Desert Playa Wetlands:

Ecological Controls of their Functioning and Responses to Climate Change

by

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ABSTRACT

The Basin and Range province of southwestern USA are composed of different grassland and shrubland ecosystems. Particularly understudied ecosystems in this region are playas, which are ephemerally-flooded wetlands located in topographic low areas of hydrologically-closed dryland catchments. There is not much known about the ecological functioning of playas and the role of playas within desert basins. Even less is known about how global change drivers may affect playas in the future. The main objective of this thesis was to better understand the ecological functioning and the impact of climate change on desert playa wetlands. I collected new data, used existing long-term data, and used simulation modelling techniques to address this objective. I compared playa soils to upland soils and found that playas were hotspots of soil organic carbon and nutrient storage within a desert basin. I also used existing data to analyze the response of above-ground net primary productivity (ANPP) to annual precipitation in playas and upland ecosystems. I found that playa ANPP responded in a non-linear concave-down relationship with annual precipitation amount. Playa ANPP peaked in moderately wet years and declined in very wet years, which was most likely due to flooding; whereas, upland ANPP increased linearly with precipitation. I measured soil organic carbon and nitrogen concentrations in a representative subset of playas and measured the biophysical characteristics of the upland catchments associated with each playa. I found that both catchment geomorphology and vegetation cover were correlated to differences in soil organic carbon and nitrogen among playas. These results showed the importance external soil-inputs delivered via surface runon to playas. Finally, I empirically measured groundwater recharge beneath playas and combined these empirical data with modelling

data to forecast how playa groundwater recharge may change in the future. I concluded that playas contribute to groundwater recharge in desert aquifers, playa runon is a strong predictor of playa groundwater recharge, and climate change will have a net-positive impact on groundwater recharge beneath playas. Overall, my thesis research increased the understanding of the role of desert playas on the functioning of dryland ecosystems.

DEDICATION

To my amazing wife Natalie and to my parents Britta and Steve, who always encouraged me to go play in the dirt.

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CHAPTER 1 – INTRODUCTION

Theoretical Background

The Basin and Range physiographic province spans ~1,000,000 km^2 (Figure 1.) and contains a majority of the deserts of The United States of America (Havstad and Schlesinger 2006). The Basin and Range province is composed of alternating mountain ranges and valley floors. Many of the valleys are internally-drained basins that have no outflow point for surface water. These internally-drained areas are known as endorheic basins, and each endorheic basin is composed of different ecosystems located across topographic gradients on erosional and depositional landforms (Wondzell et al. 1996). Desert playas are ephemerally flooded, depositional landforms located in topographic low areas of endorheic basins (Shaw and Bryant 2011). Many endorheic basins are composed of multiple sub-catchments that each drain into a lowland playa. When flooded, playas become isolated refugia for aquatic species across many trophic levels (Wondzell et al. 1996, Cohen et al. 2016).

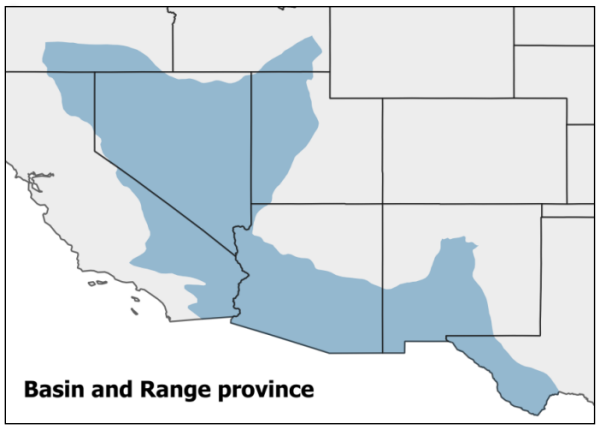


Figure 1. The Basin and Range physiographic province is highlighted in blue and makes up the majority of southwestern USA. The province consists of ~1M km^2 of land in parts of California, Oregon, Nevada, Idaho, Utah, Arizona, New Mexico, and Texas. Playa wetlands are a common feature throughout this region. Spatial data from USGS.

There are two common types of desert playas (1) discharge playas and (2) recharge playas (Rosen 1994). These playas are defined by their primary source of flood-water. Discharge playas are located close enough to the water table to be flooded by groundwater inputs. This proximity to the water table allows for frequent discharge of groundwater through evaporation. As a consequence of groundwater evaporation, salts accumulate in the soils of discharge playas and constrain biotic activity (Shaw and Bryant 2011). Recharge playas are located far enough above the water table that they do not evaporate groundwater. These playas become flooded via precipitation and surface runon from the upland areas of the closed catchment (Figure 2). Recharge playas contain clay-rich soils and support grassland communities that have highly variable net primary production (NPP) rates from year to year (Huenneke and Schlesinger 2006). These playas also have the potential to be areas of groundwater recharge (Smith 2003). In this thesis, I focused on the functioning of recharge playas and investigated how global-change drivers may alter playa functioning in the future.

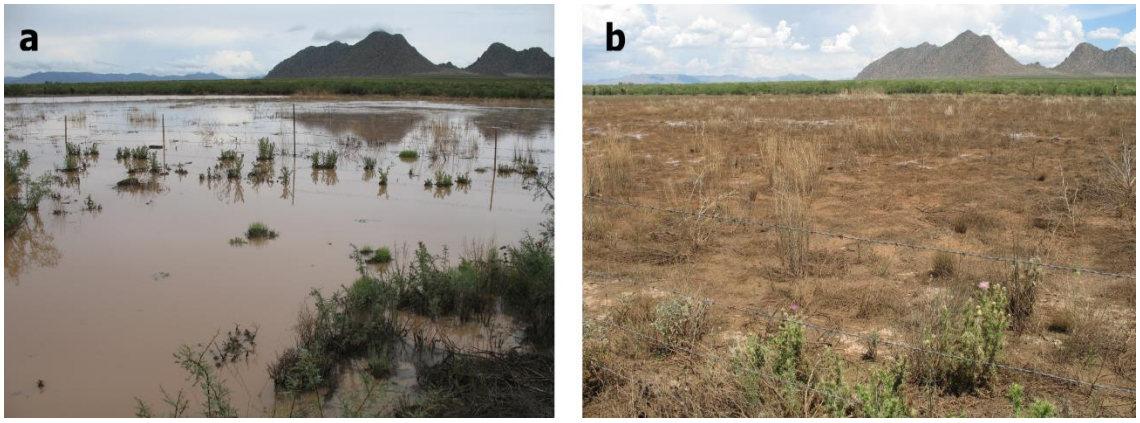


Figure 2. Side-by-side photographs of the same playa when flooded and after flood water has subsided. Photo in panel (a) was taken July 10, 2008 after a 50 mm rainfall event. Photo in panel (b) was taken July 18, 2008. Playa located at the New Mexico State University Chihuahuan Desert Rangeland Research Center with the Doña Ana Mountains in the background. Photographs taken by John Anderson.

Two important global change drivers that could impact playa ecosystem functioning are: (1) woody-plant encroachment and (2) climate change. Woody-plant encroachment in grassland ecosystems is a well-documented global phenomenon and is expected to continue in the future (Anadón et al. 2014). Woody plants are not encroaching into the dense clay soils of playas, but playas may be indirectly affected as woody-plant encroachment occurs in upland areas of catchments and alters runoff and sedimentation dynamics (Mcauliffe 1994). Increased atmospheric temperature is predicted to affect precipitation in the Basin and Range province in two ways: (1) lowered annual precipitation and (2) increased precipitation variability (Melillo et al. 2014). Higher temperatures will cause more large rainfall events that can cause runon, sedimentation, and potentially groundwater recharge in playas (Sun et al. 2007). Increased frequency of strong ENSO events will also result in more frequent extreme precipitation events (Cai et al. 2015). Increased inter-annual precipitation variability has been shown to increase soil-water availability in dryland ecosystems (Sala et al. 2015), but considerable uncertainty still exists about the overall impact of climate change on dryland groundwater recharge (Taylor et al. 2013a).

Research on desert playas has been spatially and temporally limited and many assumptions about how playas function are qualitative and anecdotal (Havstad et al. 2006). Most desert scientific studies regarding desert playas have ad dressed population and community ecology questions regarding vegetation and macroinvertebrates. These studies are limited, sometimes to only one playa, and only capture a small temporal snapshot of the ecosystem during brief flood periods (Loring et al. 1988, Mackay et al.

1990, Peters et al. 2012). The hypothesized interaction between upland ecosystems and playas through the horizontal transfer of water and nutrient-rich sediments and the functioning of playas during non-flood periods have not been tested in great detail (Okin et al. 2015). Playas also need to be studied to assess their role in facilitating focused groundwater recharge. Current models of desert aquifers in the Basin and Range province suggest that the only viable source of groundwater recharge is mountain-front recharge (Shomaker 1996, Kambhammettu 2010). Broad-based long-term data are needed to better understand playas, because playas occur across large geographic areas and playa-flood and sedimentation events are very stochastic (Loring et al. 1988, Wondzell et al. 1996). My aim is to fill this knowledge gap by quantitatively measuring different aspects of biogeochemistry among a representative subset of playas to better understand the ecological role of playas in desert basins.

Thesis Objective

The overall objective of my thesis was: to better understand the ecological functioning of and the impact of climate change on desert playa wetlands. I addressed this overall objective with three specific objectives. My first specific objective was: to understand how playa ecosystems function relative to upland desert ecosystems. My second specific objective was: to determine how catchment biophysical characteristics control ecological functioning of playas. My third specific objective was: to estimate the role of playas in groundwater recharge of dryland aquifers and to evaluate how playa groundwater recharge will change with climate change.

Approach

My approach to addressing the thesis objectives included combining multiple methodological techniques. I collected new data to measure a number of biogeochemical variables within playas and to characterize the biophysical structure of playa catchments. I used existing long-term data to explore comparisons between playas and upland ecosystems. Finally, I coupled empirical data with simulation modelling techniques to estimate recent-past playa hydrological functioning and how those dynamics may change in the future.

I conducted all of my thesis research at the Jornada Basin long-term ecological research (LTER) site. Jornada LTER is located in the northern Chihuahuan Desert in southeastern New Mexico, USA. Jornada LTER is situated in a typical closed-basin system of the Basin and Range physiographic province (Peters and Gibbens 2006). Jornada LTER contains two different grassland ecosystem types and three different shrubland ecosystem types. The grasslands are: upland Black Grama grasslands (*Bouteloua eriopoda*) and lowland playa grasslands dominated by Tobosa grass (*Pleuraphis mutica*) and Vine-mesquite grass (*Panicum obtusum*). The upland shrubland communities are: Tarbush (*Flourensia cernua*), Creosotebush (*Larrea tridentata*), and Honey Mesquite (*Prosopis glandulosa*) (Peters 2013).

I used soil, vegetation, and spatial data to address objective one. I conducted an analysis to identify if any of the five ecosystem types of the Jornada Basin were hotspots of soil organic carbon, nutrients, or aboveground net primary productivity (ANPP). I used empirical soil measurements and long-term averages of ANPP and compared them with the total area of each ecosystem type. Any ecosystem type with a concentration of soil

organic carbon and/or nutrients statistically higher than the amount proportional to their relative area within the basin was considered to be a hotspot.

I used remotely sensed catchment-biophysical data and field-collected playa soil data to address objective two. I analyzed how different catchment variables controlled soil organic carbon and nitrogen stocks among playas. I also compared the vertical distribution of soil organic carbon and nitrogen in playa and upland soils and investigated physical and biological mechanisms that controlled differences between the playas and uplands.

I empirically measured groundwater recharge beneath playas and combined those data with mathematical and statistical models to investigate how climate change will influence groundwater recharge beneath playas to address objective three.

Thesis Structure: Road Map

In Chapter 2, I addressed my first objective by analyzing the potential for playas to be hotspots of soil organic carbon, nutrients, and ANPP in a typical southwestern USA desert basin. I also used soil data to explore long-term allochthonous sedimentation rates in playa soils.

In Chapter 3, I addressed my second objective by analyzing how the catchment biophysical characteristics of upland areas control the organic carbon and nitrogen concentrations among playa soils. I also explored how ecological differences between uplands and playas controlled the vertical distribution of soil organic carbon and nitrogen

In Chapter 4, I addressed my third objective by measuring groundwater recharge beneath playas, analyzing the relationship between playa runon and playa recharge, and modelling the response of playa recharge to future climate scenarios.

In Chapter 5, I summarized and synthesized my findings into general conclusions for my thesis as a whole.

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CHAPTER 2- PLAYA WETLANDS AS HOT SPOTS OF DRYLAND BIOGEOCHEMISTRY

Abstract

I investigated the ecological role of playa wetlands within a dryland basin by sampling 30 playas in a Chihuahuan desert basin and using a 19-year aboveground net primary production (ANPP) data set of playas and the adjacent upland ecosystems. Playas store soil organic carbon and nutrients in quantities ~5 times higher than the expected value, which is proportional to the relative area of playas within the basin. The disproportionately high storage capacity of playas makes them hotspots of soil organic carbon and nutrient storage. Playas were not hotspots of ANPP because of the negative impact of flooding on playa ANPP in wet years > 300 mm. Playas received upland surface water inputs, which boosted ANPP in moderate precipitation years and decreased ANPP in high precipitation years when playas experienced prolonged flooding. These results provide evidence that playa soil hotspots are originated mostly by allochthonous sedimentation. I determined that runon increases exponentially as precipitation increases and estimated 100-year sedimentation rates of soil organic carbon and nutrients from upland soils into playas to be 30 g m^{-2} y^{-1}.

Introduction

The Basin and Range physiographic province contains most of the dryland ecosystems of North America (Havstad and Schlesinger 2006). This province contains many internally-drained catchments that are comprised of erosional and depositional landforms (Wondzell et al. 1996). Playas are ephemerally flooded, depositional landforms located in topographic low areas of hydrologically-closed dryland catchments (Shaw and Bryant 2011). There are two common types of playas and they are defined by their primary source of flood water: (1) surface-water playas and (2) groundwater playas (Rosen 1994). Surface-water playas are flooded via precipitation and surface run-on from upland areas of the catchment; because they are located far above the water table, they do not discharge groundwater. On the contrary, these playas have the potential to be areas of groundwater recharge (Smith 2003). Surface-water playas contain clay-rich soils and can support a variety of terrestrial and wetland plant species. Expanding my understanding of playa ecosystems is especially important now as the US Environmental Protection Agency (EPA) has recently emphasized the importance of protecting isolated temporary wetlands (Stokstad 2014). In this study, I focus on the role of surface-water playas in dryland basin ecosystem functioning, specifically their primary production and storage of soil organic carbon and nutrients.

Controls over above ground net primary production (ANPP) in drylands differ in both space and time. There are strong relationships between 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 space is held constant. A time lag in vegetation structure adjusting to changes in

precipitation from one year to the next explains the shallower slope of the temporal model relative to the spatial model (Sala et al. 2012). Although much is known about dryland ANPP dynamics, the majority of research has been limited to coarse-scale regional studies of upland ecosystem types such as shrublands and grasslands. Little work has been done on a spatially finer scale, nor has the work included much information about the functioning of lowland areas such as playas that receive water from precipitation, as well as run-on from upland ecosystems (Peters et al. 2012).

Connectivity of ecosystem patches is a key concept for understanding how soil- and water-redistribution processes control the ecological functioning of drylands (Okin et al. 2015). Wind- and water-driven erosional processes in drylands shape a mosaic of high and low vegetation cover ecosystem patches distributed across topographic gradients (Aguiar and Sala 1999). Differences in connectivity among ecosystem patches determine how soil organic carbon and nutrients are distributed and how they interact with vegetation (Moreno-de las Heras et al. 2012). Patches within shrubland ecosystem types are more connected than in grassland ecosystem types. In shrublands, large networks of plant interspaces allow for higher surface-water flow and greater mobility of soil organic carbon and nutrients (Schlesinger et al. 2000). In closed-basin systems, soil organic carbon and nutrient "losses" via water erosion from uplands can lead to gains for lowland ecosystems.

