



Journal of Geophysical Research: Biogeosciences

RESEARCH ARTICLE

10.1002/2016JG003545

Kev Points:

- Catchment vegetation cover was the most important predictor of soil carbon and nitrogen concentrations among playas
- Upland and playa soil C an N depth distribution correlated with differential rooting patterns
- Upland and playa soil C:N ratio through depth corresponded with soil clay content

Supporting Information:

· Supporting Information S1

Correspondence to:

O. P. McKenna, omckenna@asu.edu

Citation:

McKenna, O. P., and O. E. Sala (2016), Biophysical controls over concentration and depth distribution of soil organic carbon and nitrogen in desert playas, *J. Geophys. Res. Biogeosci.*, 121, 3019–3029, doi:10.1002/2016JG003545.

Received 11 JUL 2016 Accepted 11 NOV 2016 Accepted article online 18 NOV 2016 Published online 15 DEC 2016

Biophysical controls over concentration and depth distribution of soil organic carbon and nitrogen in desert playas

Owen P. McKenna¹ and Osvaldo E. Sala²

¹School of Life Sciences, Arizona State University, Tempe, Arizona, USA, ²School of Life Sciences and School of Sustainability, Arizona State University, Tempe, Arizona, USA

Abstract Playa wetlands are important areas of soil organic carbon and nutrient storage in drylands. We conducted this study to assess how catchment biophysical variables control soil organic carbon and nitrogen in playas and how playas function differently than upland ecosystems. We found that playa organic carbon and nitrogen corresponded primarily with catchment vegetation cover and secondarily with catchment area, slope, and soil texture. The effect of increased organic matter production associated with high catchment vegetation cover overshadowed the potential effect of reduced run-on. We also found soil carbon and nitrogen profiles to be significantly shallower in playas than uplands. This trend is correlated with evidence of sedimentation and shallow-rooted plants in playas. Upland soils had a deeper carbon and nitrogen profile, which correlated with organic matter being generated by deeply rooted vegetation. In playas, C:N ratios remained constant through depth but in uplands, C:N ratios increased through depth. We found evidence that differences in rooting depth distributions and soil texture may explain these C:N variations between uplands and playas. In uplands, clay concentration increased with depth, whereas in playas, clay concentration did not change with depth, which highlighted the important role of sedimentation in these ecosystems. Our results suggest that small changes in playa catchment vegetation cover in response to climate change or grazing intensity would greatly impact playa soil organic carbon and nitrogen stocks. This effect would be due to the playa soils dependence on allochthonous organic matter and the large upland area that drains into playas.

1. Introduction

Playas are ephemerally flooded wetlands located in the topographic low areas of hydrologically closed dryland catchments [*Thomas*, 2011]. Playas area common features of the internally drained endorheic systems of the Basin and Range physiographic province of North America, which makes up most of the Southwestern United States [*Havstad et al.*, 2006]. What makes playas unique are their geographically isolated nature, and when flooded, they contain novel aquatic ecosystems surrounded by upland terrestrial desert ecosystems [*Cohen et al.*, 2016; *Wondzell et al.*, 1996]. There are two major types of playas. Each is classified 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 run-on from the upland areas of their catchments. Flooding of these playas via surface water creates clay-rich soils that are low in salinity and can support a variety of wetland species across many trophic levels [*Smith*, 2003]. Due to frequent flooding and an absence of a water-restrictive petrocalcic soil layer—found in upland areas of most deserts—beneath surface water playas, these playas also have the potential to be areas of groundwater recharge [*Scanlon et al.*, 2012]. In this paper, we focus solely on the functioning of surface water playas.

Playas have been shown to store soil organic carbon and nutrients in quantities ~5 times higher than upland desert ecosystems [Peters and Gibbens, 2006]. Soil organic carbon can accumulate in playas 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 mainly via surface water run-on. Although playas store much more soil organic carbon storage than uplands, on average playas fix autochthonous carbon at similar rates as upland desert ecosystems [Peters et al., 2012]. The long-term ANPP of playas is not different from uplands, but their soil organic carbon stock is much higher, suggesting that the accumulation of soil organic carbon and nutrients in playas is driven by allochthonous sediment inputs from upland ecosystems. Run-on-driven sedimentation also concentrates clay particles

©2016. American Geophysical Union. All Rights Reserved.



in playa soils, which stabilize organic matter and slow the movement of water and air, that reduces the degradative effect of microbes on soil organic matter in playa soils [Peterjohn and Schlesinger, 1990; Wondzell et al., 1996]. The soil catena concept explains that soil resources accumulate in low areas of topographic gradients, such as playas [Schimel et al., 1985]. Although this general concept is qualitatively understood, the quantitative relationship between different biophysical variables and playa soil organic carbon and nitrogen stocks has not been determined. We conducted this study to answer three questions about the differences in soil organic carbon and nitrogen among playas and in relation to upland ecosystems.

