RESEARCH ARTICLE

Key Points:
- High soil-organic carbon and nutrient concentrations in playas result from runoff-mediated allochthonous inputs
- Overall, playas fix carbon at similar rates as uplands with high ANPP rates in average rain years counterbalanced by relatively low ANPP in flood years
- Differences in ANPP between playas and upland grasslands can be used to accurately estimate runoff

Supporting Information:
- Figure S1

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Playa-Wetlands Effects on Dryland Biogeochemistry: Space and Time Interactions

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Abstract Playas are ephemerally flooded wetlands found in hydrologically closed dryland catchments. Recent research showed how upland-catchment biophysical characteristics control the amount of organic carbon and nutrients that accumulates in playas from upland grasslands and shrublands. Here we further explored the role of allochthonous and autochthonous processes in fixing carbon and accruing soil nutrients in playas across a desert basin. We assessed whether playas contribute soil nutrient, organic-carbon stocks, and primary productivity rates in amounts disproportionately higher or lower than upland grasslands and shrublands. We found that playas had higher soil carbon and nutrient storage but no difference in mean annual primary production. Playas, on average, had similar primary productivity than upland systems, because they exhibited lower productivity during extremely wet years that offset the larger productivity during average or below average precipitation years. These results suggest that playas contain higher carbon and soil nutrient stocks because of runoff-mediated allochthonous inputs, rather than autochthonous sources, since long-term average productivity was similar to upland ecosystems. We also used the precipitation-aboveground net primary production (ANPP) relationships to accurately measure run-on in playas using differences between playa and upland grassland ANPP. The dependence of playa ANPP on surface-water inputs from upland catchments makes them susceptible to future changes in extreme precipitation events.

1. Introduction

Intermittently inundated wetlands are often geographically isolated and embedded in a matrix of upland grasslands, shrublands, or agroecosystems (Cohen et al., 2016). Wetlands such as prairie potholes, vernal pools, and playas are both ecologically and economically important systems in North America (Calhoun et al., 2017). Playas are ephemerally flooded, depositional landforms located in topographic low areas of hydrologically closed dryland catchments (Shaw & Thomas, 1997). The Basin and Range physiographic province contains most of the dryland ecosystems of North America (Havstad & Schlesinger, 2006) and is made up of many internally drained catchments (Wondzell et al., 1996). There are two common types of playas, and they are defined by their primary source of floodwater: (1) surface-water playas and (2) groundwater playas (Rosen, 1994). Surface-water playas are flooded via precipitation (PPT) and surface run-on from upland areas of their catchment and have the potential to be areas of groundwater recharge (Smith, 2003). In this study, we focused on the ecosystem functioning of surface-water playas and their biogeochemical role through space and time within a desert basin.

Connectivity of ecosystem patches is a key concept for understanding how nutrient- and water-redistribution processes control the ecological functioning of drylands (Bracken & Croke, 2007; Okin et al., 2015). Wind- and water-driven erosional/depositional processes, which occur at multiple scales, in drylands shape a mosaic of high and low vegetation cover patches (Aguiar & Sala, 1999; Schlesinger et al., 1990). These patches serve as sinks and sources of organic matter, soil particles, and plant propagules. The differential abiotic and biotic structure of these patches affects community structure and the functioning of ecosystems (Aguiar & Sala, 1994; Aguiar & Sala, 1997; Schlesinger et al., 1990). In closed-basin systems, surface water runoff from uplands can lead to gains for lowland ecosystems like playas and potentially influence biogeochemical processes such as primary productivity (McKenna & Sala, 2016).

Controls over aboveground net primary production (ANPP) in drylands differ in both space and time. There are strong relationships between dryland ANPP and mean annual precipitation (MAP) moving spatially from

dry to humid regions (Sala et al., 1988). There is a much weaker relationship between ANPP and annual precipitation through time when holding space constant (Sala et al., 2012). Although a number of studies have developed a firm understanding of dryland ANPP dynamics, the majority of research has been limited to coarse-scale regional studies focused on upland ecosystem types such as shrublands and grasslands. Little work has been done at a spatially finer scale nor has the work included much information about the functioning of lowland areas such as playas that are connected to upland ecosystems via surface-water run-on (Peters et al., 2012).

