PLAYA WETLAND PLANT AND SOIL RESPONSE TO PREDICTED CLIMATE AND LAND USE CHANGE IN THE SOUTHERN GREAT PLAINS

A Dissertation presented to the Faculty of the Graduate School at the University of Missouri-Columbia

In Partial Fulfillment of the Requirements for the Degree Doctor of Philosophy by

RACHEL K. OWEN

Dr. Keith Goyne, Dissertation Co-Advisor
Dr. Elisabeth Webb, Dissertation Co-Advisor

MAY 2019
The undersigned, appointed by the dean of the Graduate School, have examined the dissertation entitled

PLAYA WETLAND PLANT AND SOIL RESPONSE TO PREDICTED CLIMATE AND LAND USE CHANGE IN THE SOUTHERN GREAT PLAINS

presented by Rachel K. Owen,

a candidate for the degree of doctor of philosophy,

and hereby certify that, in their opinion, it is worthy of acceptance.

____________________________________
Dr. Keith W. Goyne

____________________________________
Dr. Elisabeth B. Webb

____________________________________
Dr. David A. Haukos

____________________________________
Dr. John Kabrick

____________________________________
Dr. Robert Kremer

____________________________________
Dr. Peter Motavalli
To strong women – friends, colleagues, mothers, and daughters – who have paved this path and held me up along the way
ACKNOWLEDGEMENTS

This research was part of the Missouri EPSCoR project, funded by the National Science Foundation under Award #IIA-1355406 and #IIA-1430427. Partial financial support was also provided by USDA-NIFA through Hatch funding (MO-HANR0007). Any opinions, findings, and conclusions or recommendations expressed in this manuscript are those of the authors and do not necessarily reflect the views of the National Science Foundation or USDA-NIFA. The Missouri Cooperative Fish and Wildlife Research Unit is jointly sponsored by the Missouri Department of Conservation, the University of Missouri, the U.S. Fish and Wildlife Service, the U.S. Geological Survey, and the Wildlife Management Institute. Any use of trade, firm or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

This research would not have been possible without the assistance of several groups of people. First, I am appreciative of the landowners in Texas, Darryl Birkenfeldt and Wade Davis, who let me dig countless holes in their playas and to Melanie Hartman and Dr. Warren Conway, who helped me identify playas to sample in Texas. Also, I would like to thank Ted LaGrange and Randy Stutheit at Nebraska Game and Parks who helped me identify waterfowl management areas in the Rainwater Basin that would be suitable sites for my project. Eric Simpson, Janith Chandrasoma, and Amanda Burnett provided lab assistance that was crucial to this research. Additionally, I would like to thank the School of Natural Resources Writing Workshop group for conceptual and technical edits, which greatly improved the quality of these manuscripts.
I would like to further thank my advisers, Dr. Keith Goyne and Dr. Lisa Webb, for their unwavering support throughout my Ph.D. program and helping me become an independent scientist. Additionally, this project would not have been possible without the technical guidance I received from my committee members – Drs. Dave Haukos, Peter Motavalli, John Kabrick, and Bob Kremer. I would also like to thank Dr. Kristen Veum, Dr. Christine Li, and other faculty and staff in the School of Natural Resources for countless hours of support and feedback they provided during my time at University of Missouri. Finally, I would like to thank members of the Webb and Goyne labs who provided lab and field assistance, technical feedback on presentations and manuscripts, and moral support at the HyVee Market Grille every week. I feel blessed to be part of this community of scientists and individuals and will be ever thankful for my time here at Mizzou.
# TABLE OF CONTENTS

**ACKNOWLEDGEMENTS** .................................................................................................................. ii  
**LIST OF FIGURES** ....................................................................................................................... vii  
**LIST OF TABLES** .......................................................................................................................... xii  
**CHAPTER 1: PROJECT JUSTIFICATION** ......................................................................................... 1  
**LITERATURE CITED** ....................................................................................................................... 6  
**CHAPTER 2: FRAMEWORK FOR USING DOWNSCALED CLIMATE MODEL DATA IN ECOLOGICAL EXPERIMENTS TO QUANTIFY PLANT AND SOIL RESPONSES** .................................................................................. 10  
**ABSTRACT** .................................................................................................................................. 10  
**INTRODUCTION** ............................................................................................................................ 11  
**MATERIALS AND METHODS** ....................................................................................................... 15  
  *Future and Historical Climate Data: Background* ................................................................. 15  
  *Future and Historical Climate Data: Approach Utilized* .................................................. 17  
  *Evaluating Plant and Soil Response to Climate Treatments* ............................................... 20  
**RESULTS** ................................................................................................................................... 22  
**DISCUSSION** ............................................................................................................................... 24  
**LITERATURE CITED** ....................................................................................................................... 28  
**TABLES** ...................................................................................................................................... 42  
**FIGURES** ...................................................................................................................................... 44  
**CHAPTER 3: BARNYARDGRASS (ECHINOCHLOA CRUSGALLI) EMERGENCE AND GROWTH IN A CHANGING CLIMATE IN GREAT PLAINS WETLANDS** ............................................................................................................. 51  
**ABSTRACT** .................................................................................................................................. 51  
**INTRODUCTION** ............................................................................................................................ 52  
**METHODS** .................................................................................................................................. 56  
  *Soil collection and sample preparation* .................................................................................... 56  
  *Growth chamber conditions* ...................................................................................................... 59  
  *Data collection* ............................................................................................................................ 59  
  *Statistical analysis* ...................................................................................................................... 60  
**RESULTS** ................................................................................................................................... 61  
  *Plant germination response* ...................................................................................................... 61  
  *Plant survival and growth responses* ....................................................................................... 63  
**DISCUSSION** ............................................................................................................................... 66  
**LITERATURE CITED** ....................................................................................................................... 72
LIST OF FIGURES

**Fig. 2.1.** Suggested flow diagram for using climate model data to create climate treatments for ecological experiments. Because each ecological experiment may have unique research questions and scope, details are intentionally omitted from blue boxes to provide a general framework. Detailed techniques used in this study are described in green boxes, but specific data and methods may not be suitable for all ecological experiments.

**Fig. 2.2.** Overall change between observed (1986-2015) and RCP 4.5 projected (2070-2099) maximum daily temperature values for Nebraska (a) and Texas (b) and minimum daily temperature values for Nebraska (c) and Texas (d) for 19 AOGCMs (see Table 2). Box plots represent the median model (horizontal line), interquartile range of model values (box), range of model values (whiskers), and outliers outside 1.5 interquartile range (dots).

**Fig. 2.3.** Monthly percent change from historical (1986-2015) to projected (2070-2099) for precipitation in Nebraska (a) and Texas (b), and number of days without precipitation for Nebraska (c) and Texas (d) point locations for 19 AOGCMs (Table 2) downscaled using gamma-based quantile mapping. Box plots represent the median model (horizontal line), interquartile range of model values (box), range of model values (whiskers), and outliers outside 1.5 interquartile range (dots).

**Fig. 2.4.** Temperature treatments for a germination study using soil collected in Nebraska (April - a) and Texas (March - b) for historical data and scenarios based on downscaled CMIP5-BCCA atmosphere ocean general circulation models for the RCP 4.5 emission scenarios (2070-2099) – future average, warm future, and cool future. Bars represent daily temperature range.

**Fig. 2.5.** Precipitation treatments for a greenhouse study for soil collected in Nebraska (a) and Texas (b) for historical data and scenarios based on downscaled CMIP5-BCCA atmosphere ocean general circulation models for the RCP 4.5 emission scenarios (2070-2099) – future average, wet future, and dry future. Precipitation treatments followed 28 days of constant moisture to allow for uniform germination conditions.

**Fig. 2.6.** Model predicted germination proportion as a function of climate scenario for Nebraska (a) and Texas (b). Error bars represent a 95% confidence interval. Letters designate differences at p < 0.05.

**Fig. 2.7.** Model predicted sum of nitrate-N and nitrite-N concentration ([NO$_3^-$-N] + [NO$_2^-$-N]) as a function of climate scenario for Nebraska (a) and Texas (b). Error bars represent a 95% confidence interval. Significant differences from historic reference level denoted at p < 0.05 (*), p < 0.01 (**), and p < 0.001 (***) for comparisons within categories separated by dashed lines.
Fig. 3.1. Temperature treatments for a germination study representing early season germination conditions for Nebraska (a) and Texas (b) for historical data and scenarios based on downscaled CMIP5-BCCA downscaled atmosphere ocean general circulation models for the RCP4.5 emission scenarios (2070-2099) – future average, warm future, and cool future. Nebraska conditions were based on historical observations and future projections for the month of April and Texas conditions were based on historical observations and future projections for the month of March. Bars represent daily temperature range that was simulated in the germination chamber.

Fig. 3.2. Model predicted means and 95% confidence interval bars for Barnyardgrass emergence rate (Table 3.2). For Nebraska, emergence percentage was impacted by soil moisture and climate scenario interactions (a; held constant at moderate seed bank density), as well as seed bank density and climate scenario interactions (b; held constant at field capacity moisture). For Texas, Barnyardgrass emergence percentage was impacted by soil moisture and climate scenario interactions (c; held constant at moderate seed bank density) and seed bank density and climate scenario interactions (d; held constant at field capacity moisture). Hosmer-Lemeshow statistics provided no indication of poor fit of logistic regression for Nebraska (p = 0.999) or Texas (p = 0.984). Letters indicate differences among climate scenario treatments within soil moisture or seed bank density treatments at p < 0.05 determined by Tukey pairwise comparisons performed on the log odds ratio scale.

Fig. 3.3. Model predicted mean and 95% confidence intervals for seedling survival between initial germination day (Table 3.2) and experiment day 28. Adjusted survival <4.5 indicates decline in seedling abundance throughout experiment. For Nebraska, adjusted survival was impacted by soil moisture and climate scenario interactions (a, $R^2 = 0.718$). For Texas, adjusted survival was impacted by soil moisture and climate scenario interactions (b, $R^2 = 0.816$) and seed bank density (c, $R^2 = 0.816$). Letters indicate differences among climate scenario treatments within soil moisture or seed bank density treatments at p < 0.05 determined by Tukey pairwise comparisons.

Fig. 3.4. Model predicted mean and 95% confidence intervals for physiological response between initial germination day (Table 3.2) and experiment day 28. For Nebraska, plant height at day 28 was impacted by soil moisture (a, $R^2 = 0.496$) and climate scenario (b, $R^2 = 0.496$). For Texas, holding seed bank density constant, ending plant height was negatively correlated with mean soil temperature (c) for low ($F = 7.531$, p = 0.021, $R^2 = 0.373$), moderate ($F = 9.495$, p = 0.005, $R^2 = 0.270$), and high ($F = 1.986$, p = 0.189, $R^2 = 0.082$) seed bank densities. Texas ending plant height was also affected by climate scenario (d, $R^2 = 0.713$). Letters indicate differences among treatments at p < 0.05 determined by Tukey pairwise comparisons.
Fig. 3.5. Model predicted mean and 95\% confidence intervals for biomass (g tray\(^{-1}\)) response between initial germination day (Table 3.2) and experiment day 28 for Nebraska samples. Total biomass at day 28 was affected by climate scenario (a, \(R^2 = 0.332\)) and seed bank density (b, \(R^2 = 0.332\)), with no interactions. Above-ground biomass (c, \(R^2 = 0.711\)) and below-ground biomass (d, \(R^2 = 0.293\)) were affected by interactions between climate scenario temperatures and soil moistures. Letters indicate differences among climate scenario treatments within soil moisture or seed bank density treatments at p < 0.05 determined by Tukey pairwise comparisons.

Fig. 4.1. Playa locations across the Great Plains. The orange playas indicate the Texas plains playa region of interest and blue playas indicate the rainwater basin playa region of interest. Playas sampled for this experiment are indicated in green. More information on each sample location can be found in Table 4.1.

Fig. 4.2. Historic monthly temperature conditions in Nebraska (solid lines) and Texas (dashed lines) playa regions averaged from 1986-2015 (grey lines). For both greenhouse studies, greenhouse mean daily air temperature was recorded and compared to actual playa temperatures for hydroperiod study in 2016 (red lines) & land use study in 2017 (blue lines).

Fig. 4.3. Precipitation treatments for a greenhouse study for soil collected in Nebraska (a) and Texas (b) playa regions for historic data and scenarios based on downscaled CMIP5-BCCA downscaled atmosphere ocean general circulation models for the RCP4.5 emission scenarios (2070-2099) – future average, wet future, and dry future. Precipitation treatments followed 28 days of constant moisture to allow for uniform germination conditions. Dashed lines indicate breaks in early-, mid-, and late-season germination.

Fig. 4.4. Estimated means and 95\% asymptotic confidence intervals for Nebraska plant abundance (a, \(R^2 = 0.312\)) and species richness (b, \(R^2 = 0.205\)) and Texas plant abundance (c, \(R^2 = 0.417\)) and species richness (d, \(R^2 = 0.250\)) as a function of hydroperiod treatment. Experiment is split into baseline conditions, early season plants (Months 1-2), mid-season plants (Months 3-4), and late season plants (Months 5-6). Interactive effects between season and hydroperiod were significant for abundance, but not for richness. Letters indicate differences among hydroperiod treatments within seasons at p < 0.05 determined by Tukey pairwise comparisons.

Fig. 4.5. Plant species dynamics in response to hydroperiod treatments represented by Ward’s cluster analysis representing similarity between treatments for Nebraska (a) and Texas (b) playas. Plant species identified in hydroperiod study can be found in Appendix 2. Height represents dissimilarity between plant community samples, where 0.0 indicates complete similarity and 1.0 indicates complete dissimilarity. Experiment is split into baseline conditions, early season plants (Months 1-2), mid-season plants (Months 3-4), and late season plants (Months 5-6).
Fig. 4.6. Plant species dynamics in response to hydroperiod treatments represented by principal component analyses between treatments for Nebraska (a) and Texas (b) playas. Plant species identified with wetland indicator status and native status can be found in Appendix 2. Wetland indicator statuses were determined for Great Plains plant region, representing wetland obligate (OBL), facultative wetland (FACW), facultative (FAC), facultative upland (FACU), and upland (UPL) plants. Ellipses represent at 95% confidence interval around the centroid of each hydroperiod treatment.

Fig. 4.7. Estimated means and 95% asymptotic confidence intervals for Nebraska plant abundance (a, $R^2 = 0.589$) and species richness (b, $R^2 = 0.432$) and Texas plant abundance (c, $R^2 = 0.134$) and species richness (d, $R^2 = 0.253$) as a function of nitrogen loading treatment. Experiment is split into baseline conditions, early season plants (Months 1-2), mid-season plants (Months 3-4), and late season plants (Months 5-6). Interactive effects between season and hydroperiod were significant for abundance, but not for richness. Letters indicate differences among hydroperiod treatments within seasons at p < 0.05 determined by Tukey pairwise comparisons.

Fig. 4.8. Plant species dynamics in response to land use change treatments represented by Ward’s cluster analysis representing similarity between treatments for Nebraska and Texas playas. Plant species identified in land use change study can be found in Appendix 2. Height represents dissimilarity between plant community samples, where 0.0 indicates complete similarity and 1.0 indicates complete dissimilarity. Experiment is split into baseline conditions, early season plants (Months 1-2), mid-season plants (Months 3-4), and late season plants (Months 5-6).

Fig. 4.9. Plant species dynamics in response to nitrogen loading treatments represented by principal component analyses between treatments for Nebraska (a) and Texas (b) playas. Plant species identified with wetland indicator status and native status can be found in Appendix 2. Wetland indicator statuses were determined for Great Plains plant region, representing wetland obligate (OBL), facultative wetland (FACW), facultative (FAC), facultative upland (FACU), and upland (UPL) plants. Ellipses represent at 95% confidence interval around the centroid of each nitrogen treatment.

Fig. 5.1. Playa locations across the Great Plains. The orange playas indicate the Texas plains playa region of interest and blue playas indicate the rainwater basin playa region of interest. Playas sampled for this experiment are indicated in green. More information on each sample location can be found in Table 4.1.

Fig. 5.2. Precipitation treatments for a greenhouse study for soil collected in Nebraska (a) and Texas (b) playa regions for historic data and scenarios based on downscaled CMIP5-BCCA downscaled atmosphere ocean general circulation models for the RCP4.5 emission scenarios (2070-2099) – future average, wet future, and dry future. Precipitation treatments followed 28 days of constant moisture to allow for uniform germination conditions. Dashed lines correspond to experiment months 1 to 6 (M1-M6).
Fig. 5.3. Estimated means and 95% confidence intervals for Nebraska soil moisture (a, $R^2 = 0.509$), pH (b, $R^2 = 0.237$), and electrical conductivity (c, $R^2 = 0.234$) and Texas soil moisture (d, $R^2 = 0.519$), pH (e, $R^2 = 0.083$), and electrical conductivity (f, $R^2 = 0.268$) as a function of hydroperiod treatment. Letters indicate differences among hydroperiod treatments within seasons at $p < 0.05$ determined by Tukey pairwise comparisons.

Fig. 5.4. Estimated means and 95% confidence intervals for Nebraska total N (a, $R^2 = 0.166$), NO$_3^-$ + NO$_2^-$-N (b, $R^2 = 0.476$), and NH$_4^+$-N (c, $R^2 = 0.701$) and Texas total N (d, $R^2 = 0.599$), NO$_3^-$ + NO$_2^-$-N (e, $R^2 = 0.614$), and NH$_4^+$-N (f, $R^2 = 0.361$) as a function of hydroperiod treatment. Letters indicate differences among hydroperiod treatments within seasons at $p < 0.05$ determined by Tukey pairwise comparisons.

Fig. 5.5. Estimated means and 95% confidence intervals for Nebraska total organic carbon (a, $R^2 = 0.156$) and Texas total organic carbon (b, $R^2 = 0.116$) as a function of hydroperiod treatment. Letters indicate differences among hydroperiod treatments within seasons at $p < 0.05$ determined by Tukey pairwise comparisons.

Fig. 5.6. Estimated means and 95% confidence intervals for Nebraska (a, $R^2 = 0.429$) and Texas (b, $R^2 = 0.257$) Bray-1 available phosphorus (P) as a function of hydroperiod treatment. Letters indicate differences among hydroperiod treatments within seasons at $p < 0.05$ determined by Tukey pairwise comparisons.

Fig. 5.7. Microbial community dynamics in response to hydroperiod treatments represented by principal component analyses between treatments for Nebraska (a) and Texas (b) playas. Microbial functional groups are described in Table 3.2. Soil variables included bulk density (BD), Bray-1 Phosphorus (BrayP), electrical conductivity (EC), pH, ammonia (NH4), gravimetric moisture (Moisture), total nitrogen (TotalN), total organic carbon (TotalOC), carbon to nitrogen ratio (CN), and nitrate plus nitrite (NO3NO2). Ellipses represent at 95% confidence interval around the centroid of each hydroperiod treatment.

Fig. 5.8. Estimated means (±SE) based on linear mixed effects regression model for Nebraska CO$_2$ (a, $R^2 = 0.082$) and CH$_4$ (b, $R^2 = 0.155$) emissions and Texas CO$_2$ (c, $R^2 = 0.067$) and CH$_4$ (d, $R^2 = 0.115$) emissions over a 22-day oxic incubation study.

Fig. 5.9. Estimated means (±SE) based on linear mixed effects regression model for Nebraska CO$_2$ (a, $R^2 = 0.085$) and CH$_4$ (b, $R^2 = 0.163$) emissions and Texas CO$_2$ (c, $R^2 = 0.037$) and CH$_4$ (d, $R^2 = 0.084$) emissions over a 105-day anoxic incubation study.

Fig. A3.1. Total biomass (a), above-ground biomass (b), and below-ground biomass (c) as a function of average soil temperature between germination day (Table 3.2) and day 28 for Texas samples. Biomass was significantly influenced by climate scenario, but soil moisture and seed bank density were not significant main effects. Regression model significance levels denoted at $p < 0.05$ (*) and $p < 0.01$ (**) and regression equations are listed in Table 3.3.
LIST OF TABLES

Table 2.1. Overview of emission and concentration scenarios for Coupled Model Intercomparison Project (CMIP) 3 and CMIP5 projection datasets, respectively, projected at year 2100 (Meehl et al. 2007, van Vuuren et al. 2011)

Table 2.2. Atmospheric Ocean Global Climate Models (AOGCMs) for CMIP5-BCCA RCP4.5 downscaled data for years 2070-2099 (Reclamation 2013).

Table 3.1. Initial soil conditions (2016) for germination experimental units based on sample location in Nebraska and Texas. Physiochemical soil analyses were completed using standard methods. Unless otherwise noted, samples were collected from publicly-managed playa wetlands. In Nebraska, bulk soil was collected from the moist-vegetation zone which represented Massie silty clay loam (Fine, smectitic, mesic Vertic Argialbolls), Scott silt loam (Fine, smectitic, mesic Vertic Argialbolls), and Fillmore silt loam (Fine, smectitic, mesic Vertic Argialbolls) soil series. Texas bulk soil was also collected from the moist-soil vegetation zone, representing the Randall clay (Very-fine, smectitic, thermic Ustic Epiaquerts) soil series.

Table 3.2. Environmental conditions at initial Barnyardgrass emergence for each climate (historical, future cool, future average, future warm), soil moisture (saturated – SAT, field capacity – FC, drawdown – DD), and seed bank density (65, 145, 400 kg ha\(^{-1}\)) treatment. First day of germination is the experiment day at which germination commenced. Maximum air temperature (T\(_{\text{MAX}}\)), minimum air temperature (T\(_{\text{MIN}}\)), and soil temperature were recorded at emergence. Texas minimum temperatures were lower than growth chamber limits (*).

Table 3.3. Regression equations and 95% confidence intervals for total, above- and below-ground biomass (g tray\(^{-1}\)) collected at the end of 28-day germination study for Texas samples under four climate scenarios. Total biomass was calculated as the sum of above- and below-ground biomass. Significance denoted at p < 0.05 (*) and p < 0.01 (**).

Table 4.1. Landscape and soil characteristics for each playa where soils were collected. Five Texas playas were used for both greenhouse experiments, but Nebraska playas varied due to hydrologic conditions when samples were collected. In Nebraska, soil cores were collected from the moist-vegetation zone which represented Massie silty clay loam (Fine, smectitic, mesic Vertic Argialbolls), Scott silt loam (Fine, smectitic, mesic Vertic Argialbolls), and Fillmore silt loam (Fine, smectitic, mesic Vertic Argialbolls) soil series. Texas soil cores were also collected from the moist-soil vegetation zone, representing the Randall clay (Very-fine, smectitic, thermic Ustic Epiaquerts) soil series.

Table 4.2. Total nitrogen loading rates for land use treatments based on historical cumulative precipitation in Hastings, Nebraska (423.8 mm) and Lubbock, Texas (209.5 mm).
Table 4.3. Estimated means for Nebraska Shannon-Weiner Diversity Index ($R^2 = 0.283$) and Simpson’s Diversity Index ($R^2 = 0.083$) and Texas Shannon-Weiner Diversity Index ($R^2 = 0.247$) and Simpson’s Diversity Index ($R^2 = 0.106$) as a function of hydroperiod treatment. Letters designate differences at $p < 0.05$ relative to historical reference conditions. Experiment is split into baseline conditions, early season plants (Months 1-2), mid-season plants (Months 3-4), and late season plants (Months 5-6). Interactive effects between season and hydroperiod were significant for Texas, but not for Nebraska.

Table 4.4. Estimated means for Nebraska Shannon-Weiner Diversity Index ($R^2 = 0.394$) and Simpson’s Diversity Index ($R^2 = 0.042$) and Texas Shannon-Weiner Diversity Index ($R^2 = 0.307$) and Simpson’s Diversity Index ($R^2 = 0.130$) as a function of nitrogen loading rate treatment. Letters designate differences at $p < 0.05$ relative to historic reference conditions. Diversity is described by Shannon-Weiner Diversity Index (SH) and Simpson’s Diversity Index (SI). Interactive effects between season and nitrogen loading rate were not significant, so diversity is combined across seasons.

Table 4.5. Relative contributions of plant variables in principal component analyses. Coefficients ($\beta$) for each variable included in the principal component analyses describe the relative contribution of that variable on a scale from 0 to 1. Wetland indicator statuses were determined for Great Plains plant region, representing wetland obligate (OBL), facultative wetland (FACW), facultative (FAC), facultative upland (FACU), and upland (UPL) plants.

Table 5.1. Landscape and soil characteristics for each playa where soils were collected. Soil analyses were conducted on surface soils (0-10 cm). In Nebraska, soil cores were collected from the moist-vegetation zone which represented Massie silty clay loam (Fine, smectitic, mesic Vertic Argialbolls), Scott silt loam (Fine, smectitic, mesic Vertic Argialbolls), and Fillmore silt loam (Fine, smectitic, mesic Vertic Argialbolls) soil series. Texas soil cores were also collected from the moist-soil vegetation zone, representing the Randall clay (Very-fine, smectitic, thermic Ustic Epiaquerts) soil series.

Table 5.2. Estimated mean phospholipid fatty acid (PLFA) abundance based on linear mixed effects regression models with hydroperiod treatment as a fixed effect and wetland replicates as random effects to account for variation between samples. Total PLFA is a sum of arbuscular mycorrhizal fungi (A.M. Fungi), gram negative bacteria (Gram Neg.), fungi, gram positive bacteria (Gram Pos.), actinomycetes, and protozoa. Letters denote differences between hydroperiod treatments at $p < 0.05$ within a given state.

Table 5.3. Estimated mean carbon and nitrogen species based on linear mixed effects regression models with hydroperiod treatment and sampling date as fixed effects and wetland replicates as random effects to account for variation between samples. Samples were collected prior to aerobic and anaerobic incubation studies (Pre-Inc.) and after aerobic (AE) and anaerobic (AN) incubation studies for Nebraska and Texas. Uppercase letters denote difference between hydroperiod treatments and lowercase letters denote differences between sampling dates at $p < 0.05$ within a given state.
Table A1.1. Growth chamber programming information. Setting codes d and h represent sunrise and sunset times, respectively, for Hastings, NE (a) and Lubbock, TX (b), with 45 minutes built in to account for dawn and dusk. Maximum and minimum temperatures derived from temperature observation data (Historical) and global climate models (Future) are represented at setting codes d and h respectively. Humidity is based on historic observations from weather stations in Nebraska and Texas. Incandescent and fluorescent lights were turned on and off to mimic outdoor solar radiation.

Table A2.1. Plant species identified in hydroperiod and land use studies. Wetland indicator statuses were determined for Great Plains plant region, representing wetland obligate (OBL), facultative wetland (FACW), facultative (FAC), facultative upland (FACU), and upland (UPL) plants.
CHAPTER 1

PROJECT JUSTIFICATION

Future climate conditions are likely to directly affect ecosystem function and services and may also combine with existing ecosystem threats to exacerbate other anthropogenic pressures (Hughes 2000; Wuethrich 2000; Walther et al. 2002). The Great Plains, USA region is accustomed to extreme weather variability on a seasonal and year-to-year scale; however, this variability is expected to increase by the end of the 21st century (Conant et al. 2018; Kloesel et al. 2018). Regional climate change models for the Great Plains project that mean annual air temperature will increase by 2.0 to 2.8 °C by 2050 and by 2.4 to 4.7 °C by 2100 (Kloesel et al. 2018). Elevated temperatures are expected to increase evapotranspiration in wetlands (Winter 2000) and may induce land use changes in the surrounding landscape, such as relative shifts between croplands and grasslands depending upon water availability (Kukal and Irmak 2018). Regional climate models also project that precipitation events in the Great Plains will become more variable and intense, leading to extended periods of drought and flooding (Melillo et al. 2014; Kloesel et al. 2018). While Great Plains ecosystems and native plant and animal species have co-evolved with extreme temporal weather variability, they may be affected by increased variability expected with projected climate change (Matthews 2008; Uden et al. 2015; Sofaer et al. 2016; Reese and Skagen 2017).

Playas are small, shallow, recharge wetlands located throughout the High Plains region that rely entirely on precipitation and runoff from the surrounding watershed for inundation (Smith 2003). Playa size and density are greatest on the Texas High Plains; however, playas are distributed as far north as Nebraska (Figure 4.1). Average playa area
is 6.3 ha, and 87% of playas are less than 12 ha in Texas (Guthery and Bryant 1982). While playas make up only 2% of the land area in the southern High Plains of the southwestern Great Plains and even less in central and northern High Plains (Haukos and Smith 1994), they provide crucial ecosystem functions, including groundwater recharge (Gurdak and Roe 2010; McKenna and Sala 2017), wildlife habitat (Johnson 2011; Smith et al. 2011), and biogeochemical cycling (McKenna and Sala 2016; Villa and Bernal 2017; Howell et al. 2019). Playas are able to provide these ecosystem services due to unique biotic and abiotic properties, such as hydrophytic vegetation (Gilbert 1989; Haukos and Smith 2004), shrink-swell soils (Allen et al. 1972), and isolated watershed hydrology (O’Connell et al. 2012; Tang et al. 2017).

Playa functions will likely be altered by changes in precipitation and temperature associated with climate change (Matthews 2008; Uden et al. 2015). Interactions between temperature and precipitation drive playa hydroperiod, thus changes in climate dynamics will affect the duration, timing, and frequency of inundation, moist-soil, and dry ecological states within playas (Bartuszevige et al. 2012). Variable hydroperiods across the landscape allow playas to support a broad range of plant and animal species that require hydric soil or standing water as part of their life history strategies (Smith 2003). Any shifts in spatial or temporal hydroperiod variability are likely to have consequences on floral and faunal diversity on the High Plains (Smith et al. 2011). While several field-scale and controlled studies have evaluated playa vegetative communities (e.g., Haukos and Smith 2004; Haukos and Smith 2006), landscape factors contributing to sedimentation and inundation (e.g., Bartuszevige et al. 2012; O’Connell et al. 2012), and dependent faunal taxa (e.g., Anderson and Smith 2000; Webb et al. 2010), very few
researchers have studied playa soil ecosystems (Smith 2003). Further, a dearth of literature exists on how playas will respond to changing climate conditions, especially compared to the abundance of literature for wetlands in the adjacent Prairie Pothole region of the northern Great Plains.