Although playas account for less than 1% of area in dryland basins, they have been qualitatively assumed to be important areas of biogeochemical activity due to allochthonous sediment and water inputs via run-on (Wondzell et al. 1996, Luo et al. 1999). The frequent allochthonous soil and water inputs received by playas and the fact

that they account for a relatively small area of dryland basins give them the potential to be "hotspots" of biogeochemical storage and cycling. Hotspots are areas where a constituent of interest is found in disproportionately high abundances relative to the surrounding area. In the case of conservation planning, biodiversity hotspots are areas containing disproportionately high numbers of species and rates of endemism. Biodiversity hotspots are also prioritized for protection, because they are highly threatened by habitat loss (Myers et al. 2000). This concept is also used in the field of biogeochemistry where hotspots are small areas of highly concentrated stocks or high reaction rates of a chemical constituent of interest, relative to the surrounding area (McClain et al. 2003). There have been no studies quantifying this hotspot effect of playas within a desert basin.

This paper addresses three questions about the potential role of playas as biogeochemical hotspots: (1) Do playas store a disproportionately large amount of soil organic carbon and nutrients relative to their area within a dryland basin? (2) Do playas account for a disproportionately high rate of ANPP relative to their area within a dryland basin? And, is this effect maintained through wet and dry years? (3) 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? In other words, question 3 addresses to what extent the origin of the hypothetical organic carbon hotspot results from allochthonous inputs into the playas from upland ecosystems or enhanced autochthonous ANPP from within the playas. Identifying hotspots of biogeochemical activity will allow us to prioritize areas in drylands that are of ecological importance and may be affected by climate change.

To answer question 1, I first estimated the total mass of soil organic carbon and nutrients within a dryland basin using data from five major ecosystem types. I then determined how the soil organic carbon and nutrients were distributed among those five major ecosystem types. Any ecosystem type that stored soil organic carbon and/or nutrients in statistically higher quantities than their relative area within the basin was considered to be a hotspot. To answer question 2, I used 19 years of data from the five major ecosystem types to determine an average ANPP rate within the same basin from question 1. I then determined how ANPP rates were distributed among those five ecosystem types. Any ecosystem type with ANPP in statistically higher rates than their relative area within the basin was considered to be a hotspot. To measure how this effect was maintained through wet and dry years, I used 19 years of ANPP data to determine how ANPP is controlled by annual precipitation in the five ecosystem types. Finally, I used my analyses from the first two questions to measure: (1) the surplus of soil organic carbon in playas compared to upland ecosystems and (2) the relative contribution of autochthonous playa ANPP to the surplus of soil organic carbon in playas. The remaining portion of organic carbon not accounted for by increased ANPP was assumed to be from allochthonous inputs.

Methods

Study site

I conducted my research at the Jornada basin long-term ecological research site (Jornada LTER). This research area is representative of a typical closed-basin system within the Basin and Range physiographic province. This 1000 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 1188 m) (http://jornada.nmsu.edu/lter). The climate is arid to semiarid with a mean annual precipitation of 247 mm and average temperature of 24 °C. Approximately 60% of this precipitation is delivered during summer monsoon season (July-September). These monsoon thunderstorms are high intensity and often generate surface runoff (Schlesinger et al. 2000). The Jornada LTER is composed of two grassland and three shrubland ecosystem types. The grassland ecosystems are: upland Black Grama grasslands (*Bouteloua eriopoda*) and lowland playa grasslands co-dominated by Tobosa grass (*Pleuraphis mutica)* and Vine-mesquite grass (*Panicum obtusum*). The shrubland ecosystems are: Tarbush (*Flourensia cernua*) on lower piedmont slopes, Creosote bush (*Larrea tridentata*) on upper piedmont slopes and bajadas, and Honey Mesquite (*Prosopis glandulosa*) on the sandy basin floor (Peters 2013).

Research Approach

To address my research questions, I combined newly collected field data with previously unpublished data from the Jornada LTER. To answer question 1, I estimated the mean soil organic carbon and nutrient concentration (Gg/km^2) from three sites within each of the five major ecosystem types of the Jornada LTER. I used Jornada LTER spatial ecosystem data to determine a total area (km^2) for each ecosystem type. To calculate the total soil organic carbon and nutrient mass (Gg) for each ecosystem type, I multiplied mean concentration by ecosystem type area. Any ecosystem type with a concentration of soil organic carbon and/or nutrients statistically higher than the amount proportional to their relative area within the basin was considered to be a hotspot. To answer question 2, I used 19 years of the Jornada LTER data to determine the mean

annual rate of ANPP (Mg km^{-2} y^{-1}) for each of the five major ecosystem types within the Jornada basin. I used Jornada LTER spatial ecosystem data to determine an area (km^2) for each ecosystem type. To calculate the total annual ANPP rate (Mg/y) for each ecosystem type, I multiplied the ANPP rate by ecosystem-type area. Any ecosystem type with a statistically higher rate of ANPP relative to their area within the basin was considered a hotspot. To measure how this effect was maintained through wet and dry years, I determined best fit models of ANPP vs. annual precipitation for all five ecosystem types using 19 years of ANPP and precipitation data. I also used the difference in upland grassland ANPP compared to playa ANPP in non-flood years to estimate run-on inputs into playas. To answer question 3, I first measured soil organic carbon and nutrient concentrations in playas and compared to the upland ecosystems. I used long-term ANPP data to determine the fraction of autochthonous carbon input. The remainder of the surplus was assumed to be derived from allochthonous sedimentation, and I calculated a long-term sedimentation rate.

Soil nutrient and organic carbon storage hotspots

First, I collected values of soil total nitrogen, phosphorus, total cations (Na^+, Ca^{2+}, K^+, Mg^+), and organic carbon concentration (g/m^2) from previously unpublished data from the Jornada LTER. These data were collected from three different sites for each of the four upland ecosystem types. 49 soil samples (0-10cm) were taken from each site. A mean value for organic carbon and soil nutrients was calculated for each upland ecosystem type from the three sites. Similarly, I used values of soil phosphorus (from extractable phosphate) and total cation mass from the same dataset from three different playa sites. In addition, I collected field measurements of soil total nitrogen and organic

carbon concentrations from 30 playas (0-10cm). Nine soil samples were taken from two transects across each playa. A mean value was determined for all 30 playas. I determined the area of all five ecosystem types using the Gibbens et al. (2005) ecosystem map for the Jornada basin. I 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.

The following methods were used 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}, Mg^{+2}) (g/g soil) were extracted using saturation extract methods, and total nitrogen was determined by Kjeldahl digestion techniques (Bremner and Mulvaney 1996). Organic carbon was determined using a modified Mebius method (Yeomans and Bremner 1988). Playa soil samples were first acid fumigated to eradicate inorganic carbon (Harris et al. 2001). Soil organic carbon and total nitrogen were measured using an elemental combustion analysis to determine organic carbon (g/g soil) and total nitrogen (g/g soil) (Sollins et al. 1999). Bulk density (g/m^3) was estimated for each ecosystem type from ten soil samples in each sample site. 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 0.1m of soil.

Aboveground net primary production hotspots

To estimate differences in ANPP among ecosystem types, I used Jornada LTER data from 1992-2010. The mean annual ANPP values ($g\ m^{-2}\ y^{-1}$) for each of the five ecosystem types was taken from three replicate 50-m^2 sample sites. Experimental setup

and sampling design are detailed in Huenneke et al. (2002b). I determined ecosystem area for all five ecosystem types using the Gibbens et al. (2005) ecosystem map of Jornada. I then multiplied the mean ANPP (g m^{-2} y^{-1}) by the area (m^2) to determine the mean rate of ANPP (Mg/y) for each ecosystem type. To assess how this effect was maintained through wet and dry years, I used annual precipitation data for each of the 19 years from one central weather station in the Jornada LTER for all ecosystem types. I also used the relationship between playa and upland grassland ANPP to estimate playa run-on. Since the Jornada LTER ecosystems are water limited, I assumed any difference in ANPP between upland grasslands and playa grasslands would be accounted for by a water addition. For years with no flooding in the playas, I was able to estimate run-on (mm/yr.) into playas.

Playa net soil organic carbon surplus source

I determined the net soil organic carbon surplus in playas by subtracting the mean upland soil organic carbon mass from the mean soil organic carbon mass of playas. I assumed surplus organic carbon to be the resultant of allochthonous and/or autochthonous sources and losses due to decomposition. Autochthonous mechanisms that may yield a surplus of carbon stocks are increased net primary production or decreased decomposition. The allochthonous mechanism is sedimentation driven by run-on into playas from upland ecosystems. To disentangle the relative importance of these two mechanisms, I 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. For other soil nutrients without autochthonous sources, I assumed all soil nutrient surpluses in the playas were the result of allochthonous sedimentation.

Statistical analysis

To determine if any ecosystem type in the Jornada basin was a biogeochemical hotspot, I measured the relative distribution of ANPP, soil organic carbon and nutrient stocks across each of the five ecosystem types. To assess statistical differences between the expected and observed mean values, I used the one-sample t-test. I tested the null hypothesis that the proportion of soil organic carbon, soil nutrients, and ANPP accounted for by each ecosystem type was not different from an expected value proportional to the relative area of each ecosystem type. Any ecosystem type with a mean organic carbon mass, nutrient mass, or ANPP rate statistically higher than the expected value rejects the null hypothesis ($p<0.05$) and is considered to be a hotspot.

I also determined models for ANPP vs. annual precipitation (1992-2010) in the five ecosystem types. Non-linear and linear models were compared. I chose the best-fit models using Akaike information criterion (AIC). Using the surplus ANPP generated in playa grasslands compared to upland grasslands in years with 130-302 mm PPT, I estimated the amount of excess water it would take to generate that playa ANPP surplus. This excess water was assumed to be delivered to the playas in the form of surface run-on. I chose the best-fit run-on versus precipitation model using Akaike information criterion (AIC) and extrapolated the relationship to estimate run-on for years of PPT above 302 mm and within the observed range of precipitation.

To estimate sedimentation rates, I first calculated a mean upland soil organic carbon and nutrient stock. I 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. 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, I estimated that my 0-10 cm data represented 100-year sedimentation rates. I performed all analyses and created all figures using R version 3.0.2 (R Core Team 2013).

Results

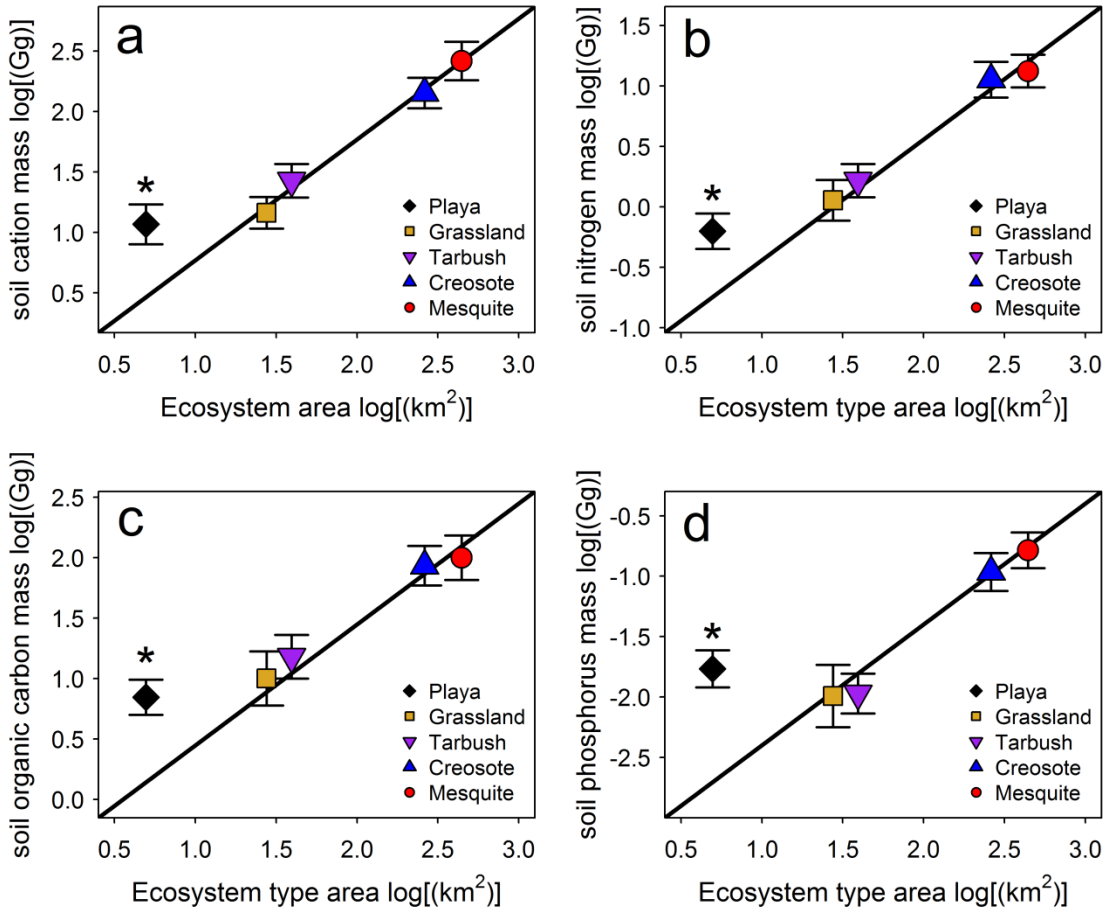


Figure 1. Log_{10} transformed relationships between soil nutrient and organic carbon mass (Gg) and ecosystem area (km^2) for the five Jornada basin ecosystem types. Black 1:1 line represents log [soil nutrient and organic carbon] values that are proportional to log [ecosystem area] values. Red circles 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. * represents signficant difference ($p < 0.05$) from expected 1:1 line value.

Soil organic carbon and nutrient storage hotspots

I found playas to be hotspots of biogeochemical soil organic carbon and nutrients, because the mean values of soil cations, organic carbon, nitrogen, and phosphorus were disproportionately high relative to their area (Figure 1a-1d). I plotted log area vs. log

organic carbon and log soil nutrients, which would yield a linear 1:1 line if ecosystem area and ecosystem mass were proportional and no hotspots were present. 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, I 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 (Figure 1a-1d).

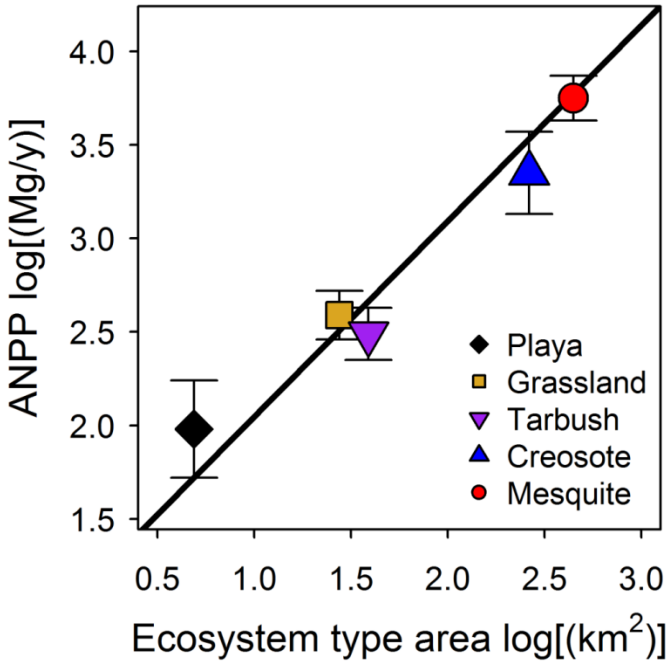


Figure 2. Log(10) transformed relationships between ANPP (Mg/y) and ecosystem area (km^2) for the five Jornada basin ecosystem types. Black 1:1 line represents log [ANPP] values that are proportional to log [ecosystem area] values. Red circles represent mesquite shrubland, blue point-up triangles represent 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.

Aboveground net primary production hotspots

I found that playas were not hotspots of ANPP because mean rates of ANPP were distributed across the ecosystem types of the Jornada basin proportionately to their area (Figure 2). I plotted log area vs. log ANPP, which would yield a straight 1:1 if ecosystem area and ecosystem ANPP were proportional and no hotspots were present. There were no statistically significant differences ($p > 0.05$) between the observed mean and the expected value for each ecosystem type. This relationship indicates that there are no hotspots of ANPP among the ecosystem types in the Jornada basin.

