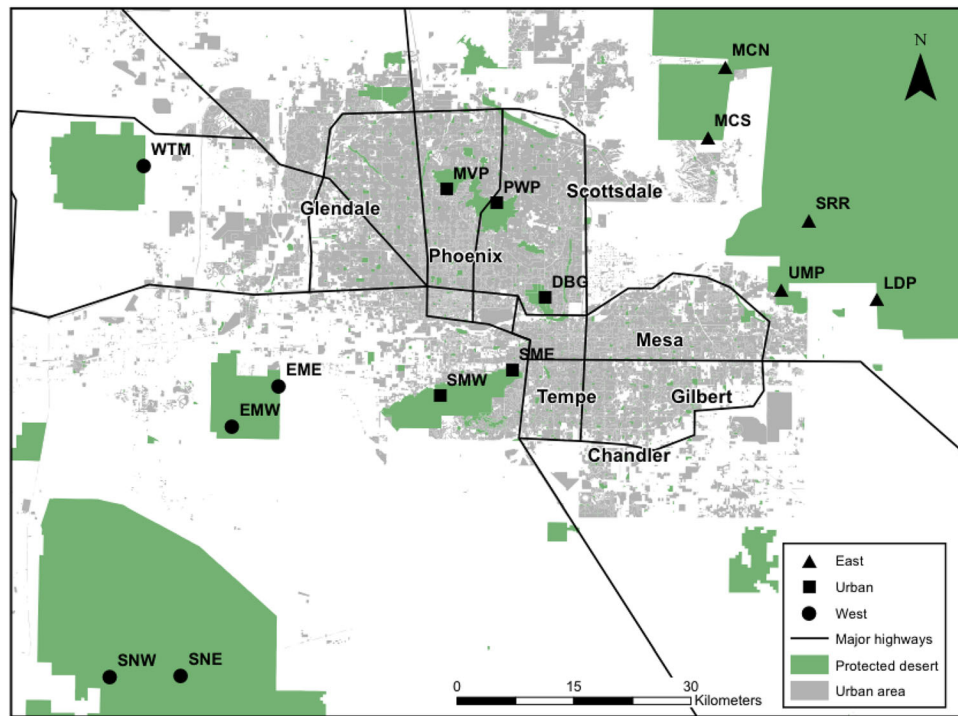
Figure 1. Map of the 15 study sites across the Phoenix, AZ metropolitan area. All sites are in protected desert preserves and are categorized by their location relative to the urban area with 'East' and 'West' outside of the city and the 'Urban' sites within the city. Three-letter codes are site names (Table 1). Four permanent 20 m × 20 m plots were established at each site to receive factorial nutrient addition treatments starting in 2006 (N, P, N and P together, and a control, that is, no nutrient addition).

potential evapotranspiration (PET)) for each year and each site. The R package 'SPEI' (Beguería and Vicente-Serrano 2016) was used to calculate PET using the Hargreaves Method (Lu and others 2005).

From these precipitation data, we calculated 'total growing season rainfall' which encompasses the critical germination window for Sonoran Desert annual plants (Venable and Pake 1999; Kimball and others 2011). To capture peak seasonal production of annuals, we used October 1 as the start of the growing season and ended the growing season at the harvest date each year. To examine the potential for rainfall effects from the previous winter growing season (lagged effects), we also collated the amount of winter precipitation in the previous year (October–March) prior to the latest biomass collection date for all years in which ANPP data were collected.

Soil Variables

Physical properties of surface soil that affect soil water availability (and are not likely to change quickly over time) were used in our analyses, including soil water-holding capacity (WHC) and particle size fraction (texture). Faster-turnover variables such as soil nutrient availability were not assessed at these sites during the full range of dates and thus were not used in this analysis. In 2009, we collected three 8 cm diameter × 2 cm depth soil cores in each patch type (under and between shrubs) and homogenized these cores within patch type for each plot. As described in Hall and others (2011) and Sponseller and others (2012), prior to analyses we first sieved the soils to 2 mm and removed all organic material. WHC was determined by the change in weight between saturated and dry soil after a 24-h drain time. Percent clay was determined using the hydrometer method (Elliot and others 1999) following removal of carbonates (modified from Gee and Bauder 1986). The sand fraction was determined gravimetrically by sieving to 53 μm, and the silt fraction was calculated by difference from combined sand and clay fractions.