To assess potential risks to playas in a changing climate, we addressed the following objectives: (1) quantify effects of changing climatic conditions on plant germination and community composition, soil chemistry, greenhouse gas emissions, and microbial community and structure; (2) compare ecosystem response to changing climatic conditions between Northern (Nebraska) and Southern (Texas) playa soils; and (3) assess effects of increased agricultural nitrogen inputs on playa plant communities. The research included four experiments with various temperature, hydroperiod, and nitrogen treatments to simulate climate and land use change projections. In the first study, a temperature-controlled growth chamber experiment was used to evaluate treatment effects on early season germination and growth of Barnyardgrass (*Echinochloa crusgalli*), a common moist-soil playa plant. A six-month greenhouse experiment was conducted to quantify hydroperiod treatment effects on seed bank plant community composition and soil biogeochemical properties. Using soils collected from the six-month greenhouse experiment, an incubation study was conducted to assess greenhouse gas emissions from playa soils under various hydroperiod conditions. Finally, a second greenhouse study was conducted to evaluate the effect of increased N inputs on playa plant community composition.

In Chapter 2, we discuss the germination experiment, which was conducted to assess potential effects of changing temperature and precipitation on moist-soil plant
communities in playas. We used a temperature-controlled growth chamber experiment to evaluate germination and growth response of a common playa moist-soil plant, Barnyardgrass (*Echinochloa crusgalli* L.), to three main effects: (i) weekly temperatures representing historical and future conditions, (ii) dry, moist, and saturated soil moisture conditions, and (iii) various seed bank densities. Our objective was to identify conditions most favorable for playa plant germination by evaluating response to various environmental conditions specific to the Northern (Nebraska) and Southern (Texas) extent of playas.

Chapter 3 combines results from the first and second greenhouse studies. These studies focused on quantifying changes in playa wetland plant community composition associated with predicted changes in precipitation and land use in the Great Plains. We conducted two six-month greenhouse studies using intact mesocosms collected from playas in Nebraska and Texas. Precipitation treatments derived from historical observations and three future CMIP5 RCP4.5 downscaled climate projections were applied to mesocosms and plant response was evaluated during the first greenhouse study. Land use treatments were represented by NH$_4$NO$_3$ applications ranging from 0 to 100 mg-N L$^{-1}$ with each precipitation event under historical rainfall patterns during the second greenhouse study.

In Chapter 4, we focused on examining various aspects of carbon (C), nitrogen (N), and phosphorus (P) cycles. We monitored soil organic C (TOC) and total N (TN), nitrate (NO$_3^-$), nitrite (NO$_2^-$), ammonium (NH$_4^+$), and Bray-1 available P (Bray P1) monthly during a six-month greenhouse experiment where samples were subjected to precipitation treatments simulating historical precipitation patterns (1986-2015) and three future
precipitation projections (2070-2099) derived from CMIP5 RCP4.5 global climate models. Soil microbial communities within the mesocosms were assessed using phospholipid fatty acid (PLFA) methods at the end of the six-month greenhouse experiment. An incubation experiment using soil collected at the end of the six-month trial was used to measure carbon dioxide (CO₂) and methane (CH₄) emissions under oxic and anoxic soil moisture conditions.

Chapters were written with the intent to publish in peer-reviewed journals, thus some introductory materials and figures are repeated throughout this dissertation and an independent literature cited section follows each chapter. Additionally, all writing uses plural nouns “we” and “our” to reflect the collaboration of co-authors.
LITERATURE CITED


Gilbert MC (1989) Ordination and mapping of wetland communities in Nebraska’s Rainwater Basin region. U.S Corps of Engineers, Omaha, NE.


CHAPTER 2

FRAMEWORK FOR USING DOWNSCALED CLIMATE MODEL DATA IN ECOLOGICAL EXPERIMENTS TO QUANTIFY PLANT AND SOIL RESPONSES

ABSTRACT

Soil and plant responses to climate change can be quantified in controlled settings. However, the complexity of projected climate data often leads researchers to evaluate ecosystem response based on general trends, rather than specific climate model outputs. Climate projections capture spatial and temporal climate extremes and variability that are lost when using mean climate trends. In addition, application of projected climate data in experimental settings remains limited. Our objective was to develop a framework to incorporate statistically downscaled climate model projections into the design of temperature and precipitation treatments for ecological experiments. To demonstrate the utility of experimental treatments derived from climate projections, we used wetlands in the Great Plains as a model ecosystem for evaluating plant and soil responses. Spatial and temporal data were selected to capture variability and intensity of projected future conditions for exemplary purposes. To illustrate climate projection application for ecological experiments, we developed temperature and precipitation treatments based on moderate emission scenario climate outputs (i.e., RCP 4.5 – 650 ppm CO₂ equivalent). Our temperature treatments captured weekly, end-of-century trends that represented cool, average, and warm temperature predictions, and our daily precipitation treatments mimicked various seasonal precipitation trends and extreme events projected for the late 21st century. Treatments were then applied within two short-term controlled experiments.
evaluating 1) plant germination (temperature treatment applied in growth chamber) and 2) soil nitrogen cycling (precipitation treatment applied in greenhouse) responses to projected future conditions in Great Plains. Our approach provides flexibility for selecting appropriate and precise climate data to design experimental treatments. Using these techniques, ecologists can better incorporate variation in climate model projections for experimentally evaluating ecosystem responses to future climate conditions, reduce uncertainty in predictive ecological models, and apply predicted outcomes when making management and policy decisions.

**INTRODUCTION**

Ecosystems face substantial threats due to increased atmospheric greenhouse gas concentrations and, subsequently, global climate change (Hughes 2000, Wuethrich 2000, Walther et al. 2002). Impacts of increasing global mean temperature, shifting precipitation patterns, and increased frequency and severity of extreme precipitation events have been documented in terrestrial, aquatic, natural, and anthropogenic ecosystems, and the consequences of climate change will likely be exacerbated in the 21st century (IPCC 2014, Melillo et al. 2014). Declines in soil moisture and increased temperature have decreased net primary production and biodiversity in terrestrial ecosystems, simultaneously reducing forest and grassland capacity to store carbon in vegetative biomass (Polley et al. 2013, Peñuelas et al. 2017). Aquatic flora and fauna have been impacted directly by atmospheric warming (Covich et al. 1997, Poff et al. 2002), and have experienced climate change effects associated with alterations to surrounding terrestrial ecosystems (Meyer et al. 1999). In addition to altering the physical environment of ecosystems, global climate change is likely to have a cascading influence
on organisms (humans and wildlife, alike) that rely on ecosystems services such as food resources (Briske et al. 2015, Howard et al. 2018), refugia (Parmesan and Yohe 2003, Root et al. 2003, Haddad et al. 2015), and water supply and quality (Meyer et al. 1999, Gosling and Arnell 2016, Vörösmarty et al. 2016).

Broad landscape-scale changes in natural ecosystems will likely be driven by small-scale changes to vegetation and soil processes, such as plant community composition and function, respiration, gas emissions, and biogeochemical cycling. Plant diversity is expected to decline (Bellard et al. 2012), causing phenotypical changes, shifts in distribution, and possible extinction for some taxa (Thuiller et al. 2005, Kelly and Goulden 2008). However, plant production is expected to increase with elevated atmospheric CO$_2$ (Parton et al. 1995, Kukal and Irmak 2018). Ecosystem carbon flux, based on the balance between photosynthesis and respiration is controlled by atmospheric CO$_2$ levels, temperature, and nutrient availability, may respond variably to changing climate drivers (Raich and Tufekciogul 2000, Schlesinger and Andrews 2000, Ryan 2008). Nitrogen cycling is also expected to be impacted by climate drivers, but to a lesser extent than carbon cycling (Pastor and Post 1986, Vitousek et al. 1997, Galloway et al. 2004). While trends have been observed over the past 40 years in a changing climate, it is much more challenging to predict how plant and soil processes may be impacted in the coming decades.

When field observations are not readily accessible, such as under future climate scenarios, plant and soil responses to changing conditions can be predicted using models generated by combining measured responses of natural systems (e.g., plant community composition, soil respiration, etc.) under simulated climate drivers such as increased

Environmental conditions expected to occur with projected climate change can, to a certain extent, be simulated in controlled settings to better identify soil and plant process responses (Stewart et al. 2013, Medlyn et al. 2015). Controlled experiments allow researchers to hold environmental variables constant and observe the effects of specific climate drivers on a variable of interest (e.g., CH$_4$ emissions, primary production, organic carbon fractionation, species richness, etc.). Experiments of this type are typically conducted in greenhouses, growth chambers, constructed facilities, or in field settings where environmental variables can be manipulated (e.g., rainout shelters for drought studies). Experiments conducted in controlled environments have been used to evaluate impacts of climate change in terrestrial (Fay et al. 2008, Harden et al. 2017) and aquatic settings (Weltzin et al. 2000, Sommer and Lengfellner 2008). However, most studies fail to capture temporal variability associated with future temperature and precipitation scenarios. Instead, studies commonly increase or decrease variables to achieve mean projected values for the duration of an experiment. With increased accessibility to climate projection data, it is likely advantageous for experimental scientists to use atmospheric-oceanic global climate model (AOGCM) output to design experiments and evaluate

Our objective was to develop a framework for creating empirical data-derived treatments that can be used in controlled experiments evaluating plant and soil responses to projected climate change. To demonstrate application of this framework, we evaluated plant germination and soil nitrogen cycles in simulated playa wetland mesocosm units. Playa wetlands are ubiquitous throughout the Southern Great Plains, U.S.A. and provide crucial ecosystem services to the region, such as aquifer recharge, wildlife habitat, nutrient filtration from agricultural runoff, and floral and faunal biodiversity (Smith 2003, Smith et al. 2011). Great Plains climate is characterized as highly variable (Melillo et al. 2014) and differs between the northern (Nebraska) and southern (Texas) extent of the playa region. We predicted that playa plant and soil processes may readily adapt to extreme conditions of the future. However, even slight perturbations to plant and soil function could have detrimental impacts when combined with other anthropogenic threats to playas (e.g., sedimentation, invasive species encroachment, hydrologic modification) (Matthews 2008, Bartuszevige et al. 2012, Johnson et al. 2012, Tsai et al. 2012). While our experimental work is ongoing, here we present a proof of concept with selected results comparing historical climate conditions with three sets of future climate conditions for two locations in the playa region. We selected Nebraska and Texas in order to capture latitudinal differences in playa wetland and climate characteristics within the Great Plains.
MATERIALS AND METHODS

Future and Historical Climate Data: Background

Several institutions worldwide archive output from atmosphere-ocean global climate models (AOGCMs), more commonly referred to as global climate models (GCMs). Climate data used to inform the IPCC Fourth and Fifth Assessment Reports are known as Coupled Model Intercomparison Project phase 3 (CMIP3), and phase 5 (CMIP5), respectively. Statistically downscaled climate projections from CMIP3 and CMIP5 are available for several future time-periods through the end of the 21st century and may be accessed at https://gdo-dcp.ucllnl.org/downscaled_cmip_projections/dcpInterface.html (Reclamation 2013) or https://cida.usgs.gov/gdp/ (Blodgett et al. 2011). The use of these projections by researchers and decision-makers can assist with evaluating impacts of climate change through controlled experiments (Maurer et al. 2007). Emission scenario terminology differs based on CMIP phase (Table A1.1), and CMIP3 data are available in monthly time frames and CMIP5 data may be obtained in monthly or daily time frames. Spatially, statistically downscaled CMIP3 and CMIP5 datasets are 12-km in resolution; however, atmospheric scientists often statistically downscale datasets to local scales (< 1-km resolution) to capture details that may be lost during spatial averaging of gridded data (Wood and Leung 2004). Temperature attributes vary slightly between CMIP3 (average daily temperature) and CMIP5 (daily minimum and maximum temperatures) datasets; whereas, precipitation (mm/day) is reported similarly for CMIP3 and CMIP5 data.

Statistical downscaling can be used to adjust climate data (e.g., precipitation and temperature) based on bias found between projected and observed values during a period of historical observation at a given spatial location (Gutmann et al. 2014). The spatial and
temporal extent of projection data dictate the appropriate downscaling method (Teutschbein and Seibert 2012, Kim et al. 2015). Monthly CMIP3 and CMIP5 data, available at Reclamation (2013) or Blodgett et al. (2011), are typically downscaled using bias corrected spatial disaggregation (BCSD) methods, and daily data are downscaled using bias correction constructed analogs (BCCA) methods (Maurer and Hidalgo 2008). Daily CMIP5 data may also be downscaled using localized constructed analogs (LOCA) (Pierce et al. 2015). Daily projection data using CMIP5 BCCA and LOCA produce fairly comparable daily downscaled temperature data, except in arid regions; whereas, LOCA projects spatial precipitation data more accurately than BCCA (Maurer and Hidalgo 2008, Pierce et al. 2014).

Climate model projection data are widely available for use, but understanding the types of data available and maximizing the appropriateness of projection data manipulations is necessary to accurately evaluate ecosystem responses to climate change (Beaumont et al. 2008, Barsugli et al. 2013). When downloading climate projection data, it is important to obtain historical and future data projections for each AOGCM output to curate data. Complementary historical observation data can be found through the National Centers for Environmental Information (NCEI; https://www.ncdc.noaa.gov/cdo-web/datatools/findstation), formerly the National Climatic Data Center (NCDC). We used a long-term dataset (> 30 years) of historical observations for Hastings, Nebraska (GHCND:USC00253660) and Lubbock, Texas (GHCND:USC00415410) to represent historical climate conditions.

Once historical observations and model projections are obtained, projected future climate data may be corrected for bias before being used to design experimental
ecological treatments. Temperature and precipitation data are most accurately corrected for local bias separately due to inherent differences in their distributions (Schoof and Pryor 2001). Temperature can typically be corrected to match monthly mean historical and projected temperature values using a delta correction method (Quilbé et al. 2008); however, more complex correction methods are appropriate if delta correction methods reduce variability in temperature projections. Several bias correction methods incorporating parametric or nonparametric transformations can be used to correct precipitation data (Gudmundsson et al. 2012, Lafon et al. 2013). Parametric bias correction methods may be appropriate for monthly precipitation data, but due to the gamma distribution of daily precipitation data (Richardson 1981), nonparametric transformations better capture the error associated with climate projections (Gudmundsson et al. 2012). Empirical quantile mapping and gamma-based (rainfall distribution) quantile mapping are two nonparametric bias correction methods commonly used to adjust daily precipitation predictions from regional climate model outputs (Lafon et al. 2013). Gamma-based quantile mapping has been reported as less sensitive to differences in climate projection time frame and emission scenarios, when compared to empirical quantile mapping (Lafon et al. 2013).

*Future and Historical Climate Data: Approach Utilized*

Great Plains playa wetlands served as a model ecosystem to demonstrate how climate model projections may be used to predict plant and soil response to future climate conditions. The framework we developed to create empirical data-derived treatments for use in controlled experiments is summarized in Figure A1.1. For all future climate projections, we aimed to capture variability within a given climate scenario, rather than
assess variability associated with low, moderate, and high emissions scenarios. A
moderate emissions scenario, CMIP5 RCP4.5, was selected to assess the impact of future
climatic conditions on our model ecosystem. Within RCP4.5, we selected models that
captured within-senario variability. For instance, models for temperature studies
represented cool, average, and warm projections for RCP4.5 and models selected for
precipitation studies represented relatively dry, average, and wet projections for RCP4.5.
Within-emission scenario variability for nineteen AOGCMs which met our selection
criteria for two locations in the playa wetlands can be observed in Figures A1.2 and A1.3.

Our first experimental study involved evaluating the influence of global climate
change induced temperature alterations on playa plant germination. Therefore, we
applied our framework for using downscaled climate model data to develop temperature
treatments from local weather station data (historical climate – 1986-2015) and three
CMIP5-BCCA AOGCMs for the RCP4.5 emission scenario (2070-2099) that could be
imposed within a temperature-controlled growth chamber.

Projected climate data were downscaled to a specific location in the playa regions of
Nebraska (GHCND:US00253660; 40.608, 98.427) and Texas (GHCND:USC00415410;
33.657, 101.824) using delta correction techniques (Quilbé et al. 2008), which is
commonly used to adjust temperature data. We assessed daily temperature maximum
(Tmax) and minimum (Tmin) values from nineteen AOGCMs (Table A1.2) and selected
the following three models to capture variability within the RCP4.5 emission scenario: 1)
least temperature change from historical climate (considering average monthly maximum
and minimum temperature values for Nebraska and Texas); 2) greatest temperature
change from historical climate; and 3) a model which represents the average temperature
change across the AOGCMs assessed. We used historical and projected 30-year average daily maximum and minimum temperatures reported for each model to develop experimental treatments. We aggregated daily temperature data into weekly treatments to simulate temporal conditions over the first four weeks of germination (e.g., 30-year average Tmax from March 1-7 for Texas location were averaged to create Week 1 Tmax treatment conditions; 30-year average Tmin from March 1-7 for Texas location were averaged to create Week 1 Tmin temperature conditions, etc.). Growth chamber settings reflected diurnal temperature cycles for the months of April and March for Nebraska and Texas, respectively (Appendix 2). Four climatic temperature treatments (historical, future cool, future average, and future warm) were represented in four-week germination studies, separated by state (Figure A1.4). Because playa plant germination is primarily driven by soil moisture (Haukos and Smith 2001) and heat units (Swanton et al. 2000), we did not incorporate daily temperature variability in our experimental design; however, this approach may not be suitable for every ecological experiment.

Our second experiment involved assessing the impact of precipitation changes on soil nitrogen cycling within wetlands of the Great Plains. To develop appropriate precipitation/hydrologic treatments that would simulate future climate projections and could be used in a greenhouse setting, we once again applied our framework for using downscaled climate model data to develop appropriate treatments. Treatments were based on historical precipitation patterns (1986-2015) and future precipitation projections (2070-2099) using CMIP5-BCCA AOGCMs for the RCP4.5 emission scenario for the wetland growing season (April to October).
We corrected precipitation data from nineteen AOGCMs (Table A1.2) to remove excess drizzle days (<0.25 mm precipitation) and used gamma-based quantile mapping to accurately capture extreme events (Teutschbein and Seibert 2012, Gautam et al. 2018). We selected gamma-based quantile mapping as a bias correction technique as it has been reported as less sensitive to differences in climate projection time frame and emission scenarios, when compared to empirical quantile mapping (Lafon et al. 2013). Comprehensive bias correction details for precipitation adjustments can be found in Gautam et al. (2018). After adjusting projected output data, we selected three models based on the following criteria: 1) an average model, representing the most typical precipitation conditions projected in RCP4.5 scenarios; 2) a model that contained the longest period of no-precipitation days over the course of the growing season; and 3) a model that contained the greatest number of runoff-inducing precipitation events (Uden et al. 2015) during the growing season. We then used projected precipitation data to determine the timing and amounts of water applied to experimental units as a means to simulate altered hydropersiods during the dominant growing season (April 1 – October 31). For historical and future data, we empirically selected a year with the lowest deviation from average model conditions over the wetland growing season. By selecting a representative future year, we could simulate drought events and inherent daily precipitation variability within our greenhouse study, thus simulating temporal variation in playa hydroperiod conditions (Figure A1.5).

_Evaluating Plant and Soil Response to Climate Treatments_

**Germination Experiment:** The germination study was conducted to evaluate the response of playa wetland vegetation to changing climate conditions. Temperature
treatments consisted of weekly aggregated temperatures for historical, future cool, future average, and future warm temperatures as described previously. Bulk soil was collected from the surface 15-cm in transitional zones (between basin floor and upland) in six playa wetlands, three in Nebraska and three in Texas. Soil was dried at 23 °C, ground to pass through 2 mm sieve, and homogenized for each wetland separately. Prior to the germination study, soils were packed into containers at a bulk density representative for each wetland, as determined by core samples collected on site. For each four-week temperature period in the germination study, we held soil moisture constant at 60% water-filled pore space and planted barnyardgrass (Echinochloa crusgali L.) seed at a density of 145 kg ha\(^{-1}\). We counted germinated plants on the first day of germination and on the last day of each four-week experiment. We used generalized mixed effects logistic regression models to test the effect of temperature on germination percentage (fitted with a binomial distribution) with random intercept term fit for sampling location. Analyses were conducted in R software package lme4 (Bates et al. 2015) and package effects and ggplot2 were used to visualize predicted germination percentage with regression model estimates (Fox 2003, Wickham 2016).

Soil Nitrogen Cycling Experiment: To assess how projected climate change will affect playa soil nitrogen cycling, we conducted a greenhouse experiment to mimic the growing season in Nebraska and Texas playas under various hydrologic conditions. Intact soil cores collected from transition zones around the outer rim of ten playas were subjected to four climate treatments (historical, future wet, future average, and future cool) described previously. Precipitation treatments were applied daily to reflect historical and projected future daily rainfall events (mm/day). We were unable to control
for temperature or atmospheric CO$_2$ in greenhouse settings; however, soil and ambient air temperatures were continuously monitored throughout experiment (Supplemental Information 2). Monthly soil samples were collected to assess shifts in biogeochemical cycling. To demonstrate the utility of assessing biogeochemical response using climate projections, we present inorganic nitrogen results. Nitrate (NO$_3$-N) and nitrite (NO$_2$-N) were extracted using 1 M potassium chloride solution (Reddy et al. 2013) and quantified using Lachat QuickChem Methods for nitrate determination (Lachat Instruments, Milwaukee, WI). Statistical analyses were completed using repeated measures mixed-effects linear models in R software package lme4 (Bates et al. 2015). Packages effects and ggplot2 were used to visualize predicted inorganic nitrogen with regression model estimates (Fox 2003, Wickham 2016).

RESULTS

This framework allowed us to incorporate a range of temperature projections into a controlled growth chamber experiment. In Nebraska and Texas, minimum and maximum temperatures are projected to increase in each month of the year (Figure A1.2) based on 19 AOGCMs available at RCP4.5. During the germination months of March for Texas and April for Nebraska, average temperature is expected to increase by a range of 1.0 to 3.8 °C for Texas and 0.1 to 4.5 °C in Nebraska. For our future temperature projection treatments, we selected the INMCM4.1 (#10 Future Cool - Volodin, Dianskii, & Gusev, 2010), IPSL-CM5A-LR.1 GCM (#11 Future Average - Dufresne et al., 2013), and MIROC5.1 (#15 Future Warm - Watanabe et al., 2011). These models captured the range of temperatures expected for the Great Plains under the RCP 4.5 emission scenario (Figure A1.4). After bias correction, the future cool model (INMCM4.1) projected a
mean temperature change of -0.9 °C to 3.1 °C for Nebraska germination period and -0.1 °C to 1.9 °C for Texas germination period. The average future model (IPSL-CM5A-LR.1 GCM) projected a temperature change in Nebraska of 0.1 °C to 4.8 °C and 0.9 °C to 2.2 °C in Texas. The warm future model (MIROC5.1) projected a temperature change of 3.2 °C to 5.2 °C for Nebraska germination period and 0.9 °C to 1.9 °C for Texas germination period.

Although temperature conditions derived from the climate models used in the germination experiment did not vary significantly between all treatments based on the standard error of 30-year average conditions, germination was impacted by increased temperatures and temporal variability associated with future climate conditions (Figure A1.6). In Nebraska, future temperature conditions reduced germination abundance when soil moisture and seed bank density were held constant. In contrast, Texas samples exhibited greater germination percentage under warm future temperatures. We found that germination commenced at air temperatures between 9.0 and 29.0 °C, with peak germination rate at 21.4 °C, however, this was likely constrained by our experimental design because peak germination may occur at higher temperatures if experimental conditions allowed (Swanton et al. 2000).

We were also interested in response of playa soil processes to hydroperiod changes associated with altered precipitation regimes in a changing climate. Precipitation is projected to increase during winter months in Nebraska and decrease during spring, summer, and fall months (Figure A1.3). Rainfall is projected to decrease throughout the entire year in Texas, but greatest decreases may be seen in early summer. Each of three models selected to capture variability in monthly precipitation and number of dry days
reflected decreased precipitation throughout the growing season compared to historical conditions [CESM1-BGC.1 (Hurrell et al. 2013); MIROC-ESM-CHEM.1 (Watanabe et al. 2011); and MPI-ESM-LR.1 (Giorgetta et al. 2013)]. Based on our selection techniques, the future average treatment had less cumulative precipitation over the growing period for Nebraska than the future dry treatment; however, the temporal conditions of these two treatments mimicked the overall model projections for end-of-century data and were selected regardless of the discrepancy (Figure A1.5).

Application of precipitation treatments derived from climate model output data within the greenhouse experiment indicated nitrogen cycling response to climate conditions (Figure A1.7). For Nebraska samples, inorganic nitrogen concentrations under future average and future wet conditions were significantly greater than historical baseline conditions in experimental months 4 and 5. During these months, very few plants were actively growing in mesocosm units representing future climate conditions, whereas plant communities remained robust for historical mesocosm units. Inorganic nitrogen concentrations were similar in Texas samples; however, future dry conditions only produced significantly greater nitrate and nitrite during experimental month 4 (Figure A1.7). There were no differences in nitrate and nitrite concentrations between future and historical conditions for experimental months 1, 2, 3, and 6 for Nebraska samples and experimental months 1, 2, 3, 5, and 6 for Texas samples.

DISCUSSION

Historically, climate change studies have used percentile changes or general temporal and spatial assumptions to develop experimental treatments evaluating ecosystem response to climate change (Weltzin et al. 2000, Sommer et al. 2007, Fay et al. 2008,
Harden et al. 2017). However, here we present a method that reduces error by adjusting downscaled data using historical observations while simultaneously capturing temporal variability and extreme events projected in future climates. We were able to assess variability of each bias corrected downscaled model output but comparing individual AOGCM outputs with mean outputs from each emission scenario (RCP4.5 in this case). In doing so, we selected models that captured low, moderate, and high changes in temperature or precipitation conditions within an emission scenario. When selecting temperature treatments, we were able to utilize a thirty-year average prediction, thus, allowing us to assess the standard error of averaging over this time period. For precipitation, we selected an individual year from a thirty-year period to capture daily precipitation trends, but we could assess error by comparing output from the selected year to thirty-year average trends.

While the specific results of our ecological experiments are not the primary outcome of this paper, the germination and greenhouse studies demonstrate how climate projections may be developed for and applied in experimental settings. We predicted that barnyardgrass would be fairly resistant to temperature and soil moisture changes associated with future climate projections because it has been found to continuously emerge throughout the early growing season in playa wetlands (Haukos and Smith 2001). Based on our study results, overall germination percentage or temporal emergence patterns will likely be impacted by temperature conditions associated with projected climate change. Other playa plants requiring more specific soil moisture and temperature conditions for germination to occur may be more or less competitive in future climate
conditions (Haukos and Smith 2001). The framework developed here may be used to further assess these plant community dynamics in controlled ecological experiments.

Similarly, we were able to capture temporal differences in inorganic nitrogen concentrations associated with various hydrologic treatments. Inorganic nitrogen availability is impacted by mineralization and denitrification pathways, which are influenced by soil moisture and precipitation, plant uptake, microbial activity, and substrate availability (Havlin et al. 2005). Using our framework, we were able to identify specific months of the growing season where differences existed between inorganic nitrogen concentrations in historical and future climate conditions. This information can be used to further explore plant, microbial, and other environmental factors that may be causing these differences to exist. In germination and greenhouse studies, controlled environments allowed ample opportunities for additional data collection (not described in this manuscript) to better understand the impacts of changing climate drivers on plant and soil ecosystem response. These data can be used to reduce uncertainty in predictive ecological modeling by improving parameterization of ecosystem response variables (i.e., germination and soil nitrogen cycling) and guide future experiments.

Changing climatic conditions have increased the need for cross-disciplinary partnerships capable of addressing ecosystem threats. Future climate conditions are likely to directly impact ecosystem function and services and may also combine with existing ecosystem threats to exacerbate other anthropogenic pressures (Hughes 2000, Wuethrich 2000, Walther et al. 2002). Through collaborative efforts among ecologists, soil scientists and climatologists, we were able to develop realistic treatment conditions in an experimental framework that will enhance understanding of ecological alterations caused
by climate change. Climate model output data are openly accessible to all scientists, and, after correcting for bias associated with downscaling, can be used to simulate future climate conditions in a variety of controlled experiments. With increasing technology used to develop projected future climate model outputs, scientists can use projection data to capture emission scenario variability and better understand how ecosystems and associated processes will respond to climate change.
LITERATURE CITED


M. Ewers, B. L. Foster, C. N. Jenkins, A. J. King, W. F. Laurance, D. J. Levey, C.
R. Margules, B. A. Melbourne, A. O. Nicholls, J. L. Orrock, D. Song, and J. R.
Townshend. 2015. Habitat fragmentation and its lasting impact on Earth’s

Harden, J. W., G. Hugelius, A. Ahlström, J. C. Blankinship, B. Bond-Lamberty, C. R.
Lawrence, J. Loisel, A. Malhotra, R. B. Jackson, S. Ogle, C. Phillips, R. Ryals, K.
Todd-Brown, R. Vargas, S. E. Vergara, M. F. Cotrufo, M. Keiluweit, K. A.
our science to characterize the state, vulnerabilities, and management opportunities

2014. Climate projections for ecologists. Wiley Interdisciplinary Reviews: Climate


159 Soil Fertility and Fertilizers: An Introduction to Nutrient Management. 7th

A. Williams, and N. Mieszkowska. 2014. Beyond long-term averages: making


Walther, G. R., E. Post, P. Convey, A. Menzel, C. Parmesan, T. J. C. Beebee, J. M.

Watanabe, S., T. Hajima, K. Sudo, T. Nagashima, T. Takemura, H. Okajima, T. Nozawa,
H. Kawase, M. Abe, T. Yokohata, T. Ise, H. Sato, E. Kato, K. Takata, S. Emori, and
M. Kawamiya. 2011. MIROC-ESM 2010: Model description and basic results of
CMIP5-20c3m experiments. Geoscientific Model Development 4:845–872.

Response of bog and fen plant communities to warming and water-table

Wickham, H. 2016. ggplot2: Elegant graphics for data analysis. Springer-Verlag, New
York.