Playas account for less than 1% of the area of dryland basins and are known to store high concentrations of soil biogeochemical constituents (McKenna & Sala, 2016). Prairie potholes have also been identified as important areas for carbon storage in North America (Euliss et al., 2006). Although playas have been found to store soil organic carbon and nutrients in much higher concentrations than upland desert ecosystems (McKenna & Sala, 2016), it is uncertain if the amount of soil organic carbon and nutrients stored in playas relative to its area is significantly higher than in other ecosystem types. Similarly, it is unknown whether enhanced water and soil nutrient inputs in playas result in rates of ANPP that are disproportionately higher than their areal extent when compared to upland grasslands and shrublands (Peters et al., 2012). A new way to think about the disproportionate biogeochemical importance of an ecosystem in both space and time is through the control point framework (Bernhardt et al., 2017). Our aim is to better understand how playas may function, not only as important areas of soil organic carbon and nutrient storage but also as important areas of ANPP. To our knowledge, there have been no studies comparing basin-scale biogeochemical responses across ecosystems in the context of the Bernhardt et al. (2017) "control points" framework. Such a study could also help further elucidate connections between surface-water processes and ecosystem functioning through space and time in dryland basins.

We conducted this study to answer two specific questions about how playas fix carbon relative to upland ecosystems and whether or not autochthonous ANPP was the main driver of differences between playas and adjacent ecosystem types. Question 1: Do playas account for a disproportionately high rate of ANPP relative to their area within a desert basin? Moreover, how does this effect change through wet and dry years? To answer this question, we used 19 years of data collected by the Jornada Basin long-term ecological research (Jornada LTER) program. We considered disproportionality as any ecosystem type with average ANPP rates statistically higher than their relative area within the basin. We also analyzed the relationship between ANPP and annual precipitation in each ecosystem type. Question 2: How much of the difference in soil-organic carbon stock between upland ecosystems and playas is accounted for by allochthonous sedimentation, and how much is accounted for by autochthonous carbon fixation? To answer this question, we first calculated the surplus of soil-organic carbon in playas relative to upland ecosystems. We then estimated what fraction of the surplus could be accounted for by autochthonous playa ANPP.

2. Methods

2.1. Study Site

We conducted all of our research at the Jornada LTER. This research area is representative of a typical closed-basin system within the Basin and Range physiographic province. This 1,000-km^2 site is located in the northern Chihuahuan Desert, approximately 25 km northeast of Las Cruces, New Mexico, USA (+32.5 N, −106.8 W, elevation 1,188 m) (http://jornada.nmsu.edu/lter).The climate is arid to semiarid with a MAP of 237 mm and average temperature of 24 °C. Approximately 60% of this precipitation comes during summer monsoon season (July–September). Some of these monsoon thunderstorms are high intensity and can generate surface runoff (Schlesinger et al., 2000). The Jornada LTER is composed of two grassland and three shrubland ecosystem types. The grassland communities are upland grasslands dominated by black grama—*Bouteloua eriopoda* Torr. (Poac.)—and lowland playa grasslands dominated by tobosa grass—*Pleuraphis mutica* Buckley (Poac.)—and vine-mesquite grass—*Panicum obtusum* H.B.K. (Poac.). The upland shrubland communities are shrublands dominated by tarbush—*Flourensia cernua* DC (Aster.)—found on lower piedmont slopes, shrublands dominated by creosote bush—*Larrea tridentata* (DC) Cov. (Zygo.)—found on upper piedmont slopes and bajadas, and shrublands dominated by leguminous honey mesquite—*Prosopis glandulosa* Torr. var. *torreyana* (Fabac.)—found on the sandy basin floor (Peters, 2013).