Surface Rock Cover

For each plot in each site at the start of the experiment, we visually estimated surface rock cover from two randomly placed 1 m × 1 m

quadrats within each of four 10 m × 10 m quadrants of each plot (for example, NW, NE, SW and SE quadrants of each plot), for a total of eight 1 m × 1 m quadrats per plot. We then visually estimated cover of the following surface rock size categories (Schoenenberger and others 2002): boulders (> 60 cm in diameter), stones (59–25 cm), cobbles (25–7.5 cm) and gravel (< 7.5 cm). We averaged the estimates from the eight quadrats for each category and summed all size categories to determine the total surface rock cover of each plot.

Statistical Analyses

We used a linear mixed model to evaluate the long-term relationship between ANPP of winter annual plants, climate, patch type (under and between shrubs) and soil variables. Winter annual ANPP was log-transformed for all analyses to meet statistical assumptions regarding normality and heteroscedasticity. We performed all statistical analyses using R statistical software version 4.2.2 (R Core Team 2021) with R Studio version 2022.7.1.554 (RStudio Team 2022). P-values ≤ 0.05 were considered statistically significant.

Prior to fitting the mixed model, we first performed bivariate correlation analyses to determine relationships among predictor variables. If two variables showed a significant correlation ($r > 0.4$), we compared full models containing one of the two correlated predictors and selected the variable in the model with the lower AIC value. Rock cover and soil variables were correlated (Figure S2), and following this comparison only gravel cover was included in the final model. To determine whether including previous year's precipitation improved the model, we also included both current and previous year growing season rainfall (rainfall lag) in the model. When plotting ANPP against seasonal rainfall, there was evidence of a nonlinear relationship, therefore we also included models with log transformations of current and previous year seasonal rainfall, and both current and previous season rainfall variables in the rainfall lag model. We used the model with the lowest AIC as our full model (Table S2).

How do Precipitation, N and P Affect ANPP of Winter Annuals and are These Effects Altered by Soil Properties and Shrub Cover?

To test our hypotheses regarding desert annual growth across time and in relation to nutrient addition and soil properties, we used a repeated measures mixed model using the R package 'nmle' (Pinheiro and others 2022) to examine main and first-order interactive effects for fixed factors: year, patch type (under or between shrubs), current growing season rainfall, previous season rainfall (to account for lag effects), N addition, P addition and total gravel cover. We also included site as a random factor to account for untested site-level differences and an auto-regressive error structure due to the repeated measurements across years. Using the 'stepAIC' function in the 'MASS' package, we performed stepwise model selection by AIC, with our full model as the upper limit and the intercept model as our lower limit, to determine the best fitting model (Ripley and others 2018). We ran the stepwise selection both forward and backward and selected the model with the lowest AIC value among the two outputs. We then used the R package 'piecewiseSEM' (Lefcheck 2016) to calculate the marginal (fixed effects only) and conditional (fixed and random effects) R^2 values of the best fitting model.

Does Proximity to an Urban Area Influence the Drivers of ANPP of Winter Annual Plants?

To test whether ANPP of desert annual plants differs by region (West, Urban core and East of the metro area), which vary in ambient rates of N deposition (Cook and others 2018) and potentially other factors, we used a linear mixed model using control and N addition plot data with growing season precipitation, previous season precipitation, year, region and patch type as fixed factors, and site as a random effect. We used an auto-regressive error structure to account for the repeated measurements across years. We then performed stepwise model selection using the R package 'piecewiseSEM' (Lefcheck 2016). As a post hoc test, we calculated estimated marginal means for simultaneous pairwise comparisons using a Tukey adjustment in the package 'emmeans' with the 'emmeans' function (Lenth and others 2018).