Wise, M., K. Calvin, A. Thomson, L. Clarke, B. Bond-lamberty, R. Sands, S. J. Smith, A.
Janetos, and J. Edmonds. 2009. Implications of limiting CO2 concentrations for land


795.
Table 2.1. Overview of emission and concentration scenarios for Coupled Model Intercomparison Project (CMIP) 3 and CMIP5 projection datasets, respectively, projected at year 2100 (Meehl et al. 2007, van Vuuren et al. 2011)

<table>
<thead>
<tr>
<th>Scenario</th>
<th>CO₂ equivalent (ppm)</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>CMIP3</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>B1</td>
<td>550</td>
<td>Low emissions</td>
</tr>
<tr>
<td>A1b</td>
<td>700</td>
<td>Moderate emissions</td>
</tr>
<tr>
<td>A2</td>
<td>820</td>
<td>High emissions</td>
</tr>
<tr>
<td><strong>CMIP5</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>RCP2.6</td>
<td>490</td>
<td>Radiative forcing peaks and declines by 2100 (van Vuuren et al. 2006, 2007)</td>
</tr>
<tr>
<td>RCP4.5</td>
<td>650</td>
<td>Radiative forcing stabilizes by 2100 at 4.5 W m⁻² (Smith and Wigley 2006, Clarke et al. 2007, Wise et al. 2009)</td>
</tr>
<tr>
<td>RCP6.0</td>
<td>850</td>
<td>Radiative forcing stabilizes by 2100 at 6 W m⁻² (Fujino et al. 2006, Hijoka et al. 2008)</td>
</tr>
<tr>
<td>RCP8.5</td>
<td>1370</td>
<td>Radiative forcing continues to rise by 2100 (Riahi et al. 2007)</td>
</tr>
</tbody>
</table>
Table 2.2. Atmospheric Ocean Global Climate Models (AOGCMs) for CMIP5-BCCA RCP4.5 downscaled data for years 2070-2099 (Reclamation 2013).

<table>
<thead>
<tr>
<th>Model #</th>
<th>Modeling Center</th>
<th>Simulations</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Commonwealth Scientific and Industrial Research Organization (CSIRO) and Bureau of Meteorology (BOM)</td>
<td>ACCESS1-0.1</td>
</tr>
<tr>
<td>2</td>
<td>Beijing Climate Center, China Meteorological Administration</td>
<td>BCC-CSM1-1.1</td>
</tr>
<tr>
<td>3</td>
<td>Canadian Centre for Climate Modeling and Analysis</td>
<td>CANESM2.1</td>
</tr>
<tr>
<td>4</td>
<td>National Center for Atmospheric Research</td>
<td>CCSM4.1</td>
</tr>
<tr>
<td>5</td>
<td>Community Earth System Model Contributors</td>
<td>CESM1-BGC.1</td>
</tr>
<tr>
<td>6</td>
<td>Centre National de Recherches Meteorologiques / Centre European de Recherche et Formation Advance en Calcul Scientifique</td>
<td>CNRM-CM5.1</td>
</tr>
<tr>
<td>7</td>
<td>CSIRO in collaboration with Queensland Climate Change Centre of Excellence</td>
<td>CSIRO-MK3-6-0.1</td>
</tr>
<tr>
<td>8</td>
<td>NOAA Geophysical Fluid Dynamics Laboratory</td>
<td>GFDL-ESM2G.1</td>
</tr>
<tr>
<td>9</td>
<td></td>
<td>GFDL-ESM2M.1</td>
</tr>
<tr>
<td>10</td>
<td>Institute for Numerical Mathematics</td>
<td>INMCM4.1</td>
</tr>
<tr>
<td>11</td>
<td>Institut Pierre-Simon Laplace</td>
<td>IPSL-CM5A-LR.1</td>
</tr>
<tr>
<td>12</td>
<td></td>
<td>IPSL-CM5A-MR.1</td>
</tr>
<tr>
<td>13</td>
<td>Japan Agency for Marine-Earth Science and Technology, Atmosphere and Ocean Research Institute, and National Institute for Environmental Studies</td>
<td>MIROC-ESM.1</td>
</tr>
<tr>
<td>14</td>
<td></td>
<td>MIROC-ESM-CHEM.1</td>
</tr>
<tr>
<td>15</td>
<td></td>
<td>MIROC5.1</td>
</tr>
<tr>
<td>16</td>
<td>Max Planck Institute for Meteorology</td>
<td>MPI-ESM-LR.1</td>
</tr>
<tr>
<td>17</td>
<td></td>
<td>MPI-ESM-MR.1</td>
</tr>
<tr>
<td>18</td>
<td>Meteorological Research Institute</td>
<td>MRI-CGCM3.1</td>
</tr>
<tr>
<td>19</td>
<td>Norwegian Climate Centre</td>
<td>NORESM1-M.1</td>
</tr>
</tbody>
</table>
**FIGURES**

**Select Appropriate Climate Data**

1. Select emission scenario(s) of interest
2. Select spatial and temporal extent
3. Select data type and resolution
4. Select climate attributes

1. Selected CMIP5 RCP4.5 scenario
2. Selected two point locations - Nebraska and Texas
3. Selected daily data at 16 km resolution
4. Selected daily precipitation (mm), maximum temperature, and minimum temperature

**Correct Bias**

1. Download historical weather data
2. Select 30-yr calibration period
3. Select appropriate bias correction method
4. Calculate bias correction by month and apply to predicted values

1. Downloaded historical data from weather stations in Hastings, NE and Lubbock, TX
2. Selected 1986-2015 as calibration period
3. Selected delta correction methods for temperature and gamma-based quartile mapping for precipitation
4. Calculated bias correction by month and apply to projected future values for years 2070-2099

**Transform Model Output to Ecological Treatments**

1. Select models that represent variability
2. Apply predicted conditions to mesocosm units through controlled experiments
   - Temperature: Aggregate data into desired timeframes or select individual year
   - Precipitation: Empirically select individual year of data

1. Selected three models that captured variability within a climate scenario based on projected change from historical conditions
2. Applied predicted conditions to controlled experiments
   - Temperature: Aggregated data into weekly timeframes for germination months
   - Precipitation: Empirically select individual year of data and applied rainfall totals daily in greenhouse study

**Figure 2.1.** Suggested flow diagram for using climate model data to create climate treatments for ecological experiments. Because each ecological experiment may have unique research questions and scope, details are intentionally omitted from blue boxes to provide a general framework. Detailed techniques used in this study are described in green boxes, but specific data and methods may not be suitable for all ecological experiments.
Figure 2.2. Overall change between observed (1986-2015) and RCP 4.5 projected (2070-2099) maximum daily temperature values for Nebraska (a) and Texas (b) and minimum daily temperature values for Nebraska (c) and Texas (d) for 19 AOGCMs (see Table 2.2). Box plots represent the median model (horizontal line), interquartile range of model values (box), range of model values (whiskers), and outliers outside 1.5 interquartile range (dots).
Figure 2.3. Monthly percent change from historical (1986-2015) to projected (2070-2099) for precipitation in Nebraska (a) and Texas (b), and number of days without precipitation for Nebraska (c) and Texas (d) point locations for 19 AOGCMs (Table 2.2) downscaled using gamma-based quantile mapping. Box plots represent the median model (horizontal line), interquartile range of model values (box), range of model values (whiskers), and outliers outside 1.5 interquartile range (dots).
Figure 2.4. Temperature treatments for a germination study using soil collected in Nebraska (April - a) and Texas (March - b) for historical data and scenarios based on downscaled CMIP5-BCCA atmosphere ocean general circulation models for the RCP 4.5 emission scenarios (2070-2099) – future average, warm future, and cool future. Bars represent daily temperature range.
Figure 2.5. Precipitation treatments for a greenhouse study for soil collected in Nebraska (a) and Texas (b) for historical data and scenarios based on downscaled CMIP5-BCCA atmosphere ocean general circulation models for the RCP 4.5 emission scenarios (2070-2099) – future average, wet future, and dry future. Precipitation treatments followed 28 days of constant moisture to allow for uniform germination conditions.
Figure 2.6. Model predicted germination proportion as a function of climate scenario for Nebraska (a) and Texas (b). Error bars represent a 95% confidence interval. Letters designate differences at $p < 0.05$. 
Figure 2.7. Model predicted sum of nitrate-N and nitrite-N concentration ([NO$_3^-$-N] + [NO$_2^-$-N]) as a function of climate scenario for Nebraska (a) and Texas (b). Error bars represent a 95% confidence interval. Significant differences from historic reference level denoted at $p < 0.05$ (*), $p < 0.01$ (**), and $p < 0.001$ (***), and $p < 0.001$ (****) for comparisons within categories separated by dashed lines.
CHAPTER 3

BARNYARDGRASS (ECHINOCLOA CRUSGALLI) EMERGENCE AND GROWTH IN A CHANGING CLIMATE IN GREAT PLAINS WETLANDS

ABSTRACT

Projected 21st century increases in temperature and precipitation intensity in the U.S. Great Plains may alter playa wetland hydroperiods. Our objective was to identify favorable germination conditions for a common moist-soil grass. Barnyardgrass (Echinochloa crusgalli L.), by evaluating emergence and growth response to various environmental conditions specific to the Northern (Nebraska) and Southern (Texas) range of playas. We used a temperature-controlled growth chamber experiment to evaluate emergence and growth response of Barnyardgrass to three main effects: (i) weekly temperatures representing historical and future conditions under a moderate emissions scenario, (ii) dry, moist, and saturated soil moisture conditions, and (iii) various seed bank densities. In Nebraska samples, projected future temperatures reduced emergence percentage by up to 20%, but increased emergence percentage by up to 15% for Texas samples. For Nebraska samples, plants were 9.6 cm taller under field capacity moisture compared to saturated moisture. Texas plant height was driven by temperature, where historical conditions produced plants that were 13 cm shorter than future warm conditions. These effects may be exacerbated in natural settings over time and when inter-specific competition exists; thus, temperature, soil moisture, and seed bank densities may be important considerations when planning for playa management in future climate conditions.
INTRODUCTION

Global climate change is affecting and will continue to affect ecosystems throughout the world for decades to come (Hughes 2000; Wuethrich 2000; Walther et al. 2002). Wetland ecosystems are affected directly by changes in temperature and precipitation associated with a changing climate (Covich et al. 1997; Poff et al. 2002). Indirectly, wetlands have experienced climate change effects associated with alterations to surrounding terrestrial ecosystems (Meyer et al. 1999; Rashford et al. 2016). In addition to altering the physical environment of ecosystems, global climate change is likely to have a cascading influence on organisms (humans and wildlife, alike) that rely on wetland ecosystems services such as food resources (Briske et al. 2015; Howard et al. 2018), refugia (Parmesan and Yohe 2003; Root et al. 2003; Haddad et al. 2015), and water supply and quality (Meyer et al. 1999; Gosling and Arnell 2016; Vörösmarty et al. 2016).

Playa wetland (hereafter referred to as “playas”) functions are likely to be altered by changes in precipitation and temperature associated with global climate change (Matthews 2008; Uden et al. 2015). Playas are hydrologically and geographically isolated and exist ubiquitously throughout the High Plains of the United States. (Smith 2003). Regional climate change models for the High Plains predict that mean air temperature will increase by 2.0 to 2.8 °C by 2050 and by 2.4 to 4.7 °C by 2100 (Kloesel et al. 2018). Elevated temperatures are expected to increase evapotranspiration from wetlands (Winter 2000) and may induce land use changes in the surrounding landscape, such as relative shifts between croplands and grasslands depending upon water availability (Kukal and Irmak 2018). Regional climate models also project that precipitation events in the High
Plains will become more variable and intense, leading to extended periods of drought and flooding (Melillo et al. 2014; Kloesel et al. 2018). Interactions between temperature and precipitation drive playa hydroperiod, thus changes in climate dynamics will affect the duration, timing, and frequency of inundation, moist-soil, and dry ecological states within playas (Bartuszevige et al. 2012). Variable hydroperiods across the landscape allow playas to support a broad range of plant and animal species that require hydric soil or standing water as part of their life history strategies (Smith 2003). Any shifts in spatial or temporal hydroperiod variability are likely to have consequences on floral and faunal diversity on the High Plains (Smith et al. 2011).

Many wetland-dependent animal species, including migratory waterbirds, rely on seasonal and spatial variability in playa plant communities to support refugia and food requirements during all or part of their life cycles (Conway et al. 2005; Webb et al. 2010; Tsai et al. 2012). Additionally, playa plant composition may assist with removing nutrients and contaminants from infiltrating water (Pezzolesi et al. 1998; McKenna and Sala 2016), improving water quality within recharging aquifers (Urban et al. 1989). Dominant plant taxa are able to survive and grow in a variety of conditions and are well adapted to the variable hydroperiod dynamics in playas. In many years, playa plant communities are dominated by moist-soil annual grasses and forbs [e.g., Barnyardgrass (*Echinochloa crusgalli*) and Smartweeds (*Polygonum* spp.)] (Gilbert 1989; Haukos et al. 1997; Haukos and Smith 2004; Federal Geographic Data Committee 2013). Plant distribution in a given year is dependent upon the timing and intensity of rainfall events, which drive soil moisture at germination throughout the playa (Grubb 1977; Welling et al. 1988b; Haukos and Smith 2004). When playas are not inundated, plant species that
typically occur in the wetland perimeter may encroach the center of the playas to compete with moist-soil plant species (Smith 2003). In the absence of a seasonal hydroperiod, the overall playa ecology may shift (Haukos and Smith 2004). Understanding effects of climate change on hydroperiod and plant communities will be important for maintaining playa ecosystem services under altered future conditions.

Plant germination experiments can provide valuable insight into how wetland plant and seed biomass production will be affected by changes in precipitation and temperature associated with future climate conditions (Seabloom et al. 1998; Casanova and Brock 2000; Haukos and Smith 2006). Germination rate and timing of moist-soil grass species primarily respond to soil moisture and temperature (McGinnies 1960; Winkel et al. 1991; Chhetri and Rawal 2017). In contrast, plant growth and overall community richness are predominantly dependent upon nutrient availability, specifically nitrogen and phosphorus (Bedford et al. 1999; Elser et al. 2000; Güsewell et al. 2003). However, plant growth and community richness may also be affected by temperature and soil moisture interactions (Haukos and Smith 1995; Haukos and Smith 2006). As temperatures warm in a changing climate, playa plant germination can occur earlier and biomass production may be enhanced or diminished. Additionally, changes in soil moisture are likely to affect plant germination in playas because saturated soils provide ideal conditions for moist-soil species in playas, (Haukos and Smith 2001). Plants experiencing adequate moisture conditions during germination and the remaining growing period may have greater biomass than those that experience water stress (Haukos and Smith 2001; Haukos and Smith 2006). Temperature patterns could potentially limit plant growth, even with adequate moisture (Thompson and Grime 1983; Seabloom et al. 1998). Diminished seed
bank density, potentially indicative of low seed production or resource competition from the previous growing season (Schepker 2017), may also reduce total germination abundance (van der Valk and Davis 1978; Haukos and Smith 2001).

Our objective was to quantify effects of simulated climate change conditions on plant emergence and early season growth. To test effects of changing climate conditions on plant germination and growth in playa ecosystems, we selected Barnyardgrass as a representative playa moist-soil plant species. Barnyardgrass is an annual, introduced grass common across the geographical range of playas (Maun and Barrett 1986; Haukos et al. 1997). Classified as a facultative plant species in the Great Plains (U.S. Army Corps of Engineers 2016), barnyardgrass may persist in a variety of hydroperiod conditions (Fredrickson and Taylor 1982), and may be resilient to changing climatic conditions; however, barnyardgrass requires moist-soil conditions to germinate (Haukos and Smith 2004). Barnyardgrass has been documented to germinate when soil temperatures range from 6.5 °C to 51.0 °C (Swanton et al 2000). Barnyardgrass has been widely noted as an important food resource for waterfowl due to substantial seed production and high nutritional value (Wieland and Bazzaz 1975; Haukos and Smith 1995; Haukos et al. 1997; Anderson and Smith 1999; Tidwell et al. 2013). Because barnyardgrass is highly prolific and wetland managers promote the species across the playa region to support migrating waterfowl, it is important to understand barnyardgrass germination response to changing climate conditions. Presented here are results of studies evaluating the emergence and initial barnyardgrass life history response to changing temperature, soil moisture, and seed bank density.
METHODS

Soil collection and sample preparation

To capture landscape-scale variability among playas, we collected soil from six playas, three in Nebraska and three in Texas, to examine trends across the playa region (Table 3.1). The three wetlands in each region were considered replicates in order to represent field-scale variability that may exist among playas. Soil from each wetland was kept separate throughout the germination experiment. Bulk soil was collected from the top 10 cm of the soil profile in transition areas surrounding the playa basin. In Nebraska, bulk soil was collected from the moist-vegetation zone which represented Massie silty clay loam (*Fine, smectitic, mesic Vertic Argialbolls*), Scott silt loam (*Fine, smectitic, mesic Vertic Argialbolls*), and Fillmore silt loam (*Fine, smectitic, mesic Vertic Argialbolls*) soil series. Texas bulk soil was also collected from the moist-soil vegetation zone, representing the Randall clay (*Very-fine, smectitic, thermic Ustic Epiaquerts*) soil series. Additional soil samples were collected and analyzed to determine bulk density, texture, pH, cation exchange capacity, and total carbon, nitrogen and phosphorus content using standard methods (USDA 2014). Soil from each playa was dried and ground separately prior to use to create homogenized conditions (texture and bulk density) for the study. Plastic trays with a surface area of 28 cm x 36.5 cm were packed with soil to a depth of 6 cm with a bulk density equivalent to field bulk density values measured for each individual playa (Table 3.1). Barnyardgrass seeds were purchased in bulk from MFA Cooperative in Columbia, Missouri. Seeds were placed approximately 1 cm below the soil surface.
Experimental design and climate treatments

We used a completely randomized design within temperature-controlled growth chambers to test barnyardgrass emergence and early growth responses to changing climate conditions. Temperature, soil moisture, and seed bank density were the main experimental effects. While barnyardgrass typically does not germinate until later in the growing season, it is considered a ‘continuous emitter’ and has been known to germinate in temperatures as low as 6.5 °C (Swanton et al. 2000; Haukos and Smith 2001; Haukos and Smith 2004); thus, we tested barnyardgrass emergence and growth with conditions common to the beginning of the playa growing season. In Nebraska and Texas, overall playa germination typically begins in April and March, respectively; thus, we used climate data from the first 28 days of these months to evaluate emergence response to changes in temperature. We aggregated daily temperature data into weekly treatments to simulate temporal conditions (Appendix 1). Four climatic temperature treatments were represented in four-week germination studies, separated by state. Therefore, we completed eight four-week temperature studies – Nebraska (4) and Texas (4).

Historical temperature treatments were derived from local weather station data (years 1986-2015) at point locations in Hastings, NE (GHCND:US00253660; 40.608, 98.427) and Lubbock, TX (GHCND:USC00415410; 33.657, 101.824). We derived future climate projections using three coupled model intercomparison project phase 5 (CMIP5) global climate models (GCMs) for the RCP4.5 emission scenario (years 2070-2099) down-scaled to the point location in the playa regions of Nebraska and Texas (available at Reclamation 2013). Future projection data were adjusted to local conditions using delta correction techniques (Quilbé et al. 2008). We evaluated daily temperature maximum and
minimum values from 19 GCMs and selected the following three models for use in this study: 1) least temperature change (considering maximum and minimum values) relative to historical climate; 2) greatest temperature change relative to historical climate; and 3) a model that represents the average temperature change across the GCMs assessed (Owen et al). We used historical and projected 30-year average daily maximum and minimum temperatures reported for each model to develop weekly experimental treatments to assess effects of changing temperature on wetland plant emergence and early growth (Figure 3.1).

For each four-week temperature study, we evaluated interactive effects of soil moisture and seed bank density. We selected three soil moisture treatments, including two constant moisture conditions at saturation and field capacity moisture, and one dynamic hydroperiod where soil was kept at field capacity moisture until emergence commenced and then allowed to dry for the remainder of the four-week study. To determine soil moisture at field capacity, we determined porosity of Nebraska and Texas samples separately using bulk density samples collected at each wetland. We then used wilting point values reported by local soil surveys to calculate field capacity moisture values as wilting point moisture subtracted from porosity (Soil Survey Staff, Natural Resources Conservation Service United States Department of Agriculture).

All experimental units with differing hydrologic treatments were subjected to a barnyardgrass seed bank density of 145 kg ha\(^{-1}\), based on seed production values common in ephemeral wetlands (Kross et al. 2008). In addition to the average rate, two additional seed density treatments (low – 65 kg ha\(^{-1}\) and high – 400 kg ha\(^{-1}\)) were tested at field capacity moisture throughout the study period (based on ranges from Fredrickson and
Taylor 1982). For each four-week study period, there were five total treatments (three moisture treatments with constant seeding rate and two additional seeding rates at field capacity moisture, only) per sampling location; thus, there were fifteen experimental units total in each four-week study. Nebraska and Texas samples were studied separately due to differences in local weather data.

**Growth chamber conditions**

Nebraska experiments were conducted in a controlled growth chamber (model CMP 3244, Conviron, Winnipeg, Canada). Photoperiod mimicked sunrise/sunset times for Hastings, Nebraska for April 1-28, and temperatures ramped up and down over 30 minutes at dawn and dusk to reach daily high and low temperatures, respectively. Light intensity was supplied by cool-white fluorescent and incandescent lamps at 130 (±14.6) μmol m⁻² s⁻¹ PAR. Relative humidity ranged from 40-85%. Texas experiments were conducted in a controlled growth chamber (model CG-36, Environmental Growth Chambers, Ltd., Winnipeg, Canada). Photoperiod mimicked sunrise/sunset times for Lubbock, Texas for March 1-28, and temperatures ramped up and down over 30 minutes at dawn and dusk to reach daily high and low temperatures, respectively. Light intensity was supplied by cool-white fluorescent and incandescent lamps at 136 (±19.2) μmol m⁻² s⁻¹ PAR. Relative humidity was held constant at 45%. Chamber conditions were adjusted on a weekly basis (details in Appendix 1).

**Data collection**

Emergence day, air temperature, and soil temperature were recorded for each four-week temperature study. Soil temperature was measured continuously using an Onset HOBO data logger and sensors (Onset Computer Corporation, Bourne, MA). We counted
plants on the first day of emergence and on the last day of each four-week experiment. Survival percentage within each experimental unit was calculated as the difference between initial and final seedling density counts divided by the total number of seeds planted. At the end of each four-week experiment, plant growth response was quantified by averaging measured height (cm) from three randomly selected plants in each experimental unit. Above- and below-ground plant biomass was collected at the end of each four-week study for each experimental unit. Above-ground biomass was removed at the soil surface, dried at 55 °C for 48 hours, and measured to 0.01 g. To collect below-ground biomass, soil was soaked in a dispersing solution (generic dish detergent – active ingredient: sodium lauryl sulfate) for 30 minutes, then passed through a 1 mm sieve. Organic materials that did not pass through the 1 mm sieve were dried at 55 °C for 48 hours and weighed to 0.01 g. Total biomass was calculated as the combined above- and below-ground biomass portions.

**Statistical analysis**

Linear mixed effects models were used to test effects of temperature, soil moisture, and seed bank density on above and below ground biomass (fitted with logarithmic response), plant height, and survival. Survival values were adjusted using the equation $Y_{adjusted} = \ln(Y_{observed} + 1 - Y_{minimum})$ to account for negative data points. Generalized linear mixed effects models with binomial distributions were used to evaluate percent seedling emergence response to temperature, soil moisture, and seed bank density. For each response variable, we tested a model with interactive effects of: 1) temperature and soil moisture; and 2) temperature and seed bank density. Interactive effects of soil moisture and seed bank density were beyond the scope of this experiment. Sampling
location (wetland where soil samples were collected) was included as a random effect in all models to account for variation among sites; models were evaluated separately for Nebraska and Texas sites. When interactive effects were significant, we conducted post-hoc least squared means comparisons using a Tukey adjustment to evaluate differences between various combinations of climate scenario, soil moisture, and seed bank density. If no main effects produced significant differences in response variables, we combined data to test for correlations between response and soil temperature using simple linear regression. Results were analyzed using the lme4 package (Bates et al. 2015) and lsmeans package (Lenth 2016) of R statistical software. We used package effects and ggplot2 to visualize estimated means derived from regression models (Fox 2003; Wickham 2016).

RESULTS

Plant germination response

Day of emergence varied by temperature treatment; however, all moisture and seed bank density treatments emerged on the same day within a temperature scenario (Table 3.2). Prior to and at emergence, field capacity and drawdown treatments were held at the same soil moisture levels, which may explain why there were no differences between these moisture treatments. With the exception of historical Nebraska conditions, increased air temperature caused emergence to occur days earlier. For instance, under future cool temperatures, emergence occurred on day 9 compared to future warm emergence, which occurred on day 6 for Nebraska samples. For Texas samples, emergence occurred on days 12, 11, 10, and 8 for historical, future cool, future average, and future warm climate scenarios, respectively. Air temperatures were warmer in Nebraska due to the reference timeframe – Nebraska temperatures represented April
conditions and Texas temperatures represented March conditions. Maximum air temperature on the day of emergence ranged from 24.0 to 29.0 °C across the four Nebraska temperature scenarios and 19.1 to 21.5 °C across the four Texas temperature scenarios. Soil temperature at emergence varied by soil moisture and seed bank density treatments. Nebraska emergence occurred when soil temperatures ranged from 17.4 to 22.6 °C; whereas, Texas emergence occurred when soil temperatures ranged from 13.9 to 16.2 °C. Within each temperature treatment, soil temperature varied <1.6 °C for various combinations of soil moisture and seed bank density (Table 3.2).

Seedling emergence percentage was influenced by the interaction between climate scenario and soil moisture, as well as the interaction between climate scenario and seed density at planting (Figure 3.2). For Nebraska, emergence percentages were greater under drawdown (held at field capacity moisture prior to emergence; 18.5% to 37.0%) and field capacity (20.5% to 26.7%) moistures compared to saturated (6.4% to 22.9%) moisture. For all soil moisture conditions, emergence under future temperature conditions was less than emergence under historical reference levels (|z| ≥ 3.88, p ≤ 0.001), with the exceptions of future warm emergence under field capacity moisture (|z| = 0.33, p = 0.99). Additionally, emergence percentage was driven by interacting effects of climate scenario and initial seed bank density. At each seed bank density treatment level, emergence percentage was greatest under historical reference temperature conditions (|z| ≥ 2.89, p ≤ 0.02), with the exception of future cool emergence at moderate seed bank density (|z| = 0.18, p = 0.99).

For Texas samples, emergence percentage was greatest under future warm temperature conditions at each soil moisture (|z| ≥ 3.70, p ≤ 0.001) and seed bank density
(|z| ≥ 4.39, p ≤ 0.0001) level (Figure 3.2-c, 3.2-d). At each Texas soil moisture level, emergence percentage under predicted future temperature conditions varied from historical reference temperatures, but with inconsistent effects (Figure 3.2-c). Under field capacity moisture, historical emergence was less than future warm emergence (|z| = 16.69, p < 0.0001), but greater than future cool and future average emergence (|z| ≥ 5.24, p < 0.0001). At saturated moisture conditions, historical emergence was again less than future warm emergence (|z| = 6.93, p < 0.0001) and greater than future average emergence (|z| = 5.13, p < 0.0001); however, historical emergence did not differ from future cool emergence (|z| = 1.62, p = 0.37). Differences between Texas historical and future conditions were also inconsistent between seed bank density treatment levels (Figure 2-d). For instance, at the moderate seed bank density treatment, historical emergence was less than future warm emergence (|z| = 6.23, p < 0.0001), greater than future average emergence (|z| = 7.23, p < 0.0001), and did not differ from future cool emergence (|z| = 2.54, p = 0.054). However, at the high seed bank density treatment, historical emergence was less than future cool (|z| = 2.62, p = 0.04) and future warm (|z| = 8.61, p < 0.0001) emergence, and greater than future average emergence (|z| = 4.04, p = 0.0003).

Plant survival and growth responses

Plant survival described differences between seedling density at emergence and seedling density after 28-day experimental period. For Nebraska, the interaction between soil moisture and climate scenario contributed to differences in estimated plant survival when comparing drawdown and field capacity moisture levels (|t| = 6.50, p < 0.0001). Samples exposed to continuous drawdown conditions after germination had lower plant
survival than samples held at field capacity ($|t| = 7.89, p < 0.0001$) and saturated moisture ($|t| = 8.65, p < 0.0001, R^2 = 0.72$). Nebraska samples subjected to warm future temperatures had greater survival than samples subjected to historical temperatures at drawdown soil moistures ($|t| = 2.75, p = 0.04$; Figure 3.3-a). Survival was positive and did not differ among climate treatments at field capacity and saturated moistures, indicating that seedlings continued to emerge at the same rate under these temperature and moisture conditions. Seed bank density did not affect plant survival for Nebraska samples ($|t| \leq 0.18, p \geq 0.86$).

Plant survival for Texas conditions was affected by the interaction between climate scenario and soil moisture when comparing drawdown ($|t| = 2.04, p = 0.046$) and saturated ($|t| = 3.78, p = 0.0004$) soil moistures to field capacity soil moisture under various climate scenarios. Similar to trends for Nebraska samples, plant survival was lowest under drawdown soil moisture for Texas samples (Figure 3.3-b). In saturated soils, future average temperature conditions promoted survival which was 17-fold greater than survival under historical reference conditions ($|t| = 5.66, p < 0.0001$) and 4-fold greater than future cool temperature conditions ($|t| = 6.44, p < 0.0001$). Under field capacity moisture conditions, survival was 2-fold greater under future average temperatures compared to future cool temperatures ($|t| = 2.95, p = 0.02$). Survival for Texas samples was also significantly affected by seed bank density ($|t| = 6.15, p < 0.0001$). High seed bank densities promoted greater survival than low ($|t| = 6.15, p < 0.0001$) and moderate ($|t| = 4.53, p = 0.0002$) seed bank densities, likely due to more seeds present in the seedbank available to emerge throughout the 28-day experiment.
Drivers of plant growth response, as measured in plant height and biomass production, differed between Nebraska and Texas. In Nebraska, plant height was influenced by soil moisture content ($|t| = 3.96$, $p = 0.0003$) and climate scenario ($|t| = 4.27$, $p = 0.0001$). Drawdown soil moisture conditions did not have living plants at end of the experiment, thus data from this treatment were not included in plant height analysis. Plants grown under constant field capacity moisture were 9.6 cm shorter than plants produced under constant saturated moisture conditions ($|t| = 3.96$, $p < 0.0003$; Figure 3.4-a). Plant height was greatest under average future temperatures (35.5 cm ± 3.4 cm) compared to other temperature scenarios (Figure 3.4-b). Under historical temperatures, plants were taller at 29.3 cm (± 3.4 cm) than plants grown in future warm temperatures which averaged 18.9 cm (± 3.4 cm; $|t| = 4.27$, $p = 0.0007$).