Addressing the second half of question 2, I found that playa ANPP decreases as precipitation increases beyond 302 mm of annual precipitation. This effect caused there to be a concave-down second-order polynomial relationship between playa ANPP and precipitation (Figure 3). I also found that all of the upland ecosystem types respond similarly to precipitation in a positive linear fashion (Figure 3). In dry years (< 200 mm precipitation), playas were similarly as productive as upland ecosystems. During moderately wet years (200-300 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).

I calculated run-on for each year of the 19-year period by first measuring the difference between playa grassland ANPP and upland grassland ANPP and then multiplying this difference by the mean precipitation use efficiency, which is the slope of the upland grassland models in Figure 3. I fit a model for the relationship between calculated run-on and annual precipitation; run-on (mm) = $8.32*e^{0.0135\ (PPT\ (mm))}$. I

extrapolated that model to the highest precipitation recorded (427 mm) during the 19-year period to estimate run-on above 302 mm of precipitation (Figure 4).

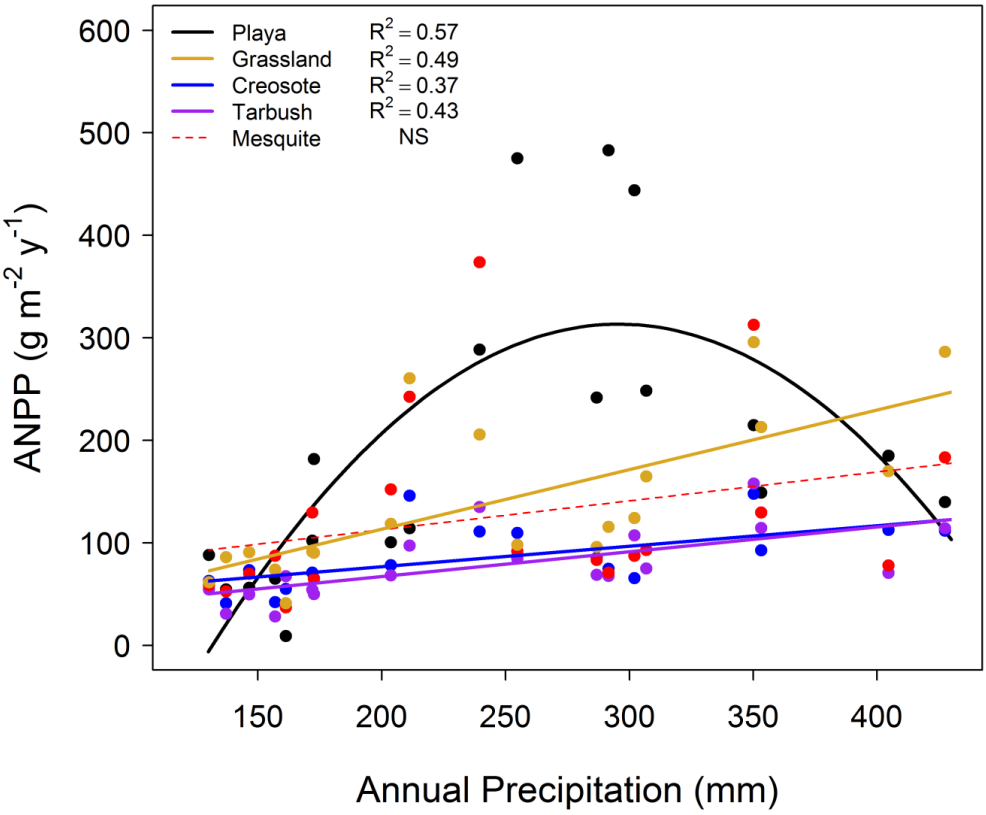


Figure 3. Relationships between mean ANPP (g m^{-2} y^{-1}) and annual precipitation (mm) for the five Jornada basin ecosystem types from 1992-2010. Red circles represent mesquite ecosystems, blue circles represent creosote shrubland, purple circles represent tarbush shrubland, gold circles upland grassland, and black circles represent playa grassland. Red dashed line represents non-significant 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).

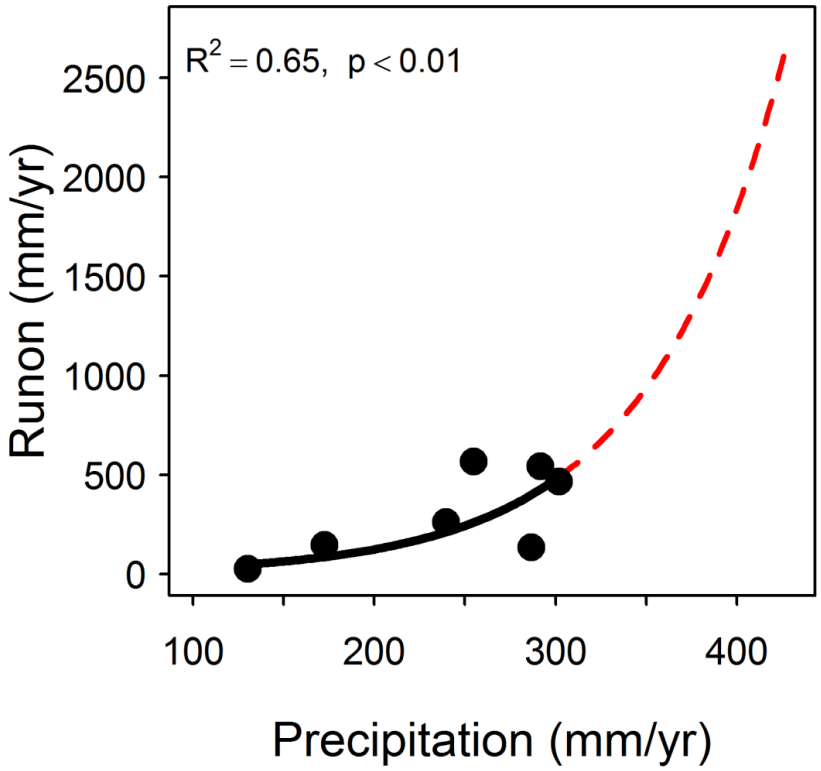


Figure 4. Relationship between annual precipitation and run-on for playa ecosystems. Black circles represent estimated run-on from comparing upland grassland ANPP to playa ANPP in non-flood precipitation years. Black solid line represents line-of-best-fit ($y = 8.32*e^{0.0135(x)}$). Red dashed line represents line-of-best-fit extrapolated to include all precipitation years.

Playa net soil organic carbon surplus source

Mean ANPP (expressed in g m^{-2} yr^{-1}) in playas was not significantly greater than the expected value of ANPP for playas (Figure 2) because the higher ANPP observed in years with lower precipitation was offset by the lower ANPP in high precipitation years (Figure 3). These findings indicate that autochthonous ANPP may be a negligible source of net soil organic carbon surplus in playas and net soil organic carbon surplus is dominated by allochthonous sedimentation. Using the difference between playa and upland soil organic carbon and nutrient concentrations, divided by the 100 years of soil development, I was able to estimate an annual deposition rate for soil organic carbon as well as soil nutrients (Table 1). I estimated average sedimentation rates of 18 g m^{-2} y^{-1}

total cation, 11 g m^{-2} y^{-1} organic carbon, 0.9 g m^{-2} y^{-1} nitrogen, and 0.03 g m^{-2} y^{-1} phosphorus into playas. Playa sedimentation rates are understandably lower than other studies conducted in depressional wetland in a more mesic climate region of the US. That study found sedimentation rates of organic carbon 56 g m^{-2} y^{-1}, nitrogen 4.7 g m^{-2} y^{-1}, and phosphorus 0.08 g m^{-2} y^{-1} (Craft and Casey 2000). Another study in the semi-arid prairie pothole region found phosphorus deposition rates similar to those I calculated from 0.3-0.57 g m^{-2} y^{-1} (Johnston 1991).

	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 yr.)	1783	3.07	88	1090
Annual deposition rate	18	0.03	0.9	11

Table 1. Estimates of 100-year sedimentation rates of soil cations and phosphorus from upland ecosystems to playas

Discussion

My results provide strong evidence that playas are hotspots of soil nutrient and organic carbon stocks in dryland basins. These high concentrations of soil organic carbon and nutrients, along with increased water availability, make playas important ecosystems by supporting plant and animal species that play an important role in the development of food-web complexity across dryland basins (Mackay et al. 1990).

Although I did not find playas to be on average hotspots of ANPP, I discovered more details about how precipitation and run-on control ANPP in playas. I also provided evidence supporting past predictions that flooding negatively impacts playa ANPP (Peters et al. 2012). Playas showed a distinct concave-down polynomial pattern of ANPP vs. annual precipitation with an inflection point ~300 mm annual precipitation (Figure 3). This inflection point matches the qualitative Jornada LTER flood record, where the five years of extensive playa flooding all received over 300 mm of rain. This relationship differs from upland grasslands, where ANPP shows a positive linear correlation with annual precipitation (Figure 3). In those high precipitation years, upland grasslands did not experience recorded flooding.

In years where precipitation was ~120-180 mm, upland grasslands and playa grasslands had similar ANPP. Also, playa grasslands had much higher ANPP than upland grasslands in years with ~180-300 mm precipitation (Figure 3). These different ANPP vs. annual precipitation models between the two grassland ecosystem types are most likely due to playas receiving run-on that released the water limitation on ANPP (Reichmann et al. 2013). I used the grassland ANPP vs. PPT model (Figure 3) to estimate how much extra water would be needed to produce the excess ANPP found in playas. This method of calculating run-on using ANPP surplus allows us to estimate conservative estimates of important hydrological processes using available data rather than needing extensive instrumentation across a number of catchments.

My results suggested that soil organic carbon and nutrients are mainly deposited into playas from run-on generated during the summer monsoon season. This run-on contains plant litter, inorganic nutrients, and soil organic carbon that have been

transported from upland ecosystems (Brazier et al. 2014). Allochthonous soil organic carbon and nutrients are deposited as sediment and stored in the heavy clay soils of the lowland playas. By using the soil as a window into the past, I was able to infer century to millennial processes. Once again, this was achieved without the need for long-term data from highly instrumented catchments.

Increased precipitation variability is predicted to cause more extreme drought and flooding in southwestern US (Janssen et al. 2014). Temperatures are also expected to rise in southwestern US (Seager et al. 2007). These climate changes may alter how precipitation both transports soil organic carbon and nutrients and controls ANPP in dryland ecosystems. My results suggest that playa ecosystems will be the most sensitive ecosystem type to reductions in precipitation because of the non-linear relationship between run-on and annual precipitation (Figure 4). Given the disproportionate amount of soil carbon and nutrients located in playas, climate-change driven droughts may have large ecosystem consequences at the basin scale.

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CHAPTER 3- BIOPHYSICAL CONTROLS OVER CONCENTRATION AND DEPTH DISTRIBUTION OF SOIL ORGANIC CARBON AND NITROGEN IN DESERT PLAYAS

Abstract

Playa wetlands are hotspots of soil organic carbon and nutrient storage in drylands. Differences in organic carbon and nitrogen among playas were controlled primarily by catchment vegetation cover and secondarily by catchment area, slope, and soil texture. The effect of higher organic matter concentration associated with high catchment vegetation cover overshadowed the potential effect of reduced runon. Carbon and nitrogen profiles were significantly shallower in playas than uplands because of the dominant effect of sedimentation and of shallow-rooted plants. Uplands had a deeper C and N profile because organic matter was predominantly autochthonous, and they were dominated by deep-rooted vegetation. In playas, C/N ratios remained constant with depth, but in uplands, C/N ratios increased as a consequence of the distribution of soil texture with depth. In uplands, clay concentration increased with depth, whereas in playas, clay concentration did not change with depth highlighting the important role of sedimentation in these ecosystems. The dependence of playas on allochthonous inputs makes them sensitive to changes in upland vegetation due to drought and/or overgrazing. Upland vegetation response to climate change in the future would have a disproportional effect on playa soil organic carbon and nitrogen stocks relative to its effect on upland C and N stocks.

Introduction

Playas are ephemerally flooded wetlands located in the topographic low areas of hydrologically closed dryland catchments (Thomas 2011). Playas are unique, because they are geographically isolated wetlands and, when flooded, they are ecologically important aquatic ecosystems surrounded by upland terrestrial ecosystems (Wondzell et al. 1996, Cohen et al. 2016). Playas can be categorized into two types determined by the source of their flood water: (1) groundwater playas and (2) surface-water playas (Rosen 1994). Surface-water playas are flooded via precipitation and surface-runon from the upland areas of their catchments. Surface-water playas contain clay-rich soils that are low in salinity and can support a variety of wetland species across many trophic levels (Smith 2003). These playas also have the potential to be areas of groundwater recharge due to frequent flooding and an absence of a water-restrictive petrocalcic soil layer – found in upland areas of most drylands – beneath them (Scanlon et al. 2012). In this paper, I focus solely on the functioning of surface-water playas. Playas are a common feature of internally draining endorheic systems of the Basin and Range physiographic province of North America, which makes up most of southwestern United States (Havstad et al. 2006).

Playas are biogeochemical hotspots that store soil organic carbon and nutrients in quantities ~5 times higher than concentrations that would be proportional to their relative area in a basin (McKenna and Sala 2016b). Playa soil organic carbon can accumulate through two different pathways: (1) autochthonous carbon that is fixed through aboveground net primary productivity (ANPP) within the playa, and (2) allochthonous carbon that is fixed outside the playa and delivered via surface-water runon. Although

playas are hotspots of soil carbon storage, playas are not hotspots of autochthonous carbon fixation rates (McKenna and Sala 2016b). During years of high precipitation, when upland ecosystems are most productive, playas become flooded and ANPP is very low. The long-term ANPP of playas is not different from uplands, but their soil organic carbon stock is much higher suggesting that the soil organic carbon and nutrient hotspot effect in playas is driven by allochthonous sediment inputs from upland ecosystems (McKenna and Sala 2016b). I conducted this study to answer three questions about the differences in soil organic carbon and nitrogen among playas and compared to upland ecosystems. I used the answers to these questions to evaluate how playas may change in the future.

Question 1: how do catchment biophysical variables influence soil organic carbon and nitrogen concentrations among playas? When climate variables are held constant, the amount of allochthonous inputs of soil organic carbon and nutrients delivered from upland ecosystems to playas should be controlled by two processes: (1) amount of surface-water runon a playa receives and (2) concentration of organic carbon and nutrients in the runon (Ludwig et al. 2005). There are a number of both geomorphic and biological variables that may be controlling these sedimentation rates. Larger and steeper catchments generate more runon and erode more sediment than smaller and gradual sloping catchments (Young et al. 2009). Catchment soil texture controls the infiltration rate of precipitation and subsequently the rate of runon generation. Sandier soils allow for more infiltration and less playa runon generation (Vivoni et al. 2006). The amount of vegetation covering a catchment may control allochthonous sediment production in two opposite ways: (1) Increased vegetation increases the amount of

organic matter produced in a catchment, which may be incorporated into allochthonous sediment that is delivered to playas (Brazier et al. 2013). (2) Increased vegetation cover also can negatively decrease surface-runoff generation by decreasing the physical impact of rainfall on soil erosion and by decreasing preferential flow paths for surface-runoff generation (Schlesinger et al. 2000). It is uncertain whether the biological or the physical processes associated with vegetation cover are most important in controlling allochthonous sedimentation of organic carbon and nutrients into playas.

Question 2: how is soil organic carbon and nitrogen distributed through depth in playas as compared to upland ecosystems? The source of organic matter, whether allochthonous or autochthonous, may be responsible for controlling the distribution of soil organic carbon and nitrogen through depth in upland and playa ecosystems. In upland ecosystems, autochthonous organic matter is deposited via deeply-rooted plants and there are smaller allochthonous organic carbon and nitrogen inputs than in lowland playas (Schlesinger et al. 1996). These deeply-rooted plants in upland ecosystems deposit organic carbon and nitrogen at depths well below one meter (Gibbens and Lenz 2001). Autochthonous soil inputs from deeply rooted plants may cause a large fraction of organic carbon and nitrogen to be stored in deeper layers. On the contrary, playas receive large allochthonous inputs from surface-runon and have shallow-rooted vegetation communities. The combination of allochthonous inputs and shallow-rooted plants may concentrate organic carbon and nitrogen at the surface of playa soils.