RESULTS

How do Precipitation, N and P Affect ANPP of Winter Annuals and are These Effects Altered by Soil Properties and Shrub Cover?

When comparing models with different rainfall variables using AIC, we found that the model that included both log-transformed current and previous year (lag effect) growing season rainfall variables produced the best fitting model to predict ANPP. The final model, selected with stepwise AIC, included the main effects of current season rainfall, previous year growing season rainfall, N, P, gravel, year and patch type (Table 2, Table S2). The significant first-order interaction terms were current season rainfall by year, current season rainfall by *P*, current season rainfall by patch type, year by patch type and N by patch type (Table 2, Table S2).

Not surprisingly, annual plant ANPP was strongly controlled by current year growing season rainfall (Table 2, Figure 2). In addition to current season rainfall, including previous year's growing season rainfall improved the model fit. Surprisingly, previous year growing season rainfall had a negative coefficient in the model (Table S3) suggesting it dampened the positive effect of current year seasonal rainfall on ANPP. The nonlinear relationship between growing season rainfall and annual plant ANPP showed a slightly diminishing effect on ANPP with increasing rainfall (Figure 3).

Soil surface characteristics and nutrient additions were important predictors of ANPP. N enrichment and P enrichment each had a significant and positive effect on annual plant ANPP, but the interaction between N and P was not significant (Table 2). In general, there was a stronger ANPP response to N enrichment than to P enrichment (Figure 2). ANPP was higher in P-fertilized plots than controls in high-rainfall years. The interaction effect of current season rainfall x N on ANPP was not significant ($P = 0.08$) (Table 2, Figure 2). Gravel cover was significantly and negatively related to ANPP, regardless of year, seasonal rainfall, soil patch type or nutrient addition (Table 2, Table S3).

Across all sites, the effect of shrub patches on ANPP depended on year (Table 2). Specifically, ANPP of winter annual plants was greater under shrubs compared to between shrubs in seasons when rainfall was higher than the long-term seasonal average of 96.6 mm (> 150 mm/season; 2008, 2010; Figure 4; Table 2). However, in low and average years (2009, 2013, 2015, 2016 and

Table 2. Linear Mixed Effects Model Exploring the Relationship Between Ecological Factors and ANPP

| Variable or interaction	df	*F*-value	*p*-value
(Intercept)	769	770.420	< 0.01*
log(Rainfall)	769	188.621	< 0.0001*
N	769	86.933	< 0.0001*
Gravel	769	32.371	< 0.0001*
Year	769	21.537	< 0.0001*
P	769	19.849	< 0.0001*
log(Prev. Rainfall)	769	4.209	0.041*
Patch type	769	3.937	0.048*
log(Rainfall) x Year	769	19.299	< 0.0001*
log(Rainfall) x P	769	8.079	< 0.01*
log(Rainfall) x Patch type	769	38.739	< 0.0001*
Year x Patch type	769	17.617	< 0.0001*
N x Patch type	769	16.554	< 0.0001*
log(Rainfall) x N	769	3.167	0.076
N x P	769	2.207	0.138

The precipitation metrics used in this model are log (current growing season rainfall) and log(previous year seasonal rainfall) based on AIC (see Table S2). Stars indicate a p-value less than 0.05. (Marginal $R^2 = 0.50$; Conditional $R^2 = 0.62$).

2017), annual plants biomass was greater in patches between shrubs.

Does Proximity to an Urban Area Influence the Drivers of ANPP of Winter Annual Plants?