For Texas samples, plant height was a function of seed bank density ($|t| = 2.25$, $p = 0.03$) and climate scenario ($|t| = 8.83$, $p < 0.0001$), separately, and did not differ between field capacity and saturated soil moisture conditions ($|t| = 1.556$, $p = 0.13$). Samples were not included from drawdown moisture conditions because no plants were living at the end of the 28-day experiment. Averaged across soil moisture treatments, plant height was negatively correlated with mean soil temperature for low ($F = 7.53$, $p = 0.02$, $R^2 = 0.37$) and moderate ($F = 9.49$, $p = 0.005$, $R^2 = 0.27$) seed bank densities (Figure 4-c). Plant height was not correlated with mean soil temperatures at high seed bank densities ($F = 1.99$, $p = 0.19$, $R^2 = 0.08$; Figure 4-c). Additionally, future average temperature conditions produced the tallest plants at 20.2 cm ± 1.3 cm compared to plant height under historical (7.4 cm; $|t| = 8.83$, $p < 0.0001$), future cool (5.5 cm; $|t| = 10.16$, $p < 0.0001$), and future warm (10.6 cm; $|t| = 6.61$, $p < 0.0001$; Figure 3.4-d) scenarios.
Total biomass (above- and below-ground) after the 28-day experimental period in Nebraska was affected by climate scenario ($|t| = 4.39, p < 0.0001$) and seed bank density ($|t| = 2.66, p = 0.01$; Figure 3.5-a, 3.5-b). Nebraska total biomass was greatest under average future climate temperatures at 3.33 g ± 0.34 g compared to biomass production in the historical (2.83 g; $|t| = 4.39, p = 0.0003$), future cool (2.34 g; $|t| = 8.68, p < 0.0001$), and future warm (2.28 g; $|t| = 9.16, p < 0.0001$) scenarios (Figure 3.5-a). Nebraska above-and below-ground biomass were influenced by interacting effects of climate scenario and soil moisture, where above-ground biomass generally increased with increasing soil moisture and below-ground biomass generally decreased with increasing soil moisture (Figure 3.5-c, 3.5-d). Similar trends were found for Texas conditions; however, total, above- and below-ground biomass in Texas samples were only influenced by historical and future climate scenarios (Table 3.3).

**DISCUSSION**

Climate patterns in the Great Plains are projected to shift dramatically, causing increased temperatures and reduced overall precipitation through the end of the 21st century. As a keystone wetland ecosystem in the Great Plains, playa wetlands will be affected by shifting climate conditions. Early season germination and growth provide an initial look at potential effects of increased temperatures and altered precipitation patterns to playa plant communities because extant plant distribution throughout the playa is dependent upon the environmental conditions at emergence (Grubb 1977; Welling et al. 1988a; Haukos and Smith 2001). In field settings, playa plant germination is primarily driven by interactions among air temperature, soil temperature, and precipitation, which produce various hydroperiod and soil moisture conditions throughout the active growing
season (Haukos and Smith 1995; Seabloom et al. 1998; Casanova and Brock 2000; Haukos and Smith 2006). We simulated interactions among air temperature, soil moisture, and seed bank density that playa plants may experience in changing climate conditions. Not surprisingly, increasing temperatures were found to be an important driver of emergence and initial growth in Nebraska and Texas playa samples. Additionally, interacting effects of air temperature and soil moisture tended to be more important drivers of emergence at higher air temperatures, as seen in Nebraska samples. Comparatively, seed bank density tended to be a more important driver when air temperatures were lower, such as in the Texas samples. Finally, emergence was enhanced by increased temperatures representing future climate conditions in Texas samples, but emergence was diminished by increased germination temperatures in Nebraska. While the drivers of emergence and early season growth were similar between the two playa regions, plant response differed.

Our results support that emergence and growth characteristics of a common playa plant (Barnyardgrass) are significantly influenced by air temperature. Swanton et al. (2000) identified base (T_b), optimal (T_o), and maximum (T_m) temperatures for various stages of Barnyardgrass phenological development. They reported that seedling emergence did not occur below 6.5 °C (T_b), peaked at 30.0 °C (T_o), and did not occur when temperatures exceeded 51.0 °C (T_m) (Swanton et al. 2000). Further, base temperature for biomass production was identified to be 20 °C (Swanton et al. 2000), similar to thermal trends identified by Kacperska-Palacz et al. (1963) and Vengris et al. (1966). We found that germination commenced at air temperatures between 9.0 and 29.0 °C, with peak germination rate at 21.4 °C; however, these temperature thresholds were
likely constrained by our experimental design. Biomass production also mimicked these temperature responses. Biomass production in Texas conditions tended to increase under warmer climate scenarios, but this trend was complicated by interactions with soil moisture and seed bank density in Nebraska samples.

In our study, soil moisture affected Barnyardgrass seedling emergence, survival, plant height, and biomass production. Haukos and Smith (2001) classified Barnyardgrass as a ‘continuous emerger’, with the majority of seedlings germinating after a drawdown event (e.g., high soil moisture without standing water), but with some seedlings continuing to emerge during other portions of the growing season as well. For all treatment combinations except those with drawdown moisture conditions with low soil moisture, seedlings continued to germinate throughout the 28-day experiment. Haukos and Smith (1994) also found that Barnyardgrass was able to germinate in several moisture conditions and adapted to rapidly changing playa conditions following germination as long as inundation did not submerge the plants. In contrast, our results indicate that moisture stress limits seedling survival and biomass production during early growth stages. We also found that field capacity moisture conditions produced shorter plants when compared to saturated moisture conditions, but saturated moisture conditions tended to have a lower germination rate. Haukos and Smith (2006) found similar biomass and germination trends for Pink smartweed (Polygonum pensylvanicum L.), another moist-soil annual playa species. Welling et al. (1988) found that seedling recruitment of seven common wetland plant species was greatest during periods with high soil moisture in prairie pothole wetlands and temperature and soil moisture played a greater role in seedling emergence and growth than did seed bank densities in field conditions.
Under controlled growth-chamber settings, we identified seed bank density as a significant driver of emergence and growth under certain environmental conditions. For instance, emergence rate peaked under moderate seed bank densities (165 kg ha\(^{-1}\)) and was reduced at high seed bank densities (400 kg ha\(^{-1}\)). Dalling and Hubbell (2002) noted that seedling recruitment (based on 38 common taxa) was a function of seed mass, but did not find a relationship between seed bank density and emergence rate in forested ecosystems. Bonis et al. (1995) found that seedling recruitment and biomass production tended to remain constant regardless of native seed bank composition and density in Mediterranean marshes. Further, several studies have noted the importance of native seed banks during wetland restoration, but few have examined the relationships between seed bank density, recruitment, and growth in individual species (e.g., van der Valk et al. 1992; Brown 1998; Galatowitsch and van der Valk 2016; Morimoto et al. 2017). In our study, effects of seed bank density on Barnyardgrass growth were confounded by interactions with soil and air temperatures. Seed bank density tended to have a greater affect at cooler temperatures, as observed in the Texas samples. High seed bank densities under warmer conditions may lead to increased resource competition in the soil, reducing germination rate and delaying phenological development.

We did not introduce inter-specific competition by adding other common playa plant species to experimental units; however, changing climate conditions may have community-wide effects on composition of plant species in playa wetlands. Playa seed banks may contain up to 346 different plant species at a regional scale (Haukos and Smith 2004). This diverse seed bank allows for seedling recruitment in a variety of environmental conditions, leading to similar plant densities regardless of hydroperiod in a
given year (Haukos and Smith 1994). No matter the moisture conditions, some combination of plants will be produced in a playa wetland; however, not all species provide equivalent ecosystem services. Moist-soil annuals, such as Barnyardgrass, Pink Smartweed, and Curly Dock (*Rumex crispus*) have been identified as containing high nutritional value for waterfowl (Sheeley and Smith 1989; Haukos and Smith 1995). These species are classified as facultative (Barnyardgrass) and facultative wet (Pink Smartweed and Curly Dock) wetland species, respectively in the Great Plains (Haukos and Smith 1997). Biomass and seed production in obligate wetland species may be reduced as hydroperiod length or soil moisture levels decrease in future climates.

Our results indicate that temperature patterns associated with future climate conditions may have a positive or negative effect on Barnyardgrass germination and growth depending upon soil moisture and seed bank density conditions. While our study aimed to mimic field conditions in a controlled setting, results may be limited by random variation introduced between replicates and short-term analyses. We also lacked interspecific resource competition that would have been introduced by a multi-species seed bank ensemble. Further, because we chose climate conditions representing variation within a moderate emission scenario, we were unable to capture the full extent of potential future temperature patterns. Despite these limitations, we identified interacting effects of temperature, soil moisture, and seed bank density that may relate to conditions faced by playa wetland plants in future climates. Altered germination patterns in a changing climate may have longer term effects on plant growth and production later in the growing season, further affecting wildlife refugia and food resources. Field studies conducted over the entire growing season or multiple years would help to inform
conservation priorities in playa wetlands in the coming decades, further protecting ecosystem services provided by playa plant communities.
LITERATURE CITED


TABLES

Table 3.1. Initial soil conditions (2016) for germination experimental units based on sample location in Nebraska and Texas. Physiochemical soil analyses were completed using standard methods. Unless otherwise noted, samples were collected from publicly-managed playa wetlands. In Nebraska, bulk soil was collected from the moist-vegetation zone which represented Massie silty clay loam (*Fine, smectitic, mesic Vertic Argialbolls*), Scott silt loam (*Fine, smectitic, mesic Vertic Argialbolls*), and Fillmore silt loam (*Fine, smectitic, mesic Vertic Argialbolls*) soil series. Texas bulk soil was also collected from the moist-soil vegetation zone, representing the Randall clay (*Very-fine, smectitic, thermic Ustic Epiaquerts*) soil series.

<table>
<thead>
<tr>
<th>Wetland</th>
<th>Collection Location</th>
<th>Clay (g kg(^{-1}))</th>
<th>Soil Textural Class</th>
<th>Bulk Density (g cm(^{-3}))</th>
<th>Total N (g kg(^{-1}))</th>
<th>Bray P(_{1}) (mg kg(^{-1}))</th>
<th>Total C (g kg(^{-1}))</th>
<th>Cation Exchange Capacity (cmol(_{c}) kg(^{-1}))</th>
<th>pH (H(_{2})O)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nebraska</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hidden Marsh WMA</td>
<td>40.71, -97.49</td>
<td>337</td>
<td>Silty Clay Loam</td>
<td>1.00</td>
<td>2.96</td>
<td>129.2</td>
<td>33.3</td>
<td>24.4</td>
<td>5.0</td>
</tr>
<tr>
<td>Marsh Duck WMA</td>
<td>40.86, -97.40</td>
<td>415</td>
<td>Silty Clay</td>
<td>0.98</td>
<td>3.19</td>
<td>47.4</td>
<td>34.0</td>
<td>25.3</td>
<td>5.5</td>
</tr>
<tr>
<td>Spike Rush WMA</td>
<td>40.91, -97.48</td>
<td>317</td>
<td>Silty Clay Loam</td>
<td>0.88</td>
<td>5.84</td>
<td>110.8</td>
<td>56.3</td>
<td>24.2</td>
<td>4.6</td>
</tr>
<tr>
<td>Texas</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Castro Co. (private)</td>
<td>34.53, -102.10</td>
<td>697</td>
<td>Clay</td>
<td>1.01</td>
<td>1.84</td>
<td>97.6</td>
<td>19.0</td>
<td>35.0</td>
<td>6.2</td>
</tr>
<tr>
<td>TTU Rangeland Playa</td>
<td>33.60, -101.90</td>
<td>688</td>
<td>Clay</td>
<td>1.00</td>
<td>1.21</td>
<td>84.4</td>
<td>12.0</td>
<td>36.9</td>
<td>7.5</td>
</tr>
<tr>
<td>Swisher Co. (private)</td>
<td>34.67, -101.85</td>
<td>542</td>
<td>Silty Clay</td>
<td>1.09</td>
<td>1.50</td>
<td>129.2</td>
<td>16.0</td>
<td>31.7</td>
<td>7.2</td>
</tr>
</tbody>
</table>
Table 3.2. Environmental conditions at initial Barnyardgrass emergence for each climate (historical, future cool, future average, future warm), soil moisture (saturated – SAT, field capacity – FC, drawdown – DD), and seed bank density (65, 145, 400 kg ha\(^{-1}\)) treatment. First day of germination is the experiment day at which germination commenced. Maximum air temperature (\(T_{\text{MAX}}\)), minimum air temperature (\(T_{\text{MIN}}\)), and soil temperature were recorded at emergence. Texas minimum temperatures were lower than growth chamber limits (*).

| Climate Scenario | Soil Moisture | Seed Bank Density (kg ha\(^{-1}\)) | Day of Emergence | Air Temperature \(^{\circ}\)C | Soil Temperature \(^{\circ}\)C | Emergence (%) |
|------------------|--------------|------------------------------------|------------------|-----------------|-----------------|----------------|---|
| Historical       | SAT          | 145                                |                  | 4               | 18.8            | 23.0           |   |
|                  | DD           | 145                                |                  |                 | 17.4            | 36.8           |   |
|                  | FC           | 145                                |                  |                 | 17.6            | 26.6           |   |
|                  | FC           | 65                                 |                  |                 | 17.2            | 35.6           |   |
|                  | FC           | 400                                |                  |                 | 18.5            | 19.6           |   |
| Future Cool      | SAT          | 145                                |                  | 9               | 18.9            | 21.4           |   |
|                  | DD           | 145                                |                  |                 | 18.7            | 33.8           |   |
|                  | FC           | 145                                |                  |                 | 19.0            | 32.4           |   |
|                  | FC           | 65                                 |                  |                 | 19.0            | 20.4           |   |
|                  | FC           | 400                                |                  |                 | 19.2            | 12.4           |   |
| Future Average   | SAT          | 145                                |                  | 8               | 18.3            | 6.2            |   |
|                  | DD           | 145                                |                  |                 | 17.9            | 25.8           |   |
|                  | FC           | 145                                |                  |                 | 17.9            | 22.3           |   |
|                  | FC           | 65                                 |                  |                 | 17.9            | 27.7           |   |
|                  | FC           | 400                                |                  |                 | 17.9            | 18.1           |   |
| Future Warm      | SAT          | 145                                |                  | 6               | 22.1            | 16.1           |   |
|                  | DD           | 145                                |                  |                 | 22.6            | 23.5           |   |
|                  | FC           | 145                                |                  |                 | 22.0            | 32.2           |   |
|                  | FC           | 65                                 |                  |                 | 22.0            | 37.5           |   |
|                  | FC           | 400                                |                  |                 | 22.0            | 13.7           |   |
| Historical       | SAT          | 145                                |                  | 12              | 14.3            | 6.8            |   |
|                  | DD           | 145                                |                  |                 | 14.2            | 8.0            |   |
|                  | FC           | 145                                |                  |                 | 13.9            | 8.0            |   |
|                  | FC           | 65                                 |                  |                 | 13.9            | 6.0            |   |
|                  | FC           | 400                                |                  |                 | 14.3            | 4.4            |   |
| Future Cool      | SAT          | 145                                |                  | 11              | 15.4            | 6.2            |   |
|                  | DD           | 145                                |                  |                 | 15.7            | 4.8            |   |
|                  | FC           | 145                                |                  |                 | 15.5            | 1.9            |   |
|                  | FC           | 65                                 |                  |                 | 15.5            | 6.2            |   |
|                  | FC           | 400                                |                  |                 | 15.9            | 1.0            |   |
| Future Average   | SAT          | 145                                |                  | 10              | 15.0            | 16.5           |   |
|                  | DD           | 145                                |                  |                 | 15.6            | 16.6           |   |
|                  | FC           | 145                                |                  |                 | 15.0            | 21.3           |   |
|                  | FC           | 65                                 |                  |                 | 15.5            | 34.8           |   |
|                  | FC           | 400                                |                  |                 | 15.1            | 12.1           |   |
| Future Warm      | SAT          | 145                                |                  | 8               | 16.2            | 16.5           |   |
|                  | DD           | 145                                |                  |                 | 15.6            | 16.6           |   |
|                  | FC           | 145                                |                  |                 | 15.0            | 21.3           |   |
|                  | FC           | 65                                 |                  |                 | 15.5            | 34.8           |   |
|                  | FC           | 400                                |                  |                 | 15.1            | 12.1           |   |
Table 3.3. Regression equations and 95% confidence intervals for total, above- and below-ground biomass (g tray⁻¹) collected at the end of 28-day germination study for Texas samples under four climate scenarios. Total biomass was calculated as the sum of above- and below-ground biomass. Significance denoted at $p < 0.05$ (*) and $p < 0.01$ (**).

<table>
<thead>
<tr>
<th>Climate Scenario</th>
<th>Total Biomass</th>
<th>Above-ground Biomass</th>
<th>Below-ground Biomass</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>y-intercept</td>
<td>slope (CI)</td>
<td>y-intercept</td>
</tr>
<tr>
<td>Historical</td>
<td>-5.47</td>
<td>0.52 (-0.02, 1.01)</td>
<td>26.46** (2.85, -0.84)</td>
</tr>
<tr>
<td>Future Cool</td>
<td>10.52</td>
<td>-0.53 (-1.28, 0.22)</td>
<td>17.25 (-2.41, 0.12)</td>
</tr>
<tr>
<td>Future Average</td>
<td>-4.44</td>
<td>0.39* (0.09, 0.69)</td>
<td>18.98** (-1.80, -0.61)</td>
</tr>
<tr>
<td>Future Warm</td>
<td>0.78</td>
<td>0.05 (-0.52, 0.61)</td>
<td>4.32 (-0.79, 0.07)</td>
</tr>
</tbody>
</table>
Figure 3.1. Temperature treatments for a germination study representing early season germination conditions for Nebraska (a) and Texas (b) for historical data and scenarios based on downscaled CMIP5-BCCA downscaled atmosphere ocean general circulation models for the RCP4.5 emission scenarios (2070-2099) – future average, warm future, and cool future. Nebraska conditions were based on historical observations and future projections for the month of April and Texas conditions were based on historical observations and future projects for the month of March. Bars represent daily temperature range that was simulated in the germination chamber.
Figure 3.2. Model predicted means and 95% confidence interval bars for Barnyardgrass emergence rate (Table 3.2). For Nebraska, emergence percentage was impacted by soil moisture and climate scenario interactions (a; held constant at moderate seed bank density), as well as seed bank density and climate scenario interactions (b; held constant at field capacity moisture). For Texas, Barnyardgrass emergence percentage was impacted by soil moisture and climate scenario interactions (c; held constant at moderate seed bank density) and seed bank density and climate scenario interactions (d; held constant at field capacity moisture). Hosmer-Lemeshow statistics provided no indication of poor fit of logistic regression for Nebraska (p = 0.999) or Texas (p = 0.984). Letters indicate differences among climate scenario treatments within soil moisture or seed bank density treatments at p < 0.05 determined by Tukey pairwise comparisons performed on the log odds ratio scale.
Figure 3.3. Model predicted mean and 95% confidence intervals for seedling survival between initial germination day (Table 2) and experiment day 28. Adjusted survival <4.5 indicates decline in seedling abundance throughout experiment. For Nebraska, adjusted survival was impacted by soil moisture and climate scenario interactions (a, $R^2 = 0.718$). For Texas, adjusted survival was impacted by soil moisture and climate scenario interactions (b, $R^2 = 0.816$) and seed bank density (c, $R^2 = 0.816$). Letters indicate differences among climate scenario treatments within soil moisture or seed bank density treatments at $p < 0.05$ determined by Tukey pairwise comparisons.
Figure 3.4. Model predicted mean and 95% confidence intervals for physiological response between initial germination day (Table 3.2) and experiment day 28. For Nebraska, plant height at day 28 was impacted by soil moisture (a, $R^2 = 0.496$) and climate scenario (b, $R^2 = 0.496$). For Texas, holding seed bank density constant, ending plant height was negatively correlated with mean soil temperature (c) for low ($F = 7.531, p = 0.021, R^2 = 0.373$), moderate ($F = 9.495, p = 0.005, R^2 = 0.270$), and high ($F = 1.986, p = 0.189, R^2 = 0.082$) seed bank densities. Texas ending plant height was also affected by climate scenario (d, $R^2 = 0.713$). Letters indicate differences among treatments at $p < 0.05$ determined by Tukey pairwise comparisons.
Figure 3.5. Model predicted mean and 95% confidence intervals for biomass (g tray⁻¹) response between initial germination day (Table 3.2) and experiment day 28 for Nebraska samples. Total biomass at day 28 was affected by climate scenario (a, $R^2 = 0.332$) and seed bank density (b, $R^2 = 0.332$), with no interactions. Above-ground biomass (c, $R^2 = 0.711$) and below-ground biomass (d, $R^2 = 0.293$) were affected by interactions between climate scenario temperatures and soil moistures. Letters indicate differences among climate scenario treatments within soil moisture or seed bank density treatments at $p < 0.05$ determined by Tukey pairwise comparisons.
CHAPTER 4

PROJECTED CLIMATE AND LAND USE CHANGES DRIVE PLANT COMMUNITY COMPOSITION IN PLAYA WETLANDS

ABSTRACT

Great Plains playa wetlands support a wide variety of plant species that are not found elsewhere in the region due to the ephemeral presence of standing water and hydric soils. If longer dry periods occur due to climate change or if changes in surrounding land use alter sedimentation rates and water storage capacity, playa plant communities will likely experience decreased diversity, with lasting effects on the ecosystem services provided by playas in the Great Plains. We aimed to quantify changes in playa wetland plant community composition associated with predicted changes in precipitation and land use in the Great Plains. We conducted two six-month greenhouse studies using intact mesocosms collected from playas in Nebraska and Texas. Precipitation treatments derived from historical observations and three future CMIP5 RCP4.5 downscaled climate projections were applied to mesocosms and plant response was evaluated during the first greenhouse study. Land use treatments were simulated by nitrogen (N) applications to soil ranging from 0 to 100 mg-N L\(^{-1}\) with each precipitation event under historical rainfall patterns during the second greenhouse study. Overall, plant abundance, richness, and diversity were not substantially affected by projected climate and land use changes. Plant communities tended to shift towards more native species under projected future climate conditions, but as N runoff increased, native species richness was decreased. These trends may suggest that...
management priorities focus on protecting playas in the face of land use change, rather than trying to mitigate for decreased or shifting precipitation patterns associated with projected climate change.

INTRODUCTION

The Great Plains, USA region is accustomed to extreme weather variability on a seasonal and year-to-year scale; however, this variability is expected to increase by the end of the 21st century (Conant et al. 2018; Kloesel et al. 2018). Regional climate change models for the Great Plains project that mean annual air temperature will increase by 2.0 to 2.8 °C by 2050 and by 2.4 to 4.7 °C by 2100 (Kloesel et al. 2018). Elevated temperatures are expected to increase evapotranspiration in wetlands (Winter 2000) and may induce land use changes in the surrounding landscape, such as relative shifts between croplands and grasslands depending upon water availability (Kukal and Irmak 2018). Regional climate models also project that precipitation events in the Great Plains will become more variable and intense, leading to extended periods of drought and flooding (Melillo et al. 2014; Kloesel et al. 2018). While Great Plains ecosystems and native plant and animal species have co-evolved with extreme temporal weather variability, they may be affected by increased variability expected with projected climate change (Matthews 2008; Uden et al. 2015; Sofaer et al. 2016; Reese and Skagen 2017).

Playas are shallow, recharge wetlands located throughout the High Plains region that rely entirely on precipitation and runoff from the surrounding watershed for inundation (Smith 2003). Playa density and size are greatest on the
Texas High Plains; however, playas are distributed as far north as Nebraska (Figure 3.1). Average playa area is 6.3 ha, and 87% of playas are less than 12 ha in Texas (Guthery and Bryant 1982). While playas make up only 2% of the land area in the southern Great Plains and even less in northern regions (Haukos and Smith 1994a), they provide crucial ecosystem functions, including groundwater recharge (Gurdak and Roe 2010; McKenna and Sala 2017), wildlife habitat (Johnson 2011; Smith et al. 2011), and biogeochemical cycling (McKenna and Sala 2016; Villa and Bernal 2017; Howell et al. 2019). Playas are able to provide these ecosystem services due to unique biotic and abiotic properties, such as hydrophytic vegetation (Gilbert 1989; Haukos and Smith 2004), shrink-swell soils (Allen et al. 1972), and isolated watershed hydrology (O’Connell et al. 2012; Tang et al. 2017).

Due to the ephemeral presence of standing water and hydric, heavy clay soil, playas support a wide variety of plant species not found elsewhere in the Great Plains. Playa plant species can be categorized by water regimes within the wetland (Federal Geographic Data Committee 2013), which tend to be divided into zones in concentric circles surrounding the inner basin representing the basin floor, transition between the basin and upland, and upland (Guthery and Bryant 1982; Smith 2003). Plant communities in playas depend on seasonal rainfall patterns. thus climate change conditions, especially long periods of drought, have the potential to alter the distribution and persistence of obligate, hydrophytic plant species [e.g., duckweed (Lemna minor), water fern (Azola mexicana), and common bladderwort (Utricularia vulgaris)] (Gilbert 1989), as well as annual
species [e.g., barnyardgrass (*Echinochloa crusgalli*) and smartweeds (*Polygonum* spp.)]. Moist-soil annual species rely on adequate soil moisture and nutrients to prolifically produce seed biomass which provides food resources to migratory waterfowl (Haukos and Smith 2006; Webb et al. 2010; Schepker et al. 2018).

Typical playa hydroperiods only briefly support obligate wetland plant species; however, emergent vegetation (e.g., *Typha* spp.) may be found in playas that lack physical disturbance (e.g., grazing, inundation events) or receive excess water inputs (Pezzolesi et al. 1998; Smith 2003). In years when the wetland is not inundated, plant species that typically occur at the wetland perimeter will develop towards the center of playas and outcompete moist-soil plant species (Smith 2003). In the absence of a seasonal hydroperiod, plant species richness may decrease and overall playa ecology is likely to change (Gilbert 1989; Haukos and Smith 2004; Tsai et al. 2012). If longer dry periods occur due to climate change or if land use changes increase sedimentation rates and reduce water storage capacity (Matthews 2008; Daniel et al. 2015), playa plant community composition may decrease in diversity and have lasting effects on biodiversity in the Great Plains.

In addition to future changes in climate, land use trends may also affect playa plant ecology. Culturally accelerated sedimentation due to cultivation of the surrounding watershed has caused widespread playa degradation in the 20th and 21st centuries (Luo et al. 1997; Daniel et al. 2015). Sediment accumulation reduces playa water storage volume, thereby altering hydrologic conditions supporting wetland plants. Several conservation-focused land use practices have been shown to reduce sedimentation and conserve playa integrity (Johnson 2011;
Vegetative buffers surrounding playas trap sediment runoff, and if planted to native grasses, allow water to flow into playas and support wetland plant communities (Bartuszevige et al. 2012; O’Connell et al. 2012). Grasslands and pastures in the surrounding watershed tend to have less affect on nutrient loading and sedimentation into playas than agricultural land uses (Tsai et al. 2012; O’Connell et al. 2013). Future land use scenarios are predicted to change based on climate shifts in the Great Plains with land area under cultivation increasing or decreasing, depending on precipitation, atmospheric carbon dioxide, and conservation policies (Sohl et al. 2007; Sohl and Sayler 2008).

Given changing environmental conditions in the Great Plains, the overall goal of this project is to understand potential alterations in playa wetland plant community composition associated with projected changes in precipitation and land use associated with global climate change. With this overarching goal, we identified the following objectives: (i.) quantify the effects of simulated hydroperiod change on plant community composition in playas; (ii.) elucidate differences in plant responses between mesocosms collected from Nebraska playas and Texas playas; (iii.) assess the effect of increased nitrogen inputs (from surface runoff) from simulated land-use change on plant community composition in mesocosms collected from Nebraska and Texas playas. To accomplish these objectives, we conducted two six-month greenhouse studies incorporating various hydroperiod and nitrogen loading rates in controlled settings. Previous studies evaluating playa plant communities have predominantly been conducted at a field
scale and indicated that playa plant communities tend to adapt to varying soil moisture conditions, with little difference in abundance, richness, and diversity in response to changing hydroperiods (Haukos and Smith 1994b; Haukos and Smith 2001; Haukos and Smith 2006b). Sedimentation and water storage loss associated with cropland surrounding playas generally create conditions favoring annual and exotic plant species (Smith and Haukos 2002; O’Connell et al. 2012; Tsai et al. 2012); however, this trend has not been evaluated relative to nutrient loading.

**METHODS**

*Site justification*

Soil mesocosm units were collected from playas surrounded by agricultural production in the Rainwater Basin of Nebraska and Southern High Plains in Texas (Figure 4.1). Due to logistical considerations, as well as management and environmental variability among playas, experts in each region were asked to select study sites based on their knowledge of the conditions and access to the sites. Many other ecological studies describe their site selection using a similar protocol (Haukos and Smith 1994b; Anderson and Smith 2000; Weltzin et al. 2000; Hol et al. 2015). Regional experts were asked to choose sites representative of the range of conditions within each region, although no two playas were managed in the same way. Nebraska sites were surrounded by cropland and occasionally grazed by livestock to reset vegetative succession and control encroachment by invasive plant species (Smith 1989; Smith et al. 2011), whereas Texas sites were surrounded by pasture and grazed frequently by livestock, according to land owners. Study sites also contained minimum sediment
accumulation (< 5 cm). We recorded historical climate patterns for each playa region (Figure 4.2) and evaluated landscape and soil characteristics for each playa (Table 4.1). In Nebraska, soil cores were collected from the moist-vegetation zone, which represented Massie silty clay loam (*Fine, smectitic, mesic Vertic Argialbolls*), Scott silt loam (*Fine, smectitic, mesic Vertic Argialbolls*), and Fillmore silt loam (*Fine, smectitic, mesic Vertic Argialbolls*) soil series. Texas soil cores were also collected from the moist-soil vegetation zone, representing the Randall clay (*Very-fine, smectitic, thermic Ustic Epiaquerts*) soil series.