Question 3: how does the ratio of soil organic carbon to nitrogen change through depth in playas as compared to upland ecosystems? Soil C/N ratio is dependent on the rate at which organic carbon and nitrogen leave the soil and how these

processes change with depth. Soil organic carbon is lost via microbial respiration leaving behind soil nitrogen (Schlesinger and Andrews 2000). Nitrogen is mainly lost under anaerobic conditions via denitrification. Therefore, under aerobic conditions, I expected C/N ratios to decrease through time. Soil texture is also an important variable in controlling decomposition rates and the rate of soil carbon to nitrogen ratio change (Hook and Burke 2000). Organic matter decomposes slower in heavy clay soils compared to more coarse upland soils (Mun and Whitford 1998). Therefore, if clay content were to decrease with depth, I expected the soil C/N ratio to change in the same direction.

To answer question 1 about how the biophysical characteristics of a catchment control soil organic carbon and nitrogen concentrations in an adjacent playa, I first measured organic carbon and nitrogen in playa soils across a dryland basin. Then, I used remotely sensed data to measure elevation, soil, and vegetation characteristics of each playa catchment. To answer question 2 about how soil organic carbon and nitrogen concentrations change through depth, I compared my playa soil measurements to previously collected upland soil measurements and evaluated differences in rooting depth between playas and uplands. To address question 3 about differential changes of C/N with depth and the mechanisms of this pattern, I used the organic carbon and nitrogen values used to answer question 2 in conjunction with information on soil texture with depth.

Methods

Study site

I conducted my research at the 100,000 ha Jornada Basin long-term ecological research site (Jornada LTER). Jornada LTER is located in the northern Chihuahuan Desert in SE New Mexico, USA (+32.5 N, -106.8 W). Jornada LTER is situated in a typical closed-basin system of the Basin and Range physiographic province (Peters and Gibbens 2006). The climate is semiarid with a mean annual precipitation of 247 mm and an average temperature of 24 °C. Jornada LTER is composed of five major plant communities consisting of two different grassland communities and three different shrubland communities. The grassland communities are: upland Black Grama grasslands (*Bouteloua eriopoda*) and lowland playa grasslands dominated by Tobosa grass (*Pleuraphis mutica*) and Vine-mesquite grass (*Panicum obtusum*). The upland shrubland communities are: Tarbush (*Flourensia cernua*) found on lower piedmont slopes, Creosotebush (*Larrea tridentata*) found on upper piedmont slopes and bajadas, and Honey Mesquite (*Prosopis glandulosa*) found on the sandy basin floor (Peters 2013).

My study focused on the lowland playa grasslands and the upland catchments adjacent to each playa. 99 distinct playas (< 1% of the total basin area) are distributed across Jornada LTER (Peters and Gibbens 2006). Upland catchments contained both shrubland and grassland communities.

Playa soil carbon, nitrogen, and bulk density

I chose 30/99 playas from across Jornada LTER to measure soil organic carbon and total nitrogen concentrations. I consulted the Jornada Basin landform map and available aerial imagery to choose 30 playas encompassed a broad range of sizes,

catchment characteristics, and proximities to different geological features (Peters and Gibbens 2006). The perimeter of each playa was ground-truthed using a Trimble Geo 7X handheld GPS (Trimble Navigation Limited, Sunnyvale, CA). In each study playa, I collected 36 soil samples of 100g each using a 70-mm-diameter one-piece hand auger (Forestry Suppliers Inc., Jackson, MS). The soil samples were collected from nine locations along two perpendicular transect-lines to account for a topographic gradient from the edge of the playa to the center of the playa. At each of the nine locations, one sample was collected at four depths (0 – 10 cm, 10 – 30 cm, 30 – 60 cm, 60 – 100 cm). Each soil sample was dried at 105 °C for 24 hours, homogenized, sieved through 2 mm mesh screen, and frozen before analysis.

I measured soil organic carbon and total nitrogen concentrations using elemental combustion analysis. I first ground homogenized soil subsamples using a ball mill. I then prepared 45 mg of ground soil samples in silver tins and acid fumigated the soils to eradicate inorganic carbon (Harris et al. 2001). Lastly, I sealed each fumigated sample and combusted them to estimate organic carbon (g/g) and total nitrogen (g/g) in each soil sample using an ECS 4010 elemental analyzer (Costech Analytical Technologies, Valencia, CA, USA). I also estimated soil bulk density (g/m^3) from three locations at each sample depth for all 30 playas using the core volume sampling method (Sollins et al. 1999). Using bulk density measurements for each depth range (m), I converted each soil measurement (g/g) to calculate concentrations of organic carbon and nitrogen per unit area (g/m^2).

Characterization of catchments

I used remotely-sensed data to delineate area, calculate average slope, vegetation cover, and soil texture for each of the 30 upland catchments adjacent to my study playas. I measured the area and slope of each upland catchment by analyzing 5 m resolution digital elevation model data using spatial analyst tools in ArcGIS (ESRI, San Diego, CA). The catchment slope (% gradient) was calculated by calculating an average slope value for each catchment. I used the 250 m^2 - resolution Terra MODIS Vegetation Continuous Fields (VCF 051) to determine the annual average percent vegetation cover value for each catchment (DiMiceli et al. 2011). I calculated weighted mean soil texture (% sand, silt, clay) from USDA-NRCS soil survey data (Soil Survey Staff). A mean value of soil texture was used for each soil class and a weighted mean was determined using the relative area of each soil class within the catchment.

Upland soil carbon, nitrogen, and bulk density

Soil organic carbon and nitrogen concentrations were measured at the same four depths as in the playas (0 – 10 cm, 10 – 30 cm, 30 – 60 cm, 60 – 100 cm). These soil samples were taken by Jornada LTER staff. Soil sampling was conducted within twelve 4900 m^2 plots representative of the upland ecosystems. 49 soil samples were collected from each plot at each depth 10 m apart in a 7-by-7 square grid. I averaged the 49 organic carbon (g/g soil) and nitrogen (g/g soil) measurements from each plot, and then I averaged the values at each depth for all 12 upland ecosystem plots. Total nitrogen was determined by Kjeldahl digestion techniques (Bremner and Mulvaney 1996). Organic carbon was determined using a modified Mebius method (Yeomans and Bremner 1988). Bulk density (g/m^3) was estimated for each ecosystem type from ten soil samples in each

sample site and depth. The soil weight and core volume were recorded using methods from Elliot et al. (1999), and soil carbon and nitrogen (g/g soil) were converted to per unit area (g/m^2) at each depth (m).

Playa and upland rooting depth distribution

I combined previously collected information about vegetation composition and rooting depth by species for playas and uplands. Species composition was recorded annually (2004-2014) in 12 upland ecosystems and three playas across Jornada LTER (Huenneke et al. 2002a). From this 10-year record, I calculated average percent grasses, forbs, and shrubs of playas and upland ecosystems. I used literature values from Gibbens and Lenz (2001) to determine the average rooting depth for grasses, forbs, and shrubs across Jornada LTER. These values were used to calculate the slope of the cumulative root fraction through depth for playas and upland ecosystems. This is a commonly used metric for comparing rooting depth distributions among ecosystem types (Jackson et al. 1996).

Playa and upland soil texture

I collected nine soil samples at each of the four depths in each playa and determined soil texture using the Bouyoucos hydrometer method (Elliot et al. 1999). Soil samples were oven dried for 24 hours at 105 °C and mixed for 16 hours with 100 mL of 50 g/L sodium hexametaphosphate solution. Hydrometer readings were taken at 40 s and 7 h to determine the percent sand, silt, and clay of each soil sample (Bouycous 1962). A mean value of % sand, silt, clay was calculated from the nine samples collected at each depth. For upland soil texture, I used values of % sand, silt, clay from USDA-NRCS soil survey data taken from the 12 upland sites across Jornada LTER that soil carbon and

nitrogen were measured (Soil Survey Staff). A mean value of % sand, silt, and clay was calculated for each soil depth (0 – 10 cm, 10 – 30 cm, 30 – 60 cm, 60 – 100 cm).

Statistical analysis

I used multiple regression analysis to assess how biophysical catchment characteristics controlled soil organic carbon and nitrogen concentrations in playas. All analyses were conducted using R version 3.0.2 (R Core Team 2013). Data were determined to be normal, had constant error, and did not display multicollinearity. Non-linear models and interactions between all four variables were also evaluated. The best-fit model was chosen using Akaike information criterion (AIC) (Kutner 2005). Partial regression plots were constructed to visualize the effect of each independent variable on the dependent variable while holding all other variables constant (Moya-Laraño and Corcobado 2008). I determined the relative importance of each explanatory variable in the final best-fit model using the Lindemann-Merenda-Gold (*lmg*) method for calculating sequentially weighted partial-R^2 (Lindeman et al. 1980). The *lmg* method used the individual contribution of each explanatory variable by calculating an average coefficient of partial determination for each model permutation. Values for *lmg* were calculated using the 'relaimpo' package in R (Gromping 2006).

I assessed differences in soil organic carbon and nitrogen as well as C/N ratio through depth using analysis of variance (ANOVA) and the post hoc Tukey's honest significant difference (HSD) multiple comparisons test. Soil organic carbon and nitrogen concentrations were standardized (g m^{-2} $10cm^{-1}$) for each soil depth class (0-10cm, 10-30cm, 30-60cm, 60-100cm). I calculated the C/N ratio at each depth by dividing organic

carbon concentration by total nitrogen concentration and measured changes in C/N ratio at depth for both uplands and playas using ANOVA and Tukey's HSD.

Results

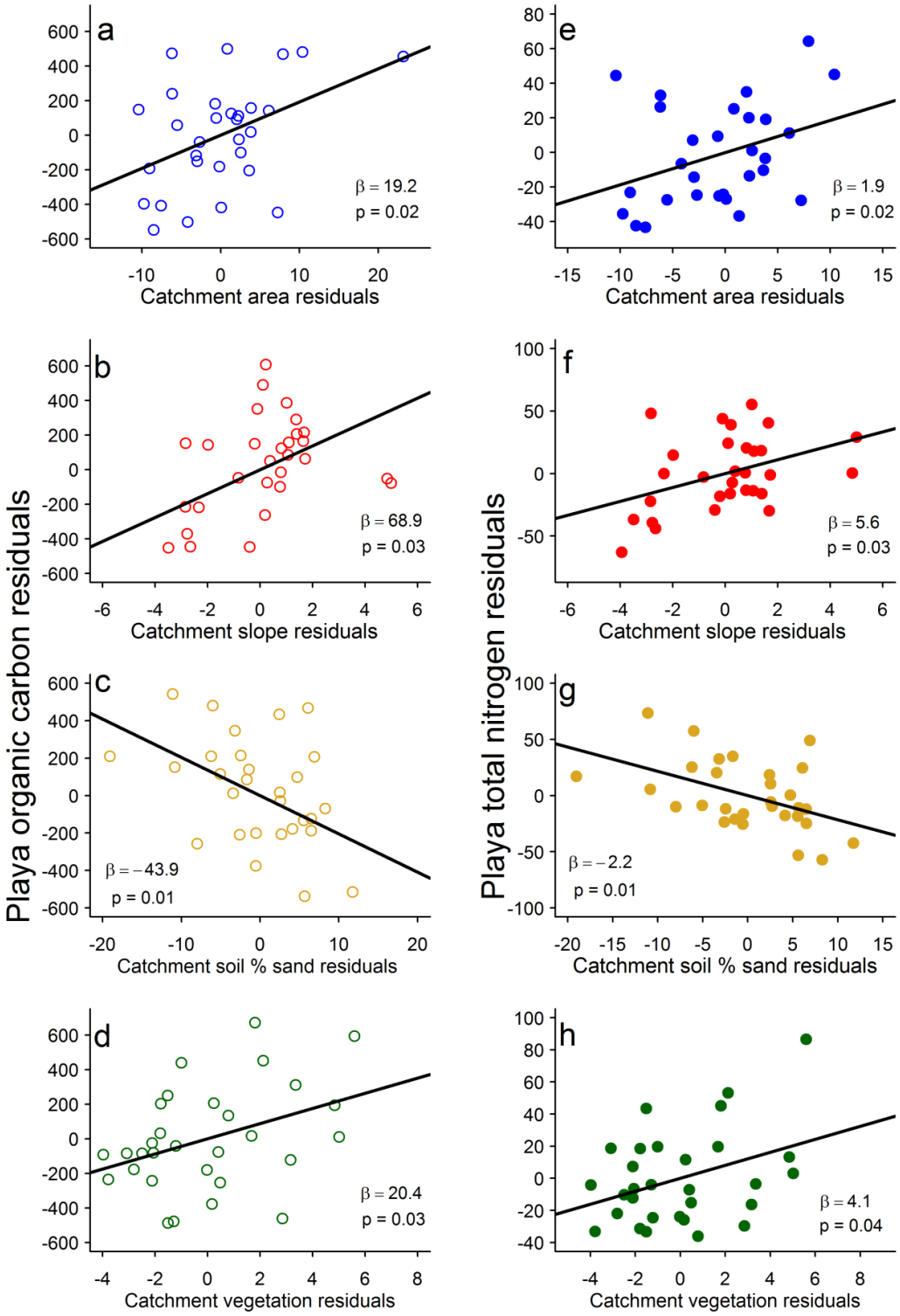

a
β = 19.2
p = 0.02
Catchment area residuals
e
β = 1.9
p = 0.02
Catchment area residuals
b
β = 68.9
p = 0.03
Catchment slope residuals
f
β = 5.6
p = 0.03
Catchment slope residuals
c
β = −43.9
p = 0.01
Catchment soil % sand residuals
g
β = −2.2
p = 0.01
Catchment soil % sand residuals
d
β = 20.4
p = 0.03
Catchment vegetation residuals
h
β = 4.1
p = 0.04
Catchment vegetation residuals
Playa organic carbon residuals
Playa total nitrogen residuals

Figure 1. Pair-wise relationships between each catchment biophysical variable and each playa soil variable from the best-fit regression models. Partial regression plots were constructed by first regressing the explanatory variable of interest (e.g. catchment vegetation) against all other explanatory variables (e.g. catchment soil texture, slope and area) of the full regression model. Next, the response variable of interest (e.g. organic carbon) is regressed against all other response variables (e.g. catchment soil texture, slope and area). The residuals of those two regressions ($e = Y_{expexted} - Y_{observed}$) were then plotted against each other to partial out the effect of each explanatory variable on each response variable. Each column shows the partial regressions for all of the explanatory variables: catchment area (blue), catchment slope (red), catchment soil texture (yellow), catchment vegetation cover (green). Organic carbon relationships are represented by open circles in the left column (a-d) and total nitrogen relationships are represented by closed circles the right column (e-h). Black trend lines represent the best fit model for each partial regression.

How do catchment biophysical variables influence soil organic carbon and nitrogen concentrations among playas?

Differences in soil organic carbon and nitrogen among playas were correlated to: catchment area, slope, soil texture, and vegetation cover of each playa. Soil organic carbon (R^2=0.86, p<0.001, AIC=207) and nitrogen (R^2=0.83, p<0.001, AIC=346) increased with size, slope, soil clay fraction and vegetation cover of a catchment (Figure 1). Below are the best-fit models explaining how catchment biophysical characteristics controlled playa organic carbon and nitrogen concentrations:

(Equation 1)

$$\text{Organic Carbon} = 1222.1 + 19.2(\text{Area}) + 68.9(\text{Slope}) - 43.9(\text{Percent sand}) + 20.4(\text{Vegetation cover})$$

(Equation 2)

$$\text{Nitrogen} = 132.3 + 1.9(\text{Area}) + 5.6(\text{Slope}) - 2.2(\text{Percent sand}) + 4.1(\text{Vegetation cover})$$

Catchment vegetation cover was the most important variable controlling soil organic carbon concentrations among playas, explaining 38% of variability (range from 430-3800 g/m^2). Playa soil organic carbon concentration increased by 20 g C/m^2 for

every percentage increased by catchment vegetation cover when all other variables were held constant (Eq. 1). The geomorphic variables explained the remainder of the variability in organic carbon among playas in the following order: catchment slope, (25%), catchment area (22%), and catchment soil texture (15%) (Table 1).