1.1. Question 1: How Do Catchment Biophysical Variables Influence Soil Organic Carbon and Nitrogen Concentrations Among Playas?

Being the endpoint of catchment runoff, playas receive substantial allochthonous inputs of organic matter [Smith, 2003]. When climate variables are held constant, allochthonous organic carbon and nitrogen inputs are controlled by two major factors: (1) the amount of water that reaches the playa from across the watershed in the form of surface run-on and (2) the concentration of organic carbon and nitrogen in the run-on water [Brazier et al., 2013].

1.2. Question 2: How Is Soil Organic Carbon and Nitrogen Distributed Through Depth in Playas as Compared to Upland Ecosystems?

We predict that the combination of allochthonous inputs and shallow-rooted plants may concentrate organic carbon and nitrogen at the surface of playa soils. On the contrary, upland soils that generate most of their organic matter locally and are dominated by deeper rooted shrubs will store soil organic carbon and nitrogen more evenly through depth.

1.3. 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 depends on the rate at which organic carbon and nitrogen enter and leave the soil relative to each other. Organic matter inputs to soils can occur both at the surface from aboveground detritus and belowground through root turnover. The resultant soil C:N ratio then depends on soil texture that controls the rate of decomposition and the distribution of roots in the soil profile.

To address Question 1 about how the biophysical characteristics of a catchment control soil organic carbon and nitrogen concentrations in an adjacent playa, we first measured organic carbon and nitrogen in playa soils across a desert basin. Then, we used remotely sensed data to measure elevation, soil, and vegetation characteristics of each playa catchment. To address Question 2 about how soil organic carbon and nitrogen concentrations change through depth, we compared our 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, we took the organic carbon and nitrogen values used to answer Question 2 and compared those values with information on soil texture with depth.

2. Methods

2.1. Study Site

We conducted our research at the 100,000 ha Jornada Basin Long-term Ecological Research Site (JRN). JRN is located in the northern Chihuahuan Desert in SE New Mexico, USA (+32.5 N, -106.8 W). JRN is situated in a typical endorheic 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. JRN is composed of five major plant communities consisting of two different grassland communities and three different shrubland communities. The grassland communities are upland grasslands dominated by Black Grama—Bouteloua eriopoda Torr. (Poac.) and lowland playa grasslands dominated by Tobosa grass—Pleuraphis mutica Buckley (Poac.) and Vine-mesquite grass—Panicum obtusum H.B.K. (Poac.). The upland shrubland communities are Tarbush—Flourensia cernua DC (Aster.) dominated shrublands found on lower piedmont slopes, Creosotebush—Larrea tridentata Larrea tridentata (DC) Cov. (Zygo.) dominated shrublands found on upper piedmont slopes and bajadas, and leguminous Honey Mesquite—Prosopis glandulosa Torr. var. torreyana (Fabac.) dominated shrublands found on the sandy basin floor [Peters, 2013].



Our study focused on the lowland playa grasslands and the upland catchments adjacent to each playa. Ninety-nine distinct playas (<1% of the total basin area) are distributed across JRN [Peters and Gibbens, 2006]. Upland catchments contained both shrubland and grassland communities.

2.2. Playa Soil Carbon, Nitrogen, and Bulk Density

We chose 30 playas from across JRN to measure soil organic carbon and total nitrogen concentrations. We consulted the Jornada Basin landform map and available aerial imagery to choose 30 out of 99 potential playas that encompassed a broad range of sizes, catchment characteristics, and proximities to different geological features [*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, we collected 36 soil samples of 100 g 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 h, homogenized, sieved through 2 mm mesh screen, and frozen before analysis.

We measured soil organic carbon and total nitrogen concentrations using elemental combustion analysis. We first ground homogenized soil subsamples using a ball mill. We then prepared 45 mg of ground soil samples in silver tins. We acid fumigated the soils to eradicate inorganic carbon [Harris et al., 2001]. Lastly, we sealed each fumigated sample and combusted them to estimate organic carbon (g C/g soil) and total nitrogen (g N/g soil) in each soil sample using an ECS 4010 elemental analyzer (Costech Analytical Technologies, Valencia, CA, USA). We also estimated soil bulk density (g/m³) 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), we converted each soil measurement (g/g) to calculate concentrations of organic carbon and nitrogen per unit area (g/m²).