In control (unfertilized) plots, the effect of region (West, Urban and East) on ANPP depended on current season rainfall and year (Table 3; Figs. 3 and 5). Also, there were significant current season rainfall by year and current season rainfall by region interactions (Table 3, Table S4). Rainfall and region were highly correlated with Eastern sites having consistently higher rainfall than Western and Urban sites (Figure 3). ANPP in Urban and Western sites declined over time, while there was no significant relationship between ANPP and year in the Eastern sites (Figure 5). In Western sites ANPP was significantly lower between shrub patches than under shrubs in most years (Figure 4). In all but two years (2009 and 2015), the ratio of average annual ANPP under compared to between shrubs was lower in the Urban and East sites compared to the West sites (Figure 4). Eastern and Urban sites did not have significantly different ANPP between and under shrubs (Figure 4, Table S4). Finally, responses to N addition differed regionally. Nitrogen addition increased ANPP in all three regions, but the increase in Eastern and
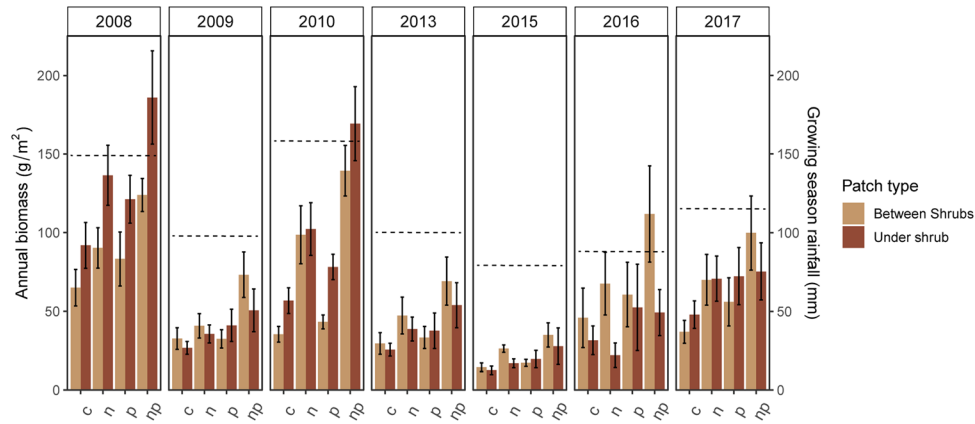
Figure 2. ANPP of annual plants across all sites, beneath and between shrubs. Patches beneath shrubs support higher rates of annual plant ANPP only when winter rainfall exceeded > 150 mm (2008, 2010). In years with lower winter rainfall, ANPP is highest in patches between shrubs. Error bars are ± 1 SE. Growing season rainfall averaged across all sites shown with dotted line. c = control, n = nitrogen addition, p = phosphorus addition, np = nitrogen plus phosphorus addition.

Western regions was greater than in the Urban core (Table 4).

DISCUSSION

Drivers of Annual Plant ANPP

Not surprisingly, water was the primary limiting resource for annual plant ANPP in this dryland system, as indicated by the significant relationship between total seasonal rainfall and ANPP. However, we found a diminishing positive effect of additional water on ANPP, as water limitation decreased. N and P were secondary limiting nutrients with a strong positive effect on ANPP in high-rainfall years. However, even in low-rainfall years, there was slightly higher ANPP in plots with nutrient addition, suggesting that these resources limit ANPP of winter annuals and that annual plants are able to readily utilize soil nutrients to support rapid growth with the addition of water. We observed higher ANPP in annual plants with the addition of N and P together, but no significant interaction between N and P, suggesting that the nutrients are co-limiting and have an additive effect on ANPP. Together, these results suggest that annual plant growth is driven by sequential limitation of water followed by co-limiting nutrients. Under sequential limitation of water followed by nutrients, future N deposition scenarios are unlikely to increase ANPP and seasonal nutrient retention without a simultaneous shift in rainfall

Table 3. Linear Mixed Effects Model Exploring the Relationship Between Ecological Factors and ANPP by Region (West, Urban and East) Within Unfertilized Control Plots