Catchment vegetation cover was also the most important variable controlling soil total nitrogen concentrations among playas, explaining 43% of variability (range from 30-400 g/m^2). Playa soil nitrogen concentration increased by 4 g N/m^2 for every percentage increased by catchment vegetation cover when all other variables were held constant (Eq. 2). The geomorphic variables explained the remainder of the variability in soil nitrogen among playas in the following order: catchment slope (21%), catchment area (21%), and catchment soil texture (14%) (Table 1).

	Explanatory variable	Range	*lmg* partial R^2	
			Carbon	Nitrogen
Geomorphic Variables	Catchment Area	0.1 - 48.9 km^2	0.19	0.18
	Catchment Slope	1.4 - 14.1% rise	0.21	0.18
	Catchment Soil Texture	54 – 89 % sand	0.13	0.12
Biological Variable	Catchment Vegetation	21-42 % cover	0.32	0.36

Table 1. Summary of the contributions of geomorphic and biological explanatory variables to the best-fit model R^2 for soil playa organic carbon and nitrogen models. Values were calculated using partial coefficient of determination *lmg* analysis. Ranges of each explanatory variable are also listed for reference.

How is soil organic carbon and nitrogen distributed through depth in playas as compared to upland ecosystems?

In playa soils, concentrations of soil organic carbon and nitrogen were very high in the top 10 cm of and sharply decreased below 10 cm (Figure 2). In contrast in upland soils, organic carbon and nitrogen were stored in relatively low concentrations that gradually decreased through depth. Playa organic carbon and nitrogen concentrations were statistically higher ($p > 0.001$) in the top 10 cm of soil than the rest of soil layers from 10 – 100 cm. (Figure 2a-b). Concentrations of soil organic carbon and nitrogen did not significantly change in playas from 10 – 100 cm. Mean organic carbon and nitrogen values for the top 10 cm were 1400 g C/m^2 and 130 g N/m^2. Mean organic carbon and nitrogen values from 10 - 100 cm were 570 g C/m^2 and 50 g N/ m^2. Upland soil organic carbon and nitrogen concentrations gradually decreased at deeper soil layers with significant differences found between the soils in the top 10 cm and soils between 60 – 100 cm ($p = 0.04$) (Figure 2c – d). Mean organic carbon and nitrogen values for the top 10 cm of soil were 570 g C/m^2 and 60 g N/m^2. Mean organic carbon and nitrogen values from 60 – 100 cm were 340 g C/m^2 and 30 g N/ m^2.

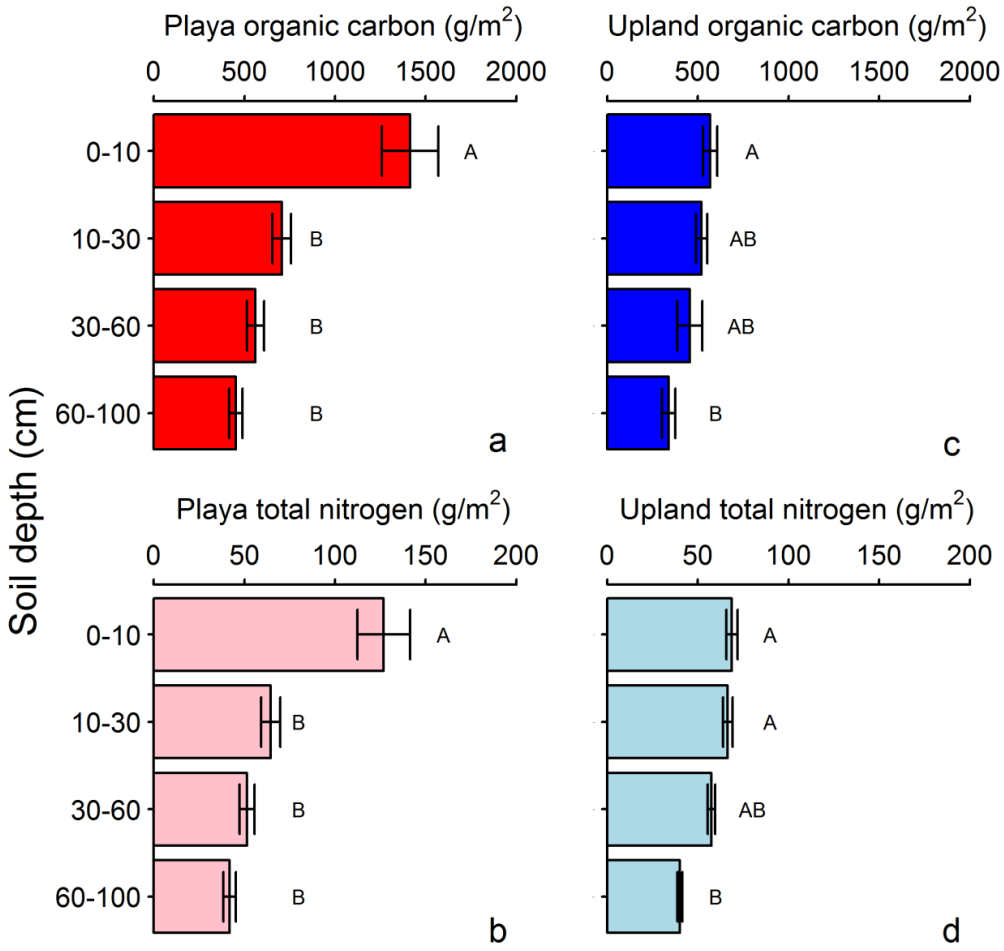


Figure 2. Soil organic carbon (a, c) and total nitrogen (b, d) concentrations in playas (a, b) and uplands (c, d) at four soil depths from 0 – 100 cm. Significant differences between soil depths are represented by different letters. Playa soil organic carbon (dark red bars) and nitrogen (light red bars) concentrations are significantly higher in the top 10 cm than the rest of the soil layers 10 – 100 cm. Upland soil organic carbon (dark blue) and nitrogen (light blue) concentrations do not significantly change from 0 – 60 cm and significantly decrease below 60 cm. Error bars represent standard error.

Differences in organic carbon and nitrogen storage through depth also paralleled the differences in rooting depths of plants in uplands and playas. Plant roots were mostly concentrated in the top 30 cm of playa soils and below 50 cm in upland soils (Figure 3). The average rooting depths across plant functional types at Jornada LTER were 30 cm for

grasses, 80 cm for forbs, and 130 cm for shrubs (Gibbens and Lenz 2001). Differences in plant community composition caused differences in root distributions through depth between playas and upland ecosystems (Figure 3). Playa vegetation communities consisted of 70% grasses and 30% forbs; shrubs were not found growing in any playas. In playa soils, 70% of roots were located around 30 cm depth and no roots were below 80 cm depth. Upland ecosystems supported vegetation communities that were composed of 35% grasses, 20% forbs, and 45% shrubs. In upland ecosystems, 55% of roots were in the top 80 cm and 45% of the roots were located around 130 cm depth (Gibbens and Lenz 2001).

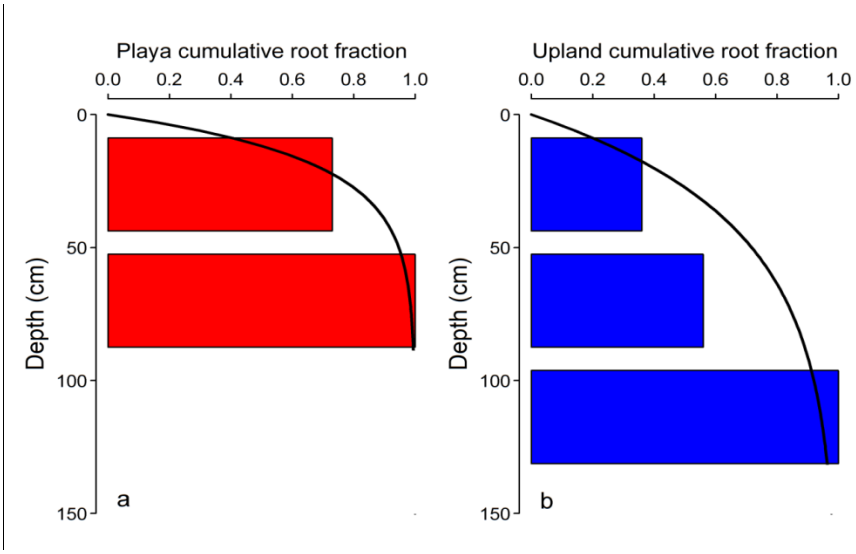


Figure 3. The distribution of root biomass plotted through soil depth for playas and upland ecosystems. Panel (a) shows the distribution of roots through depth in playas (red bars). 70% of playa roots are found in the top 30 cm of soil and 30% of roots are found between 30 and 80 cm. Panel (b) shows the distribution of roots through depth in uplands (blue bars). 35% of upland roots are found in the top 30 cm, 20% from 30 – 80 cm, and 45% from 80 – 130 cm. Black curves represent continuous rooting distributions through depth for uplands ($\beta = 0.98$) and playas ($\beta = 0.94$).

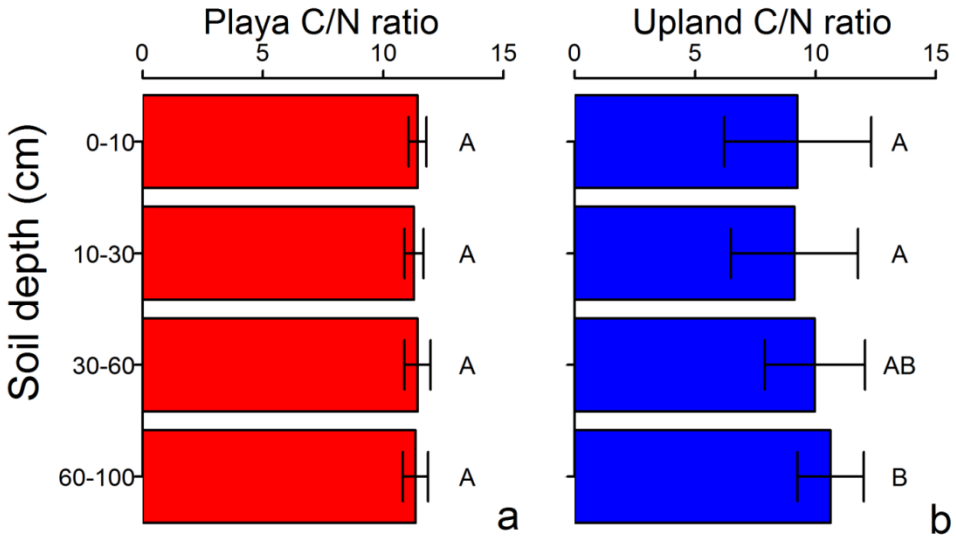


Figure 4. Soil C/N ratio for playa ecosystems and upland ecosystems at four soil depths from 0 – 100 cm. Panel (a) shows playa soil C/N ratio (red bars) did not change significantly through depth. Panel (b) shows upland soil C/N ratio (blue bars) was significantly greater in deep soil layers than in surface layers. Letters located to the right of the bars represent significant differences between depths. Black error bars represent standard error.

How does the ratio of soil organic carbon to nitrogen change through depth in playas as compared to upland ecosystems?

In playas, soil C/N ratio remained unchanged through depth and increased through depth in uplands. Playa soil C/N ratio averaged 11.2 and did not significantly change throughout the top 100 cm of soil (Figure 4a). In upland soils, soil C/N ratio significantly increased from the top 30 cm to 60 – 100 cm ($p = 0.03$, Figure 4b). The average soil C/N ratio in the top 30 cm of upland soils was 9.3 cm and the average C/N ratio from 60 – 100 cm was 10.6 cm.

Changes in soil C/N ratio through depth in playas and uplands paralleled changes in soil texture. Playa soils were composed, on average, of 34% clay particles and did not statistically change at any soil layer from the surface down to 100 cm (Figure 5a). Upland

soils increased significantly (p = 0.02) in clay content from 11% in the top 10 cm to 20% at 60-100 cm depth (Figure 5b).

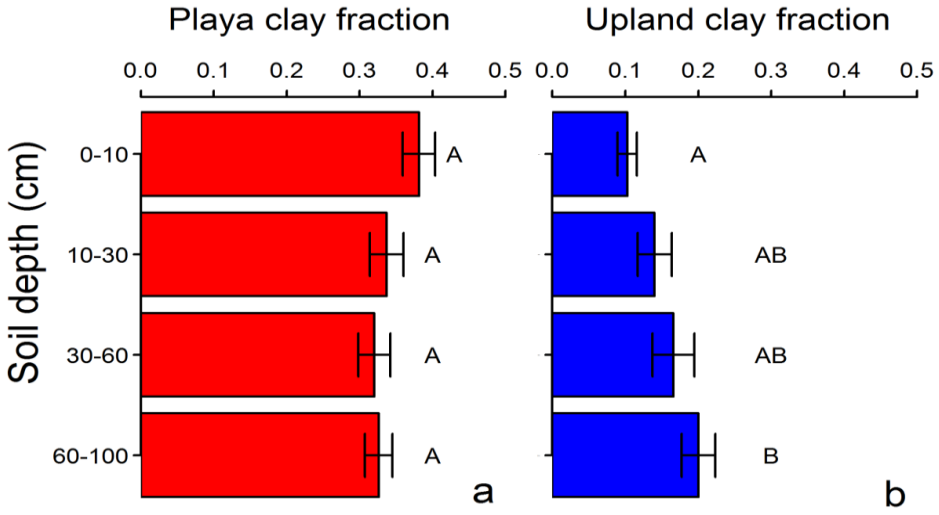


Figure 5. Percent of soil composed of clay for playas and upland ecosystems at four soil depths from 0 – 100 cm. Panel (a) illustrates clay concentration in playa soils (red bars) remained constant through different soil depths. Panel (b) illustrated how clay concentration in upland soils (blue bars) increase significantly through depth. Letters located to the right of the bars represent significant differences between depths. Black error bars represent standard error.

Discussion

Soil organic carbon and nitrogen concentrations among playas strongly corresponded to biophysical variables that control both runon and allochthonous organic matter production. Most interestingly, I found that vegetation cover in a catchment corresponded positively to the concentration of soil organic carbon and nitrogen in the adjacent playa. These results showed that the organic matter production from upland catchment vegetation was more important to playa soil organic carbon and nitrogen concentration than the physical impediment vegetation cover can have on runon production. The size, slope, and soil texture of each catchment controlled playa runon production, and the catchment vegetation controlled the concentration of organic matter

in playa runon. All of these variables combined controlled the amount of allochthonous organic matter that was deposited and stored in playa soils.

Playa soils amplify the vegetation signal of uplands and could be used as a window to view past variations of upland vegetation cover. Using radiometric dating techniques on soil cores, scientists could estimate how much organic matter was deposited and stored in playas at a given time (Craft and Casey 2000). Certain areas of playa soil cores with low organic carbon and nitrogen could represent periods of overgrazing or drought, and areas with high concentrations would be indicative of high upland primary productivity.

Concentrations of organic carbon and nitrogen sharply decreased through depth in playa soils and gradually decreased through depth in upland soils. These differential patterns in playas and uplands corresponded to: (1) vegetation rooting depths and (2) the influence of allochthonous inputs to soils. Playas were dominated by shallow-rooted grasses and most of their C and N inputs came as allochthonous organic matter. Allochthonous inputs to playas were deposited on the surface of playas, which concentrated organic carbon and nitrogen in the top 10 cm of soil. Upland soils have more deeply rooted vegetation that provided autochthonous inputs into deeper layers. The absence of allochthonous sediments in upland ecosystems results in an even pool of organic carbon and nitrogen throughout the soil profile.