2.3. Characterization of Catchments

We used remotely sensed data to delineate area and calculate average slope, vegetation cover, and soil texture for each of the 30 upland catchments adjacent to our study playas. We measured the area and slope of each upland catchment by analyzing 5 m resolution digital elevation model data using spatial analyst tools in ArcGIS (Environmental Systems Research Institute, San Diego, CA). The catchment slope (% gradient) was calculated by calculating an average slope value for each catchment. We used the 250 m² resolution Terra Moderate Resolution Imaging Spectroradiometer Vegetation Continuous Fields (VCF 051) to determine the annual average percent vegetation cover value for each catchment [DiMiceli et al., 2011]. We calculated weighted mean soil texture (% sand, silt, and clay) from U.S. Department of Agriculture (USDA)-Natural Resources Conservation Service, 2016]. 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.

2.4. 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, and 60–100 cm). These soil samples were taken by JRN staff. Soil sampling was conducted within 12 4900 m² plots representative of the upland ecosystems. Forty-nine soil samples were collected from each plot at each depth. The samples were collected 10 m apart in a 7-by-7 square grid. We averaged the 49 organic carbon (g/g soil) and nitrogen (g/g soil) measurements from each plot, and then we 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/m³) was estimated for each ecosystem type from 10 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/m²) at each depth (m).

2.5. Playa and Upland Rooting Depth Distribution

We 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 3 playas across JRN [Huenneke et al., 2002]. From this 10 year record, we calculated average percent grasses, forbs, and shrubs of playas and upland ecosystems. We used literature values from Gibbens and Lenz [2001] to determine the average rooting depth for grasses, forbs, and shrubs across JRN. These values were used to calculate the slope of the cumulative root fraction through depth for playas and upland ecosystems. This metric is commonly used for comparing rooting depth distributions among ecosystem types [Jackson et al., 1996].

2.6. Playa and Upland Soil Texture

We collected nine soil samples (see section 2.2 for the experimental design) 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 h at 105°C and mixed for 16 h with 100 mL of 50 g/L sodium hexametaphosphate solution. Hydrometer readings were taken at 40 s and 7 h to determine the % sand, silt, and clay of each soil sample [*Bouycous*, 1962]. A mean value of % sand, silt, and clay was calculated from the nine samples collected at each depth. For upland soil texture, we used values of % sand, silt, and clay from USDA-NRCS soil survey data taken from the 12 upland sites across JRN that soil carbon and nitrogen were measured [*Soil Survey Staff, Natural Resources Conservation Service*, 2016]. 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).

2.7. Statistical Analysis

We used multiple regression analysis to assess how biophysical catchment characteristics corresponded to 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. Nonlinear models and interactions between all four variables were also evaluated. The model of best fit 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]. We determined the relative importance of each explanatory variable in the final best fit model using the Lindemann-Merenda-Gold (Img) method for calculating sequentially weighted partial R² [Lindeman et al., 1980]. The Img method used the individual contribution of each explanatory variable by calculating an average coefficient of partial determination for each model permutation. Values for Img were calculated using the "relaimpo" package in R [Gromping, 2006].

We 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 Turkey's honest significant difference (HSD) multiple comparisons test. Soil organic carbon and nitrogen concentrations were standardized (g m $^{-2}$ × 10 cm) for each soil depth class (0–10 cm, 10–30 cm, 30–60 cm, 60–100 cm). We 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.

3. Results

3.1. 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 corresponded with playa organic carbon and nitrogen concentrations:

Organic carbon
$$(g/m^2) = 1222.1 + 19.2 * area (km^2) - 43.9 * soil sand fraction (% sand) + 20.4 * vegetation cover (% cover) (1)$$

Total nitrogen
$$(g/m^2) = 132.3 + 1.9 * area (km^2) - 5.6 * soil sand fraction (% sand) + 4.1 * vegetation cover (% cover) (2)$$

Catchment vegetation cover was the variable that influenced the most soil organic carbon concentrations among playas, explaining 38% of variability (range from 430 to 3800 g/m²). Playa soil organic carbon

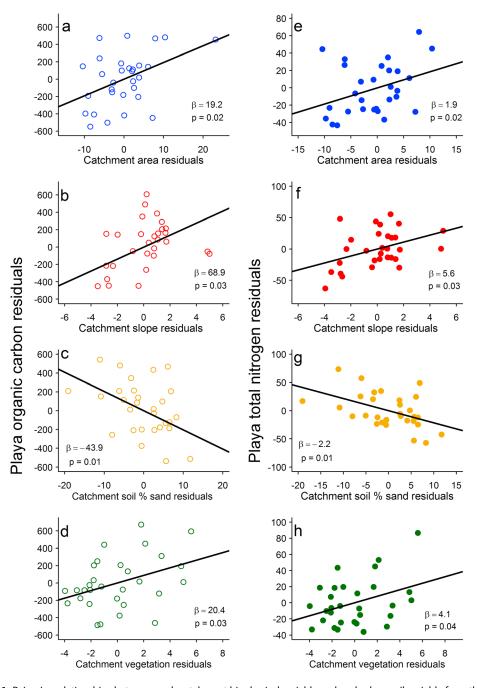


Figure 1. Pair-wise relationships between each catchment biophysical variable and each playa soil variable from the best fit regression models. Partial regression plots were constructed by first regressing the explanatory variable of interest (e.g., catchment vegetation) against all other explanatory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