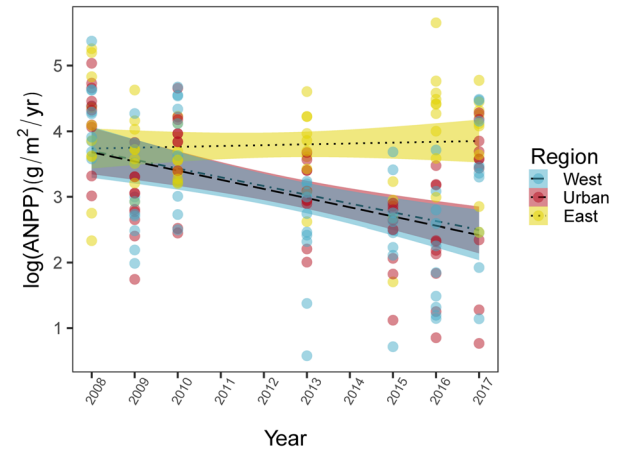| Variable or Interaction	df	*F*-value	*p*-Value
(Intercept)	176	590.202	< 0.0001*
log(Rainfall)	176	71.732	< 0.0001*
Year	176	8.190	< 0.01*
Region	12	0.101	0.905
Patch type	176	2.019	0.157
log(Prev. Rainfall)	176	0.7635	0.383
log(Rainfall) x Year	176	15.252	< 0.001*
log(Rainfall) x Region	176	13.940	< 0.0001*
log(Rainfall) x Patch type	176	2.260	0.135
Region x Patch type	176	6.294	< 0.01*

Asterisks indicate a p-value less than 0.05.

characteristics that increase soil water availability during the short winter/spring growing season.
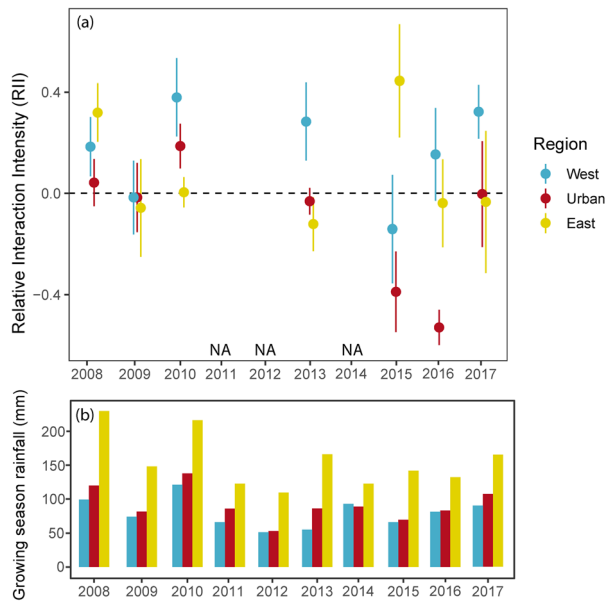
Dryland ecosystems are characterized by pulsed rainfall regimes (Noy-Meir 1973; Collins and others 2014) that vary in the size and frequency of rain events over the growing season. Theory (Knapp and others 2008) and short-term experiments (Heisler-White and others 2009; Thomey and others 2011) have shown that dryland ANPP responds positively to large, infrequent rain events more so than small, frequent events. Wet years generally result from the addition of a few large rain events in these systems (Knapp and others 2017a). Thus, interannual variability in desert annual ANPP could also be a function of not just total rainfall but
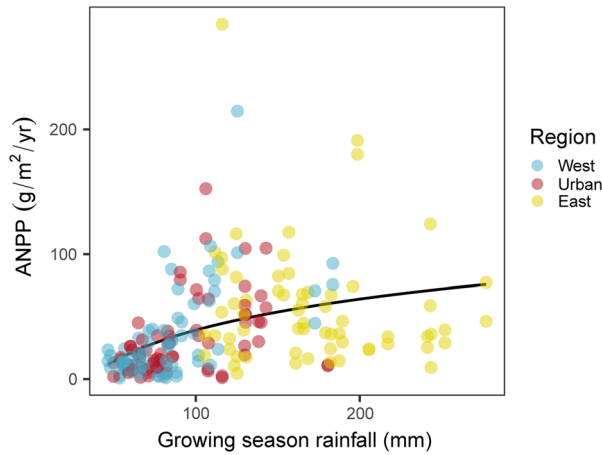
Figure 3. Relationship between winter rainfall and ANPP of Sonoran Desert annual plants across 8 years in unfertilized control plots, from 2006 to 2017. Colors represent regions. The line was fit using the formula (Annual Biomass + 1) ~ (Rainfall), which had an adjusted $R^2 = 0.234$, $P < 0.0001$.