Clay content is the most important variable controlling global soil organic carbon stocks (Jobbágy and Jackson 2000). Clay-sized particles physically bind to organic matter and sequester organic carbon and nitrogen in soils (Vogel et al. 2013). My results show the stabilizing effect of clay particles on organic matter concentrations and soil C/N

ratios. Clay-rich playa soils maintain high concentrations of organic carbon and nitrogen and unchanged soil C/N ratio through depth. Upland soils contain overall less clay-sized particles than playas and store less organic carbon and nitrogen. Upland soil clay content increased through depth, which would cause higher carbon losses in the surface soil layers than in deeper soil layers. Decreased carbon losses through depth in upland soils relative to playas corresponded to increased soil C/N ratios. In synthesis, the increasing C/N ratio with depth observed in upland soils resulted from increasing clay content with depth. In playas, a constant C/N ratio with depth resulted from high clay content in all the profile and specifically in the upper layers.

Two important global change drivers that could potentially impact playa functioning in the future are: (1) woody-plant encroachment and (2) climate change. Woody-plant encroachment into grassland ecosystems is a well-documented global phenomenon and is expected to continue in the future (Anadón et al. 2014). Woody plants are not encroaching into the dense clay soils of playas, but playas may be indirectly affected as woody-plant encroachment occurs in upland areas of catchments (Mcauliffe 1994). Despite changes in ecosystem structure, woody-plant encroachment is not expected to cause a net change in primary production for arid grasslands of southwestern US (Knapp et al. 2008). Based on the results of this study, I concluded that if woody-plant encroachment does not change biomass, it most likely will have no effect on playa C and N stocks.

In addition to woody-plant encroachment, climate change is also predicted to affect southwestern US in two ways: (1) lower annual precipitation, and (2) increased precipitation variability (Melillo et al. 2014). A decrease in mean annual precipitation

may cause a decrease in aboveground net primary production and vegetation cover (Sala et al. 2012) that may decrease, according to this study, soil organic carbon and nitrogen storage. The predicted increase in precipitation variability results from higher temperatures that change the atmospheric water holding capacity, which in turn increases the size of precipitation events (Sun et al. 2007). Increased precipitation variability is expected to decrease overall vegetation cover, which would cause a decrease of allochthonous inputs of organic carbon and nitrogen in playas (Gherardi and Sala 2015). In synthesis, both dimensions of climate change will operate in the same direction by reducing organic and nitrogen stocks in playa ecosystems.

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Supplementary Information

Model	R^2	AIC
y1=x1	0.663	231.61
y1=x2	0.654	232.40
y1=x3	0.463	245.59
y1=x4	0.784	218.32
y1=x1+x2	0.800	216.83
y1=x1+x3	0.768	221.26
y1=x1+x4	0.805	216.15
y1=x2+x3	0.743	224.39
y1=x2+x4	0.806	215.94
y1=x3+x4	0.822	213.44
y1=x1+x2+x3	0.849	209.37
y1=x1+x2+x4	0.831	212.71
y1=x1+x3+x4	0.843	210.40
y1=x2+x3+x4	0.839	211.30
y1=x1+x2+x3+x4	0.864	207.02

Table 1: Total nitrogen vs. catchment characteristics regression model comparisons (y1=Total Nitrogen (g/m^2), x1=Catchment Area (km^2), x2=Catchment Slope (% rise), x3=Catchment Soil Texture (% sand), x4=Catchment Vegetation Cover (% cover))

Model	R^2	AIC
y1=x1	0.666	373.83
y1=x2	0.686	371.97
y1=x3	0.447	388.94
y1=x4	0.798	358.71
y1=x1+x2	0.823	355.78
y1=x1+x3	0.762	364.58
y1=x1+x4	0.817	356.68
y1=x2+x3	0.761	364.75
y1=x2+x4	0.829	354.60
y1=x3+x4	0.829	354.75
y1=x1+x2+x3	0.861	349.27
y1=x1+x2+x4	0.852	351.15
y1=x1+x3+x4	0.848	352.02
y1=x2+x3+x4	0.854	350.79
y1=x1+x2+x3+x4	0.877	346.41

Table 2: Soil organic carbon vs. catchment characteristics regression model comparisons. (y1=Organic Carbon (g/m^2), x1=Catchment Area (km^2), x2=Catchment Slope (% rise), x3=Catchment Soil Texture (% sand), x4=Catchment Vegetation Cover (% cover))

CHAPTER 4 - GROUNDWATER RECHARGE IN DRYLAND PLAYAS: CURRENT RATES AND FUTURE EFFECTS OF CLIMATE CHANGE

Abstract

Groundwater resources in southwestern USA continue to decline due to human consumption outpacing natural recharge of aquifers. Topographic low areas called playas flood annually and may be important areas for concentrated recharge. Here, I investigated the role of dryland playas in recharging groundwater and how climate change will affect playa-mediated recharge in the future. I empirically measured groundwater recharge rates of 0.1-28.0 mm per year beneath dryland playas in southwestern USA. I also found that playas located in large and steep catchments with less-sandy soils had the highest rates of recharge although they were insensitive to vegetation cover. I modelled playa runon generation and found that the amount of runon a playa receives annually is linearly related to the groundwater recharge beneath that playa. Runon was generated by precipitation events larger than 20 mm and increased linearly with rainfall events above this threshold. I found that projected climate change in southwestern USA will have a net positive impact over playa runon and groundwater recharge beneath playas. Expected increased precipitation variability will cause up to a 300% increase in annual groundwater recharge overshadowing the effect of decreased precipitation amount that will cause up to a 50% decrease in recharge beneath playas.

Introduction and Approach

Groundwater supplies ~40% of the agricultural and residential water needs in southwestern USA, which occupies 1.8 M Km^2 and ~20% of the United States of America (Maupin et al. 2014). Consumption of groundwater in this large region continues to increase due to: (1) demand from growing populations (Sabo et al. 2010) and (2) larger droughts that have decreased the reliability of surface water for human consumption (MacDonald 2010). Increased demand has outpaced recharge rates and caused groundwater storage to decline. Consequently, the lifespan of some dryland aquifers in southwestern USA has been estimated to be as short as 100 years (Scanlon et al. 2012). High rates of evapotranspiration in drylands limit the potential for groundwater recharge to large precipitation events that generate surface-water runoff (Taylor et al. 2013b). Groundwater recharge in drylands is also geographically limited to ephemeral streams and lowland areas called playas, because wetting depth in upland ecosystems rarely goes beyond 100 cm (Sala et al. 1992) and in some cases water penetration is constrained by water-restrictive soil layers (Scanlon et al. 2006, Gurdak and Roe 2010).

Playas are wetlands located in the topographic low areas of hydrologically-closed catchments (Thomas 2011). Playas can be categorized into two types determined by the source of their flood-water: (1) groundwater playas and (2) surface-water playas (Rosen 1994). In this paper, I focused solely on surface-water playas, which are flooded by runon generated from upland areas during high intensity rainfall events. Runon deposits sediments to playa soils and concentrates organic carbon and nutrients in quantities ~5 times higher than upland ecosystems (McKenna and Sala 2016b). The biophysical characteristics of playa catchments control differences in soil organic carbon and nutrient

concentrations among playas. Playas found in the largest, steepest, and most highly-vegetated catchments contain the highest concentrations of soil carbon and nitrogen. Runon-driven allochthonous soil inputs also concentrate soil organic carbon and nutrients closer to the surface in playas than in upland soils (McKenna and Sala 2016a). The role of playas as areas of groundwater recharge in southwestern USA and the effect of climate change on groundwater recharge beneath playas remains uncertain.

The most recent climate-change projections from the 2014 US National Climate Assessment were based on the "Coupled Model Intercomparison Project phase 5" (CMIP5) (Wuebbles et al. 2014). CMIP5 predicted changes in climate for different atmospheric CO_2 concentration scenarios called representative concentration pathways (RCPs). In these scenarios, increased atmospheric CO_2 concentrations directly increased atmospheric temperatures. Increased temperatures can influence precipitation in two ways by: (1) increasing inter-annual variability and (2) decreasing the amount of annual precipitation for southwestern USA in all RCPs (Melillo et al. 2014). Increased atmospheric temperatures are predicted to increase the size of large precipitation events and decrease the size of small precipitation events (Sun et al. 2007). Increased inter-annual precipitation variability has been shown to increase soil-water availability in dryland ecosystems, (Sala et al. 2015) but considerable uncertainty still exists about the overall impact of climate change on dryland groundwater recharge (Taylor et al. 2013a).

Our study addressed three questions about playa groundwater recharge rates and how recharge rates will change in the future. My first question was: **how much do playas contribute to groundwater recharge in southwestern USA?** To answer this question, I empirically measured recent-past groundwater recharge beneath a subset of playas in a

representative area of the Basin and Range Physiographic province. My second question was: **how do catchment-scale variables influence groundwater recharge among playas?** To address this question, I used remotely sensed data to measure elevation, soil, and vegetation characteristics of each playa catchment and analyzed relationships between catchment characteristics and playa recharge rates. My third question was: **how will climate change influence groundwater recharge beneath playas through changes in precipitation variability and amount?** To answer this question, I first modelled playa runon events from a recent 20-year period and determined how runon controls groundwater recharge beneath playas. I used those modelling results to determine how the size of a precipitation event controls playa-runon generation. I created two new 20-year rainfall time series to reflect scenarios of (1) increased precipitation variability and (2) decreased precipitation amount. I used my best-fit rainfall-runon relationship to measure how playa runon will change in the future. Finally, I used my best-fit runon-recharge relationship to measure how groundwater recharge beneath playas will change under different climate-change scenarios.

Results and Discussion

I empirically measured groundwater recharge in the unsaturated zone beneath playas with the commonly used chloride mass balance method (Scanlon et al. 2002). Groundwater recharge occurred in 100% of playas that were sampled (Fig. 1). The average playa recharge rate was 6 mm/yr, which is 2% of the annual rainfall for the study area. Recharge beneath playas ranged from 0.1 – 28 mm/yr, and 65% of the playas sampled had recharge rates below 5 mm/yr (Fig. 1). I measured recharge rates higher than 15 mm/yr in only 15% of playas (Fig. 1). Groundwater recharge rates beneath high-

recharge playas compared to estimates of mountain-front recharge of 22 mm/yr for the Jornada del Muerto aquifer (Kambhammettu 2010).

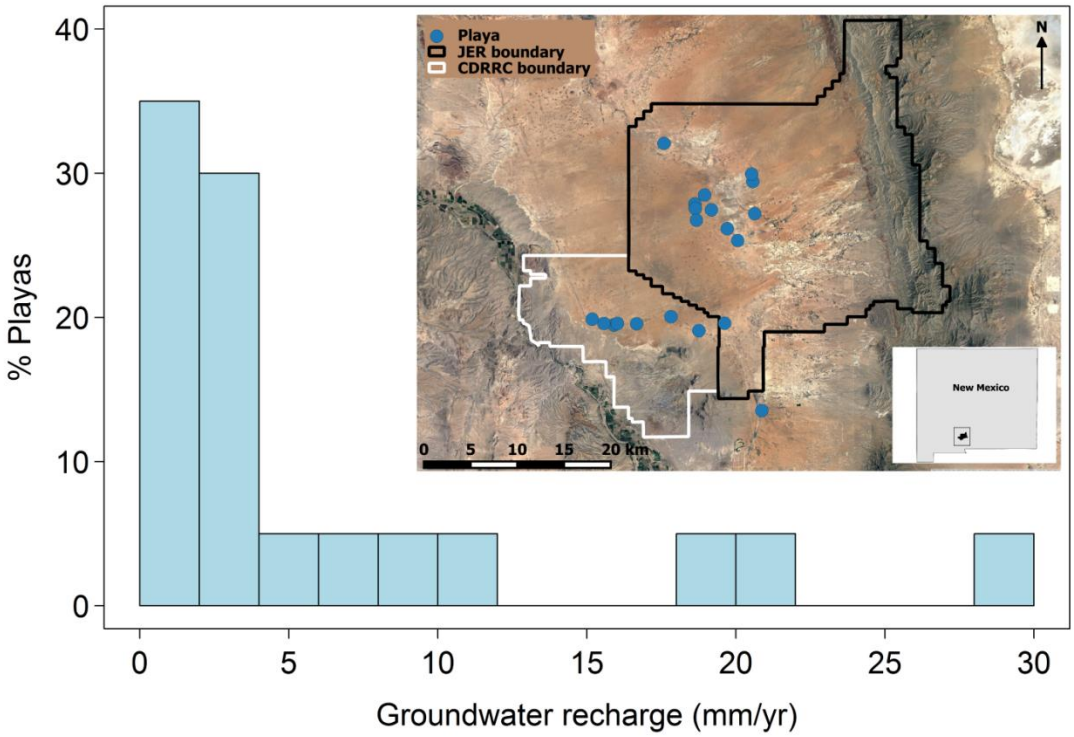


Figure 1. Frequency distribution of empirically measured past groundwater recharge rates beneath playas. Each bin of the histogram is 2 mm wide, and the height of blue bars represents percent of playas in each bin. Average recharge beneath playas was 6 mm/yr and 65% of playas (n = 20) had below-average recharge rates. Map inset of the Jornada Basin and all sampled playas. Jornada Experimental Range is outlined in black and Chihuahuan Desert Rangeland Research Center is outlined in white. Playas are represented by blue dots.

I found that differences in groundwater recharge rates among playas were correlated to the size, slope, and soil texture of each catchment (R^2=0.78, p<0.001, AIC=53.6). Recharge rate increased with area and slope, and decreased with percent sand of a catchment (Fig. 2). Catchment vegetation cover was not significantly correlated to playa groundwater recharge. These results suggested either vegetation cover did not physically impact runoff production or the range of vegetation cover in catchments I studied was not large enough to capture the physical effect of vegetation cover on runoff

production. My findings matched previous work that found that catchment vegetation as a source of organic matter was more important than the physical impediment vegetation cover can have on reducing playa runon (McKenna and Sala 2016a). These results also suggest that playa groundwater recharge would not be impacted by projected decreases in dryland vegetation cover caused by increased precipitation variability or drought (Gherardi and Sala 2015).

I used the Limburg Soil Erosion Model (LISEM) De Roo et al. (1996) to simulate the amount of runon each of my study playas received during a 20-year period (1992-2011). LISEM is a well-known hydrologic model that has been successfully used to simulate runoff for a variety of catchments around the world (Cuomo et al. 2015). I found that there was a highly significant ($p<0.05$) linear relationship between the simulated amount of annual runon a playa received and the observed amount of annual groundwater recharge that occurred beneath that playa (Fig. 3). In order to estimate how future changes in precipitation would impact groundwater recharge, I also analyzed how the size of individual precipitation events controlled playa runon. Playa runon was only generated from precipitation events larger than 20 mm, which occurred twice a year on average, and only 8% of all rainfall events were above 20 mm (Fig. 4). When rainfall events were above 20 mm, the size of a rainfall event correlated linearly to the average amount of playa runon generated (Fig. 4). I used the rainfall-runon and runon-recharge relationships to assess how projected changes in precipitation event size will influence runon and subsequently change playa groundwater recharge rates.