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^a

		Img Partial R ²	
Explanatory Variable	Range	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

^aValues were calculated using partial coefficient of determination Img analysis. Ranges of each explanatory variable are also listed for reference.

concentration increased by 20 g C/m² for every percentage increased by catchment vegetation cover when all other variables were held constant (equation (1)). The relative contribution of each geomorphic variable in the final organic carbon model was catchment slope (25%), catchment area (22%), and catchment soil texture (15%) (Table 1).

Catchment vegetation cover was also the most important variable correlated with soil total nitrogen concentrations among playas, explaining

43% of variability (range from 30 to 400 g/m²). Playa soil nitrogen concentration increased by 4 g N/m² for every percentage increased by catchment vegetation cover when all other variables were held constant (equation (2)).

The relative contribution of each geomorphic variable in the final nitrogen model was catchment slope (21%), catchment area (21%), and catchment soil texture (14%) (Table 1).

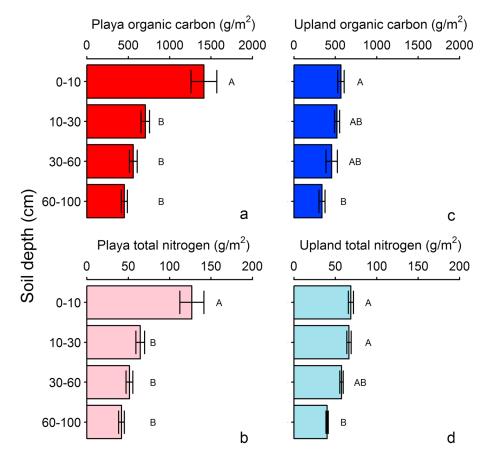


Figure 2. (a and c) Soil organic carbon and (b and d) total nitrogen concentrations in playas (Figures 2a and 2b) and uplands (Figures 2c and 2d) at four soil depths from 0 to 100 cm. Significant differences between soil depths are represented by different letters. Playa soil organic carbon (dark red 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 to 60 cm and significantly decrease below 60 cm. Error bars represent standard error.

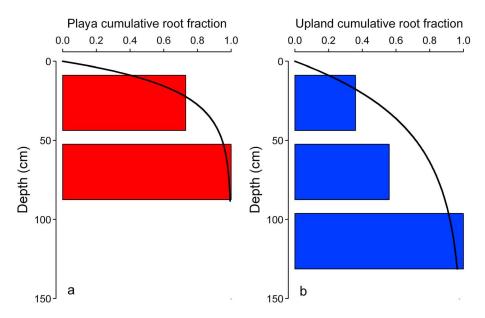


Figure 3. The distribution of root biomass plotted through soil depth for playas and upland ecosystems. (a) The distribution of roots through depth in playas (red bars). Seventy percent of playa roots are found in the top 30 cm of soil and 30% of roots are found between 30 and 80 cm. (b) The distribution of roots through depth in uplands (blue bars). Thirty-five percent of upland roots are found in the top 30 cm, 20% from 30 to 80 cm, and 45% from 80 to 130 cm. Black curves represent continuous rooting distributions through depth for uplands (β = 0.98) and playas (β = 0.94).

3.2. 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 the soil profile 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 to 100 cm. (Figures 2a and 2b). Concentrations of soil organic carbon and nitrogen did not significantly change in playas from 10 to 100 cm. Mean organic carbon and nitrogen values for the top 10 cm were 1400 g C/m² and 130 g N/m². Mean organic carbon and nitrogen values from 10 to 100 cm were 570 g C/m² and 50 g N/m². 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 and 100 cm (p = 0.04) (Figures 2c and 2d). Mean organic carbon and nitrogen values for the top 10 cm of soil were 570 g C/m² and 60 g N/m². Mean organic carbon and nitrogen values from 60 to 100 cm were 340 g C/m² and 30 g N/m².

Differences in organic carbon and nitrogen storage through depth also paralleled the differences in rooting depths of plants in uplands and playas (Figure 3). 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 JRN 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 existed 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 below 80 cm [Gibbens and Lenz, 2001].