Intact soil cores were collected by hand for two separate studies. The first set of cores was collected in March and April 2016 for use in the hydroperiod study (Experiment #1) and the second set was collected in February and March 2017 for the land use study (Experiment #2). Soil samples were placed into plastic tubs (15-cm depth, 30-cm length, 20-cm width), and stored at 4 °C until hydroperiod and land use greenhouse studies were initiated in June 2016 and April 2017, respectively. Texas samples were collected from the same five wetlands for each greenhouse study, but Nebraska sites varied between experiments because several sites where samples were collected in 2016 were completely inundated in spring 2017, making soil collection impractical. We collected and analyzed additional soil samples (0-10 cm) from the same area in the playa for texture, bulk density, total organic carbon, total nitrogen, and pH using standard methods (Reddy et al. 2013).
Hydroperiod effects on playa plant ecology

We derived hydrologic treatments to assess the effect of precipitation changes on wetland ecosystems in the Great Plains (Chapter 2). Based on historic precipitation patterns (1986-2015) and future precipitation projections (2070-2099) using Coupled Model Intercomparison Project phase 5 (CMIP5) downscaled global climate model (GCM) data for the RCP4.5 emission scenario (obtained at Reclamation 2013), we developed daily hydrologic treatments for the wetland growing season (April to October). We corrected precipitation data from nineteen GCMs to remove excess drizzle days (<0.25 mm precipitation) and used gamma-based quantile mapping to accurately capture extreme events (Teutschbein and Seibert 2012; Gautam et al. 2018). Comprehensive bias correction details for precipitation adjustments can be found in Gautam et al. (2018). After adjusting projected output data, we selected three models, including: 1) an average model, representing the most typical precipitation conditions predicted in RCP4.5 scenarios; 2) a model that contained the longest period of no-precipitation days over the course of the growing season; and 3) a model that contained the greatest number of runoff-inducing precipitation events (Uden et al. 2015) during the growing season. We then used projected precipitation data to determine the timing and amounts of deionized water applied to experimental units to simulate altered hydroperiods during the dominant growing season.

To assess how projected climate change will affect playa plant production, we conducted a greenhouse experiment that simulated the growing season in Nebraska and Texas playas under various hydrologic conditions. Before initiating
hydrologic treatments, all soil samples were wetted to field capacity moisture conditions for a duration of four weeks starting in June 2016 to promote germination (Haukos and Smith 2001). Precipitation treatments were carried out for the remaining five months, from July 2016 to November 2016.

Land use change effects on playa plant ecology

To assess how predicted land use changes could affect playa plant production, a greenhouse experiment was conducted to mimic the historic growing season in Nebraska and Texas playas under seven N loading rates. Various N runoff rates represented scenarios of increased or decreased cropland area surrounding playas. Much of the cropland surrounding playas is irrigated, and thus, runoff into playas is generally more dependent on land area cropped than on overall precipitation. We conducted the land use change experiment from April 2017 to September 2017. Before treatments began, all soil samples were wetted to field capacity moisture conditions for 4 weeks. Nitrogen in the following concentrations of ammonia-nitrate (NO$_3$NH$_4$) was added to each rainfall event throughout the remaining five-month growing season under historic conditions for Nebraska and Texas playas, separately (Figure 4.3). Total nitrogen loading rates can be found in Table 4.2.

i. Control: Deionized water

ii. Grassland Low Runoff: 0.5 mg-N L$^{-1}$

iii. Grassland High Runoff: 2.0 mg-N L$^{-1}$

iv. Modern Cropland Low Runoff: 10.0 mg-N L$^{-1}$

v. Modern Cropland High Runoff: 25.0 mg-N L$^{-1}$
vi. Intensified Cropland Low Runoff: 62.5 mg-N L\(^{-1}\)

vii. Intensified Cropland High Runoff: 100 mg-N L\(^{-1}\)

*Plant community evaluation*

The greenhouse temperature was continuously monitored during both studies using Onset HOBO data loggers and sensors (Onset Computer Corporation, Bourne, MA) and compared to atmospheric conditions in the same time period from the greenhouse location and soil sampling sites. Plants were identified to species and plant species abundance was noted monthly for each experimental unit. Species were identified using Bryson and DeFelice (2009) and Bryson and DeFelice (2010) and cross-checked using Haukos et al. (1997). We measured abundance as total plant count and species richness as the total number of unique species present. Plant community dynamics were measured monthly using the Shannon-Weiner Diversity Index, Simpson’s Diversity Index, and by species composition similarities to determine if plant community composition shifted when exposed to different environmental conditions (Magurran 1988; Haukos and Smith 2004).

For both greenhouse studies, plant community dynamics were evaluated seasonally. Baseline measurements were collected before water was added to mesocosm units each year to account for any pre-existing plants that had germinated between sample collection in the field and beginning of the greenhouse experiments. Following baseline conditions, we considered three stages of plant growth, based on season precipitation (Figure 4.3). Early-season plants were those counted in experimental months 1 and 2, mid-season plants
grew in months 3 and 4, and late-season plants were present in months 5 and 6. Statistical analyses were conducted on a seasonal, rather than monthly time-scale.

Statistical analyses

Repeated-measures generalized linear mixed effects models were used to test effects of hydroperiod and land use on plant community composition in playa wetland soils. Samples were analyzed independently for soils collected in Nebraska and Texas. Sampling date and main treatment (hydroperiod or N loading rate) were designated as interacting fixed effects in the global model and individual wetland was designated as a random effect. We accounted for repeated measurements over time by using a sample ID for each experimental unit as a random model effect. When no statistical interactions existed between sampling date and main treatment effect, we used an additive global model with the same fixed and random effects to account for all variables in predicted means estimates. Abundance and richness data were fitted with a Poisson distribution in the global model. When fixed effects were significant, we conducted post-hoc least squared means comparisons using a Tukey adjustment to evaluate differences between various combinations of hydroperiod and sampling date or nitrogen loading rate and sampling date. All analyses were conducted using the R statistical software (version 3.3.2). Results were analyzed using the lme4 package (Bates et al. 2015) and emmeans package (Lenth 2018), and package ggplot2 was used to visualize estimated means derived from regression models (Wickham 2016).

To assess plant communities, plant compositions were clustered using Ward’s cluster analysis with Bray-Curtis distance measurements of similarity (hclust
function of *vegan* package by Oksanen 2015). Additionally, we used principal component analysis (*PCA* function of *FactoMineR* package by Kassambara 2017) to relate plant characteristics (i.e., wetland indicator status, native/exotic status) to community composition by treatment. Species wetland indicator statuses used for principal component analysis were obligate (OBL), facultative wet (FACW), facultative (FAC), facultative upland (FACU), and upland (UPL). We used package *ggdendro* to visualize results of cluster analyses (Wickham 2016) and package *factoextra* to visualize results of principal component analyses (Kassambara 2017).

**RESULTS**

*Hydroperiod effects on playa plant ecology*

Models projected that precipitation will decrease throughout the growing season for Nebraska and Texas, and seasonal precipitation patterns will likely shifted (Figure 4.3). Each of three models suggested decreased precipitation throughout the growing season compared to historical conditions [CESM1-BGC.1 (Hurrell et al. 2013); MIROC-ESM-CHEM.1 (Watanabe et al. 2011); and MPI-ESM-LR.1 (Giorgetta et al. 2013)]. Based on our treatment development techniques, the future average treatment had less cumulative precipitation during the growing period for Nebraska than the future dry treatment; however, the temporal conditions of these two treatments mimicked the overall model projections for end-of-century data and were selected despite the discrepancy (Figure 4.3). In simulated rainfall conditions for Nebraska, the future wet scenario had the greatest cumulative rainfall in experiment month two (M2), but
experienced no precipitation events during experiment M3. Seasonal patterns for historical, future average, and future dry climate scenarios were similar for Nebraska, but future average and future dry scenarios had less cumulative rainfall than historical conditions. For simulated conditions in Texas samples, historical, future average, and future wet scenarios experienced similar cumulative rainfall until experiment M5; however, rainfall was consistently lower for the future dry climate scenario.

In the hydroperiod study, 10 unique plant species were identified in each of the Nebraska and Texas mesocosm units, with six species identified in both Nebraska and Texas samples (Appendix 2). Plants species identified in the hydroperiod study represented 12 plant families commonly found in playas throughout the High Plains region (Haukos and Smith 2004). Plant species wetland indicator statuses ranged from obligate wetland species to upland species (Federal Geographic Data Committee 2013). *Echinochloa crusgalli* and *Leptochloa fusca* were the most common species identified in Nebraska samples (40.0%), whereas *Ambrosia grayi* was the most common species identified in Texas samples (65.0%).

Plant abundance, richness, and diversity were evaluated seasonally for Nebraska and Texas experimental units. Abundance generally remained constant over early- and mid-season of the experiment, but decreased during the late-season under future climate conditions. In Nebraska, plant abundance was greater under historical conditions compared to future wet ($|z| = 5.14$, $p < 0.0001$) and future dry ($|z| = 2.96$, $p = 0.02$) conditions in the late season (Figure 4.4-a). Plant
abundance in Texas samples decreased progressively over the growing season for all hydroperiod treatments, but there were no differences between treatments (Figure 4.4-c). There were no interactions between sampling date and hydroperiod treatment for species richness, so comparisons are made over all seasons for either Nebraska or Texas. In Nebraska, species richness did not differ among hydroperiod treatments (Figure 4.3-b). In Texas, richness under future dry conditions was less than historical, future wet, and future average hydroperiod conditions (|z| ≥ 2.90, p ≤ 0.02; Figure 4.3-d). Plant diversity was highly variable among site replications in Nebraska and Texas samples, so climate scenario had little effect on Shannon-Weiner or Simpson Diversity (Table 4.3). In Nebraska samples, Shannon-Weiner Diversity was greater under historical climate conditions when compared to future wet climate conditions over all seasons (|z| = 3.09, p = 0.04).

While hydroperiod treatments did not have substantial effects on plant abundance, richness, and diversity, individual species and community compositions differed among simulated hydroperiods. Using cluster analysis, plant communities tended to visually cluster by hydroperiod treatment for Nebraska samples (Figure 4.5-a). Nebraska plant communities under historical conditions contained 13 of 16 species (81.3%) identified in Nebraska samples, including two species (Polygonum pensylvanicum and Verbascum thapsus) not found in any other climate scenario treatment. Plants that emerged under Nebraska future wet precipitation conditions contained 8 of 16 species (50%), including no unique species, and missing three species (Rumex crispus, Solanum
ptycanthum, and Panicum dichotomiflorum) found in the other three climate scenario samples. Samples that emerged in future average precipitation conditions contained 11 of 16 species (68.8%), including one unique species, Xanthium strumarium, commonly considered a nuisance plant in wetlands (Strader and Stinson 2005). Plant communities under future dry conditions had the greatest separation in the cluster analysis. Nebraska future dry plant communities contained 10 of 16 species (62.5%), including two unique species (Amaranthus tuberculatus and Marsilea vestita). Two species (Euphorbia prostrata and Setaria verticillata) missing from future dry samples were found in the other three climate scenario treatments for Nebraska samples. Five species were identified in samples from all Nebraska hydroperiod treatments – Coreopsis tinctoria, Polygonum persicaria, Eleocharis palustris, Echinochloa crusgalli, and Leptichloa fusca. Samples from each hydroperiod contained native and exotic plant species; however, the greatest proportion of native plants was observed under future dry climate conditions (70% native), compared to historical (53.8% native), future wet (50.0% native), and future average (54.5% native) conditions.

For Texas samples, plant communities exposed to historical precipitation contained 11 of 16 species (68.8%) identified in Texas samples, including two species (Amaranthus retroflexus and Lythrum califorunicum) not found in any other hydroperiod treatment. Plants which emerged under Texas future wet precipitation conditions contained 10 of 16 species (62.5%), including one unique species (Digitaria sanguinalis). Samples in average future precipitation conditions for Texas contained 10 of 16 species (62.5%), including one unique
species (*Eriochloa contracta*), and one species (*Cyperus esculentus*) was missing. Plant communities exposed to Texas future dry conditions contained 10 of 16 species (62.5%), including one unique species (*Panicum dichotomiflorum*). One species (*Marsilea vestita*) was missing from future dry samples that was found in the other three hydroperiod treatments for Texas samples. Six species were identified in samples from all Texas hydroperiod treatments – *Amaranthus tuberculatus, Ambrosia grayi, Chenopodium leptophyllum, Polygonum amphibium, Portulaca thapsus*, and *Echinochloa crusgalli*. Similar to Nebraska, the greatest proportion of native plants in Texas samples was found under future average climate conditions (80% native), followed closely by future dry climate conditions (70% native), compared to historical (63.6% native) and future wet (60.0% native) conditions.

Principal component analyses for Nebraska and Texas further allowed us to visualize trends in plant community data in response to hydroperiod treatments (Figure 3.6). The first two principal components accounted for 30.4% and 25.2%, respectively, of variance in community data for Nebraska. Coefficients (β) for each variable included in the principal component analyses describe the relative contribution of that variable on a scale from 0 to |1|. Native (β = 0.835) and exotic (β = -0.811) status made the strongest contribution to the first principal component (Table 4.4). The second principal component was strongly driven by FACW (β = 0.860) and FAC (β = -0.851) status. Historical plant communities were most strongly pulled in the negative direction of the first principal component, associated with exotic plant species. Plant communities under future
wet conditions were most strongly pulled in the positive direction of the first principal component, associated with native plant species. Nebraska plant communities under future dry and future average hydroperiod conditions were pulled in a negative direction on the second principal component, associated with FAC plant species.

For Texas samples, the first two principal components accounted for 36.6% and 22.8%, respectively, of variance in plant community samples. The first principal component was strongly driven by native (β = 0.816) and exotic (β = -0.826) plant status. The top two factors that contributed to the second principal component were FACW (β = 0.730) and OBL (β = -0.666) status. The centroids for all hydroperiod treatments were located close together near the intersection of the two principal component axes; thus, it is difficult to identify trends in the plant community data based on this analysis.

Land use change impacts on playa plant ecology

During the land use study, Nebraska rainfall decreased after experiment day 100, and plant growth was limited after this point when soil moisture became limited. During the last two months of the Nebraska experiment, greenhouse temperatures exceeded typical field temperatures by > 10°C, which likely exacerbated late-season moisture stress (Figure 4.2). Texas daily rainfall was limiting during the mid-growing season, but precipitation events after experiment day 115 led to late-season plant growth. Temperatures in the greenhouse mimicked typical field temperatures for the last three months of greenhouse
experiment, but in the first half of the experiment, greenhouse temperatures exceeded typical field temperatures by 5 to 10°C (Figure 4.2).

In the land use study, eight unique plant species were identified in Nebraska mesocosm units and 11 unique plant species were identified in Texas mesocosm units, with 15 species identified in Nebraska and Texas samples (Appendix 2). Plants species identified in the land use study represented 12 plant families commonly found in the playa region (Haukos and Smith 2004). For all species, the wetland indicator status ranged from obligate wetland species to upland species (Federal Geographic Data Committee 2013). *Echinochloa crusgalli* was the most abundant species identified in Nebraska samples (68.6%) and *Ambrosia grayi* was the most abundant species identified in Texas samples (80.0%).

Plant abundance, species richness, and diversity were measured for land use study mesocosm units each season (Figure 4.7). In Nebraska samples, abundance was greater under intensified cropland conditions (62.5, 100 mg-N L\(^{-1}\)) in the late-season, compared to control (0.0 mg-N L\(^{-1}\); |\(z| = 4.37, p = 0.0001\), grassland (0.5, 2.0 mg-N L\(^{-1}\); |\(z| = 4.93, p < 0.0001\), and modern cropland treatments (10, 25 mg-N L\(^{-1}\); |\(z| = 5.56, p < 0.0001\). Texas trends were not as clear for plant abundance. In mid-season, Texas modern cropland N rates produced greater abundance than grassland N rates (|\(z| = 3.80, p = 0.0009\). By late-season, abundance under grassland rates began to recover and was comparable to higher N rate treatments. No species richness differences were found among N treatments for Nebraska samples; however, in Texas samples, the control N rate produced species richness values greater than grassland N rates over all seasons (|\(z| = 3.55, p = 0.002\).
Diversity trends for the land use study were similar to the hydroperiod study, where the only differences were observed using Shannon-Weiner Diversity Index values. In Nebraska, there were no differences in diversity between N rates. In Texas samples, the control N rate had the greatest plant diversity, producing greater diversity than all other N rates over all seasons (|z| ≥ 2.89, p ≤ 0.04; Table 4.4).

Unlike the hydroperiod experiment, plant communities did not tend to cluster by main treatment effect for Nebraska and Texas samples in the land use study (Figure 4.8). Plant communities exposed to the control N rate (0 mg-N L⁻¹) contained 7 of 23 species (30.4%) identified in Nebraska samples. The control treatment did not contain *Rumex crispus* which was found in all other N treatments when grouping by land use type (i.e., grassland N rates, modern cropland rates, and intensified cropland rates). Plant communities under Nebraska grassland N rates (0.5, 2.0 mg-N L⁻¹) contained 16 of 23 species (69.6%), including three unique species (*Lythrum californicum*, *Marsilea vestita*, and *Bromus arvenis*). Samples under modern cropland N rates (10, 25 mg-N L⁻¹) contained 10 of 23 species (43.5%), including no species unique to these treatment rates. Plants that emerged under intensified cropland N rates (62.5, 100 mg-N L⁻¹) contained 18 of 23 species (78.3%), including five unique species (*Ambrosia grayi*, *Bassia scoparia*, *Setaria pumila*, *Setaria magna*, and *Alopecurus carolinianus*). Seven species (30.4% of total identified species) were identified in samples from all Nebraska N treatments – *Ameranthus tuberculatus*, *Coreopsis tinctoria*, *Polygonum pensylvanicum*, *Polygonum lapathifolium*,...
Echinochloa crusgalli, Panicum dicotomiflorum, and Hordeum jubatum. In Nebraska mesocosms, samples from each N treatment rate contained native and exotic plant species; however, the greatest proportion of native plants was found under control N rates (85.7% native), compared to grassland N rates (62.5% native), modern cropland N rates (80.0% native), and intensified cropland N rates (72.2% native).

For Texas samples, plant communities under control N rate contained 12 of 26 species (46.2%) identified in Texas samples, including one species (Alopecurus carolinianus) that was not found in any other N treatment group. Additionally, one species (Cyperus esculentus) that was identified in all other N rate categories was missing from control N rate samples. Plants communities for Texas grassland N rates contained 14 of 26 species (53.8%), including two unique species (Ambrosia trifida and Symphyotrichum subulatum), with one missing species (Eriochloa contracta). Plant communities in modern cropland N rates for Texas contained 17 of 26 species (65.4%), including five unique species (Amaranthus spinosus, Xanthium strumarium, Polygonum lapathifolium, Digitaria sanguinalis, and Bouteloua dactyloides). Samples that emerged under Texas intensified cropland N rates contained 12 of 26 species (46.2%), including three unique species (Amaranthus retroflexus, Euphorbia prostrata, and Portulaca olearacea). Five species were identified in samples from all Texas N rates – Ambrosia grayi, Coreopsis tinctoria, Rumex crispus, Eleocharis palustris, and Echinochloa crusgalli. Similar to Nebraska, the greatest proportion of native plants in Texas samples was found under the control N rate (75% native), compared to grassland
N rates (57.1% native), modern cropland N rates (64.7% native), and intensified cropland N rates (58.3% native).

Principal component analyses for Nebraska and Texas further allowed us to visualize trends in plant community data in response to nitrogen loading treatments (Figure 3.9). The first two principal components accounted for 44% and 19.8%, respectively, of variance in community data for Nebraska. Native (β = 0.792), exotic (β = -0.861), and FAC (β = -0.816) status made the strongest contributions to the first principal component (Table 4.5). The second principal component was strongly driven by OBL (β = 0.902) status. Plant communities under control N rate were most strongly pulled in the negative direction of the first principal component, associated with exotic and FAC plant species. Plant communities under the cropland N rates were most strongly pulled in the positive direction of the first principal component, associated with native and FACW plant species. Plant communities grown under modern cropland conditions were pulled in a negative direction on the second principal component, associated with FACW plant species.

For Texas samples, the first two principal components accounted for 35.2% and 17.7%, respectively, of variance in plant community samples. The first principal component was strongly driven by native (β = 0.818) and exotic (β = -0.859) plant status. The top factor contributing to the second principal component was FACW (β = -0.584) status. The centroid for control N rates aligned with the vector for native plant species, also potentially associated with FAC species.
status. Grassland N rate plant communities aligned with the vector for exotic plant species.

**DISCUSSION**

Based on climate change projections, precipitation is expected to decrease throughout the growing season in playa wetlands for Nebraska and Texas, and rainfall patterns will likely shift (Conant et al. 2018; Kloesel et al. 2018). In addition to changes in climate, land use change could shift towards more grassland or more intensified agriculture, depending upon conservation policies, commodity prices, and resource limitations in the Great Plains (Haukos and Smith 2003; Sleeter et al. 2012; Sohl et al. 2012). To quantify the effects of changing climate and land use conditions on playa plant communities, we conducted two greenhouse studies with intact mesocosm units collected from playas in Nebraska and Texas. In Nebraska and Texas playas, shorter, drier hydroperiods favored native plant species, but other community parameters (i.e., abundance, richness) responded inconsistently to hydroperiod treatments. Similarly, native plant species richness was the predominant response of Nebraska and Texas plant communities when subjected to varying N runoff rates associated with projected land use change.

In our study, plant communities were generally resilient to varying hydroperiod conditions; however, shorter, drier hydroperiods consistently favored native plant species. Common plant species identified in the hydroperiod study were consistent with previous studies on playa wetland plant communities (Gilbert 1989; Haukos et al. 1997; Haukos and Smith 2004). Overall, there were
few consistent differences in abundance, richness, and diversity among hydroperiod treatments for Nebraska and Texas samples. Playa seed banks contain a large diversity of species capable of adapting rapidly to changing moisture conditions (Haukos and Smith 1994b), so it is not surprising that plants germinated and grew regardless of soil moisture conditions. Further, we predict drier or shorter hydroperiods in the future may lead to relative shifts between plants adapted to varying moisture conditions based on previous studies across topographical and moisture gradients in playas (Haukos and Smith 2001; Haukos and Smith 2004). Results from the cluster analyses indicated that plant communities across seasons tended to cluster by hydroperiod treatments in Nebraska more strongly than in Texas; however, when examining the plant composition of various hydroperiod treatments, there are few clear trends in soil moisture preference, possibly due to variation among wetland replications. In the principal component analyses native and exotic status of plant species was the strongest indicator of plant communities for Nebraska and Texas samples, where, in general, projected future hydroperiods favored native species. Both O’Connell et al. (2012) and Tsai et al. (2012) found that exotic species richness in playas was associated with greater proportions of cropped watersheds, but neither study found an association between hydroperiod and exotic species richness. Native plants may be better adapted to variable climate conditions over the course of a growing season; however, as growing season lengthens due to warmer and drier conditions, cool season exotic species may have greater opportunities to establish and persist in playas (Ojima and Lackett 2002). In playas, exotic species richness
is not necessarily a negative factor for ecosystem services. Dominant exotic species, such as *Echinochloa crusgalli* and *Rumex crispus*, have been identified as an important food resource for migrating waterfowl (Haukos and Smith 1993; Haukos and Smith 1995).

In the land use study, increased N rates generally resulted in greater abundance and decreased diversity, but trends were not consistent across seasons or between Nebraska and Texas samples. Few studies have linked soil nutrients in playas to vegetative dynamics; however, several studies have linked surrounding land use practices to playa plant communities (Smith and Haukos 2002; O’Connell et al. 2012; Tsai et al. 2012). Cropped watersheds tend to increase exotic species richness. This trend has been linked to increased sediment accumulation and subsequent water volume loss in playas (O’Connell et al. 2012); however, increased exotic species richness could also be linked to greater nitrogen runoff associated with cropped watersheds. In this study, plant communities did not cluster consistently by N treatment; however, the control treatment (0 mg-N L⁻¹) had the greatest proportion of native plant species. Principal component analyses did not show clear trends for N rate treatments related to native and exotic plant status, likely due to variation between wetland replications. Elgersma et al. (2017) linked invasive emergent vegetation abundance, specifically *Typha* spp., to increased nutrient loading in wetlands globally; however, no *Typha* spp. were identified in our study. Further, different plant species may have variable nitrogen uptake capacities (von Wiren et al. 1997), a factor that was not evaluated as part of this study. For example, Williams et al. (2017) found that *Eleocharis*
macrostachya had greater concentrations of vegetative N compared to other wetland species, such as Polygonum spp.

One of the most consistent trends we observed was that native plant species may be better adapted to future climate conditions than exotic species, but increased N loading associated with land use change may favor exotic species. In the playa region, many of the exotic species identified in our study are considered beneficial to migratory waterfowl (Haukos and Smith 1993; Haukos and Smith 1995); however, a shift to exotic and annual plant species may decrease overall primary production and reduce plant biodiversity over time (Smith et al. 2011).

Based on our results, native and exotic plant species richness will also depend upon the relative magnitude of precipitation and land use shifts in the future. With increasingly detailed future climate and land use projections, we may soon be able to better model conditions likely to occur in the Great Plains playa region. Our future scenarios captured the range of variability of RCP4.5 climate projection models, a moderate emissions scenario. Thus, the trends we see in our hydroperiod study plant communities are likely conservative estimates of future conditions. If temperatures warm to a greater extent than modeled in our experiment, perhaps comparable with a high emissions scenario (i.e., RCP8.0), native species may continue to be well adapted or other invasive species may begin to intrude upon playa ecosystems (Smith 2003; Matthews 2008). Our land use change treatments captured a broad range of N loading rates associated with grassland and cropland dominated watersheds; however, native species richness was greatest when no N was added. Without vegetative buffers to reduce
sedimentation and nutrient loading (Luo et al. 1997; Johnson et al. 2012), playa plant communities may be vulnerable to exotic and invasive species encroachment based on our results.

Ecosystem services provided by playa plant communities are dependent upon landscape-scale variability driven by hydrology, surrounding land use, and watershed characteristics throughout the southern High Plains (Haukos and Smith 2004; O’Connell et al. 2012; Tang et al. 2017). We aimed to capture this variability by collecting intact soil cores from multiple playas in Nebraska and Texas to represent replications. This variability among the replicates likely contributed to inconsistent results in the hydroperiod and land use experiments; however, the results may be more representative of field conditions. Due to high variability among replicates collected from different playas, as well as variability within samples from the same playa, future studies at a field scale and in greater replication may help to identify more detailed shifts occurring in playa plant communities in the face of changing precipitation and land use.

In designing these studies, we aimed to capture variability within and among playas across the landscape through spatial replications, while also simulating a wide range of climate and land use scenarios. The statistical inference of our results are limited to the playas from which our samples were collected, because the sites were not randomly selected. However, the results for the samples collected from Nebraska and Texas are likely biophysically relevant on a regional scale. We were able to capture responses in the northern and southern extent of the playa region, but we did not conduct our studies using samples collected from
central playas in Kansas and Colorado. While the properties of these playas are similar to those in Texas, we cannot extend the inference of our study to include these ecosystems.

Overall, abundance, richness and diversity were not greatly affected by climate and land use changes in playas, which was expected based on the previous studies conducted in the playa region. Plant communities under projected future climate conditions and minimal N loading rates tended to shift to favor native species; however, as N runoff increased, native species richness decreased. These trends may suggest that management priorities focus on protecting playas in the face of land use change, rather than trying to manage for decreased or shifting rainfall patterns. Limited water resources exist in the Great Plains region (e.g., Steiner et al. 2017), thus, implementing traditional moist-soil management techniques (i.e., adding and drawing down water) may be challenging. Existing efforts to reduce sedimentation and increase water storage (e.g., Bartuszevige et al. 2012; O’Connell et al. 2012) in playas may also increase ecosystem resilience to future land use change.
LITERATURE CITED


Bryson CT, DeFelice MS (2009) Weeds of the South. University of Georgia Press, Athens, GA.


( Typha spp. ) management techniques depends on exogenous nitrogen
inputs. Elementa Science of the Anthropocene 5:19. doi:
10.1525/elementa.147

Federal Geographic Data Committee (2013) Classification of wetlands and
deepwater habitats of the United States. FGDC-STD-004-2013. Second
Edition 79. doi: FWS/OBS-79/31

impact of climate change using ensemble approach and comparison with
global gridded model: A case study on Goodwater Creek Experimental

Gilbert MC (1989) Ordination and mapping of wetland communities in
Nebraska’s Rainwater Basin region. U.S Corps of Engineers, Omaha, NE.

Giorgetta MA, Jungclaus J, Reick CH, et al. (2013) Climate and carbon cycle
changes from 1850 to 2100 in MPI-ESM simulations for the Coupled Model
Intercomparison Project phase 5. Journal of Advances in Modeling Earth

Gurdak J, Roe C (2010) Review: Recharge rates and chemistry beneath playas of
the High Plains aquifer, USA. Hydrogeology Journal 18:1747–1772. doi:
10.1007/s10040-010-0672-3


Table 4.1. Landscape and soil characteristics for each playa where soils were collected. Five Texas playas were used for both greenhouse experiments, but Nebraska playas varied due to hydrologic conditions when samples were collected. In Nebraska, soil cores were collected from the moist-vegetation zone which represented Massie silty clay loam (*Fine, smectitic, mesic Vertic Argialbolls*), Scott silt loam (*Fine, smectitic, mesic Vertic Argialbolls*), and Fillmore silt loam (*Fine, smectitic, mesic Vertic Argialbolls*) soil series. Texas soil cores were also collected from the moist-soil vegetation zone, representing the Randall clay (*Very-fine, smectitic, thermic Ustic Epiaquerts*) soil series.