2.2. Desert Soil Resources

In order to assess how playas store soil organic carbon and nutrients relative to the area they encompass within a desert basin, we collected new soil samples and measured total nitrogen and organic carbon concentrations from 30 of the 99 playas in the Jornada Basin (0–10 cm). We consulted the Jornada Basin landform map and available aerial imagery to choose 30 out of 99 potential playas that encompassed a broad range of sizes, catchment characteristics, and proximities to different geological features (Monger & Bestelmeyer, 2006; Peters & Gibbens, 2006). We collected nine soil samples from two transects across each playa. A mean value was determined for all 30 playas. Second, we collected values of soil total nitrogen, phosphorus, total cations (Na^+, Ca^{2+}, K^+, and Mg^+), and organic carbon concentration (g/m^2) from previously unpublished data from the Jornada LTER. Jornada personnel collected these data from three different sites for each of the four upland ecosystem types (black grama grasslands, tarbush shrublands, creosote bush shrublands, and mesquite shrublands) in year 2000. Site selection and sampling scheme can be found in Huenneke et al. (2002). They sampled 49 soil samples (0–10 cm) from each site. They calculated a mean value for organic carbon and soil nitrogen for each upland ecosystem type from the three sites. Similarly, we used values of soil phosphorus (from extractable phosphate) and total cation mass from the same data set that also included three different playa sites. In addition, we determined the area of all five ecosystem types using the Gibbens et al. (2005) ecosystem map for the Jornada basin. We then multiplied soil nutrient and organic carbon concentration (g/m^2) by the area (m^2) to determine the mean total mass of soil organic carbon and nutrient (Gg) for each ecosystem type.

Jornada personnel used the following methods in collecting the soil organic carbon and nutrient data from the Jornada LTER. Available phosphorus was analyzed as $NaHCO_3^-$ extractable (PO_4^-; g/g soil), soluble cations (K^+, Na^+, Ca^{+2}, and Mg^{+2}; g/g soil) were extracted using saturation extract methods, and organic carbon was determined using a modified Mebius method (Yeomans & Bremner, 1988). Total nitrogen was determined by Kjeldahl digestion techniques (Bremner & Mulvaney, 1996). We compared our total nitrogen results from dry combustion methods in playas to the Kjeldahl nitrogen estimations in upland soils. The difference between the two methods in desert soils is known to be less than 5% difference (Craft et al., 1991; Yeomans & Bremner, 1991). We also validated this in our system by comparing measurements from the same playas using both methods and found that the Kjeldahl method underestimated total nitrogen by a nonsignificant ($p = 0.49$) 2% (Table S1 in the supporting information).

We measured organic carbon (g/g soil) and total nitrogen (g/g soil) in soils from the 30 sample playas using an elemental combustion analysis (Sollins et al., 1999). Playa soil samples were first acid fumigated to eradicate inorganic carbon (Harris et al., 2001). We chose this method to capture the high variability between playas with a larger sample size ($n = 30$). Jornada personnel also measured available phosphorus as $NaHCO3^-$ extractable ($PO4^-$; g/g soil) and soluble cations (K^+, Na^+, Ca^{+2}, and Mg^{+2}; g/g soil) for playas. We estimated bulk density (g/m^3) for all five ecosystem types from 10 soil samples in each sample site. Soils in the upland sites were collected from the sites selected by Huenneke et al. (2002) to be representative of each ecosystem type. The soil weight and core volume were recorded using methods from Elliot et al. (1999) to convert soil organic carbon and nutrients (g/g soil) to areal measurements (g/m^2) for 0.1 m of soil.

2.3. Aboveground Net Primary Production

To estimate differences in ANPP among ecosystem types, we used Jornada LTER data from 1992 to 2010. We took the mean annual ANPP values ($g \cdot m^{-2} \cdot year^{-1}$) for each of the five ecosystem types from three replicate 50-m^2 sample sites. Experimental setup and sampling design are detailed in Huenneke et al. (2002). We determined ecosystem area for all five ecosystem types using the Gibbens et al. (2005) ecosystem map of Jornada. We then multiplied the mean ANPP ($g \cdot m^{-2} \cdot year^{-1}$) by the area ($m^2$) to determine the mean rate of ANPP (Mg/year) for each ecosystem type. To assess this effect through wet and dry years, we used annual precipitation data for each of the 19 years from one central weather station in the Jornada LTER for all ecosystem types.