3.3. 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

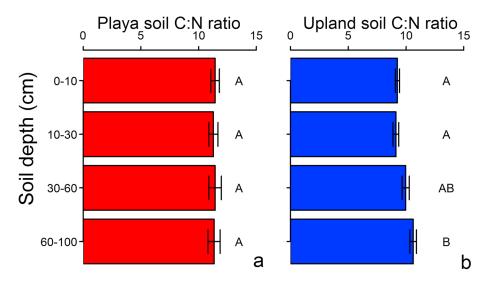


Figure 4. Soil C:N ratio for playa ecosystems and upland ecosystems at four soil depths from 0 to 100 cm. (a) Playa soil C:N ratio (red bars) did not change significantly through depth. (b) Upland soil C:N ratio (blue bars) was significantly greater in deep soil layers than in surface layers. Letters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

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 and the average C:N ratio from 60 to 100 cm was 10.6

Changes in soil C:N ratio through depth in playas and uplands (Figure 4) paralleled changes in soil texture (Figure 5) as well as root distribution (Figure 3). Playa soils were composed, on average, of 34% clay particles and did not statistically change at any soil layer from the surface down to $100 \, \text{cm}$ (Figure 5a). Upland soils increased significantly (p = 0.02) in clay content from 11% in the top $10 \, \text{cm}$ to 20% at $60-100 \, \text{cm}$ depth (Figure 5b).

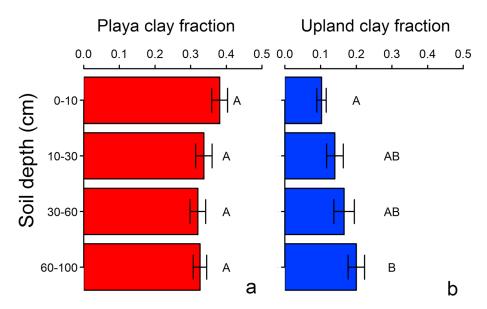


Figure 5. Percent of soil composed of clay for playas and upland ecosystems at four soil depths from 0 to 100 cm. (a) Clay concentration in playa soils (red bars) remained constant through different soil depths. (b) Clay concentration in upland soils (blue bars) increase significantly through depth.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



4. Discussion

Differences in soil organic carbon and nitrogen concentrations among playas were strongly correlated with biophysical variables that are known to control both run-on and allochthonous organic matter production. Most interestingly, we found that vegetation cover in a catchment was positively related to the concentration of soil organic carbon and nitrogen in the adjacent playa (Figure 1d). Catchments with higher vegetation cover are known to have higher amounts of soil organic matter and produce less surface runon [Schlesinger et al., 2000]. These results indicated that organic matter production from upland catchment vegetation was more important to playa soil organic carbon and nitrogen concentration than the physical impediment that vegetation cover had on run-on production [Puigdefabregas, 2005]. We expect that these results may differ in more mesic systems where vegetation cover is greater and has a greater potential to influence runoff production [Bormann et al., 1968]. We also found evidence that geomorphic variables known to control catchment runoff generation—which delivers allochthonous organic matter to playas—also correlated with playa organic carbon and nitrogen concentrations (Figure 1). Our results indicated that larger and steeper catchments with less sandy soils are correlated to playas with greater concentrations of soil organic carbon and nitrogen than playas found in smaller, gradual sloping catchments with sandier soils (Figure 1). The size, slope, and soil texture of a catchment are all known to contribute to runoff production [Vivoni et al., 2006]. Catchment soil sand content is negatively correlated with playa organic carbon and nitrogen (Figure 1), which supports evidence that catchment soil texture influences infiltration and runoff generation [Young et al., 2009]. Sandier soils are most likely allowed for more precipitation to infiltrate in upland soils and less run-on generated into playas.

Playa soils amplified the vegetation signal of uplands and should be used as a window to view past variations of upland vegetation cover. Using radiometric dating techniques on soil cores, scientists should be able to 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 could be indicative of years with 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 with both vegetation rooting depths and the influence of allochthonous inputs to soils. Playas were dominated by shallow-rooted grasses (Figure 3a), and we found evidence that mechanisms known to control allochthonous organic matter production are correlated strongly with the soil organic carbon and nitrogen stocks in playas (Figure 1). Allochthonous inputs to playas would have been deposited on the soil surface, which showed high concentrations of organic carbon and nitrogen in the top 10 cm of soil (Figure 2a). Upland soils had more deeply rooted vegetation that provided autochthonous inputs into deeper layers. These deeply rooted plants in upland ecosystems have been shown to deposit organic carbon and nitrogen at depths well below 1 m [Gibbens and Lenz, 2001]. In upland ecosystems, there has been evidence presented to suggest that surface soil organic matter can be lost due to exports via runoff [Schlesinger et al., 1996]. The presence of deep-rooted shrubs and the absence of allochthonous sediments in upland ecosystems likely resulted in the observed even pool of organic carbon and nitrogen throughout the top 100 cm of the soil profile (Figures 2c and 2d).