Figure 4. A Relative interaction intensity of the mean annual plant ANPP in plots under shrubs versus between shrubs in non-fertilized control plots across all study sites as estimated by aboveground biomass. Symbol colors indicate the urban–rural gradient of protected desert sites to the West, East and within the city (Urban). Symbols above the dotted line have higher average biomass under shrubs and symbols below the dotted line have higher average biomass under shrubs. **B** Growing season precipitation across the urban gradient. X-axis is the winter–spring growing year (for example, 2008 = Winter 2007–Spring 2008 growing season). NA = no data. Error bars are ± 1 SE.

Figure 5. Relationship between year and log(ANPP) across years for each region. Asterisks (*) represent a significant linear relationship ($P < 0.05$). Shaded bands represent 95% confidence intervals.

differences in the size and frequency of rain events. However, results from a 14-year long rainfall manipulation experiment in Chihuahuan Desert grassland found no difference in summer ANPP under frequent-small vs infrequent-large rain events under ambient soil nutrient conditions (Brown 2022). However, large-infrequent rain events did result in the highest seasonal ANPP on plots fertilized with nitrogen. That is, rainfall pulses interacted with resource availability to drive growing season ANPP. This is consistent with the large response of desert annual ANPP in our system on fertilized plots during years of high seasonal rainfall.

Abiotic factors such as surface rocks and WHC were expected to be important determinants of patterns of winter annual ANPP through moderation of or interactions with limiting resources. Contrary to our hypothesis, gravel cover in our sites was negatively related to ANPP regardless of year, patch type or nutrient addition, and WHC was not retained in any of our statistical models. While surface rocks can reduce evaporation and increase moisture retention (Nobel and others 1992; Pérez 1998; Peters and others 2008), at high cover they can impede water infiltration and increase soil temperature (Poesen and others 1990; Martin 2008). Additionally, the negative relationship between gravel cover and ANPP could be due to the high amount of surface gravel cover (average 55%), leaving little bare soil where plants can take root. Cantón and others (2004) determined that rock cover between 20 and 50% can impede vegetative colonization because rocks are occupying

Table 4. Linear Mixed Effects Model Exploring the Relationship Between Nitrogen Addition and ANPP Within and Between Regions (West, Urban and East)

Comparison	Estimate	SE	df	t ratio	p value	Significant
West region control vs N addition	0.58	0.07	594	7.79	< **0.001**	*
Urban region control vs N addition	0.26	0.08	594	3.47	< **0.001**	*
East region control vs N addition	0.48	0.08	594	6.16	< **0.001**	*
Effect of N—West vs Urban	−0.31	0.11	594	−2.98	< **0.01**	*
Effect of N—Urban vs East	0.22	0.11	594	2.04	**0.04**	*
Effect of N—West vs East	−0.09	0.11	594	−0.85	0.40	

Asterisks indicate a p-Value less than 0.05.

colonizable space. High gravel cover, when packed tightly and accompanied by fine-textured soils, can also lead to desert pavements, which prevent water infiltration (Young and others 2004). In addition to the spatial impediment presented by gravel, the size classes of the rocks could differentially affect annual growth. In our study, gravel cover made up the majority of the rock cover, which is likely to have less of a 'nurse rock' effect than stones, cobbles or boulders as a perch for seed dispersers, or providers of shade, intercepted water and habitable microclimates (Nobel and others 1992; Nobel and Zutta 2007; Carlucci and others 2011).