We also used ANPP data to estimate the value of supplemental water inputs to playas via run-on (mm/year). We calculated run-on into playas as the difference in ANPP between playa and upland grasslands multiplied by the rain-use efficiency (RUE) of upland grasslands (RUE = ANPP/PPT; Le Houérou, 1984). We used RUE of upland grasslands because RUE is similar across plant communities in drylands (Huxman et al., 2004; Sala

et al., 2012). Since the Jornada LTER ecosystems are water limited (Reichmann et al., 2013), we assumed that water addition was the cause of any difference in ANPP between upland and playa grasslands.

2.4. Source of Playa Soil Organic Carbon

We determined the net soil organic carbon surplus in playas by subtracting the mean upland soil organic carbon mass per unit area from the mean soil organic carbon mass per unit area of playas. We assumed surplus organic carbon to be the resultant of allochthonous and/or autochthonous sources minus losses due to decomposition. Autochthonous mechanisms that may yield a surplus of carbon stocks are increased net primary production or decreased decomposition. We did not measure direct rates of decomposition. The allochthonous mechanism is sedimentation driven by run-on into playas from upland ecosystems. To disentangle the relative importance of allochthonous and autochthonous mechanisms, we first assessed whether mean playa ANPP was proportional to the relative playa area compared to upland ecosystems. Small changes or no changes in ANPP relative to other upland ecosystem types would suggest a dominance of the allochthonous pathway. Higher ANPP in playas relative to upland ecosystems would suggest a shared importance of allochthonous and autochthonous mechanisms. Since playas do not contain plant species most commonly associated with nitrogen fixing microbes, we assumed that major nitrogen inputs were also allochthonous (McKenna & Sala, 2016). For other soil nutrients without autochthonous sources, we assumed all soil nutrient surpluses in the playas were the result of allochthonous sedimentation.

To estimate minimum sedimentation rates, we first calculated a mean upland soil organic carbon and nutrient stock. We took the playa soil surplus values and divided them by the estimated age of the playa soil to determine a long-term net sedimentation rate for soil organic carbon and nutrients. This value is a minimum rate as it represents sedimentation minus any decomposition or leaching of soil organic matter and nutrients from playa soils. Playa soils of the Jornada basin are part of the Lank Tank geomorphic surface, which rests on sandy to gravelly fluvial deposits of the Camp Rice formation. The Camp Rice formation soils date back to 18,000 years B.P. at the deepest depths (Gile et al., 1981). Nearby Chihuahuan Desert wetland soils have been radiocarbon dated, and it was found that soils at 50 cm were ~700 years old (Minckley et al., 2009). Knowing this information, and assuming a constant sedimentation rate, we estimated that the top 10 cm of playa soil represented ~100 years.

2.5. Statistical Analysis

To assess how different ecosystem types functioned relative to their area within the Jornada basin, we measured the relative distribution of ANPP, soil organic carbon, and nutrient stocks across each of the five ecosystem types. Statistical differences between the expected and observed mean values were assessed using the one-sample t test. We tested the null hypothesis that the proportion of soil organic carbon, soil nutrients, and ANPP accounted for by each ecosystem type was similar to an expected value proportional to the relative area of each ecosystem type.

We also developed models for ANPP versus annual precipitation (1992–2010) in the five ecosystem types. We considered both nonlinear and linear models. We chose the best-fit models using Akaike information criterion. Using the surplus ANPP generated in playa grasslands compared to upland grasslands in years with 130- to 302-mm PPT, we estimated the amount of excess water—delivered via run-on—that would be necessary to generate that playa ANPP surplus. We chose the best-fit run-on versus precipitation model using Akaike information criterion. We performed all analyses and created all figures using R version 3.0.2 (R-Core-Team, 2016).