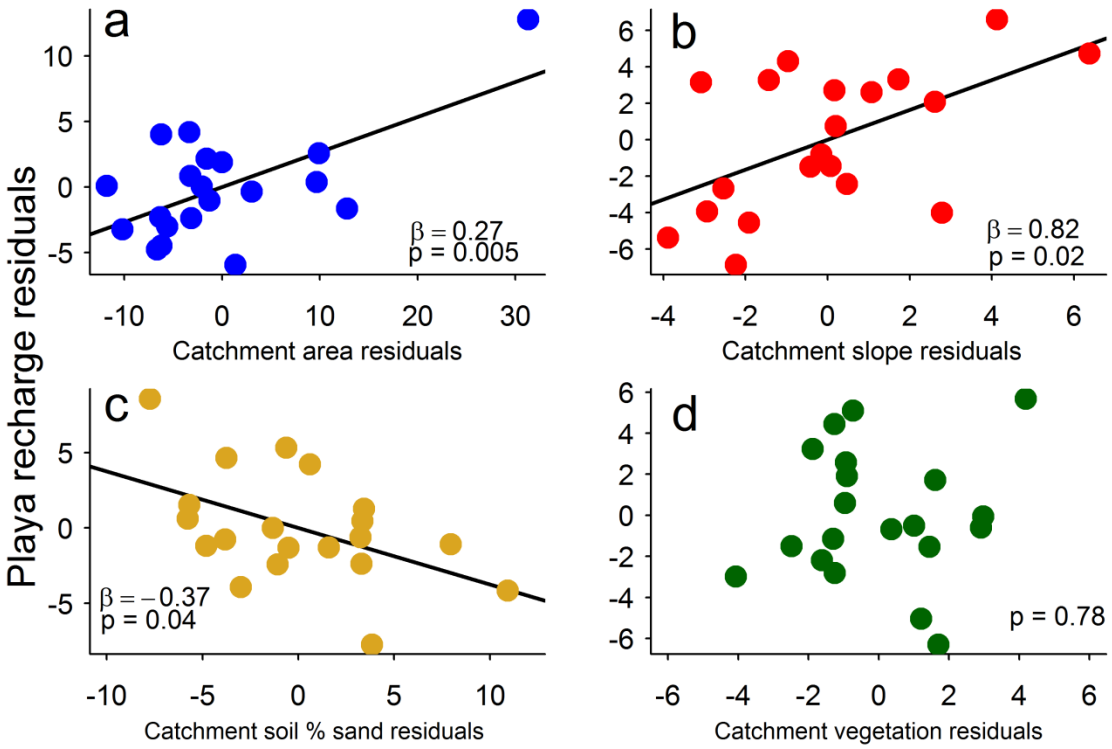


Figure 2. Pair-wise relationships from multiple regression analysis each catchment biophysical variable and playa groundwater recharge. Panels a, b, and c are from the best-fit regression models, and panel d is from the full model. Partial regression plots were constructed by first regressing the explanatory variable of interest (e.g. catchment vegetation) against all other explanatory variables (e.g. catchment soil texture, slope and area) of the regression model. Next, the response variable (groundwater recharge) was regressed against all other explanatory variables (e.g. catchment soil texture, slope and area). The residuals of those two regressions ($e = Y_{expexted} - Y_{observed}$) were then plotted against each other to partial out the effect of each explanatory variable on the response variable. Each panel shows the partial regressions for all of the explanatory variables: catchment area (blue), catchment slope (red), catchment soil texture (yellow) and catchment vegetation cover (green). Black trend lines represent the best-fit model for each partial regression. The best-fit model for explaining groundwater recharge was: ***Groundwater recharge (mm/yr) = 29.82 + 0.27*Catchment Area (ha) + 0.82*Catchment slope (% rise) – 0.38*Catchment soil texture (% sand).***

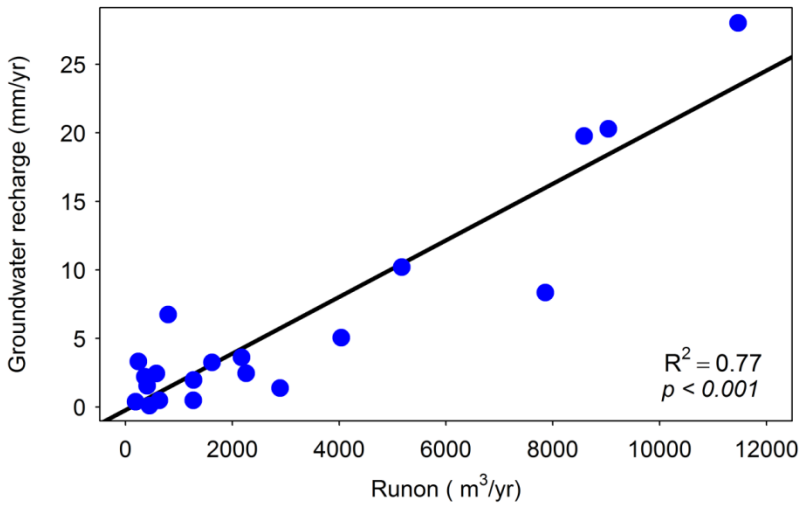


Figure 3. Relationship between modelled annual runon and observed annual groundwater recharge beneath playas. The amount of annual runon received by a playa was positively correlated with the annual rate of groundwater recharge beneath that playa. Open circles represent empirically measured average annual groundwater recharge rates beneath 20-playas and modelled annual runon for each of the same 20 playas. The best-fit model for predicting groundwater recharge was: ***Groundwater recharge =-0.23+ 0.0021*runon (m^3/yr)***. The best-fit model of runon vs. recharge is represented by the black line.

After modelling runon from recent-past precipitation events, I independently evaluated the effects of increased precipitation variability and decreased mean annual precipitation on playa groundwater recharge. I manipulated a 20-year rainfall record to reflect two different climate change scenarios: (1) increased precipitation variability and (2) decreased precipitation amount. I then used my rainfall-runon-recharge models (Fig. 3 & Fig. 4) to calculate the response of groundwater recharge beneath playas to changes in precipitation variability and mean under RCP 4.5, RCP 6.0, and RCP 8.5 scenarios. Climate models predict increased atmospheric temperatures will increase precipitation variability and decrease precipitation amount in southwestern USA (Melillo et al. 2014).

Under different climate change scenarios for southwestern USA, average atmospheric temperature is predicted to increase between 2 and 6 °C for RCP 4.5 and RCP 8.5.

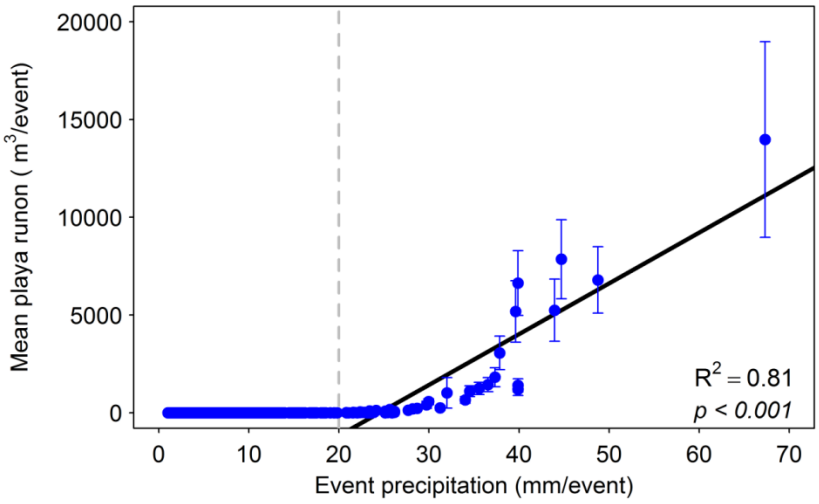


Figure 4. Relationship between rainfall event size and average playa (n = 20) runon generated from each rainfall event. The vertical dashed gray line at 20 mm represents the runon production threshold. All rainfall events below the 20 mm threshold did not generate playa runon. Above 20 mm, precipitation-event size was positively correlated with playa runon. Closed blue circles represent the average runon produced on playas (n = 20) for 560 rainfall events (1992-2011). Blue Error bars represent standard error of runon among 20 playas for each rainfall event. The best-fit model for predicting playa runon was: ***Mean playa runon = -6369.86+ 259.78*rainfall event size (mm)***. The best-fit model of rainfall vs. runon is represented by the solid black line.

A rise in temperature would decrease the size of small rainfall events and increase the size of large rainfall events (Sun et al. 2007). The overall effect of changing rainfall event sizes would be a 5 - 17% increase in precipitation variability (see supplemental information). I found that for every 1% increase in precipitation variability, average playa groundwater recharge rates increased 18%. In the most extreme scenario, average playa groundwater recharge rates increased 300% from 6 mm/yr to 22 mm/yr (Fig. 5). Increased temperatures are also predicted to decrease the mean annual precipitation 2% for southwestern USA for every degree Celsius increase in temperature. Mean annual

precipitation would decrease 4 - 12% under the RCP 4.5 - RCP 8.5 scenarios (Pierce et al. 2013). I found that for every 1% decrease in precipitation amount, average playa groundwater recharge rates decreased 5%. In the most extreme scenario, average playa groundwater recharge rates decreased 50% from 6 mm/yr to 3 mm/yr (Fig. 5). Overall, I found that climate change will have a net positive effect on playa groundwater recharge.

The different responses of groundwater recharge to changes in precipitation variability and amount were due to the distribution of precipitation events in southwestern USA. Recent-past precipitation records show that 92% of rainfall events are too small to generate runon (see supplemental information). There were 47/560 precipitation events greater than 20 mm from 1992-2011. Increased temperature is projected to increase the size of these large rainfall events and decrease the size of small events that do not produce runon (Sun et al. 2007). By decreasing precipitation mean, there would be a much smaller impact on large rainfall events.

Regional climate phenomena such as El Niño/Southern Oscillation (ENSO) also influence precipitation and groundwater recharge events on a decadal time scale. During the warm "El Niño" periods, more frequent large rainfall events have been shown to cause higher groundwater recharge rates in southwestern USA (Pool 2005). The current consensus is that continued greenhouse warming will increase the frequency of strong ENSO events (Cai et al. 2015). Increased ENSO frequency would increase the amount of runon-generating rainfall events and cause more groundwater recharge beneath playas.

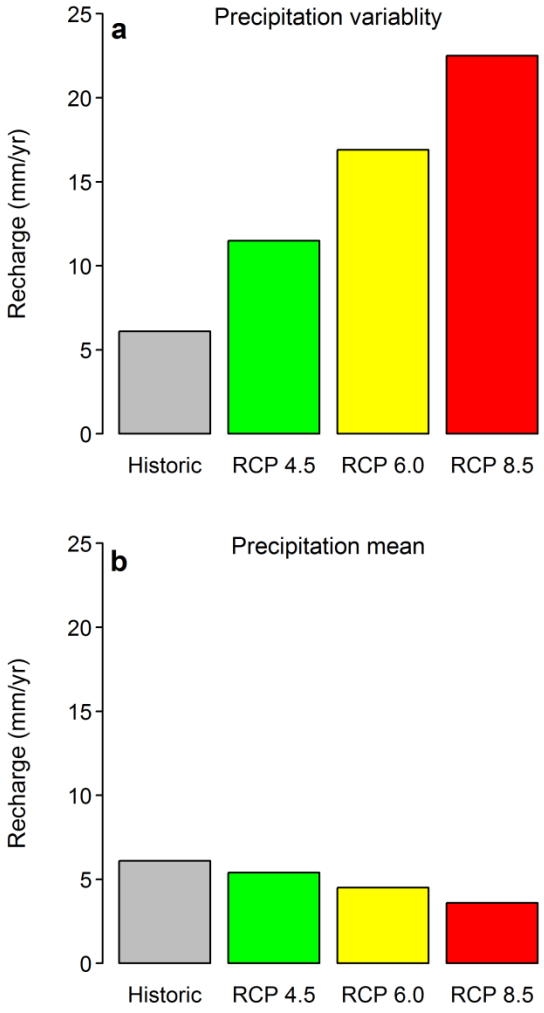


Figure 5. Response of mean annual playa groundwater recharge to different climate- change scenarios that modify precipitation variability and amount. Grey bars represent average playa recharge under recent-past climate. Green, yellow, red bars represent average playa recharge under future representative concentration pathways (RCPs) scenarios of increased CO_2 emissions. Panel (**a**) shows the response of increased precipitation variability under warmer climate while maintaining precipitation amount constant. Panel (**b**) shows the effect of decreased precipitation amount as predicted by global circulation models while maintaining precipitation variability constant.

Conclusions

In conclusion**,** groundwater recharge beneath playas in southwestern USA is significant and should be considered in dryland aquifer budgets. Recharge beneath playas is controlled by large rainfall events that generate surface-water runon to playas.

Predicted future increases in the magnitude of large rainfall events will increase groundwater recharge beneath playas and enhance the sustainability of dryland in southwestern USA aquifers. These findings also have global implications for groundwater sustainability and ecosystem water budgets, because lateral groundwater flow has been found to influence ecosystem evapotranspiration at large scales (Maxwell and Condon 2016)

Increased large rainfall and runon events would increase flood frequency in drylands with negative economic impact (Donat et al. 2016). On the contrary, increased runon-generating storms would recharge reliable drinking water and irrigation sources. Increased precipitation variability would cause groundwater to be an even more dependable source of water for rapidly growing human populations in drylands.

Methods

I combined both empirical and modelling techniques to answer my three research questions regarding past and future rates of groundwater recharge beneath dryland playas. Here, I have detailed the study site where all of the field work and modelling were focused, followed by the specific methods used to address each research question.

Study site

Both the empirical and modelling components of this study were conducted at the Jornada Basin long-term ecological research site (Jornada LTER). This site is located near Las Cruces, NM, USA (+32.5 N, -106.8 W, elevation 1188 m) and contains all of the ecosystem types and geomorphic landforms that are typical for systems in the Basin and Range province (Peters and Gibbens 2006). A warm and semi-arid climate exists at Jornada LTER with 36 °C mean maximum summer temperature and mean annual precipitation of 237 mm/yr. Over 60% of annual precipitation is delivered during the summer monsoon season from July to September. The Jornada Basin is composed of many internally-draining catchments that each span a topographic gradient from the piedmont slopes to the basin floor (Fig. 1). These upland catchments are comprised of both desert grasslands and shrublands. The low areas of most of these internally-draining catchments form playa grasslands (Peters 2013). The upland soils range from sandy to loamy and contain variable amounts of carbonates, whereas the playa soils are much more dense clays that contain less carbonates (Havstad et al. 2006). There are 100 playas that account for ~1% of Jornada LTER area.

How much do playas contribute to groundwater recharge in southwestern USA?

I empirically measured groundwater recharge using an environmental tracer mass balance beneath a representative subset of playas. I used the chloride mass balance (CMB) approach to measure groundwater recharge rates beneath playas (Wood and Sanford 1995). CMB is the most common method for estimating relatively low rates of groundwater recharge in unsaturated soil zones (Scanlon et al. 2006). Chloride occurs naturally as wet and dry deposition and is not biologically active, which enabled a long-term mass balance of chloride to be calculated (Allison and Hughes 1978, Scanlon 1991). Surface inputs of chloride (Cl^-_p) (mg/l) and precipitation (P) (mm/yr) are balanced by the mass out of the playa via chloride in the unsaturated zone (Cl_{uz}) (mg/l) and deep percolation that results in groundwater recharge (R) (mm/yr) (Equation 1). Recharge is calculated by solving Equation 1 for R (Eq. 1).

$$R = \frac{(Cl_p)(P)}{(Cl_{uz})} \quad (1)$$

I used a Giddings hydraulic soil auger to collect one continuous soil core from the center of each study playa (n = 20). Each soil core measured 5 meters in length. Five 100 g soil samples were taken from below the playa rooting zone at 1 m increments (1 - 5 m). Soil samples were weighed, dried for 24 hours at 105 °C, and re-weighed to determine gravimetric water content (g/g). Volumetric water content was calculated using soil bulk density (g/m^3) measurements from each playa at 1 m depth using methods from Elliot et al. (1999). Dried soil samples were mixed with 0.2 µm filtered water at a ratio of 2:1 water to soil. ISA stabilization solution was also added to soil-water mixture. Soil slurries were mixed on a shaker table for 12 hours and filtered. Cl^- was measured (mg/l) from the supernatant using a calibrated Orion ion selective electrode. Average Soil Cl^-

measurements were taken from across 1 – 5 m depths for each playa. To calculate recharge using CMB, I used values of annual precipitation and wet and annual dry deposition values from Jornada LTER data. Mean annual precipitation was calculated from the 100-year record of the centrally-located Jornada weather station. Annual rates of wet and dry Cl^-_p deposition (mg/l) were calculated using a 20-year record (1992-2011). Wet and dry deposition of Cl^-_p were measured monthly at the same centrally-located weather station using AeroChem Metrics collector.

How do catchment-scale variables influence groundwater recharge rates among playas?

I used remotely-sensed data to measure catchment biophysical characteristics for each of the 20 study catchments. Elevation data were used to delineate area and calculate average slope. Satellite NDVI data were used to calculate average vegetation cover. Digital soil maps were used to measure an average soil texture for each playa catchment. I measured the area and slope of each upland catchment by analyzing 5 m resolution digital elevation model data using spatial analyst tools in ArcGIS (ESRI, San Diego, CA). The catchment slope (% gradient) was measured by calculating an average slope value for each catchment. I used the 250 m^2 - resolution Terra MODIS Vegetation Continuous Fields (VCF 051) to determine the annual average percent vegetation cover value for each catchment (DiMiceli et al. 2011). I calculated weighted mean soil texture (% sand, silt, clay) from USDA-NRCS soil survey digital mapping products (Soil Survey Staff). A mean value of soil texture was used for each soil class and a weighted mean was determined using the relative area of each soil class within the catchment.