<table>
<thead>
<tr>
<th>Wetland</th>
<th>Collection Date(s)</th>
<th>Collection Location</th>
<th>Clay (g kg⁻¹)</th>
<th>Textural Class</th>
<th>Bulk Density (g cm⁻³)</th>
<th>Total N (mg kg⁻¹)</th>
<th>Organic C (g kg⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nebraska</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Father Hupp WMA</td>
<td>2017</td>
<td>40.34, -97.61</td>
<td>400</td>
<td>Silty Clay</td>
<td>0.92</td>
<td>316</td>
<td>35.6</td>
</tr>
<tr>
<td>Hidden Marsh WMA</td>
<td>2016</td>
<td>40.71, -97.49</td>
<td>337</td>
<td>Silty Clay Loam</td>
<td>1.00</td>
<td>296</td>
<td>33.3</td>
</tr>
<tr>
<td>Marsh Hawk WMA</td>
<td>2017</td>
<td>40.64, -97.72</td>
<td>753</td>
<td>Clay</td>
<td>0.64</td>
<td>598</td>
<td>79.9</td>
</tr>
<tr>
<td>Red Head WMA</td>
<td>2017</td>
<td>40.43, -97.81</td>
<td>358</td>
<td>Silty Clay Loam</td>
<td>0.86</td>
<td>360</td>
<td>37.5</td>
</tr>
<tr>
<td>Renquist WMA</td>
<td>2016, 2017</td>
<td>41.03, -97.70</td>
<td>329</td>
<td>Silty Clay Loam</td>
<td>0.82</td>
<td>452</td>
<td>47.7</td>
</tr>
<tr>
<td>Sandpiper WMA</td>
<td>2016</td>
<td>40.50, -97.71</td>
<td>245</td>
<td>Silt Loam</td>
<td>0.98</td>
<td>77</td>
<td>10.0</td>
</tr>
<tr>
<td>Sora WMA</td>
<td>2016</td>
<td>40.38, -97.66</td>
<td>403</td>
<td>Silty Clay</td>
<td>1.08</td>
<td>238</td>
<td>23.8</td>
</tr>
<tr>
<td>Spike Rush WMA</td>
<td>2016, 2017</td>
<td>40.91, -97.48</td>
<td>317</td>
<td>Silty Clay Loam</td>
<td>0.88</td>
<td>584</td>
<td>56.3</td>
</tr>
<tr>
<td>Texas</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Castro Co.</td>
<td>2016, 2017</td>
<td>34.53, -102.10</td>
<td>697</td>
<td>Clay</td>
<td>1.01</td>
<td>184</td>
<td>19.0</td>
</tr>
<tr>
<td>Hale Co.</td>
<td>2016, 2017</td>
<td>33.99, -101.58</td>
<td>828</td>
<td>Clay</td>
<td>0.80</td>
<td>245</td>
<td>28.0</td>
</tr>
<tr>
<td>Lubbock Co.</td>
<td>2016, 2017</td>
<td>33.60, -101.90</td>
<td>688</td>
<td>Clay</td>
<td>1.00</td>
<td>121</td>
<td>12.0</td>
</tr>
<tr>
<td>Randall Co.</td>
<td>2016, 2017</td>
<td>34.75, -101.93</td>
<td>641</td>
<td>Clay</td>
<td>0.94</td>
<td>98</td>
<td>10.0</td>
</tr>
<tr>
<td>Swisher Co.</td>
<td>2016, 2017</td>
<td>34.67, -101.85</td>
<td>542</td>
<td>Silty Clay</td>
<td>1.09</td>
<td>150</td>
<td>16.0</td>
</tr>
</tbody>
</table>
Table 4.2. Total nitrogen loading rates for land use treatments based on historical cumulative precipitation in Hastings, Nebraska (423.8 mm) and Lubbock, Texas (209.5 mm).

<table>
<thead>
<tr>
<th>Rate (mg-N L⁻¹)</th>
<th>Nebraska Loading (mg-N)</th>
<th>Texas Loading (mg-N)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Control</td>
<td>0.0</td>
<td>0.0</td>
</tr>
<tr>
<td>Grassland - Low</td>
<td>0.5</td>
<td>27.1</td>
</tr>
<tr>
<td>Grassland – High</td>
<td>2.0</td>
<td>108.5</td>
</tr>
<tr>
<td>Modern Cropland – Low</td>
<td>10.0</td>
<td>542.5</td>
</tr>
<tr>
<td>Modern Cropland – High</td>
<td>25.0</td>
<td>1356.2</td>
</tr>
<tr>
<td>Intensified Cropland – Low</td>
<td>62.5</td>
<td>3390.4</td>
</tr>
<tr>
<td>Intensified Cropland - High</td>
<td>100.0</td>
<td>5424.6</td>
</tr>
</tbody>
</table>
Table 4.3. Estimated means for Nebraska Shannon-Weiner Diversity Index ($R^2 = 0.283$) and Simpson’s Diversity Index ($R^2 = 0.083$) and Texas Shannon-Weiner Diversity Index ($R^2 = 0.247$) and Simpson’s Diversity Index ($R^2 = 0.106$) as a function of hydroperiod treatment. Letters designate differences at $p < 0.05$ relative to historical reference conditions. Experiment is split into baseline conditions, early season plants (Months 1-2), mid-season plants (Months 3-4), and late season plants (Months 5-6). Interactive effects between season and hydroperiod were significant for Texas, but not for Nebraska.

<table>
<thead>
<tr>
<th></th>
<th>Shannon-Weiner Diversity Index</th>
<th>Simpson’s Diversity Index</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Historical</td>
<td>Future Wet</td>
</tr>
<tr>
<td>Nebraska</td>
<td></td>
<td></td>
</tr>
<tr>
<td>All Seasons</td>
<td>0.593A</td>
<td>0.146B</td>
</tr>
<tr>
<td>Baseline</td>
<td>0.721A</td>
<td>0.483A</td>
</tr>
<tr>
<td>Early</td>
<td>0.612A</td>
<td>0.441A</td>
</tr>
<tr>
<td>Mid</td>
<td>0.243A</td>
<td>0.524A</td>
</tr>
<tr>
<td>Late</td>
<td>0.066A</td>
<td>0.422A</td>
</tr>
</tbody>
</table>

128
Table 4.4. Estimated means for Nebraska Shannon-Weiner Diversity Index ($R^2 = 0.394$) and Simpson’s Diversity Index ($R^2 = 0.042$) and Texas Shannon-Weiner Diversity Index ($R^2 = 0.307$) and Simpson’s Diversity Index ($R^2 = 0.130$) as a function of nitrogen loading rate treatment. Letters designate differences at $p < 0.05$ relative to historic reference conditions. Diversity is described by Shannon-Weiner Diversity Index (SH) and Simpson’s Diversity Index (SI). Interactive effects between season and nitrogen loading rate were not significant, so diversity is combined across seasons.

<table>
<thead>
<tr>
<th>Season</th>
<th>Control (0.0 mg-N L$^{-1}$)</th>
<th>Grassland (0.5, 2.0 mg-N L$^{-1}$)</th>
<th>Modern Cropland (10.0, 25.0 mg-N L$^{-1}$)</th>
<th>Intensified Cropland (62.5, 100.0 mg-N L$^{-1}$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nebraska</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>All Seasons</td>
<td>SH: 0.430$^\text{A}$</td>
<td>SH: 0.619$^\text{A}$</td>
<td>SH: 0.406$^\text{A}$</td>
<td>SH: 0.554$^\text{A}$</td>
</tr>
<tr>
<td></td>
<td>SI: 0.392$^\text{a}$</td>
<td>SI: 0.481$^\text{a}$</td>
<td>SI: 0.339$^\text{a}$</td>
<td>SI: 0.360$^\text{a}$</td>
</tr>
<tr>
<td>Texas</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>All Seasons</td>
<td>SH: 0.796$^\text{A}$</td>
<td>SH: 0.418$^\text{B}$</td>
<td>SH: 0.505$^\text{B}$</td>
<td>SH: 0.495$^\text{B}$</td>
</tr>
<tr>
<td></td>
<td>SI: 0.450$^\text{a}$</td>
<td>SI: 0.354$^\text{a}$</td>
<td>SI: 0.324$^\text{a}$</td>
<td>SI: 0.298$^\text{a}$</td>
</tr>
</tbody>
</table>
Table 4.5. Relative contributions of plant variables in principal component analyses. Coefficients (β) for each variable included in the principal component analyses describe the relative contribution of that variable on a scale from 0 to |1|. Wetland indicator statuses were determined for Great Plains plant region, representing wetland obligate (OBL), facultative wetland (FACW), facultative (FAC), facultative upland (FACU), and upland (UPL) plants.

<table>
<thead>
<tr>
<th>Variable</th>
<th>First Principal Component</th>
<th>Second Principal Component</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>β</td>
<td>Contribution</td>
</tr>
<tr>
<td>OBL</td>
<td>0.556</td>
<td>17.0%</td>
</tr>
<tr>
<td>FACW</td>
<td>0.000</td>
<td>0.0%</td>
</tr>
<tr>
<td>FAC</td>
<td>-0.244</td>
<td>2.8%</td>
</tr>
<tr>
<td>FACU</td>
<td>0.000</td>
<td>0.0%</td>
</tr>
<tr>
<td>UPL</td>
<td>-0.322</td>
<td>6.1%</td>
</tr>
<tr>
<td>Native</td>
<td>0.835</td>
<td>38.2%</td>
</tr>
<tr>
<td>Exotic</td>
<td>-0.811</td>
<td>36.0%</td>
</tr>
<tr>
<td>OBL</td>
<td>0.378</td>
<td>6.5%</td>
</tr>
<tr>
<td>FACW</td>
<td>-0.458</td>
<td>9.6%</td>
</tr>
<tr>
<td>FAC</td>
<td>0.392</td>
<td>7.0%</td>
</tr>
<tr>
<td>FACU</td>
<td>0.582</td>
<td>15.5%</td>
</tr>
<tr>
<td>UPL</td>
<td>0.000</td>
<td>0.0%</td>
</tr>
<tr>
<td>Native</td>
<td>0.816</td>
<td>30.4%</td>
</tr>
<tr>
<td>Exotic</td>
<td>-0.826</td>
<td>31.1%</td>
</tr>
<tr>
<td>OBL</td>
<td>0.331</td>
<td>4.1%</td>
</tr>
<tr>
<td>FACW</td>
<td>0.691</td>
<td>18.1%</td>
</tr>
<tr>
<td>FAC</td>
<td>-0.816</td>
<td>25.2%</td>
</tr>
<tr>
<td>FACU</td>
<td>0.140</td>
<td>0.7%</td>
</tr>
<tr>
<td>UPL</td>
<td>0.000</td>
<td>0.0%</td>
</tr>
<tr>
<td>Native</td>
<td>0.792</td>
<td>23.7%</td>
</tr>
<tr>
<td>Exotic</td>
<td>-0.861</td>
<td>28.0%</td>
</tr>
<tr>
<td>OBL</td>
<td>0.433</td>
<td>7.6%</td>
</tr>
<tr>
<td>FACW</td>
<td>-0.730</td>
<td>21.6%</td>
</tr>
<tr>
<td>FAC</td>
<td>0.563</td>
<td>12.8%</td>
</tr>
<tr>
<td>FACU</td>
<td>0.109</td>
<td>0.5%</td>
</tr>
<tr>
<td>UPL</td>
<td>0.101</td>
<td>0.4%</td>
</tr>
<tr>
<td>Native</td>
<td>0.818</td>
<td>27.1%</td>
</tr>
<tr>
<td>Exotic</td>
<td>-0.859</td>
<td>29.9%</td>
</tr>
</tbody>
</table>
Figure 4.1. Playa locations across the Great Plains. The orange playas indicate the Texas plains playa region of interest and blue playas indicate the rainwater basin playa region of interest. Playas sampled for this experiment are indicated in green. More information on each sample location can be found in Table 4.1.
Figure 4.2. Historic monthly temperature conditions in Nebraska (solid lines) and Texas (dashed lines) playa regions averaged from 1986-2015 (grey lines). For both greenhouse studies, greenhouse mean daily air temperature was recorded and compared to actual playa temperatures for hydroperiod study in 2016 (red lines) & land use study in 2017 (blue lines).
Figure 4.3. Precipitation treatments for a greenhouse study for soil collected in Nebraska (a) and Texas (b) playa regions for historic data and scenarios based on downscaled CMIP5-BCCA downscaled atmosphere ocean general circulation models for the RCP4.5 emission scenarios (2070-2099) – future average, wet future, and dry future. Precipitation treatments followed 28 days of constant moisture to allow for uniform germination conditions. Dashed lines indicate breaks in early-, mid-, and late-season germination.
Figure 4.4. Estimated means and 95% asymptotic confidence intervals for Nebraska plant abundance (a, $R^2 = 0.312$) and species richness (b, $R^2 = 0.205$) and Texas plant abundance (c, $R^2 = 0.417$) and species richness (d, $R^2 = 0.250$) as a function of hydroperiod treatment. Experiment is split into baseline conditions, early season plants (Months 1-2), mid-season plants (Months 3-4), and late season plants (Months 5-6). Interactive effects between season and hydroperiod were significant for abundance, but not for richness. Letters indicate differences among hydroperiod treatments within seasons at $p < 0.05$ determined by Tukey pairwise comparisons.
Figure 4.5. Plant species dynamics in response to hydroperiod treatments represented by Ward’s cluster analysis representing similarity between treatments for Nebraska (a) and Texas (b) playas. Plant species identified in hydroperiod study can be found in Appendix 2. Height represents dissimilarity between plant community samples, where 0.0 indicates complete similarity and 1.0 indicates complete dissimilarity. Experiment is split into baseline conditions, early season plants (Months 1-2), mid-season plants (Months 3-4), and late season plants (Months 5-6).
Figure 4.6. Plant species dynamics in response to hydroperiod treatments represented by principal component analyses between treatments for Nebraska (a) and Texas (b) playas. Plant species identified with wetland indicator status and native status can be found in Appendix 2. Wetland indicator statuses were determined for Great Plains plant region, representing wetland obligate (OBL), facultative wetland (FACW), facultative (FAC), facultative upland (FACU), and upland (UPL) plants. Ellipses represent at 95% confidence interval around the centroid of each hydroperiod treatment.
Figure 4.7. Estimated means and 95% asymptotic confidence intervals for Nebraska plant abundance (a, $R^2 = 0.589$) and species richness (b, $R^2 = 0.432$) and Texas plant abundance (c, $R^2 = 0.134$) and species richness (d, $R^2 = 0.253$) as a function of nitrogen loading treatment. Experiment is split into baseline conditions, early season plants (Months 1-2), mid-season plants (Months 3-4), and late season plants (Months 5-6). Interactive effects between season and hydroperiod were significant for abundance, but not for richness. Letters indicate differences among hydroperiod treatments within seasons at p < 0.05 determined by Tukey pairwise comparisons.
Figure 4.8. Plant species dynamics in response to land use change treatments represented by Ward’s cluster analysis representing similarity between treatments for Nebraska and Texas playas. Plant species identified in land use change study can be found in Appendix 2. Height represents dissimilarity between plant community samples, where 0.0 indicates complete similarity and 1.0 indicates complete dissimilarity. Experiment is split into baseline conditions, early season plants (Months 1-2), mid-season plants (Months 3-4), and late season plants (Months 5-6).
Figure 4.9. Plant species dynamics in response to nitrogen loading treatments represented by principal component analyses between treatments for Nebraska (a) and Texas (b) playas. Plant species identified with wetland indicator status and native status can be found in Appendix 2. Wetland indicator statuses were determined for Great Plains plant region, representing wetland obligate (OBL), facultative wetland (FACW), facultative (FAC), facultative upland (FACU), and upland (UPL) plants. Ellipses represent at 95% confidence interval around the centroid of each nitrogen treatment.
CHAPTER 5

SOIL BIOGEOCHEMISTRY IN PLAYA WETLANDS IN RESPONSE TO CHANGING CLIMATE CONDITIONS

ABSTRACT

Great Plains playas are shallow, recharge wetlands that provide essential ecosystem functions; however, projected precipitation changes over the next century have the potential to alter these ecosystem services. We conducted controlled mesocosm experiments to quantify effects of predicted precipitation change on wetland biogeochemical cycles in Nebraska and Texas playas. Nebraska and Texas playas were selected to capture the geographic range of playas. Primarily, we focused on examining various aspects of carbon (C), nitrogen (N), and phosphorus (P) cycles. We monitored soil organic C (TOC) and total N (TN), nitrate (NO\textsubscript{3}\textsuperscript{−}), nitrite (NO\textsubscript{2}\textsuperscript{−}), ammonium (NH\textsubscript{4}\textsuperscript{+}), and Bray-1 available P (Bray P1) monthly during a six-month greenhouse experiment where samples were subjected to precipitation treatments simulating historical precipitation patterns (1986-2015) and three future precipitation projections (2070-2099) derived from CMIP5 RCP4.5 global climate models. Soil microbial communities within these mesocosms were assessed using phospholipid fatty acid (PLFA) methods at the end of the six-month greenhouse experiment. An incubation experiment using soil collected at the end of the six-month trial was used to measure carbon dioxide (CO\textsubscript{2}) and methane (CH\textsubscript{4}) emissions under aerobic and anaerobic conditions. Overall, few consistent differences were detected between historical and future precipitation treatments irrespective of the parameter that was quantified (e.g., soil C, N, P content; CO\textsubscript{2} and CH\textsubscript{4} emissions); however, this study provides the first known glimpse into playa soil
microbial communities. The lack of biogeochemical response may indicate ecosystem resilience to changing climate conditions due to variability among wetlands across the landscape or inherent resistance to change because of extreme wetting and drying conditions with which playa ecosystems co-evolved. Based on our results, playas throughout the region may require different management strategies in future climate conditions; however, overall, playa soils tend to be resilient and able to buffer environmental conditions.

**INTRODUCTION**

Playa wetlands (hereafter playas) are shallow, palustrine wetlands and each playa is located within a small, isolated watershed (Smith 2003). Playas are classified as palustrine, emergent, freshwater marshes and often mistakenly thought to be similar to the prairie pothole wetlands in the Midwest, but playas differ in their geographic isolation, soil composition, ecology, and hydrologic inputs (Bolen et al. 1989; Mushet et al. 2015; Calhoun et al. 2016). Playas only receive water through precipitation and runoff; a feature that distinguishes playas from prairie potholes and other freshwater wetlands influenced by groundwater (Smith 2003). Playas are most commonly found in the High Plains region of the southern Great Plains, but can also be found as far north as Nebraska and Wyoming (Fig. 5.1). Formation theories vary, but most agree that playas were formed through a combination of wind and water processes (Osterkamp and Wood 1987; Wood and Osterkamp 1987; Gustavson et al. 1994; Gustavson et al. 1995; Sabin and Holliday 1995; Reeves and Reeves 1996).

Playas are mineral soil wetlands that exhibit hydric soil properties, but soil organic matter content does not dominate the soil composition (Allen et al. 1972; Luo et al.
The most common playa soil series in the Southern High Plains is the Randall clay (very-fine, smectitic, thermic Ustic Epiaquerts). Other common soil series within playas and the adjacent watershed are fine with smectitic or mixed mineralogy and comprised of the following USDA taxonomic soil Great Groups: Haplusterts, Epiaquersts, Argiustolls, and Paleustolls (Allen et al. 1972; Guthery and Bryant 1982; Nelson et al. 1983; Sabin and Holliday 1995; Soil Survey Staff 2017). In Nebraska, the Butler (fine, smectitic, mesic Vertic Argiaquolls), Fillmore (fine, smectitic, mesic Vertic Argialbolls), Scott (fine, smectitic, mesic Vertic Argialbolls), and Massie (fine, smectitic, mesic Vertic Argialbolls) soil series are most common in playas (Gilbert 1989; Soil Survey Staff 2017). Playa soils contain substantial concentrations (50-75%) of smectitic (shrink-swell) clays (Allen et al. 1972; Smith 2003). When playa soils dry and shrink, they develop large, vertical cracks that permit rapid water infiltration through the soil profile during precipitation events, resulting in recharge of the underlying aquifers until these soils swell sufficiently to seal the playa and cause water to stand. Due in part to the shrink-swell mineralogy, playas recharge aquifers twice as rapidly as the surrounding landscape and are the main recharge source for the Ogallala aquifer (Gurdak and Roe 2010). Playas also act as a buffer to environmental conditions, providing ecosystem services such as improved water quality and enhanced biodiversity (Bolen et al. 1989; Haukos and Smith 1994); however, the combination of sedimentation, land use change, and climate change threatens the primary functions of these wetlands.

Playa soils likely contain a diverse array of microbial populations that are highly adaptable to various hydrologic conditions (Mitsch and Gosselink 2000). Under oxic soil conditions, aerobic microbes use oxygen as an electron acceptor to decompose organic
matter. However, when suboxic or anoxic soil conditions occur due to inundated or flooded conditions, facultative and obligate anaerobic bacteria, those that are capable of using alternative electron receptors, will dominate the microbial population. The most common respiration product of aerobic organisms is CO\(_2\), and the concentration gradient between CO\(_2\) in the soil air and atmospheric air causes CO\(_2\) to be emitted from the soil. In water-logged environments, facultative and obligate anaerobic bacteria capable of anaerobic respiration will begin to emit N\(_2\)O, H\(_2\)S, and CH\(_4\), with each gas corresponding to a specific microbial community. The soil microbial community structure is sensitive to changes in moisture (Kim et al. 2008), thus climate induced changes to playa hydroperiods may change the soil microbial community structure and gene abundance. If playas are saturated for longer periods of time, anaerobic bacteria and some archaea (i.e., methanogens, denitrifiers, and sulfur-reducers) may begin to dominate the microbial community, and populations of these anaerobes may become dormant during periods of extended drought.

Regional climate change models for the High Plains project that mean annual air temperature will increase by 2.0 to 2.8 °C by 2050 and by 2.4 to 4.7 °C by 2100 (Kloesel et al. 2018). Elevated temperatures are expected to increase evapotranspiration from wetlands (Winter 2000) and may induce land use changes in the surrounding landscape, such as relative shifts between croplands and grasslands depending upon water availability (Kukal and Irmak 2018). Regional climate models also project that precipitation events in the High Plains will become more variable and intense, leading to extended periods of drought and flooding (Melillo et al. 2014; Kloesel et al. 2018).
Previous studies on playa soil biogeochemistry have focused on effects of surrounding buffers and watershed land use. In playa surface soils (0-5 cm), Daniel et al. (2017) found mean bulk density values ranging from 1.15 to 1.26 g cm\(^{-3}\), organic carbon (OC) percentages ranging from 3.2 to 4.7\%, and total nitrogen (TN) percentages ranging from 0.28 to 0.39\% in a variety of Rainwater Basin playas in Nebraska. McKenna and Sala (2016) describe surface (0-10 cm) playa mean OC values ranging from 1300 to 1600 g m\(^{-2}\) and mean TN values ranging from 110 to 140 g m\(^{-2}\). To date, no studies have evaluated the response of soil biogeochemistry in playas to altered hydroperiods. Further, little is known about soil microbial populations in playa wetlands and greater understanding of how abundance and diversity of the below-ground biological community may respond to projected climate change is warranted.

Given changing conditions in the Great Plains, the overall goal of this project was to understand alterations to playa wetland soil biogeochemical processes associated with predicted changes in precipitation and land use associated with global climate change. With these overarching goals in mind, the following objectives were identified: (i.) quantify the effects of simulated climate change conditions on soil carbon (C), nitrogen (N), and phosphorus (P), greenhouse gas emissions, and soil biological communities in playas; and (ii.) elucidate differences in plant responses between mesocosms collected from Northern playas (Nebraska) and Southern playas (Texas). To do so, we conducted a six-month greenhouse study and subsequent incubation study to evaluate various hydroperiod patterns in controlled settings. We postulated that moisture-sensitive nutrients, such as nitrogen and carbon, will be altered by changing hydroperiods associated with projected future climate change.
METHODS

Site selection

In spring 2016, we collected soil mesocosm units from playas in the Rainwater Basin of Nebraska and southern High Plains in Texas (Figure 5.1). In an effort to collect intact cores from playas that were representative of each region, regional experts were asked to choose sites. All Nebraska sites were located on state-owned public land, predominantly surrounded by cropland and grazed by livestock. Texas sites were located on publicly-owned and privately-owned land, predominantly surrounded by pasture and grazed frequently by livestock. Bulk soil samples were collected from the soil surface (0-10 cm) to evaluate baseline soil characteristics for each playa on the same date when intact cores were collected (Table 5.1). Intact soil cores, including root matter, were collected in March and April 2016 and placed into plastic tubs (15-cm depth, 30-cm length, 20-cm width), and stored cold until hydroperiod greenhouse study began in June 2016. In Nebraska, soil cores were collected from the moist-vegetation zone which was comprised of Massie silty clay loam (fine, smectitic, mesic Vertic Argialbolls), Scott silt loam (fine, smectitic, mesic Vertic Argialbolls), and Fillmore silt loam (fine, smectitic, mesic Vertic Argialbolls) soil series. Texas soil cores were also collected from the moist-soil vegetation zone, representing the Randall clay (very-fine, smectitic, thermic Ustic Epiaquerts) soil series.

Hydroperiod effects on playa soil biogeochemistry

To assess how predicted climate change will affect playa plant production, a greenhouse experiment was conducted to simulate the growing season in Nebraska and Texas playas under various hydrologic conditions. Before hydrologic treatments began in
June 2016, all soil samples were wetted to field capacity moisture with deionized water for a duration of four weeks to promote germination (Haukos and Smith 2001). Precipitation treatments were carried out for the remaining five months, from July 2016 to November 2016, again using deionized water.

We used historical observations and projected climate conditions to derive hydrologic treatments that permitted the assessment of precipitation changes on wetland ecosystems in the Great Plains (Chapter 2). Based on historic precipitation patterns (1986-2015) and future precipitation projections (2070-2099) using Coupled Model Intercomparison Project phase 5 (CMIP5) downscaled global climate model (GCM) data for the RCP4.5 emission scenario (Reclamation 2013), we developed daily hydrologic treatments for the wetland growing season (April to October). We corrected precipitation data from nineteen GCMs to remove excess drizzle days (<0.25 mm precipitation) and used gamma-based quantile mapping to accurately capture extreme events (Teutschbein and Seibert 2012; Gautam et al. 2018). Comprehensive bias correction details for precipitation adjustments can be found in Gautam et al. (2018). After adjusting projected output data, we selected three models based on the following criteria: 1) an average model, representing the most typical precipitation conditions predicted in RCP4.5 scenarios; 2) a model that contained the longest period of no-precipitation days over the course of the growing season; and 3) a model that contained the greatest number of runoff-inducing precipitation events (Uden et al. 2015) during the growing season. We then used projected precipitation data to determine the timing and amounts of water applied to experimental units by choosing a representative year from the 30-year data set of climate observations or projections. Precipitation patterns for the selected year of each
climate model allowed us to simulate altered hydroperiods during the dominant growing season.

Sample collection and analyses for greenhouse studies

Soil temperature was measured continuously using an Onset HOBO data logger and sensors (Onset Computer Corporation, Bourne, MA). Bulk soil samples were collected monthly throughout the experiments and analyzed for the following properties: pH and electrical conductivity (EC) from a 1:1 dilution with deionized water using an Accumet benchtop meter (Fisher Scientific, Waltham, MA); total N and organic carbon (OC) from dry combustion using a LECO CN analyzer (LECO Corp., St. Joseph, MI); available P from a Bray-1 P extraction (Reddy et al. 2013); and NO$_3^-$-N + NO$_2^-$-N and NH$_4^+$-N using Lachat QuickChem Methods for nitrate/nitrite and ammonium determination (Lachat Instruments, Milwaukee, WI). Phospholipid fatty-acid (PLFA) analysis was used to determine the active microbial communities on select soil samples collected during the hydroperiod greenhouse study. In this procedure, lipids were first separated by a chloroform:methanol:phosphate buffer, then phospholipids were separated from glycolipids and subjected to a mild alkaline methanolysis to recover fatty acid methyl esters. Functional groups of soil microorganisms were then determined using MIDI methods (Sherlock Microbial Identification System version 6.2, MIDI Inc., Newark, DE; Buyer and Sasser 2012; Rinklebe and Langer 2013).

Incubation study for measuring greenhouse gas emissions

Using soil collected from the greenhouse study, we conducted a lab-based incubation study to evaluate the effects of hydroperiod on soil carbon dioxide (CO$_2$) and methane (CH$_4$) emissions. Soil samples were subjected to both oxic (60% water-filled pore space -
WFPS) and anoxic (90% WFPS) soil moisture conditions. Gas samples were collected from the ambient air space above soil samples through a septum over the duration of 22 days and 16 weeks in oxic and anoxic incubation, respectively. Emissions from soils held under oxic conditions were measured using a 22-day incubation laboratory study (Hatch et al. 2005; Chen et al. 2015; Kannenberg et al. 2015). Oxic soils were brought to 60% WFPS, an optimal moisture for microbial activity (Linn and Doran 1984), and equilibrated for nine days at room temperature to allow the microbial activity to stabilize (Kemmitt et al. 2008). Gas samples were then collected from incubation vials on days 1, 2, 4, 6, 8, 11, 15, 18, and 22 after pre-equilibrium period. Gas concentrations were determined with a Shimadzu gas chromatograph (Shimadzu Corp., Kyoto, Japan) capable of measuring CO₂ and CH₄ using a helium carrier gas and a methanizer and flame ionization detector set at 250 °C. For the anoxic incubation study, soils were brought to 60% WFPS and equilibrated for fourteen days at room temperature. After the pre-equilibration period, soils were brought to 90% WFPS to create anoxic soil conditions. Gas samples were then collected daily for one week and weekly for the remaining fourteen weeks of the experiment (Chintala et al. 2015). To further investigate substrate availability before and after incubation studies, we measured active C based on a potassium permanganate oxidation method using 2.5 g of air-dried soil (Weil et al. 2003) and potentially mineralizable nitrogen (PMN) using a seven day anaerobic incubation period with a 1:7 soil to extracting solution ratio (Rhine et al. 1998, Reddy et al. 2013).

Statistical analyses

Repeated-measures linear mixed effects regression models were used to test the effects of hydroperiod on biogeochemical response variables in playa wetland soils over
six-month greenhouse studies. When data were not normally distributed, response variables were log-transformed prior to analysis. Samples were analyzed independently for Nebraska and Texas playa regions. Sampling date and hydroperiod treatment were designated as fixed effects in the model and wetland was designated a random effect. We accounted for repeated measures by using sample identification as a random model effect. When interactive effects were significant, we conducted post-hoc least squared means comparisons using a Tukey adjustment (α = 0.05) to evaluate differences between various combinations of hydroperiod and sampling date. Results were analyzed using the lme4 package (Bates et al. 2015), emmeans package (Lenth 2018), and vegan package (Oksanen 2015) of R statistical software. We used package ggplot2 to visualize estimated means derived from regression models (Wickham 2016).

RESULTS

Baseline soil samples were collected to assess initial nutrient concentrations in playa soils (Table 5.1). Nebraska samples, which are primarily classified as Mollisols, had surface soil textures of silt loam and silty clay loam with clay contents of 245 to 403 g kg$^{-1}$. Initial soil bulk density for Nebraska samples ranged from 0.82 to 1.08 g cm$^{-3}$, pH was slightly acidic (pH 4.3 to 6.6), and base saturation ranged from 76 to 83%. Nebraska soils contained 10.0 to 56.3 g-C kg$^{-1}$, 77 to 584 mg-N kg$^{-1}$, and 98 to 129 mg-Bray P1 kg$^{-1}$. Primarily classified as Vertisols, Texas soil samples had surface soil textures of clay and silty clay with clay contents ranging from 542 to 828 g kg$^{-1}$. The initial soil bulk density for Texas samples ranged from 0.80 to 1.09 g cm$^{-3}$. Soil pH values were slightly alkaline, ranging from 6.5 to 7.7, and exchangeable base saturation ranged from 92 to 128%.
Texas samples contained 10.0 to 28.0 g-C kg\(^{-1}\), 98 to 245 g-N kg\(^{-1}\), and 43 to 116 g-Bray P\(_{1}\) kg\(^{-1}\).