3. Results

3.1. Soil Resources

We found that playas stored soil organic carbon and nutrients in disproportionately high amounts relative to their area within the Jornada Basin (Figures 1a–1d). Our first figure shows log area versus log organic carbon and log soil nutrients that would yield a linear 1:1 line if ecosystem area and carbon/nutrient mass were proportional to their relative area within the Jornada Basin. Playa soil-organic carbon and nutrient masses were all significantly larger ($p < 0.05$) than the expected proportional values from the 1:1 line. On the contrary, we found no statistical differences ($p > 0.05$) between the observed mean values of soil organic carbon and the expected values for upland grassland, creosote, mesquite, and tarbush ecosystems (Figures 1a–1d).
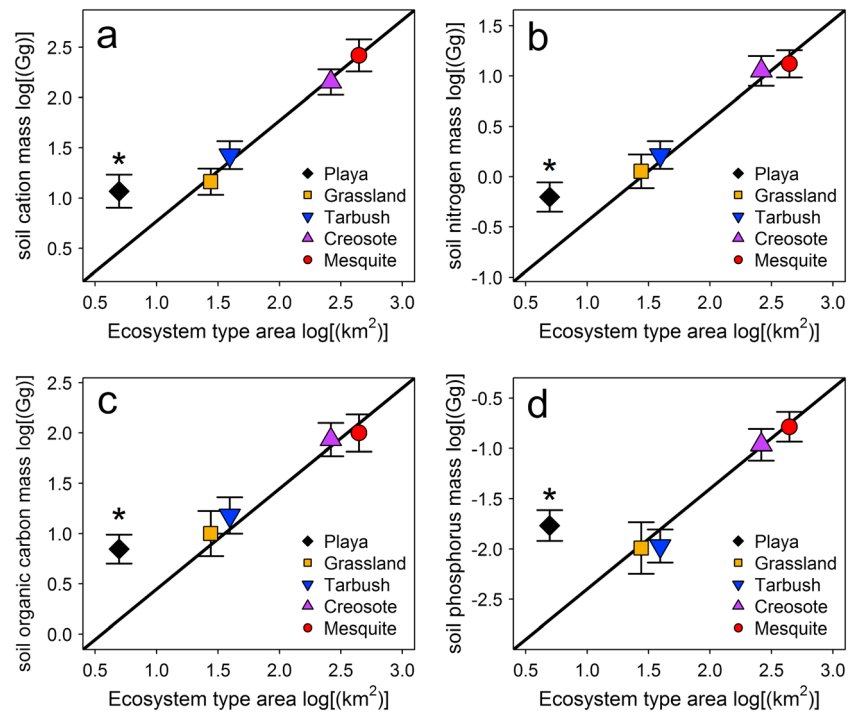
Figure 1. Log_{10} transformed relationships between soil nutrient and organic carbon mass (Gg) and ecosystem area (km^2) for the five Jornada basin ecosystem types. Relationships for different soil nutrients are displayed in four panels: (a) soil cation mass, (b) soil nitrogen, (c) soil organic carbon, and (d) soil phosphorous. Black 1:1 line represents log [soil nutrient and organic carbon] values that are proportional to log [ecosystem area] values. Red circles represent mesquite shrubland, blue point-up triangles represent creosote shrubland, purple point-down triangles represent tarbush shrubland, gold squares represent upland grassland, and black diamonds represent the playa grassland. Error bars represent standard error. The asterisk "*" represents significant difference ($p < 0.05$) from expected 1:1 line value.
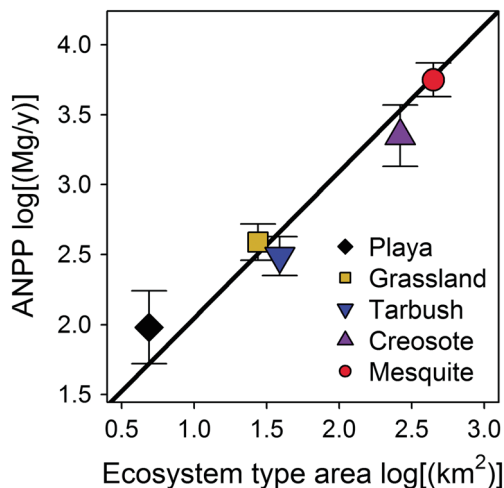

Figure 2. Log (10) transformed relationships between ANPP (Mg/year) and ecosystem area (km^2) for the five Jornada basin ecosystem types. Black 1:1 line represents log [ANPP] values that are proportional to log [ecosystem area] values. Red circles represent mesquite shrubland, blue point-up triangles represent creosote shrubland, purple point-down triangles represent tarbush shrubland, gold squares represent upland grassland, and black diamonds represent the playa grassland. Error bars represent standard error. ANPP = aboveground net primary production.