I used multiple regression analysis to assess how biophysical catchment characteristics were correlated with groundwater recharge in playas. All analyses were

conducted using R version 3.0.2 (R Core Team 2013). Data were determined to be normal, had constant error, and did not display multicollinearity. Non-linear models and interactions among all four variables were also evaluated. The best-fit-model was chosen using Akaike information criterion (AIC) (Kutner 2005). Partial regression plots were constructed to visualize the effect of each independent variable on the dependent variable while holding all other variables constant (Moya-Laraño and Corcobado 2008).

How will climate change influence groundwater recharge beneath playas through changes in rainfall variability and amount?

I quantified annual playa runon using mathematical simulation modelling. I established the relationships between rainfall, playa runon, and playa groundwater recharge using statistical models. I then independently altered 20-year precipitation records to simulate (1) increased precipitation variability and (2) decreased precipitation amount according to different climate-change scenario projections. Using the statistical models, I then calculated how groundwater recharge would change in response to changes in precipitation under different climate change scenarios.

I used the Limburg Soil Erosion Model (LISEM) De Roo et al. (1996) to simulate playa runon for 20 playa catchments over a 20-year period. This model has been used to simulate runoff and soil erosion during and immediately after rainfall events in dryland catchments from 0.1 – 100 km (De Roo and Jetten 1999, Hessel et al. 2006, Baartman et al. 2012, Cuomo et al. 2015). Hydrological equations are detailed in Baartman et al. (2012). Runoff, infiltration, and interception are calculated in LISEM using data from spatially distributed soil, vegetation, and elevation maps for each catchment. Local drainage direction and outlet maps were created from 5-m digital elevation model (DEM)

data using the PCRaster GIS framework (Schmitz et al. 2014). Each catchment drained to one central 5- m^2 pixel at the lowest point of the playa. Soil characteristics for each catchment were derived from USDA NRCS soil survey data (Soil Survey Staff 2016). Using the soil texture sand-to-silt-to-clay ratios for each soil type, I calculated different soil-physical characteristic from literature values (Rawls et al. 1983). Saturated conductivity (mm/hr), soil water tension (cm) and saturated volumetric soil moisture content for each soil type were taken from Rawls et al. (1983). Initial volumetric soil moisture values for the soil types were taken from average Jornada LTER neutron probe measurement for the month of each rainfall event. This sampling design is detailed in Nash et al. (1991). Catchment vegetation was divided into grassland and shrubland based on dominated vegetation of each pixel from Jornada LTER vegetation map (Gibbens et al. 2005). Literature values for Manning's surface resistance to flow (n) and random roughness coefficients and vegetation height (cm) for Chihuahuan desert shrublands and grasslands were used from Weltz et al. (1992). I generated all maps using PCRaster (Karssenberg et al. 2010).

I modelled playa runon using rainfall inputs from Jornada LTER hourly precipitation record 1992-2011. Throughout those 20 years, there were 560 unique rainfall events above 1 mm in size (See supplementary information). To validate the model, I compared model outputs of runon to observed playa flood volume for 14 rainfall events. Modelled runon explained 89% of the observed variability in flood volumes (See supplementary information). I then ran the model for all 560 rainfall events from 1992-2011.

After modelling runon from recent-past precipitation events, I independently evaluated the effect of increased precipitation variability and decreased mean annual precipitation. I used predictions of both precipitation variability and mean from three different CMIP5 representative concentration pathways (RCPs), which represent climate predictions for the year 2100 under different CO_2 emission scenarios (Wuebbles et al. 2014). RCP 4.5 predicts a 2 °C increase in temperature, RCP 6.0 predicts a 4 °C increase in temperature, and RCP 8.5 predicts a 6 °C increase in temperature. I manipulated the 560 rainfall events from my historical 20-year record and generated a new 560-event series for RCP 4.5, RCP 6.0, and RCP 8.5 scenarios. Using the Sun et al. (2007) calculations, I decreased 0-10 mm events by 2% per °C increase. I increased 10-20 mm events by 5%, 20-50 mm events by 6%, and >50 mm events by 7% per °C increase. These changes kept the mean event size constant at 5.56 mm and increased the standard deviation by 5%, 10%, and 15% (See supplementary information). Precipitation amount was predicted to decrease 2% per °C increase in atmospheric temperature (Pierce et al. 2013). To simulate a decrease in mean precipitation for RCP 4.5, RCP 6.0, and RCP 8.5, I reduced the size of all precipitation events by 4%, 8%, and 12%.

I used regression analysis to determine the relationships between playa groundwater recharge (mm/yr) and modelled runon (m^3/yr), as well as the playa runon (m^3/event) and event precipitation (mm/event). I used the rainfall-runon and runon-recharge regression models to calculate how changes in both precipitation variability and mean precipitation amount through changes in precipitation event size.

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Supplementary Information

	Climate	$\bar{x}$ PPT event size (mm)	σ PPT event size (mm)
	Historical	5.56	2.45
Variability	+2 °C	5.56	2.58
	+4 °C	5.56	2.73
	+6 °C	5.56	2.85
Mean	-4% MAP	5.34	2.45
	-8% MAP	5.12	2.45
	-12% MAP	4.89	2.45

Table S1. 20-year precipitation event size mean and variability for historical period and future climate scenarios.

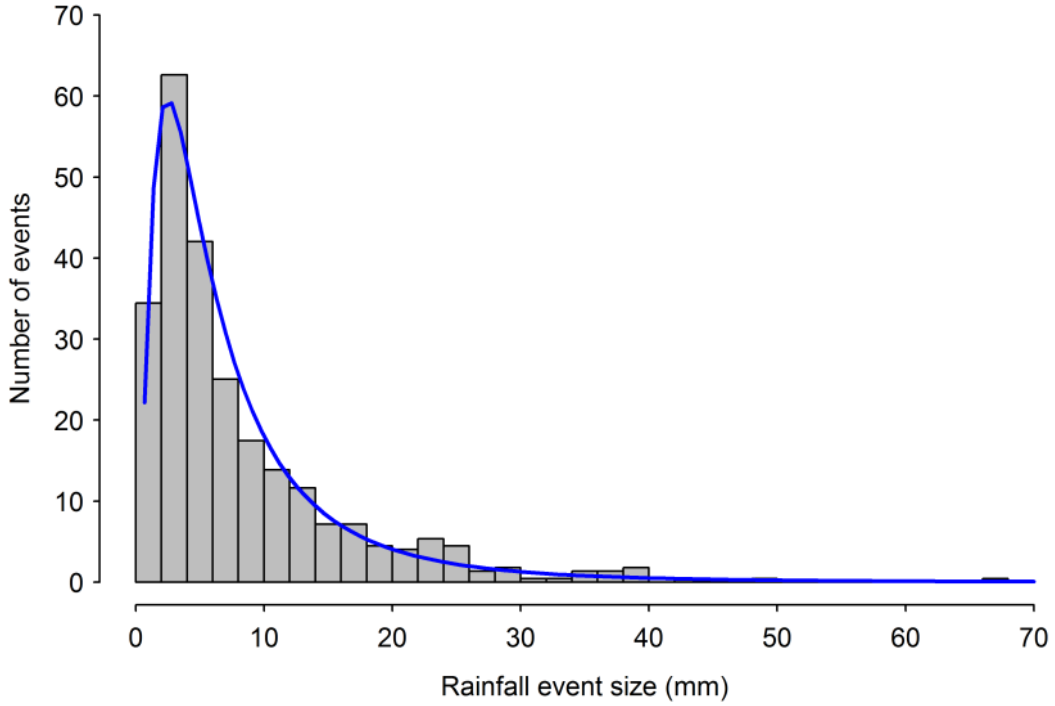


Figure S1. Size distribution of rainfall events at Jornada LTER 1992-2011. Histogram bins are 2 mm in width. Grey bars represent number of rainfall events within a given rainfall size bin. Rainfall events were lognormally distributed, and the blue curve represents the best-fit density function.

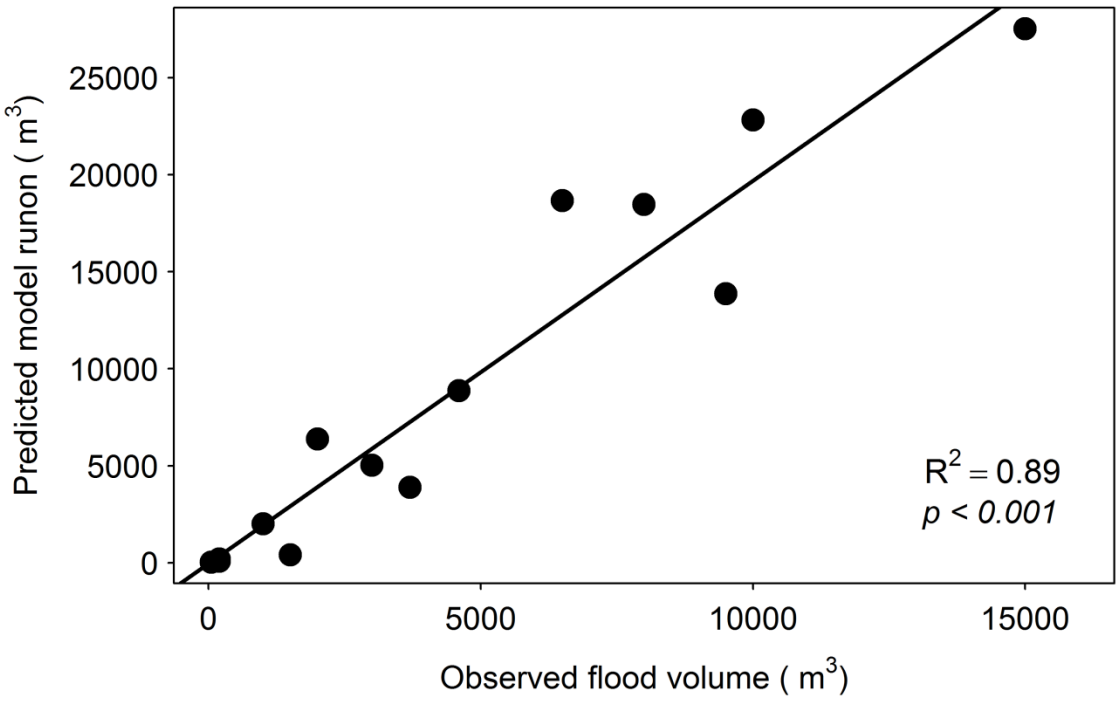


Figure S2. Analysis of predicted model runon vs. observed flood volume. Results of regression analysis for validating hydrologic simulation model. Model predictions of runon were compared to observed flood volumes for the College Playa. Fourteen rainfall events (1999-2011) were used for the validation.

CHAPTER 5- CONCLUSIONS AND SYNTHESIS

The overall objective of my thesis was: to better understand the ecological functioning of and the impact of climate change on desert playa wetlands. I used a multifaceted methodological approach to address different aspects of this objective. My specific objectives focused on improving the understanding of current carbon, nitrogen, and water dynamics in playas and forecasting how they may change in the future. Here, I presented the conclusions and syntheses of the entirety of my thesis research.

My first specific objective was: to understand how playa ecosystems function relative to upland desert ecosystems. In chapter 2, I collected new field data regarding playas and coupled them with existing long-term data regarding upland desert grasslands and shrublands to understand how playas function relative to the upland ecosystems. Specifically, I analyzed how playa productivity and soil resource storage, relative to their area, compared to upland ecosystems. I found that playas were "hotspots," which meant they stored soil organic carbon and nutrients in amounts that were disproportionately higher than their relative area (Chapter 2, Figure 1). Playas were not hotpots of ANPP (Chapter 2, Figure 2), because playas were less productive in very wet years when uplands were most productive (Chapter 2, Figure 3). The effect of wet years stunting playa ANPP was hypothesized to be due to anoxic soil conditions and physical disruption of vegetation communities due to flooding. These results also suggested that a large portion of organic matter and nutrients found in playa soils were delivered from upland ecosystems via sedimentation. I was able to use these soil data to estimate long-term sedimentation rates (Chapter 2, Table 1) as well as use the differences in ANPP, in non-

flood periods, between playas and upland grasslands to estimate runon water inputs to playas (Chapter 2, Figure 4).

My second specific objective was: to determine how catchment biophysical characteristics controlled the ecological functioning of playas. In chapter 3, I combined new soil and GIS-based ecosystem data with existing LTER soil data to address different aspects of this objective. I analyzed how different biophysical characteristics of upland catchments related to playa soil organic carbon and nitrogen stocks across a large number of playas within a desert basin. I also analyzed how differences in soil texture and root distribution between playas and uplands control the vertical distribution of soil organic carbon and nitrogen. I found that catchment vegetation cover was the most important variable for predicting soil organic carbon and nitrogen concentrations in playa soils (Chapter 3, Table 1). Other geomorphic variables, that are known to control runoff, also were found to be important for controlling playa soil resources (Chapter 3, Figure 1). These results indicated that playa soil resource concentrations depended on external allochthonous inputs, and those inputs were controlled by both the amount of organic matter in a catchment and the volume of surface-water runoff that is generated to transport organic matter and other sediments.

Playas also had much higher clay content (Chapter 3, Figure 3) and were dominated by much more shallow-rooted vegetation (Chapter 3, Figure 5) than upland ecosystems. I found that these biophysical differences between uplands and playas caused multiple distinct soil patterns. For example, uplands stored soil resources very evenly through depth and playas stored the majority of their soil resources near the surface. Also,

soil C/N ratios through depth remained constant in playas but increased through depth in uplands (Chapter 3, Figure 4).

My third specific objective was: to estimate the role of desert playas in recharging groundwater recharge and to evaluate how climate change may influence future rates of playa groundwater recharge. In chapter 4, I combined empirical measurements of groundwater recharge with hydrological modelling to address objective 3. I quantified how much playas contribute to groundwater, on an annual basis, and analyzed how different catchment biophysical variables controlled playa groundwater recharge rates. I used hydrological modelling to estimate the relationship between precipitation, playa runon, and playa recharge and then calculated the response of playa groundwater recharge to future changes in precipitation. I concluded that playas contribute to groundwater recharge in desert aquifers (Chapter 4, Figure 1), playa runon is a strong predictor of playa groundwater recharge (Chapter 4, Figure 2), and climate change will have a net-positive impact on groundwater recharge beneath playas (Chapter 4, Figure 5). These findings showed the power of combining empirical and modelling techniques to address complex ecosystem processes and could be useful for land and water managers in southwestern USA.

Ecosystem ecology is an intrinsically interdisciplinary field. On the whole, my thesis research exemplified the complex nature of the ecosystem science by combining concepts and methods from biology, geology, chemistry, and hydrology to understand different patterns and processes relating to desert playas. My thesis results also reinforce the need for long-term ecosystem research through programs such as NSF LTER. Without long-term soil and ANPP records, I could not place playa functioning into the

landscape context. Also, without playa flood records, I would not have been able to have an empirical record to validate the numerical hydrologic model. My thesis provided an example of utilizing a suite of tools, both empirical and modelling based, to address the complexity of an ecosystem. My thesis research also provided a dual contribution of understanding the basic science behind playa ecosystem functioning and developing products that could be useful to rangeland managers. Playas soils can be utilized as a window into the past to track changes in climate and vegetation structure of upland ecosystems. I can conclude that there is now a better understanding of the role of desert playas on the ecosystem level. Playas should be considered in future groundwater, carbon, and nitrogen budgets in drylands.

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APPENDIX I

STATEMENT OF CO-AUTHOR PERMISSION

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The information presented in Chapter 2, Chapter 3, and Chapter 4 of my dissertation has been submitted for review in various peer-reviewed journals. Each journal submission is co-authored by Dr. Osvaldo Sala, my dissertation committee chair. I have received permission from Dr. Sala to include these manuscripts in my dissertation.