The observed increase in C:N ratio through depth in upland soils (Figure 4b) may have been explained by the observed increase in soil clay content through depth (Figure 5b). Clay content is known to be 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]. Upland soil clay content increased through depth, which would cause higher carbon losses in the surface soil layers than in deeper soil layers [Schlesinger and Andrews, 2000]. In playas, a constant C:N ratio with depth (Figure 4a) corresponded with a uniform high clay content throughout the full one meter soil profile (Figure 5a).

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]. Across the Jornada Basin, beginning in the 1850s, there has been a well-documented encroachment of



Prosopis glandulosa into areas that were formally Bouteloua eriopoda grasslands [Gibbens et al., 2005]. Woody plants such as *Prosopis glandulosa* 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]. We found that as the vegetation cover increased across a catchment, so did playa soil organic carbon and nitrogen (Figures 1d and 1h). Despite changes in ecosystem structure and resource heterogeneity, woody plant encroachment is not expected to cause a net change in primary production for arid grasslands of the southwestern U.S. [Knapp et al., 2008]. Based on the results of this study, we concluded that if woody plant encroachment does not change upland biomass production, there most likely will not be an impact on playa organic carbon and nitrogen stocks. However, the identity of the woody invaders may affect the nitrogen content of the sediments flowing into the playas. For example, invasion by Prosopis glandulosa, which is a legume with the capacity to develop symbiotic relationships with microbes that fix atmospheric nitrogen, may result in nitrogen enriched sediments. This phenomenon may not occur when grasslands are invaded by nonleguminous woody plants such as Larrea tridentata and Flourensia cernua.

In addition to woody plant encroachment, climate change is also predicted to affect the southwestern U.S. by lowering mean annual precipitation and increasing interannual precipitation variability [Melillo et al., 2014]. A decrease in mean annual precipitation may cause a decrease in runoff, primary production, and vegetation cover [Sala et al., 2012]. These ecosystem impacts may cause a decrease, according to this study, in the amount of soil organic carbon and nitrogen stored in playas. The predicted increase in interannual 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 interannual precipitation variability may have opposite effects by increasing runoff and reducing vegetation cover. It has been experimentally shown that increased interannual precipitation variability decreased overall vegetation cover in semiarid grasslands [Gherardi and Sala, 2015], which would cause a decrease of allochthonous inputs of organic carbon and nitrogen in playas. In synthesis, the net effect of increased interannual precipitation variability on playa soil organic carbon and nitrogen stocks is still uncertain and will depend on the relative effect of these changes on runoff amount and organic matter concentration in runoff water.

Acknowledgments

We would like to thank Laureano Gherardi, Greg Okin, Josh Haussler, and Kelsey McGurrin for field and lab support. Thanks to Sharon Hall, Curtis Monger, and Dan Childers for invaluable input and contributions to this manuscript. Data sets were provided by the Jornada basin LTER project. Funding for this work was provided by the U.S. National Science Foundation (grant DEB-1235828) and Arizona State University School of Life Sciences. We would also like to thank the Jornada LTER and JER USDA personnel, especially to Debra Peters, Kris Havstad, David Thatcher, Joe Ramirez, and John Anderson for their incredible support. Special thanks to Natalie McKenna for her help with editing this manuscript. The data used are available through Jornada LTER http://jornada.nmsu.edu/ Iter. Additional statistical analysis information is available in supporting information Text S1 and Tables S1 and S2.

References

Anadón, J. D., O. E. Sala, and F. T. Maestre (2014), Climate change will increase savannas at the expense of forests and treeless vegetation in tropical and subtropical Americas, J. Ecol., 102(6), 1363-1373.

Bormann, F. H., G. E. Likens, D. W. Fisher, and R. S. Pierce (1968), Nutrient loss accelerated by clear-cutting of a forest ecosystem, Science, 159(3817), 882-884.

Bouycous, G. (1962), Hydrometer method improved for making particle size analysis of soil, Agron. J., 54, 464-465.

Brazier, R. E., L. Turnbull, J. Wainwright, and R. Bol (2013), Carbon loss by water erosion in drylands: Implications from a study of vegetation change in the south-west USA, Hydrol. Processes, 28(4), 2212-2222.

Bremner, J. M., and C. S. Mulvaney (1996), Methods of soil analysis. Part 3: Chemical methods, in Agronomy, edited by D. L. Sparks et al., pp. 1085-1122. Soil Science Society of America, Inc., Madison.