3.2. Aboveground Net Primary Production

Playa mean annual ANPP rates were proportional to their relative area within the Jornada Basin. In fact, all of the ecosystem types had rates of ANPP proportional to their area within the Jornada Basin (Figure 2). Our second figure shows log area versus log ANPP, which would yield a straight 1:1 if ecosystem area and ecosystem ANPP were proportional. There were no statistically significant differences ($p > 0.05$) between the observed mean and the expected value for each ecosystem type.

Addressing the second part of Question 2, which asked how playa ANPP responds to MAP, we found that playa ANPP increased with annual precipitation up to 300 mm/year. and then decreased (Figure 3). There were recorded multiday playa flooding events during the years with PPT higher than 300 mm (1992, 1997, 2005, 2006, and 2008). The strong concave second-order polynomial correlation between playa ANPP and precipitation illustrated this effect (Figure 3). All of the upland ecosystem types responded similarly to precipitation in a positive linear fashion (Figure 3). In dry years (<200 mm precipitation), playas were as productive as upland ecosystems. During moderately wet years (200- to 300-mm precipitation), playas were the most productive ecosystems in the Jornada Basin, and in wet years (>300-mm precipitation), playas were less productive than upland ecosystems (Figure 3).

We estimated surface-water run-on to playas during years where playa ANPP > upland ANPP and when there were no multiday standing
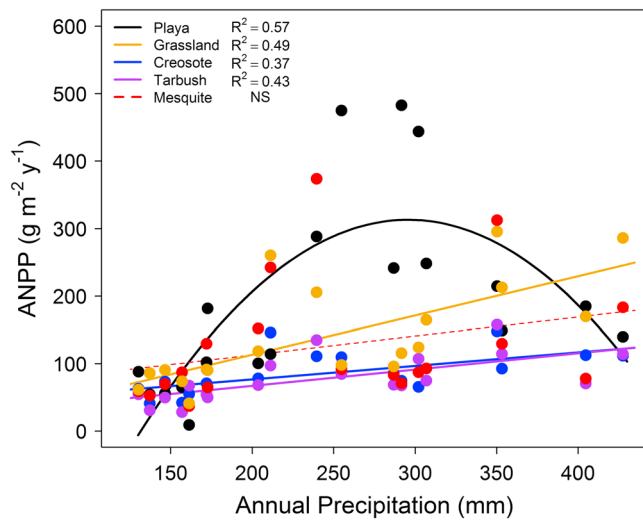
Figure 3. Relationships between mean ANPP $(g \cdot m^{-2} \cdot year^{-1})$ and annual precipitation (mm) for the five Jornada Basin ecosystem types from 1992 to 2010. Red circles represent mesquite ecosystems, blue circles represent creosote shrubland, purple circles represent tarbush shrubland, gold circles upland grassland, and black circles represent playa grassland. Red dashed line represents nonsignificant mesquite shrubland model, blue solid line represents the line of best fit for the creosote shrubland ($y = 36.60 + 0.2x$), purple solid line represents the line of best fit for the tarbush shrubland ($y = 18.90 + 0.24x$), gold solid line represents the line of best fit for the upland grassland ($y = 0.50 + 0.58x$), and the black line represents the line of best fit for the playa grassland ($y = -705.10 + 6.90x - 0.01x^2$). ANPP = aboveground net primary production.

water events in playas (Figure 4). We found that precipitation correlated with run-on in a positive and exponential fashion. The best-fit model for the relationship between calculated run-on and annual precipitation was run-on (mm) = $8.32 * e^{0.0135 \, (PPT \, (mm))}$ (Figure 4).