The Importance of the Diminishing Effect of Rainfall and Lag Effects

Climate change models in the Southwestern United States predict high interannual precipitation variability, with both wet years characterized by extreme precipitation events and sequential dry years leading to extended periods of drought (Easterling and others 2000; Polade and others 2014; Cook and others 2015), events that are already evident in the recent climate record (Williams and others 2022). The sequential limitation of water and then nutrients suggests that extreme precipitation events will have less of an effect on annual plant ANPP than prolonged dry periods because above a rainfall threshold, growth will become limited by nutrient availability rather than water. Therefore, additional water above this threshold will not lead to an increase in ANPP. Our findings are consistent with recent syntheses of both empirical and modeled data that found that rare, extreme precipitation years can be negatively asymmetric in their effect on ANPP (for example, Jensen's inequality: Hsu and others 2012; Rudgers and others 2018),

meaning that the net negative impact of extreme dry years on plant growth (more dry days between rain events) will outweigh the net positive impact of extreme wet years when there is a higher frequency of large rain events (Knapp and others 2017b; Wilcox and others 2017). However, a recent meta-analysis (Gherardi and Sala 2019) and modeling study (Hou and others 2021) found that sites with low mean precipitation ($< \sim 300$ mm/year) had a positive ANPP response to increased precipitation variability. Furthermore, herbivory (Davis and others 2015) and other pollutants, such as ozone (Cook and others 2018), may confound this response, along with nutrient limitation, as indicated by our experimental results and the findings of Yahdjian and others (2011). Overall, interactions among regional drivers, such as atmospheric deposition, will interact with small-scale variables, such as gravel cover and presence of shrubs, to govern how desert annual ANPP will respond to increased precipitation variability in the future.

Negative and positive lag effects are among the proposed mechanisms driving nonlinear responses of ANPP to precipitation (Felton and others 2021). For example, in annual plant communities, high rates of seed production during a wet year could result in a positive effect on composition and production the following growing season. Consistent with this prediction, a synthesis of rainfall lag effects across systems found that dry years have a negative effect on ANPP in the following year while wet years have a positive effect in the following year (Gherardi and Sala 2019). Wheeler and others (2021) reported that species richness of Sonoran Desert winter annuals increased following a wet year, but there was little effect of current season water availability on species richness following a dry year. Our study period had more average or

below average rainfall seasons than above average years, which may account for the overall negative effect of previous year's rainfall in our model. The observed dampening effect of previous year's rainfall is consistent with observed mechanisms of lag effects. For example, dry years can limit the amount or composition of seeds in the seedbank (Hobbs and Mooney 1995; Dudney and others 2017; DeMalach and others 2021). The significant lag term in our model demonstrates how the predicted increase in dry years in the Southwestern United States (Archer and Predick 2008; Cook and others 2015; Williams and others 2022) can have reverberating effects on production and potentially community structure (Wheeler and others 2021) in this water-limited system. Further, the nonlinear relationship between ANPP and precipitation suggests that although wet years may have a positive lag effect, the magnitude of the effect size may be limited even with increased nutrient availability.

The Interaction Between Annual Plants and Shrubs Depends on Rainfall

Understanding the interplay between different mechanisms of plant–plant interaction is difficult in drylands because of complex relationships between resource availability (Holzapfel and Mahall 1999; Maestre and others 2005; O'Brien and others 2017), soil texture (Devitt and Smith 2002; Ryel and others 2004) and environmental stress (Soliveres and Maestre 2014; Butterfield and others 2016). Theory predicts that interactions between competition and facilitation structure plant communities in stressful environments (Bertness and Calloway 1994). In deserts, for example, competition will prevail under benign conditions, whereas facilitation increases as abiotic stress increases. Indeed, long-term patterns in desert annual ANPP were significantly influenced by the distribution of shrub patches in our study system. However, contrary to our expectation but similar to Tielbörger and Kadmon (2000), we found that winter annual ANPP was higher between shrubs than under shrub canopies in medium- to low-rainfall years. In years with more than about 150 mm of seasonal precipitation, the reverse pattern emerged and ANPP of winter annual plants was greater under shrub canopies than between them, but this pattern was driven primarily by sites in the dryer Western region of our study area.