Cohen, M. J., et al. (2016), Do geographically isolated wetlands influence landscape functions?, Proc. Natl. Acad. Sci. U.S.A., 113(8), 1978-1986.

Craft, C. B., and W. P. Casey (2000), Sediment and nutrient accumulation in floodplain and depressional freshwater wetlands of Georgia, USA, Wetlands, 20(2), 323-332.

DiMiceli, C. M., M. L. Carroll, R. A. Sohlberg, C. Huang, M. C. Hansen, and J. R. G. Townshend (2011), Vegetation Continuous Fields MOD44B, Collection 5, Univ. of Maryland, College Park, Maryland. [Available at http://reverb.echo.nasa.gov/.]

Elliot, E. T., J. W. Heil, E. F. Kelly, and H. C. Monger (1999), Soil structural and other physical properties, in Standard Soil Methods for Long-Term Ecological Research, edited by G. P. Robertson et al., pp. 74–88, Oxford Univ. Press, New York.

Gherardi, L. A., and O. E. Sala (2015), Enhanced precipitation variability decreases grass- and increases shrub-productivity, Proc. Natl. Acad. Sci. U.S.A., 112(41), 12,735-12,740.

Gibbens, R. P., and J. M. Lenz (2001), Root systems of some Chihuahuan Desert plants, J. Arid Environ., 49(2), 221-263.

Gibbens, R. P., R. P. McNeely, K. M. Havstad, R. F. Beck, and B. Nolen (2005), Vegetation changes in the Jornada basin from 1858 to 1998, J. Arid Environ., 61(4), 651-668.

Gromping, U. (2006), Relative importance for linear regression in R: The package relaimpo, J. Stat. Softw., 17(1), 1-27.

Harris, D., W. R. Horwath, and C. van Kessel (2001), Acid fumigation of soils to remove carbonates prior to total organic carbon or carbon-13 isotopic analysis, Soil Sci. Soc. Am. J., 65(6), 1853-1856.

Havstad, K. M., L. F. Huenneke, and W. H. Schlesinger (2006), Structure and Function of a Chihuahuan Desert Ecosystem: The Jornada Basin Long-term Ecological Research Site, 465 pp., Oxford Univ. Press, Oxford, New York.

Huenneke, L. F., J. Anderson, M. Remmenga, and W. H. Schlesinger (2002), Desertification alters patterns of aboveground net primary production in Chihuahuan ecosystems, Global Change Biol., 8(3), 247–264.

Jackson, R. B., J. Canadell, J. R. Ehleringer, H. A. Mooney, O. E. Sala, and E. D. Schulze (1996), A global analysis of root distributions for terrestrial biomes, Oecologia, 108(3), 389-411.

Jobbágy, E. G., and R. B. Jackson (2000), The vertical distribution of soil organic carbon and its relation to climate and vegetation, Ecol. Appl., 10(2), 423-436.