3.3. Source of Playa Soil Organic Carbon

Autochthonous ANPP appeared to be a small contributing factor to the disproportionate soil organic carbon accumulation in playas. The long-term ANPP in playas is similar to that on upland ecosystem types providing further evidence that allochthonous sedimentation was driving soil organic carbon accumulation in playas. This mechanism would also explain why we found disproportionately high accumulation of soil organic carbon as well as nitrogen, phosphorus, and cations (Figure 1). Using the difference between playa and upland soil organic carbon and nutrient concentrations, divided by the 100 years of soil development, we were able to estimate an annual deposition rate for soil organic carbon as well as soil nutrients (Table 1). We estimated average sedimentation rates of 18 $g \cdot m^{-2} \cdot year^{-1}$ total cation, 11 $g \cdot m^{-2} \cdot year^{-1}$ organic carbon, 0.9 $g \cdot m^{-2} \cdot year^{-1}$ nitrogen, and 0.03 $g \cdot m^{-2} \cdot year^{-1}$ phosphorus into playas.

4. Discussion

Our results address Question 1 showing that overall, long-term average ANPP rates in playas were not different from that of all other upland ecosystem types. Although we did not find enhanced ANPP in playas, we discovered more details about how precipitation and run-on controlled ANPP in playas. We also provided evidence that flooding negatively impacts playa ANPP, which had been hypothesized by Peters et al. (2012). Similar patterns of high precipitation years resulting in low primary productivity have been well documented in wetlands of the North American Prairie Pothole Region (van der Valk & Mushet, 2016). The peak in playa productivity in years where playas did not flood, but still received localized run-on, was most likely due to a reduction in the frequency of water limitation on ANPP (Reichmann et al., 2013).
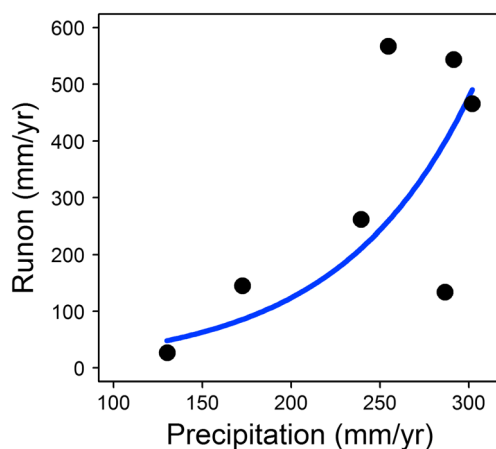

Figure 4. Relationship between annual precipitation and run-on for playa ecosystems. Black circles represent estimated run-on from comparing upland grassland ANPP to playa ANPP in nonflood precipitation years. Blue solid line represents line of best fit ($y = 8.32 * e^{0.0135(x)}$). ANPP = aboveground net primary production.

We also estimated that playas received twice as much water via run-on as compared to direct precipitation during moderately wet years (Figure 4). This method of calculating run-on using ANPP surplus allowed us to make conservative estimates of important hydrological processes using available data rather than needing extensive instrumentation across a number of catchments and years. We also compared these estimates of run-on with simulation modeling results from McKenna and Sala (2018). On average the ANPP-run-on estimates were within 10% of the simulation model estimates of run-on (Table S2). These findings further strengthen the validity of using differences in ANPP between playa and upland grasslands to calculate runoff. These methods could be further expanded by using biological responses to infer complex hydrological processes in other systems—such as the Great Plains playas and the Prairie Pothole Region—that consistently generate surface water flow from upland ecosystems to lowland ecosystems (Leibowitz, 2003). Prairie pothole wetland biological community assemblages are especially linked to hydrological and chemical processes (Mushet et al., 2018) that are associated with wet and dry climate periods (McKenna et al., 2017).

Although the long-term productivity of playas is the same as uplands, during 53% of the years, playas produce more biomass and forage

Table 1
Estimates of 100-year Sedimentation Rates of Soil Cations and Phosphorus From Upland Ecosystems to Playas

	Total cations (g/m^2)	Phosphorus (g/m^2)	Nitrogen (g/m^2)	Carbon (g/m^2)
Weighted upland average	586	0.38	39	325
Playa deposition surplus (100 years)	1,783	3.07	88	1,090
Annual deposition rate	18	0.03	0.9	11

than uplands (Figure 3). In terms of ANPP these results suggest that playas fit into the control point framework proposed by Bernhardt et al. (2017). Playas serve as "activated control points" that support high process rates under the right conditions. Playas play a key role in sustaining livestock and wildlife during these high-productivity years (Smith et al., 2011) since they produce high-quality forage that allows animals an alternative to the low-quality forage characteristic of mixed grassland/shrubland uplands (Eldridge et al., 2011). It has been estimated that over 50% of playas in the Southern High Plains of Texas are used for livestock grazing (Bolen et al., 1989). The downside is that, because of the disparity in forage quality, playas tend to be overgrazed if not managed separately from uplands (Haukos & Smith, 2003). Overgrazing may also increase soil compaction and rapidly downgrade the carbon and nutrient stocks of playas (Dlamini et al., 2016).