**Soil biogeochemical response**

Cumulative rainfall associated with Nebraska precipitation treatments over the six-month growing season totaled 423.8 mm for the historical treatment, 375.5 mm for the future wet treatment, 207.6 mm for the future average treatment, and 263.4 mm for the future dry treatment (Figure 5.2). While Nebraska historical precipitation treatment had the greatest cumulative rainfall over the six-month greenhouse experiment, the future wet precipitation treatment had the greatest cumulative rainfall through month three (M3). The future average precipitation treatment had the lowest cumulative rainfall due to methods used to select an average year from the projected 30-year dataset. We continued to use this projected rainfall data for the future average precipitation treatment despite the discrepancy because the seasonal rainfall patterns were consistent with average trends for the associated downscaled climate model projections. Due to rapid wetting and drying cycles in playa soils, soil moisture did not necessarily correspond to monthly cumulative rainfall totals (Figure 5.3-a), but rather was more representative of rainfall during the last few days of each month. Based on average bulk density (0.92 g cm\(^{-3}\)) for Nebraska soils, saturation, field capacity, and wilting point gravimetric water contents were calculated to be 0.707, 0.545, and 0.162 g H\(_2\)O g soil\(^{-1}\), respectively. For the majority of the experiment, soil moistures fell between the wilting point moisture and field capacity moisture.

Likely due to inherent variation among wetland replicates, there were few prominent trends in soil physiochemical analyses associated with the various Nebraska precipitation
treatments. Mean soil pH ranged from pH 5.4 to 6.3 throughout the growing season, with the greatest pH occurring during M4 for all treatments (Figure 5.3-b). Mean electrical conductivity ranged from 1.5 and 2.0 dS m\(^{-1}\) throughout the growing season and varied among precipitation treatments in M2 and M3 (Figure 5.3-c). Although soil EC values approached slightly saline thresholds, soils did not exhibit any visible signs of soluble salt accumulation when dry. Mean total N for Nebraska samples ranged from 200 to 400 mg-N kg\(^{-1}\) throughout the growing season and did not differ among treatments (Figure 4.4-a); however, extractable inorganic N species varied throughout the growing season. Summed extractable NO\(_3^-\) and NO\(_2^-\) concentration for future precipitation treatments differed from extractable NO\(_3^-\) + NO\(_2^-\) concentration for historical precipitation in M4 and M5, but trends were inconsistent (Figure 5.4-b). Extractable NH\(_4^+\) concentration for the future dry precipitation treatment was less than extractable NH\(_4^+\) concentration for all other treatments during M2 and M4 of Nebraska experiment (Figure 5.4-c). Soil OC content remained fairly stable throughout the growing season, ranging from 25 to 50 g-OC kg soil\(^{-1}\) among treatments (Figure 5.5-a). Soil Bray P1 did not differ among precipitation treatments for Nebraska samples. Mean soil Bray P1 content ranged from 15 to 30 mg-Bray P1 kg soil\(^{-1}\) during M1 and M2 and increased to mean values near 40 mg-Bray P1 kg soil\(^{-1}\) for M3 to M6 (Figure 5.6-a).

Cumulative rainfall associated with Texas precipitation treatments over the six-month growing season totaled 209.5 mm for historical treatment, 174.5 mm for future wet treatment, 171.1 mm for future average treatment, and 98.8 mm for future dry treatment (Figure 5.2). Seasonal rainfall patterns were fairly comparable between historical precipitation treatment and future dry precipitation treatment, but overall cumulative
rainfall for the future dry treatment was less than 50% of historical treatment. Future wet and future average precipitation treatments followed slightly different seasonal trends, typically experiencing rainfall events 7 to 10 days prior to historical and future dry precipitation events. Similar to Nebraska, soil moisture for Texas samples was more representative of rainfall during the last few days of each month, rather than cumulative monthly rainfall (Figure 5.3-d). Based on average bulk density (0.96 g cm\(^{-3}\)) for Texas soils, saturation, field capacity, and wilting point gravimetric water contents were calculated to be 0.667, 0.400, and 0.267 g H\(_2\)O/g soil, respectively. Throughout the greenhouse experiment, mean gravimetric soil moisture content for all Texas treatments tended to be at or below wilting point.

Similar to Nebraska samples, there were few prominent trends in soil physiochemical analyses associated with the various Texas precipitation treatments. Mean soil pH ranged from pH 6.0 to 7.1 throughout the growing season, with the most basic pH occurring during M3 for historical and future average treatments and during M4 for future wet and future dry treatments (Figure 5.3-e). Mean EC ranged from 0.2 and 0.7 dS m\(^{-1}\) throughout the growing season for all treatments (Figure 5.3-f). The mean soil EC of future dry samples in M6 was lower than mean EC of the other three precipitation treatments. Mean total N ranged from 100 to 200 mg-N kg\(^{-1}\) throughout the growing season and did not vary among precipitation treatments (Figure 5.4-d). Similar to Nebraska samples, inorganic N species varied throughout the growing season for Texas samples. Summed extractable NO\(_3^-\) + NO\(_2^-\) concentrations for some or all future precipitation treatments tended to be greater than extractable NO\(_3^-\) + NO\(_2^-\) concentration for historical precipitation for M4 to M6 (Figure 5.4-e). Extractable NH\(_4^+\) concentration for future dry
precipitation treatment was less than extractable NH$_4^+$ concentration for historical and future wet treatments during M4 of the Texas experiment (Figure 5.4-f). Soil OC varied among precipitation treatments in M4, where the soil OC content of the future average treatment was less than the soil OC content of the future wet treatment (Figure 5.5-b). Lastly, Bray P1 concentration for future precipitation treatments did not differ from historical Bray P1 concentration during the Texas experiment, consistent with trends for Nebraska samples.

Soil microbial communities

Soil microbial community response to precipitation treatments at the end of the six-month greenhouse study was compared using multiple metrics. For Nebraska and Texas soil samples, each functional group – arbuscular mycorrhizal fungi, gram-negative bacteria, fungi, gram-positive bacteria, actinomycetes, and protozoa – as well as total PLFA were compared using the global linear mixed-effects regression model, with precipitation treatment as a fixed effect and wetland as a random effect to account for variability among replicates. Gram-negative and gram-positive bacteria were the most abundant PLFAs (Table 5.2), composing approximately 75% of the total PLFA for all Nebraska and Texas treatments. Significant differences were found for fungi PLFAs and protozoa PLFAs for Nebraska samples, where future dry samples had the greatest abundance of fungi and protozoa (Table 5.2). No differences were found among treatments for other microbial markers in Nebraska or any markers in Texas, likely due to variation among treatments.

Additionally, we used principal component analyses to visualize soil microbial communities compared to several soil variables, including bulk density, Bray P1,
electrical conductivity, pH, extractable NH$_4^+$, gravimetric soil moisture, total N, total OC, carbon to nitrogen ratio, and extractable NO$_3^-$ + NO$_2^-$ (Figure 5.7). For Nebraska samples, the first principal component explained 38% of variability, and was most strongly influenced by microbial functional groups. The second principal component for Nebraska explained 15.3% of variability, and was most strongly influenced by soil variables. For Texas samples, the first principal component explained 48.9% of variability, and was again primarily driven by microbial functional groups. The second principal component for Texas accounted for 17.2% of variability and was driven primarily by soil factors. For both Nebraska and Texas, ellipses representing 95% confidence intervals around the centroid of each precipitation treatment overlapped to varying extents. Future dry samples cluster slightly away from the other three treatments for Nebraska and future wet clusters slightly separate from the other three treatments in Texas.

Greenhouse gas emissions

Following the greenhouse study, soils from each mesocosm unit were collected to be used for oxic and anoxic incubation studies to evaluate greenhouse gas emissions from the soil. In the oxic incubation study, carbon dioxide (CO$_2$) and methane (CH$_4$) emissions were captured and analyzed over a 22-day study. For both Nebraska and Texas, CO$_2$ flux peaked on the second day following the incubation period to a maximum near 55 mg-C kg-soil$^{-1}$ day$^{-1}$ for Nebraska and 45 mg-C kg-soil$^{-1}$ day$^{-1}$ for Texas (Figure 5.8). No statistical differences in soil CO$_2$ flux were observed among precipitation treatments. During the oxic incubation study, mean daily CH$_4$ emissions tended to remain below 5 mg-C kg-soil$^{-1}$ day$^{-1}$. An exception was the Nebraska future dry precipitation treatment, where CH$_4$ emissions ranged from 20 to 50 mg-C kg-soil$^{-1}$ day$^{-1}$. While no statistical
differences in CH$_4$ emissions existed among these samples, future dry emissions were consistently greater for the Nebraska study. Additionally, flux associated with historical precipitation were consistently greater for the Texas study.

The anoxic incubation study took place over 16 weeks. Trends over the first 30 days were similar to trends for the aerobic incubation study (Figure 5.9). For Nebraska and Texas, CO$_2$ emissions peaked near the beginning of the study at approximately 45 mg-C kg-soil$^{-1}$ day$^{-1}$ for Nebraska samples and 35 mg-C kg-soil$^{-1}$ day$^{-1}$ for Texas samples. There were no statistical differences in CO$_2$ emissions among precipitation treatments for either Nebraska or Texas. Similar to the oxic study, no statistical differences in CH$_4$ emissions were found among precipitation treatments for the anaerobic study (Figure 5.9). Nebraska future dry precipitation treatment had an early CH$_4$ emissions flux, reaching a maximum of nearly 70 mg-CH$_4$-C kg-soil$^{-1}$ day$^{-1}$ two days after the incubation period ended; however, by the end of the anaerobic study, CH$_4$ emissions from historical treatment conditions were greatest for Nebraska samples. Conversely, CH$_4$ emissions for the historical precipitation treatment peaked early in the Texas incubation study, with a maximum concentration near 8 mg-C kg-soil$^{-1}$ day$^{-1}$.

Although there were no differences in soil CO$_2$ or CH$_4$ emissions among precipitation treatments, we did detect differences in soil labile carbon (i.e., active C) and nitrogen before and after incubation studies (Table 5.3). However, no differences were detected in stable carbon and nitrogen fractions. Active C increased significantly during the anoxic incubation study for the historical precipitation treatment, from 0.103 to 0.202 ng-C kg-soil$^{-1}$. After the anoxic incubation study, active C was greater for historical precipitation treatment samples than for samples from the future average precipitation treatment. The
most striking differences were in the potentially mineralizable nitrogen (PMN) fraction. Over all precipitation treatments for Nebraska and Texas, PMN was reduced during the anoxic incubation study. For Nebraska samples, PMN was also reduced during the oxic study.

**DISCUSSION**

From Nebraska to Texas, precipitation is expected to decline by the end of the 21st century over the active growing season for playa wetlands (Conant et al. 2018; Kloesel et al. 2018). Many of the ecosystem services provided by playa wetlands rely on seasonal periods of inundation associated with rainfall events (Smith 2003; Smith et al. 2011). Playa soils are unique on the High Plains landscape, containing a high abundance of shrink-swell clays that allow for rapid infiltration after rainfall events and hold relatively large volumes of water when saturated (Allen et al. 1972; Luo et al. 1997; Gurdak and Roe 2010; Daniel et al. 2015). Because precipitation is projected to decline and seasonal rainfall patterns are projected to shift in the playa region, this study aimed to quantify changes in playa soil biogeochemical processes in response to changing precipitation. A six-month greenhouse study was conducted to evaluate changes in carbon, nitrogen, and phosphorus over the active growing season for playa vegetation. Following the greenhouse study, soils were collected and subjected to incubation studies to measure soil CO2 and CH4 fluxes under various precipitation regimes associated with future climate conditions. Overall, few consistent differences were detected between historical and future precipitation treatments irrespective of the quantified parameter. The lack of biogeochemical response may indicate ecosystem resilience to changing climate conditions due to variability among wetlands across the landscape or inherent resistance.
to change because of extreme wetting and drying conditions with which playa ecosystems co-evolved. Further, this study provides the first information on playa microbial communities. While trends were not detected among precipitation treatments, we quantified microbial markers using PLFA analyses.

Throughout the greenhouse study, soil moisture values tended to be reflective of precipitation during the few days prior to sample collection, rather than monthly cumulative totals. Based on historical observations and future climate projections, precipitation events were small enough that they did not induce inundation or saturated conditions (Uden et al. 2015). The greenhouse mesocosm units went through several wet and dry cycles over the length of the experiment and within each month. Total soil organic carbon was not sensitive to changes in soil moisture within the six-month experiment, and concentrations were comparable to values found by Daniel et al. (2017) - 10.0 to 56.3 g-C kg⁻¹. Total soil N content was also stable among precipitation treatments, but fell below the range of values (2791-3945 mg-N kg⁻¹) found by Daniel et al. (2017). Extractable inorganic N (NO₃⁻, NO₂⁻, and NH₄⁺) concentrations are primarily driven by soil moisture, plant uptake, and microbial decomposition (Mitsch and Gosselink 2000; Brown et al. 2017b). There were no clear patterns between soil moisture and extractable inorganic nitrogen content, thus differences seen in this experiment may be due to plant uptake. Plant communities differed among precipitation treatments and contained 16 different species in Nebraska and Texas mesocosm units (see Chapter 3). Further, different plant species may have variable N uptake capacities (von Wiren et al. 1997), a factor that was not evaluated as part of this study. For example, Williams et al. (2017) found that Eleocharis macrostachya had greater concentrations of vegetative N compared
to other wetland species, such as *Polygonum* spp. Pezzelesi et al. (1998) also identified differential plant uptake of nutrients in playas. Soil available phosphorus content is typically driven by plant uptake, microbial decomposition, and concentrations of soluble cations, such as calcium (Ca$^{2+}$) and iron (Fe$^{3+}$) (Mitsch and Gosselink 2000; Montgomery and Eames 2008; Brown et al. 2017a). We did not measure soluble cation concentrations as part of this study, but based on season trends, Bray P1 content may have also been driven by plant uptake dynamics.

While we did not find statistical differences in soil CO$_2$ and CH$_4$ flux among precipitation treatments, there were clear patterns in the oxic and anoxic incubation studies. For Nebraska and Texas samples, soil CO$_2$ flux peaked shortly following the pre-equilibration period during both incubation studies. In soil environments, CO$_2$ emissions are correlated with microbial respiration (Schlesinger and Andrews 2000), which is dependent on relative carbon and nutrient concentrations available for metabolic processes, as well as temperature and available moisture (Skopp et al. 1990; Raich and Schlesinger 1992). We found that labile N was reduced during oxic and anoxic incubation studies, thus it is possible that microbes utilized labile N rapidly at the beginning of the incubation studies and were then limited by N availability during the remainder of the incubation studies.

Soil methane flux differed between Nebraska and Texas samples in this study. In Nebraska, future dry precipitation treatments produced the greatest soil CH$_4$ flux initially, but the historical precipitation treatment had the greatest cumulative CH$_4$ emissions. In Texas, the historical precipitation treatment produced the greatest CH$_4$ flux at the beginning of the incubation study, and emissions were minimal from all treatments.
thereafter. Bansal et al. (2016) found that temporary prairie pothole wetlands had greater soil CH$_4$ emissions than semi-permanent wetlands, and predicted that substrate availability allowed *methanogens* to more rapidly evolve CH$_4$ following wetting and drying cycles. Throughout the greenhouse study, Nebraska historical precipitation treatments occasionally reached saturated moisture conditions, which may have reduced carbon decomposition; however, Texas historical precipitation samples rarely reached saturated conditions and maintained ideal moisture levels for microbial decomposition. More information is needed to better understand these relationships and how gas emissions may be affected by future climate conditions.

As ephemeral wetlands, playas do not necessarily experience extended periods of anoxic soil conditions, thus playa microbial communities may be well adapted to precipitation conditions associated with future climate conditions. While future precipitation treatments had less than half of historical cumulative precipitation, few differences existed in microbial markers at the end of the greenhouse study. Texas samples, which were collected from a more arid climate, had no differences in the microbial community. Nebraska samples, however, had differences in fungi and protozoa PLFA abundances among historical and future precipitation treatments. Typically, fungi are not abundant in saturated conditions due to aerobic cellular metabolic processes (Sylvia et al. 2005); however, playas likely do not often hold enough water to limit fungal growth. The greatest fungal PLFA abundance was under future dry conditions in Nebraska samples. As soil moisture declined, associated with future climate conditions, fungal abundance may have been driven by other soil physiochemical properties, such as pH, P or Ca content, or by the plant community (Tedersoo et al. 2014). Protozoa PLFA
abundance was also greatest under the future dry precipitation treatment for Nebraska in this study. Protozoa, typically more abundant in disturbed ecosystems, may consume >50% of bacterial biomass in soil environments, and are thus an important component of nutrient cycling and the soil food web (Foissner 1999; Sylvia et al. 2005). In ephemeral ecosystems, protozoa communities have responded to nutrient availability and aerobic methane oxidation (Murase and Frenzel 2007; van Dijk et al. 2009). To date, this study is the first to evaluate soil microbial communities in playa wetlands. Overall, results show that soil microbial communities are resilient to changes in soil moisture, particularly in Texas where climate conditions are highly variable (Kloesel et al. 2018).

Playa soils act as buffers between surrounding agricultural watersheds and underlying aquifer water (Urban et al. 1989; Reeves and Reeves 1996; Gurdak and Roe 2010). This study suggests that inorganic soil N may be more abundant during certain periods of the growing season under future climate conditions, which may pose a threat to groundwater quality. Previous studies have linked vegetative buffers to reduced nutrient runoff into playas (O’Connell et al. 2012; Haukos et al. 2016); however, buffers may not be the only management strategy to employ if nutrient cycles are changing within the playa independent of runoff. Because soil N and P content may have varied among hydroperiod treatments based on plant communities, managers may consider seeding or managing for plants with greater nutrient uptake to mitigate increased nutrient availability associated with future climate conditions. Due to variation among wetlands across the landscape, it may also remain important to conserve wetland complexes to maintain ecosystem services provided by playas in the Great Plains (Webb et al. 2010; Johnson et al. 2012; Tsai et al. 2012; McIntyre et al. 2018).
Ecosystem services provided by playa soils are dependent upon landscape-scale variability driven by hydrology, surrounding land use, and watershed characteristics throughout the southern High Plains (Haukos and Smith 2004; O’Connell et al. 2012; Tang et al. 2017). We aimed to capture this variability by collecting intact soil cores from multiple playas in Nebraska and Texas to represent replications. This variability among the replicates likely contributed to inconsistent response of soil biogeochemical cycles to changes in hydroperiod; however, the results are likely representative of field conditions. Due to high variability among replicates collected from different playas, as well as variability within samples from the same playa, future studies at a field scale and in greater replication may help to identify more detailed shifts occurring in playa soil biogeochemical cycles in the face of changing precipitation.

In designing these studies, we aimed to capture variability within and among playas across the landscape through spatial replications, while also simulating a wide range of climate and land use scenarios. The statistical inference of our results are limited to the playas from which our samples were collected, because the sites were not randomly selected. However, the results for the samples collected from Nebraska and Texas are likely biophysically relevant on a regional scale. We were able to capture responses in the northern and southern extent of the playa region, but we did not conduct our studies using samples collected from central playas in Kansas and Colorado. While the properties of these playas are similar to those in Texas, we cannot extend the inference of our study to include these ecosystems.

With this study, we identified biogeochemical soil processes in playa wetlands that may be sensitive to changes in precipitation associated with projected future climate
change. Soil moisture varied with precipitation treatments, and subsequently, moisture-sensitive processes (e.g., soil inorganic nitrogen content) were also affected by precipitation treatments. While there were few effects of precipitation treatments on soil microbial communities, this study is the first to quantify soil microbial communities using PLFA analyses in playa wetlands. Our incubation studies provided evidence that anaerobic methane production was likely occurring in playas, and supported previous studies that ephemeral wetlands have a greater greenhouse gas flux potential relative to more permanently inundated wetlands due to surges of methane production following flooding and drawdown events. Soil biogeochemical processes measured in our study were not directly correlated with moisture, and may be more dependent upon plant dynamics within wetlands. Further field and long-term studies to evaluate soil and plant communities may elucidate the relationships among playa soils, plants, and ecosystem services. Based on results of this study, playas throughout the High Plains may require different management strategies in future climate conditions; however, overall, playa soils may be resilient and able to buffer environmental conditions.


Gilbert MC (1989) Ordination and mapping of wetland communities in Nebraska’s Rainwater Basin region. U.S Corps of Engineers, Omaha, NE.


Gustavson TC, Holliday VT, Hovorka SD (1995) Origin and development of playa basins, sources of recharge to the Ogallala Aquifer, Southern High Plains, Texas and New Mexico. Austin, TX


Montgomery JA, Eames JM (2008) Prairie Wolf Slough Wetlands demonstration project:
A case study illustrating the need for incorporating soil and water quality assessment in wetland restoration planning, design and monitoring. 16:618–628. doi: 10.1111/j.1526-100X.2008.00492.x


Table 5.1. Landscape and soil characteristics for each playa where soils were collected. Soil analyses were conducted on surface soils (0-10 cm). In Nebraska, soil cores were collected from the moist-vegetation zone which represented Massie silty clay loam (*Fine, smectitic, mesic Vertic Argialbolls*), Scott silt loam (*Fine, smectitic, mesic Vertic Argialbolls*), and Fillmore silt loam (*Fine, smectitic, mesic Vertic Argialbolls*) soil series. Texas soil cores were also collected from the moist-soil vegetation zone, representing the Randall clay (*Very-fine, smectitic, thermic Ustic Epiaquerts*) soil series.

<table>
<thead>
<tr>
<th>Wetland</th>
<th>Collection Location</th>
<th>Clay (g kg(^{-1}))</th>
<th>Texture Class</th>
<th>Bulk Density (g cm(^{-3}))</th>
<th>pH (H(_2)O)</th>
<th>Total N (mg kg(^{-1}))</th>
<th>Total C (g kg(^{-1}))</th>
<th>Bray P1 (mg kg(^{-1}))</th>
<th>Base Saturation (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Hidden Marsh WMA</td>
<td>40.71, -97.49</td>
<td>337</td>
<td>Silty Clay Loam</td>
<td>1.00</td>
<td>5.0</td>
<td>296</td>
<td>33.3</td>
<td>129</td>
<td>81</td>
</tr>
<tr>
<td>Renquist WMA</td>
<td>41.03, -97.70</td>
<td>329</td>
<td>Silty Clay Loam</td>
<td>0.82</td>
<td>4.3</td>
<td>452</td>
<td>47.7</td>
<td>98</td>
<td>76</td>
</tr>
<tr>
<td>Sandpiper WMA</td>
<td>40.50, -97.71</td>
<td>245</td>
<td>Silt Loam</td>
<td>0.98</td>
<td>6.6</td>
<td>77</td>
<td>10.0</td>
<td>86</td>
<td>83</td>
</tr>
<tr>
<td>Sora WMA</td>
<td>40.38, -97.66</td>
<td>403</td>
<td>Silty Clay</td>
<td>1.08</td>
<td>5.1</td>
<td>238</td>
<td>23.8</td>
<td>118</td>
<td>83</td>
</tr>
<tr>
<td>Spike Rush WMA</td>
<td>40.91, -97.48</td>
<td>317</td>
<td>Silty Clay Loam</td>
<td>0.88</td>
<td>4.6</td>
<td>584</td>
<td>56.3</td>
<td>111</td>
<td>74</td>
</tr>
<tr>
<td>Castro Co.</td>
<td>34.53, -102.10</td>
<td>697</td>
<td>Clay</td>
<td>1.01</td>
<td>6.5</td>
<td>184</td>
<td>19.0</td>
<td>94</td>
<td>92</td>
</tr>
<tr>
<td>Hale Co.</td>
<td>33.99, -101.58</td>
<td>828</td>
<td>Clay</td>
<td>0.80</td>
<td>6.0</td>
<td>245</td>
<td>28.0</td>
<td>43</td>
<td>94</td>
</tr>
<tr>
<td>Lubbock Co.</td>
<td>33.60, -101.90</td>
<td>688</td>
<td>Clay</td>
<td>1.00</td>
<td>7.7</td>
<td>121</td>
<td>12.0</td>
<td>75</td>
<td>116</td>
</tr>
<tr>
<td>Randall Co.</td>
<td>34.75, -101.93</td>
<td>641</td>
<td>Clay</td>
<td>0.94</td>
<td>7.2</td>
<td>98</td>
<td>10.0</td>
<td>74</td>
<td>128</td>
</tr>
<tr>
<td>Swisher Co.</td>
<td>34.67, -101.85</td>
<td>542</td>
<td>Silty Clay</td>
<td>1.09</td>
<td>7.2</td>
<td>150</td>
<td>16.0</td>
<td>116</td>
<td>104</td>
</tr>
</tbody>
</table>
Table 5.2. Estimated mean phospholipid fatty acid (PLFA) abundance based on linear mixed effects regression models with hydroperiod treatment as a fixed effect and wetland replicates as random effects to account for variation between samples. Total PLFA is a sum of arbuscular mycorrhizal fungi (A.M. Fungi), gram negative bacteria (Gram Neg.), fungi, gram positive bacteria (Gram Pos.), actinomycetes, and protozoa. Letters denote differences between hydroperiod treatments at p < 0.05 within a given state.

<table>
<thead>
<tr>
<th>Microbial Marker</th>
<th>Nebraska</th>
<th></th>
<th></th>
<th></th>
<th>Texas</th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Historical</td>
<td>Future Wet</td>
<td>Future Average</td>
<td>Future Dry</td>
<td></td>
<td>Historical</td>
<td>Future Wet</td>
<td>Future Average</td>
<td>Future Dry</td>
</tr>
<tr>
<td></td>
<td>(nmol PLFA g soil⁻¹)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>(nmol PLFA g soil⁻¹)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>A.M. Fungi ((R^2 = 0.115))</td>
<td>2.17⁵</td>
<td>1.76⁵</td>
<td>2.32⁵</td>
<td>3.05⁵</td>
<td>A.M. Fungi ((R^2 = 0.061))</td>
<td>2.01⁵</td>
<td>1.54⁵</td>
<td>2.09⁵</td>
<td>1.80⁵</td>
</tr>
<tr>
<td>Fungi ((R^2 = 0.291))</td>
<td>1.09⁵B</td>
<td>0.57B</td>
<td>0.65AB</td>
<td>1.37A</td>
<td>Fungi ((R^2 = 0.258))</td>
<td>1.27⁵A</td>
<td>0.77B</td>
<td>1.66A</td>
<td>1.02A</td>
</tr>
<tr>
<td>Gram Neg. ((R^2 = 0.165))</td>
<td>26.95⁵A</td>
<td>28.28A</td>
<td>33.12A</td>
<td>42.34A</td>
<td>Gram Neg. ((R^2 = 0.054))</td>
<td>21.52⁵A</td>
<td>17.99A</td>
<td>22.76A</td>
<td>22.33A</td>
</tr>
<tr>
<td>Gram Pos. ((R^2 = 0.130))</td>
<td>22.00⁵A</td>
<td>22.13A</td>
<td>26.97A</td>
<td>30.72A</td>
<td>Gram Pos. ((R^2 = 0.031))</td>
<td>18.25⁵A</td>
<td>16.32A</td>
<td>18.73A</td>
<td>19.37A</td>
</tr>
<tr>
<td>Actinomycetes ((R^2 = 0.137))</td>
<td>11.03⁵A</td>
<td>11.10A</td>
<td>13.88A</td>
<td>15.97A</td>
<td>Actinomycetes ((R^2 = 0.115))</td>
<td>10.27⁵A</td>
<td>9.32A</td>
<td>10.80A</td>
<td>11.16A</td>
</tr>
<tr>
<td>Protozoa ((R^2 = 0.404))</td>
<td>0.50B</td>
<td>0.37B</td>
<td>0.49B</td>
<td>1.06A</td>
<td>Protozoa ((R^2 = 0.146))</td>
<td>0.52⁵A</td>
<td>0.48A</td>
<td>0.72A</td>
<td>0.57A</td>
</tr>
<tr>
<td>Total PLFA ((R^2 = 0.154))</td>
<td>64.40⁵A</td>
<td>64.97⁵A</td>
<td>78.24A</td>
<td>95.76A</td>
<td>Total PLFA ((R^2 = 0.051))</td>
<td>54.23⁵A</td>
<td>46.74A</td>
<td>57.13A</td>
<td>56.70A</td>
</tr>
</tbody>
</table>
Table 5.3. Estimated mean carbon and nitrogen species based on linear mixed effects regression models with hydroperiod treatment and sampling date as fixed effects and wetland replicates as random effects to account for variation between samples. Samples were collected prior to aerobic and anaerobic incubation studies (Pre-Inc.) and after aerobic (AE) and anaerobic (AN) incubation studies for Nebraska and Texas. Uppercase letters denote difference between hydroperiod treatments and lowercase letters denote differences between sampling dates at $p < 0.05$ within a given state.