Changes in species interactions with changes in precipitation are common in dryland ecosystems (McCluney and others 2012; Wheeler and others 2021). For desert annuals, it is likely that precipi-

tation interacts with resource availability to drive spatial patterns of ANPP. Soil water and nutrients are often higher under shrubs following rains compared to areas between shrubs (Schlesinger and others 1996; Turnbull and others 2010; Mudrak and others 2014). If annual precipitation declines with climate change as predicted (Cook and others 2015), years with high enough rainfall levels to switch the shrub–annual plant interactions from competitive to facilitative will become rarer and growing under shrubs will be less advantageous, despite higher levels of soil resources (Butterfield and Briggs 2009). Moreover, the homogenization of resource availability between and under shrubs via N deposition could reduce the advantage of growing under a shrub in high-rainfall years.

Variation at the Regional Scale

Observed differences in ANPP among regions were well explained by differences in the amount of seasonal rainfall. The lack of response to differing rainfall amounts across years in the eastern sites suggests that all years had sufficient rainfall to prevent water limitation, whereas western and urban sites were still water-limited. In addition to adequate water, the higher ANPP in eastern sites could be due to higher utilization of deposited N. During winter, wind carries emissions, pollutants and particulates from the urban core to eastern sites downwind where they are deposited as either wet or dry deposition (Lohse and others 2008; Cook and others 2018; Williamson and Ball 2023). Therefore, sites in the east are expected to be less water and nutrient limited than western and urban sites, explaining the higher average ANPP. Wind directionality, precipitation patterns and elevation are crucial components for interpreting future impacts of nutrient deposition on natural areas near urban centers and the ability of ephemeral species to take up and retain excess nutrients. If N deposition continues to increase in drylands as cities expand, the flush of winter annual species during wet years may help retain nitrogen in the system when nutrients might otherwise be lost to leaching and runoff.

CONCLUSIONS

Our long-term dataset allowed us to parse out complex trends that are important to determine how the spatial and temporal dynamics of annual primary production are affected by rainfall amount and nutrient availability. Winter ephemeral species

can utilize additional soil nitrogen due to their rapid growth in response to rainfall pulses and their short lifespans, under a range of total seasonal rainfall. Furthermore, our study highlights how often-overlooked small-scale abiotic factors, such as gravel cover, can influence annual plant growth through their interactions with patch type and seasonal precipitation. This understanding is important because winter annuals are a significant resource for higher trophic levels, including herbivores, pollinators and granivores (Lan and Zhang 2008; Sun and others 2015; Davis and others 2015; Manlick and others 2021; Maron and others 2022). Climate predictions for the Southwestern United States forecast a far more variable precipitation regime including prolonged droughts, which will likely result in less predictable ANPP (Archer and Predick 2008). This significant alteration in annual primary production may create negative feedbacks within carbon and nitrogen cycles by reducing nutrient storage and inputs in desert systems, contributing to climate model uncertainty (Ahlström and others 2015). Overall, our study demonstrated how small-scale biotic and soil physical characteristics interact with large-scale patterns in precipitation and resource availability to drive spatial and temporal variation in ANPP of winter annuals in the northern Sonoran Desert. Understanding the relative role of biotic and abiotic interactions and their impacts on the spatial distribution of ANPP will improve predictions of how desert annuals will respond to both climate change and urban encroachment in the future.

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DATA AVAILABILITY

Data for this study are available through the Environmental Data Initiative (Grimm and others 2022).

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