Our results also addressed Question 2 showing that playa soil biogeochemical stocks are highly dependent on allochthonous inputs and that the main mechanism for addition of soil organic carbon and nutrients to playas is surface-water run-on. This run-on contains plant litter, inorganic nutrients, and soil-organic carbon transported from upland ecosystems (Brazier et al., 2014). Run-on delivers the allochthonous organic carbon and nutrients to playas via sedimentation (Table 1). Rates of soil nutrients and organic carbon erosion have been measured at the plot scale in grasslands and shrublands of the Jornada Basin (Brazier et al., 2014; Schlesinger et al., 2000). Schlesinger et al. (2000) found that nitrogen losses via runoff averaged ~0.2 $g \cdot m^{-2} \cdot year^{-1}$, and Brazier et al. (2014) found that soil-organic carbon losses via runoff averaged ~2 $g \cdot m^{-2}$ over 10 runoff events. Our estimates of sedimentation in playas were also comparable and understandably lower than wetlands in more mesic systems. For example, in one case in southeastern United States, sedimentation rates were 56 $g \cdot m^{-2} \cdot year^{-1}$ for organic carbon, 4.7 $g \cdot m^{-2} \cdot year^{-1}$ for nitrogen, and 0.08 $g \cdot m^{-2} \cdot year^{-1}$ for phosphorus (Craft & Casey, 2000). Another study in the North American Prairie Pothole Region found phosphorus deposition rates similar to those that we calculated from 0.3 to 0.57 $g \cdot m^{-2} \cdot year^{-1}$ (Johnston, 1991). Evidence of sedimentation in playas is supported by McKenna and Sala (2016), who found the highest concentrations of soil organic carbon and nitrogen stored near the surface of the heavy clay playa soils. By using the soil as a window into the past, we are able to infer century to millennial processes. Once again, we achieved this without the need for long-term data from highly instrumented catchments.

Increased precipitation variability in the future could increase runoff and sedimentation to playas from uplands. Current climate predictions call for more extreme drought and flooding in southwestern United States (Janssen et al., 2014). These climate changes may alter how precipitation both transports organic carbon and nutrients and controls ANPP in dryland ecosystems. Recent studies showed that the expected increase in climate variability resulting from climate change might have a positive effect on runoff and groundwater recharge overshadowing the effects of reduced precipitation amount (McKenna & Sala, 2018). Our results suggest that playa ecosystems will be the most sensitive desert ecosystem type to changes in precipitation variability and amount. The reason behind this sensitivity is the exponential relationship between precipitation and run-on (Figure 4), which can influence the rate of soil-resource deposition in playas. Longer droughts could lead to longer periods with minimal runoff and allochthonous inputs to playas. Increases in extreme precipitation events will also cause future runoff events to be very large. These future runoff events will be important for continued allochthonous inputs to playas. The effect of future climate on playa stocks cannot be seen independently of the effects on upland ecosystems. Increased precipitation variability may increase runoff and short-term organic matter inputs into playas (McKenna & Sala, 2018) but may have a negative effect on the productivity and stocks of upland ecosystems (Gherardi & Sala, 2015). Given the disproportionately high amount of organic carbon and nutrients located in playas, the climate-

change-driven impacts of droughts and deluges may have large ecosystem consequences at the basin scale. Expanding our understanding of playa ecosystems is especially important since recent research has found that geographically isolated wetlands, such as playas, influence numerous ecosystem functions at large spatial scales (Cohen et al., 2016), and since the U.S. Environmental Protection Agency has emphasized the landscape-scale importance of protecting isolated temporary wetlands (Stokstad, 2014).

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