- Knapp, A. K., J. M. Briggs, S. L. Collins, S. R. Archer, M. S. Bret-Harte, B. E. Ewers, D. P. Peters, D. R. Young, G. R. Shaver, and E. Pendall (2008), Shrub encroachment in North American grasslands: Shifts in growth form dominance rapidly alters control of ecosystem carbon inputs, *Global Change Biol.*, 14(3), 615–623.
- Kutner, M. H. (2005), Applied Linear Statistical Models, 5th ed., 1396 pp., McGraw-Hill, Boston, Mass.
- Lindeman, R. H., P. F. Merenda, and R. Z. Gold (1980), *Introduction to Bivariate and Multivariate Analysis*, 444 pp., Scott, Foresman, Glenview, Ill. Mcauliffe, J. R. (1994), Landscape evolution, soil formation, and ecological patterns and processes in Sonoran Desert Bajadas, *Ecol. Monogr.*, 64(2), 111–148.
- Melillo, J. M., T. C. Richmond, and G. W. Yohe (Eds.) (2014), Climate Change Impacts in the United States: The Third National Climate Assessment, 841 pp., U.S. Global Change Research Program, Washington, D. C., doi:10.7930/J0Z31WJ2.
- Moya-Laraño, J., and G. Corcobado (2008), Plotting partial correlation and regression in ecological studies, Web Ecol., 8(1), 35-46.
- Peterjohn, W., and W. Schlesinger (1990), Nitrogen loss from deserts in the southwestern United States, *Biogeochemistry*, 10(1), 67–79.
- Peters, D. P. C. (2013), Appendix 1: Jornada (JRN) (USDA-ARS, LTER), in Long-Term Trends in Ecological Systems: A Basis for Understanding Responses to Global Change, edited by D. P. C. Peters et al., pp. 269–272, United States Department of Agriculture (USDA), Washington, D. C.
- Peters, D. P. C., and R. P. Gibbens (2006), Plant communities in the Jornada Basin: The dynamic landscape, in *Structure and Function of a Chihuahuan Desert Ecosystem: The Jornada Basin Long-Term Ecological Research Site*, edited by K. M. Havstad, L. F. Huenneke, and W. H. Schlesinger, pp. 211–231, Oxford Univ. Press, Oxford, U. K.
- Peters, D. P. C., J. Yao, O. E. Sala, and J. P. Anderson (2012), Directional climate change and potential reversal of desertification in arid and semiarid ecosystems, *Global Change Biol.*, 18, 151–163.
- Puigdefabregas, J. (2005), The role of vegetation patterns in structuring runoff and sediment fluxes in drylands, *Earth Surf. Processes Landforms*, 30(2), 133–147.
- Rosen, M. R. (1994), Paleoclimate and basin evolution of playa systems, Geol. S. Am. S., 289(1), 1–18.
- Sala, O. E., L. Gherardi, L. Reichmann, E. Jobbágy, and D. Peters (2012), Legacies of precipitation fluctuations on primary production: Theory and data synthesis, *Phil. Trans. R. Soc. B*, 367, 3135–3144.
- Scanlon, B. R., C. C. Faunt, L. Longuevergne, R. C. Reedy, W. M. Alley, V. L. McGuire, and P. B. McMahon (2012), Groundwater depletion and sustainability of irrigation in the US High Plains and Central Valley, *Proc. Natl. Acad. Sci. U.S.A.*, 109(24), 9320–9325.
- Schimel, D., M. A. Stillwell, and R. G. Woodmansee (1985), Biogeochemistry of C, N, and P in a soil catena of the Shortgrass Steppe, *Ecology*, 66(1), 276–282.
- Schlesinger, W. H., and J. A. Andrews (2000), Soil respiration and the global carbon cycle, Biogeochemistry, 48(1), 7-20.
- Schlesinger, W. H., T. J. Ward, and J. Anderson (2000), Nutrient losses in runoff from grassland and shrubland habitats in southern New Mexico: II. field plots, *Biogeochemistry*, 49(1), 69–86.
- Schlesinger, W. H., J. A. Raikes, A. E. Hartley, and A. F. Cross (1996), On the spatial pattern of soil nutrients in desert ecosystems, *Ecology*, 77(2), 364–374.
- Smith, L. M. (2003), Playas of the Great Plains, Univ. of Texas Press, Austin, Tex.
- Soil Survey Staff, Natural Resources Conservation Service (2016), Soil Survey Geographic (SSURGO) database. [Available at http://sdmdataaccess.nrcs.usda.gov/.]
- Sollins, P., C. Glassman, E. A. Paul, C. Swanston, K. Lajtha, J. Heil, and T. E. Elliott (1999), Soil carbon and nitrogen pools and fractions, in Standard Soil Methods for Long-Term Ecological Research, edited by G. P. Robertson et al., pp. 89–105, Oxford Univ. Press, New York.
- Sun, Y., S. Solomon, A. Dai, and R. W. Portmann (2007), How often will it rain?, J. Clim., 20(19), 4801-4818.
- Thomas, D. S. G. (2011), Arid Zone Geomorphology: Process, Form and Change in Drylands, 3rd ed., 624 pp., Wiley-Blackwell, Hoboken, N. J. Vivoni, E. R., R. S. Bowman, R. L. Wyckoff, R. T. Jakubowski, and K. E. Richards (2006), Analysis of a monsoon flood event in an ephemeral
- tributary and its downstream hydrologic effects, Water Resour. Res., 42, W03404, doi:10.1029/2005WR004036.
- Vogel, A. L., et al. (2013), In situ submicron organic aerosol characterization at a boreal forest research station during HUMPPA-COPEC 2010 using soft and hard ionization mass spectrometry, *Atmos. Chem. Phys.*, *13*(21), 10,933–10,950.
- Wondzell, S. M., G. L. Cunningham, and D. Bachelet (1996), Relationships between landforms, geomorphic processes, and plant communities on a watershed in the northern Chihuahuan Desert, *Landscape Ecol.*, 11(6), 351–362.
- Yeomans, J. C., and J. M. Bremner (1988), A Rapid and precise method for routine determination of organic-carbon in soil, Commun. Soil Sci. Plant Anal., 19(13), 1467–1476.
- Young, C., B. McEnroe, and A. Rome (2009), Empirical determination of rational method runoff coefficients, J. Hydrol. Eng., 14(12), 1283–1289.