<table>
<thead>
<tr>
<th>Sampling Date</th>
<th>Historical</th>
<th>Future Wet</th>
<th>Future Average</th>
<th>Future Dry</th>
<th>Historical</th>
<th>Future Wet</th>
<th>Future Average</th>
<th>Future Dry</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Nebraska</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pre-Inc.</td>
<td>0.067(^{Aa})</td>
<td>0.067(^{Aa})</td>
<td>0.052(^{Aa})</td>
<td>0.051(^{Aa})</td>
<td>0.103(^{Ab})</td>
<td>0.102(^{Ab})</td>
<td>0.078(^{Ab})</td>
<td>0.088(^{Ab})</td>
</tr>
<tr>
<td>--</td>
<td>--</td>
<td>--</td>
<td>--</td>
<td>--</td>
<td>--</td>
<td>--</td>
<td>--</td>
<td>--</td>
</tr>
<tr>
<td>After AE</td>
<td>0.082(^{Aa})</td>
<td>0.107(^{Aa})</td>
<td>0.088(^{Aa})</td>
<td>0.070(^{Aa})</td>
<td>0.100(^{Ab})</td>
<td>0.130(^{Aa})</td>
<td>0.143(^{Ab})</td>
<td>0.132(^{Aa})</td>
</tr>
<tr>
<td>After AN</td>
<td>0.079(^{Aa})</td>
<td>0.085(^{Aa})</td>
<td>0.088(^{Aa})</td>
<td>0.044(^{Aa})</td>
<td>0.202(^{Aa})</td>
<td>0.132(^{Aa})</td>
<td>0.117(^{Ba})</td>
<td>0.134(^{Aa})</td>
</tr>
<tr>
<td>Texas</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Active Carbon (ng-C kg-soil(^{-1}))</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pre-Inc.</td>
<td>39.3(^{Aa})</td>
<td>36.5(^{Aa})</td>
<td>38.4(^{Aa})</td>
<td>40.6(^{Aa})</td>
<td>21.9(^{Aa})</td>
<td>18.8(^{Aa})</td>
<td>22.7(^{Aa})</td>
<td>22.8(^{Aa})</td>
</tr>
<tr>
<td>--</td>
<td>--</td>
<td>--</td>
<td>--</td>
<td>--</td>
<td>--</td>
<td>--</td>
<td>--</td>
<td>--</td>
</tr>
<tr>
<td>After AE</td>
<td>37.0(^{Aa})</td>
<td>36.8(^{Aa})</td>
<td>37.8(^{Aa})</td>
<td>49.4(^{Aa})</td>
<td>21.5(^{Aa})</td>
<td>18.1(^{Aa})</td>
<td>21.9(^{Aa})</td>
<td>21.2(^{Aa})</td>
</tr>
<tr>
<td>After AN</td>
<td>36.5(^{Aa})</td>
<td>35.8(^{Aa})</td>
<td>36.9(^{Aa})</td>
<td>43.3(^{Aa})</td>
<td>20.1(^{Aa})</td>
<td>17.5(^{Aa})</td>
<td>21.8(^{Aa})</td>
<td>20.8(^{Aa})</td>
</tr>
<tr>
<td>Total Carbon (g-C kg-soil(^{-1}))</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pre-Inc.</td>
<td>165.3(^{Aa})</td>
<td>164.8(^{Aa})</td>
<td>163.2(^{Aa})</td>
<td>160.2(^{Aa})</td>
<td>82.8(^{Aa})</td>
<td>71.6(^{Aa})</td>
<td>96.8(^{Aa})</td>
<td>64.5(^{Aa})</td>
</tr>
<tr>
<td>--</td>
<td>--</td>
<td>--</td>
<td>--</td>
<td>--</td>
<td>--</td>
<td>--</td>
<td>--</td>
<td>--</td>
</tr>
<tr>
<td>After AE</td>
<td>95.7(^{ABb})</td>
<td>91.2(^{ABb})</td>
<td>71.5(^{Bb})</td>
<td>104.5(^{ABb})</td>
<td>46.3(^{Aa})</td>
<td>48.0(^{Aa})</td>
<td>63.8(^{Aa})</td>
<td>37.2(^{Ab})</td>
</tr>
<tr>
<td>After AN</td>
<td>0.0(^{Ac})</td>
<td>0.0(^{Ac})</td>
<td>0.0(^{Ac})</td>
<td>0.0(^{Ac})</td>
<td>0.1(^{Ab})</td>
<td>0.0(^{Ab})</td>
<td>0.0(^{Ab})</td>
<td>0.0(^{Ab})</td>
</tr>
<tr>
<td>Potentially Mineralizable Nitrogen (mg-N kg-soil(^{-1}))</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pre-Inc.</td>
<td>3460(^{Aa})</td>
<td>3300(^{Aa})</td>
<td>3400(^{Aa})</td>
<td>3694(^{Aa})</td>
<td>2060(^{Aa})</td>
<td>1760(^{Aa})</td>
<td>2020(^{Aa})</td>
<td>2080(^{Aa})</td>
</tr>
<tr>
<td>--</td>
<td>--</td>
<td>--</td>
<td>--</td>
<td>--</td>
<td>--</td>
<td>--</td>
<td>--</td>
<td>--</td>
</tr>
<tr>
<td>After AE</td>
<td>3360(^{Aa})</td>
<td>3380(^{Aa})</td>
<td>3420(^{Aa})</td>
<td>4240(^{Aa})</td>
<td>1920(^{Aa})</td>
<td>1660(^{Aa})</td>
<td>1900(^{Aa})</td>
<td>1980(^{Aa})</td>
</tr>
<tr>
<td>After AN</td>
<td>3160(^{Aa})</td>
<td>3200(^{Aa})</td>
<td>3280(^{Aa})</td>
<td>3780(^{Aa})</td>
<td>1960(^{Aa})</td>
<td>1700(^{Aa})</td>
<td>2000(^{Aa})</td>
<td>1960(^{Aa})</td>
</tr>
<tr>
<td>Total Nitrogen (mg-N kg-soil(^{-1}))</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Figure 5.1. Playa locations across the Great Plains. The orange playas indicate the Texas plains playa region of interest and blue playas indicate the rainwater basin playa region of interest. Playas sampled for this experiment are indicated in green. More information on each sample location can be found in Table 4.1.
Figure 5.2. Precipitation treatments for a greenhouse study for soil collected in Nebraska (a) and Texas (b) playa regions for historic data and scenarios based on downscaled CMIP5-BCCA downscaled atmosphere ocean general circulation models for the RCP4.5 emission scenarios (2070-2099) – future average, wet future, and dry future. Precipitation treatments followed 28 days of constant moisture to allow for uniform germination conditions. Dashed lines correspond to experiment months 1 to 6 (M1-M6).
Figure 5.3. Estimated means and 95% confidence intervals for Nebraska soil moisture (a, $R^2 = 0.509$), pH (b, $R^2 = 0.237$), and electrical conductivity (c, $R^2 = 0.234$) and Texas soil moisture (d, $R^2 = 0.519$), pH (e, $R^2 = 0.083$), and electrical conductivity (f, $R^2 = 0.268$) as a function of hydroperiod treatment. Letters indicate differences among hydroperiod treatments within seasons at $p < 0.05$ determined by Tukey pairwise comparisons.
Figure 5.4. Estimated means and 95% confidence intervals for Nebraska total N (a, \( R^2 = 0.166 \)), \( \text{NO}_3^- + \text{NO}_2^- \cdot \text{N} \) (b, \( R^2 = 0.476 \)), and \( \text{NH}_4^+ \cdot \text{N} \) (c, \( R^2 = 0.701 \)) and Texas total N (d, \( R^2 = 0.599 \)), \( \text{NO}_3^- + \text{NO}_2^- \cdot \text{N} \) (e, \( R^2 = 0.614 \)), and \( \text{NH}_4^+ \cdot \text{N} \) (f, \( R^2 = 0.361 \)) as a function of hydroperiod treatment. Letters indicate differences among hydroperiod treatments within seasons at \( p < 0.05 \) determined by Tukey pairwise comparisons.
**Figure 5.5.** Estimated means and 95% confidence intervals for Nebraska total organic carbon (a, $R^2 = 0.156$) and Texas total organic carbon (b, $R^2 = 0.116$) as a function of hydroperiod treatment. Letters indicate differences among hydroperiod treatments within seasons at $p < 0.05$ determined by Tukey pairwise comparisons.
Figure 5.6. Estimated means and 95% confidence intervals for Nebraska (a, $R^2 = 0.429$) and Texas (b, $R^2 = 0.257$) Bray-1 available phosphorus (P) as a function of hydroperiod treatment. Letters indicate differences among hydroperiod treatments within seasons at $p < 0.05$ determined by Tukey pairwise comparisons.
Figure 5.7. Microbial community dynamics in response to hydroperiod treatments represented by principal component analyses between treatments for Nebraska (a) and Texas (b) playas. Microbial functional groups are described in Table 4.2. Soil variables included bulk density (BD), Bray-1 Phosphorus (BrayP), electrical conductivity (EC), pH, ammonia (NH4), gravimetric moisture (Moisture), total nitrogen (TotalN), total organic carbon (TotalOC), carbon to nitrogen ratio (CN), and nitrate plus nitrite (NO3NO2). Ellipses represent at 95% confidence interval around the centroid of each hydroperiod treatment.
Figure 5.8. Estimated means (±SE) based on linear mixed effects regression model for Nebraska CO$_2$ (a, $R^2 = 0.082$) and CH$_4$ (b, $R^2 = 0.155$) emissions and Texas CO$_2$ (c, $R^2 = 0.067$) and CH$_4$ (d, $R^2 = 0.115$) emissions over a 22-day oxic incubation study.
Figure 5.9. Estimated means (±SE) based on linear mixed effects regression model for Nebraska CO$_2$ (a, $R^2 = 0.085$) and CH$_4$ (b, $R^2 = 0.163$) emissions and Texas CO$_2$ (c, $R^2 = 0.037$) and CH$_4$ (d, $R^2 = 0.084$) emissions over a 105-day anoxic incubation study.
CHAPTER 6

EXECUTIVE SUMMARY

Climate patterns in the Great Plains are projected to shift dramatically, causing increased temperatures and reduced overall precipitation through the end of the 21st century. As a keystone wetland ecosystem in the Great Plains, playa wetlands will be affected by shifting climate conditions. In addition to future changes in climate, land use trends may also affect playa ecosystems. Culturally accelerated sedimentation due to cultivation of the surrounding watershed has caused widespread playa degradation in the 20th and 21st centuries (Luo et al. 1997; Daniel et al. 2015). While several field-scale and controlled studies have evaluated playa vegetative communities (e.g., Haukos and Smith 2004; Haukos and Smith 2006), landscape factors contributing to sedimentation and inundation (e.g., Bartuszevige et al. 2012; O’Connell et al. 2012), and dependent faunal taxa (e.g., Anderson and Smith 2000; Webb et al. 2010), very few researchers have studied how playas will respond to changing climate conditions. To assess potential risks to playas in a changing climate, this research quantified effects of changing climatic conditions on plant germination and community composition, soil chemistry, greenhouse gas emissions, and microbial community and structure; compared ecosystem response to changing climatic conditions between Northern (Nebraska) and Southern (Texas) playa soils; and assessed effects of increased agricultural nitrogen inputs on playa plant communities.

Early season germination and growth provide an initial look at potential effects of increased temperatures and altered precipitation patterns to playa plant communities because extant plant distribution throughout the playa is dependent upon the
environmental conditions at germination (Grubb 1977; Welling et al. 1988a; Haukos and Smith 2001). In field settings, playa plant germination is primarily driven by interactions among air temperature, soil temperature, and precipitation, which produce various hydroperiod and soil moisture conditions throughout the active growing season (Haukos and Smith 1995; Seabloom et al. 1998; Casanova and Brock 2000; Haukos and Smith 2006). In Chapter 2, we simulated interactions among air temperature, soil moisture, and seed bank density that playa plants may experience in changing climate conditions. Increasing temperatures were found to be an important driver of germination and growth of Barnyardgrass in Nebraska and Texas playa samples. Additionally, interacting effects of air temperature and soil moisture tended to be more important drivers of germination at higher air temperatures, as seen in Nebraska samples. Comparatively, seed bank density tended to be a more important driver when germination air temperatures were lower, such as in the Texas samples. Finally, germination was enhanced by increased germination temperatures representing future climate conditions in Texas samples, but germination was diminished by increased germination temperatures in Nebraska. While the drivers of germination and early season growth were similar between the two playa regions, plant response differed.

Described in Chapter 3, we conducted two greenhouse studies with intact mesocosm units collected from playas in Nebraska and Texas to quantify effects of changing climate and land use conditions on playa plant communities. Overall, abundance, richness and diversity were not greatly affected by climate and land use changes in playas, which was expected based on the previous studies conducted in the playa region. Plant communities under projected future climate conditions and minimal nitrogen loading rates tended to
shift to favor native species; however, as nitrogen runoff increased, native species richness decreased. These trends may suggest that management priorities focus on protecting playas in the face of land use change, rather than trying to manage for decreased or shifting rainfall patterns. Limited water resources exist in the Great Plains region (e.g., Steiner et al. 2017), thus, implementing traditional moist-soil management techniques may be challenging. Existing efforts to reduce sedi mentation and increase water storage (e.g., Bartuszevige et al. 2012; O’Connell et al. 2012) in playas may also increase ecosystem resilience to future land use change. Due to high variability among replicates in this study, future studies at a field scale and in greater replication may help to identify more detailed shifts occurring in playa plant communities in the face of changing precipitation and land use.

Playas soils are unique on the High Plains landscape, containing a high abundance of shrink-swell clays that allow for rapid infiltration after rainfall events and hold relatively large volumes of water when saturated (Allen et al. 1972; Luo et al. 1997; Gurdak and Roe 2010; Daniel et al. 2017). Because precipitation is projected to decline and seasonal rainfall patterns are projected to shift in the playa region, studies described in Chapter 4 aimed to quantify changes in playa soil biogeochemical processes in response to changing precipitation. A six-month greenhouse study was conducted to evaluate changes in carbon, nitrogen, and phosphorus over the active growing season for playa vegetation. Following the greenhouse study, soils were collected and subjected to incubation studies to measure CO$_2$ and CH$_4$ emissions under various precipitation regimes associated with future climate conditions. Overall, few consistent differences were detected between historical and future precipitation treatments irrespective of the parameter that was
quantified. The lack of biogeochemical response may indicate ecosystem resilience to changing climate conditions due to variability among wetlands across the landscape or inherent resistance to change because of extreme wetting and drying conditions with which playa ecosystems co-evolved. Further, this study provided the first known glimpse into playa microbial communities. While trends were not detected among precipitation treatments, we quantified microbial markers using PLFA analyses.

Ecosystem resilience can be defined in several ways, but generally refers to an ecosystem’s ability to withstand external forces and maintain form and function (Holling 1973; Holling 2001). For playas, resilience may be driven by landscape scale variability. Across the four experiments completed for this project, inconsistency remained the most consistent trend. In the germination study, we found that emergence and growth were affected by altered temperatures associated with projected future climate change; however, increased temperatures did not promote a uniform response among treatments or between Nebraska and Texas regions. Similar inconsistencies were observed in greenhouse studies quantifying plant community composition response to changing precipitation patterns and nitrogen loading rates; however, native plant species richness was consistently greatest under future dry conditions and control N rates (0 mg-N L\(^{-1}\)). Moisture-sensitive soil biogeochemical processes tended to be impacted by hydroperiod treatments conducted in the greenhouse study, yet differences were not well correlated with soil moisture content. While the lack of consistent results in these studies may be due to variability among the wetland replicates utilized for the experiments, this may also indicate resilience in playa plant and soil processes. Playas evolved in a region with extreme weather variability and may be able to buffer against climate and land use...
changes projected for the future and continue providing crucial ecosystems services on the Great Plains landscape (Smith et al. 2011; Kloesel et al. 2018).

This work identified components of playa plants and soils that may be sensitive to changing climate and land use conditions, but also provided evidence that playas are able to buffer against external alterations. Due to variation among wetlands across the landscape, it may remain important to conserve wetland complexes to maintain ecosystem services provided by playas in the Great Plains (Webb et al. 2010; Johnson et al. 2012; Tsai et al. 2012; McIntyre et al. 2018). Existing efforts to reduce sedimentation and increase water storage (e.g., Bartuszevige et al. 2012; O’Connell et al. 2012) in playas may also increase ecosystem resilience to future climate and land use change. Field studies conducted over multiple years would help to inform conservation priorities in playa wetlands in the coming decades, further protecting the ecosystem services provided by playa plants and soils.
LITERATURE CITED


APPENDIX 1

GROWTH CHAMBER PROGRAMMING INFORMATION

Table A1.1. Growth chamber programming information. Setting codes d and h represent sunrise and sunset times, respectively, for Hastings, NE (a) and Lubbock, TX (b), with 45 minutes built in to account for dawn and dusk. Maximum and minimum temperatures derived from temperature observation data (Historical) and global climate models (Future) are represented at setting codes d and h respectively. Humidity is based on historic observations from weather stations in Nebraska and Texas. Incandescent (INC) and fluorescent (FLU) lights were turned on and off to mimic outdoor solar radiation.
### (a) Nebraska environmental conditions

<table>
<thead>
<tr>
<th>Setting Code</th>
<th>Time</th>
<th>Historic (°C)</th>
<th>Future Cool (°C)</th>
<th>Future Average (°C)</th>
<th>Future Warm (°C)</th>
<th>Humidity (%)</th>
<th>INC (#)</th>
<th>FLU (#)</th>
</tr>
</thead>
<tbody>
<tr>
<td>a</td>
<td>6:40</td>
<td>15</td>
<td>13</td>
<td>15</td>
<td>17</td>
<td>40</td>
<td>2</td>
<td>0</td>
</tr>
<tr>
<td>b</td>
<td>6:55</td>
<td>18</td>
<td>17</td>
<td>18</td>
<td>21</td>
<td>60</td>
<td>4</td>
<td>2</td>
</tr>
<tr>
<td>c</td>
<td>7:10</td>
<td>21</td>
<td>20</td>
<td>21</td>
<td>25</td>
<td>75</td>
<td>6</td>
<td>4</td>
</tr>
<tr>
<td>d</td>
<td>7:25</td>
<td>24</td>
<td>23.6</td>
<td>24.4</td>
<td>29</td>
<td>85</td>
<td>8</td>
<td>4</td>
</tr>
<tr>
<td>e</td>
<td>19:47</td>
<td>21</td>
<td>20</td>
<td>21</td>
<td>25</td>
<td>85</td>
<td>6</td>
<td>4</td>
</tr>
<tr>
<td>f</td>
<td>20:02</td>
<td>18</td>
<td>17</td>
<td>18</td>
<td>21</td>
<td>75</td>
<td>4</td>
<td>2</td>
</tr>
<tr>
<td>g</td>
<td>20:17</td>
<td>15</td>
<td>13</td>
<td>15</td>
<td>17</td>
<td>60</td>
<td>2</td>
<td>0</td>
</tr>
<tr>
<td>h</td>
<td>20:32</td>
<td>11.1</td>
<td>10.7</td>
<td>11.2</td>
<td>13.2</td>
<td>40</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>a</td>
<td>6:27</td>
<td>15</td>
<td>16</td>
<td>18</td>
<td>20</td>
<td>40</td>
<td>2</td>
<td>0</td>
</tr>
<tr>
<td>b</td>
<td>6:42</td>
<td>18</td>
<td>18</td>
<td>22</td>
<td>26</td>
<td>60</td>
<td>4</td>
<td>2</td>
</tr>
<tr>
<td>c</td>
<td>6:57</td>
<td>21</td>
<td>22</td>
<td>22</td>
<td>26</td>
<td>75</td>
<td>6</td>
<td>4</td>
</tr>
<tr>
<td>d</td>
<td>7:12</td>
<td>25.1</td>
<td>24.8</td>
<td>26.4</td>
<td>29.9</td>
<td>85</td>
<td>8</td>
<td>4</td>
</tr>
<tr>
<td>e</td>
<td>19:55</td>
<td>21</td>
<td>22</td>
<td>22</td>
<td>26</td>
<td>85</td>
<td>6</td>
<td>4</td>
</tr>
<tr>
<td>f</td>
<td>20:10</td>
<td>18</td>
<td>19</td>
<td>22</td>
<td>27</td>
<td>75</td>
<td>4</td>
<td>2</td>
</tr>
<tr>
<td>g</td>
<td>20:25</td>
<td>15</td>
<td>16</td>
<td>18</td>
<td>20</td>
<td>60</td>
<td>2</td>
<td>0</td>
</tr>
<tr>
<td>h</td>
<td>20:40</td>
<td>11.8</td>
<td>12.1</td>
<td>13.1</td>
<td>15.5</td>
<td>40</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>a</td>
<td>6:18</td>
<td>16</td>
<td>17</td>
<td>19</td>
<td>21</td>
<td>40</td>
<td>2</td>
<td>0</td>
</tr>
<tr>
<td>b</td>
<td>6:33</td>
<td>19</td>
<td>21</td>
<td>23</td>
<td>25</td>
<td>60</td>
<td>4</td>
<td>2</td>
</tr>
<tr>
<td>c</td>
<td>6:48</td>
<td>22</td>
<td>25</td>
<td>26</td>
<td>28</td>
<td>75</td>
<td>6</td>
<td>4</td>
</tr>
<tr>
<td>d</td>
<td>7:03</td>
<td>26.6</td>
<td>28.6</td>
<td>29.8</td>
<td>31.6</td>
<td>85</td>
<td>8</td>
<td>4</td>
</tr>
<tr>
<td>e</td>
<td>20:01</td>
<td>22</td>
<td>25</td>
<td>26</td>
<td>28</td>
<td>85</td>
<td>6</td>
<td>4</td>
</tr>
<tr>
<td>f</td>
<td>20:16</td>
<td>19</td>
<td>21</td>
<td>23</td>
<td>26</td>
<td>75</td>
<td>4</td>
<td>2</td>
</tr>
<tr>
<td>g</td>
<td>20:31</td>
<td>16</td>
<td>17</td>
<td>19</td>
<td>21</td>
<td>60</td>
<td>2</td>
<td>0</td>
</tr>
<tr>
<td>h</td>
<td>20:46</td>
<td>13.4</td>
<td>14.8</td>
<td>16.1</td>
<td>17.6</td>
<td>40</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>a</td>
<td>6:08</td>
<td>17</td>
<td>20</td>
<td>22</td>
<td>21</td>
<td>40</td>
<td>2</td>
<td>0</td>
</tr>
<tr>
<td>b</td>
<td>6:23</td>
<td>20</td>
<td>24</td>
<td>26</td>
<td>25</td>
<td>60</td>
<td>4</td>
<td>2</td>
</tr>
<tr>
<td>c</td>
<td>6:38</td>
<td>24</td>
<td>27</td>
<td>29</td>
<td>28</td>
<td>75</td>
<td>6</td>
<td>4</td>
</tr>
<tr>
<td>d</td>
<td>6:53</td>
<td>28.1</td>
<td>30.5</td>
<td>32.1</td>
<td>31.9</td>
<td>85</td>
<td>8</td>
<td>4</td>
</tr>
<tr>
<td>e</td>
<td>20:10</td>
<td>24</td>
<td>27</td>
<td>29</td>
<td>28</td>
<td>85</td>
<td>6</td>
<td>4</td>
</tr>
<tr>
<td>f</td>
<td>20:25</td>
<td>20</td>
<td>24</td>
<td>26</td>
<td>25</td>
<td>75</td>
<td>4</td>
<td>2</td>
</tr>
<tr>
<td>g</td>
<td>20:40</td>
<td>17</td>
<td>20</td>
<td>22</td>
<td>21</td>
<td>60</td>
<td>2</td>
<td>0</td>
</tr>
<tr>
<td>h</td>
<td>20:55</td>
<td>14.5</td>
<td>17.4</td>
<td>18.4</td>
<td>18</td>
<td>40</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>
### (b) Texas environmental conditions

<table>
<thead>
<tr>
<th>Setting Code</th>
<th>Time</th>
<th>Historic (°C)</th>
<th>Future Cool (°C)</th>
<th>Future Average (°C)</th>
<th>Future Warm (°C)</th>
<th>Humidity (%)</th>
<th>INC (#)</th>
<th>FLU (#)</th>
</tr>
</thead>
<tbody>
<tr>
<td>a</td>
<td>6:41</td>
<td>13.5</td>
<td>14</td>
<td>14</td>
<td>14</td>
<td>45</td>
<td>2</td>
<td>0</td>
</tr>
<tr>
<td>b</td>
<td>6:56</td>
<td>15</td>
<td>15</td>
<td>16</td>
<td>16</td>
<td>45</td>
<td>4</td>
<td>2</td>
</tr>
<tr>
<td>c</td>
<td>7:11</td>
<td>16.5</td>
<td>16</td>
<td>18</td>
<td>18</td>
<td>45</td>
<td>6</td>
<td>4</td>
</tr>
<tr>
<td>d</td>
<td>7:26</td>
<td>18.2</td>
<td>17.8</td>
<td>19.4</td>
<td>20.1</td>
<td>45</td>
<td>8</td>
<td>4</td>
</tr>
<tr>
<td>e</td>
<td>18:31</td>
<td>16.5</td>
<td>16</td>
<td>18</td>
<td>18</td>
<td>45</td>
<td>6</td>
<td>4</td>
</tr>
<tr>
<td>f</td>
<td>18:46</td>
<td>15</td>
<td>15</td>
<td>16</td>
<td>16</td>
<td>45</td>
<td>4</td>
<td>2</td>
</tr>
<tr>
<td>g</td>
<td>19:01</td>
<td>13.5</td>
<td>14</td>
<td>14</td>
<td>14</td>
<td>45</td>
<td>2</td>
<td>0</td>
</tr>
<tr>
<td>h</td>
<td>19:16</td>
<td>9.0</td>
<td>9.0</td>
<td>9.0</td>
<td>9.0</td>
<td>45</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Week 2</th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>a</td>
<td>6:32</td>
<td>13</td>
<td>14</td>
<td>14</td>
<td>14</td>
<td>45</td>
<td>2</td>
<td>0</td>
</tr>
<tr>
<td>b</td>
<td>6:47</td>
<td>15</td>
<td>16</td>
<td>17</td>
<td>17</td>
<td>45</td>
<td>4</td>
<td>2</td>
</tr>
<tr>
<td>c</td>
<td>7:02</td>
<td>17</td>
<td>18</td>
<td>19</td>
<td>20</td>
<td>45</td>
<td>6</td>
<td>4</td>
</tr>
<tr>
<td>d</td>
<td>7:17</td>
<td>19.1</td>
<td>19.6</td>
<td>21.5</td>
<td>22.5</td>
<td>45</td>
<td>8</td>
<td>4</td>
</tr>
<tr>
<td>e</td>
<td>18:37</td>
<td>17</td>
<td>18</td>
<td>19</td>
<td>20</td>
<td>45</td>
<td>6</td>
<td>4</td>
</tr>
<tr>
<td>f</td>
<td>18:52</td>
<td>15</td>
<td>16</td>
<td>17</td>
<td>17</td>
<td>45</td>
<td>4</td>
<td>2</td>
</tr>
<tr>
<td>g</td>
<td>19:07</td>
<td>13</td>
<td>14</td>
<td>14</td>
<td>14</td>
<td>45</td>
<td>2</td>
<td>0</td>
</tr>
<tr>
<td>h</td>
<td>19:22</td>
<td>9.0</td>
<td>9.0</td>
<td>9.0</td>
<td>9.0</td>
<td>45</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Week 3</th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>a</td>
<td>7:23</td>
<td>13</td>
<td>15</td>
<td>15</td>
<td>14</td>
<td>45</td>
<td>2</td>
<td>0</td>
</tr>
<tr>
<td>b</td>
<td>7:38</td>
<td>15</td>
<td>17</td>
<td>18</td>
<td>17</td>
<td>45</td>
<td>4</td>
<td>2</td>
</tr>
<tr>
<td>c</td>
<td>7:53</td>
<td>17</td>
<td>20</td>
<td>20</td>
<td>20</td>
<td>45</td>
<td>6</td>
<td>4</td>
</tr>
<tr>
<td>d</td>
<td>8:08</td>
<td>20.1</td>
<td>21.6</td>
<td>22.1</td>
<td>22.9</td>
<td>45</td>
<td>8</td>
<td>4</td>
</tr>
<tr>
<td>e</td>
<td>19:42</td>
<td>17</td>
<td>20</td>
<td>20</td>
<td>20</td>
<td>45</td>
<td>6</td>
<td>4</td>
</tr>
<tr>
<td>f</td>
<td>19:57</td>
<td>15</td>
<td>17</td>
<td>18</td>
<td>17</td>
<td>45</td>
<td>4</td>
<td>2</td>
</tr>
<tr>
<td>g</td>
<td>20:12</td>
<td>13</td>
<td>15</td>
<td>15</td>
<td>14</td>
<td>45</td>
<td>2</td>
<td>0</td>
</tr>
<tr>
<td>h</td>
<td>20:27</td>
<td>9.0</td>
<td>9.0</td>
<td>9.0</td>
<td>9.0</td>
<td>45</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Week 4</th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>a</td>
<td>7:13</td>
<td>14</td>
<td>15</td>
<td>15</td>
<td>15</td>
<td>45</td>
<td>2</td>
<td>0</td>
</tr>
<tr>
<td>b</td>
<td>7:27</td>
<td>17</td>
<td>17</td>
<td>18</td>
<td>18</td>
<td>45</td>
<td>4</td>
<td>2</td>
</tr>
<tr>
<td>c</td>
<td>7:43</td>
<td>19</td>
<td>20</td>
<td>21</td>
<td>21</td>
<td>45</td>
<td>6</td>
<td>4</td>
</tr>
<tr>
<td>d</td>
<td>7:57</td>
<td>21.2</td>
<td>21.4</td>
<td>23.2</td>
<td>25.5</td>
<td>45</td>
<td>8</td>
<td>4</td>
</tr>
<tr>
<td>e</td>
<td>19:48</td>
<td>19</td>
<td>20</td>
<td>21</td>
<td>21</td>
<td>45</td>
<td>6</td>
<td>4</td>
</tr>
<tr>
<td>f</td>
<td>20:03</td>
<td>17</td>
<td>17</td>
<td>18</td>
<td>18</td>
<td>45</td>
<td>4</td>
<td>2</td>
</tr>
<tr>
<td>g</td>
<td>20:18</td>
<td>14</td>
<td>15</td>
<td>15</td>
<td>15</td>
<td>45</td>
<td>2</td>
<td>0</td>
</tr>
<tr>
<td>h</td>
<td>20:33</td>
<td>9.0</td>
<td>9.0</td>
<td>9.0</td>
<td>9.0</td>
<td>45</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>
**APPENDIX 2**

**PLANT SPECIES IDENTIFIED IN HYDROPERIOD AND LAND USE STUDIES**

*Table A2.1.* Plant species identified in hydroperiod and land use studies. Wetland indicator statuses were determined for Great Plains plant region, representing wetland obligate (OBL), facultative wetland (FACW), facultative (FAC), facultative upland (FACU), and upland (UPL) plants.

<table>
<thead>
<tr>
<th>Scientific Name</th>
<th>Family</th>
<th>Native Status</th>
<th>Wetland Indicator Status (NE(^b)</th>
<th>TX(^c))</th>
<th>Hydroperiod Study Frequency Identified</th>
<th>Land Use Study Frequency Identified</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Amaranthus retroflexus</em></td>
<td>Amaranthaceae</td>
<td>Native</td>
<td>FACU</td>
<td>FACU</td>
<td>0.0%</td>
<td>5.0%</td>
</tr>
<tr>
<td><em>Amaranthus spinosus</em></td>
<td>Amaranthaceae</td>
<td>Native</td>
<td>FACU</td>
<td>FACU</td>
<td>0.0%</td>
<td>0.0%</td>
</tr>
<tr>
<td><em>Amaranthus tuberculatus</em></td>
<td>Amaranthaceae</td>
<td>Native</td>
<td>FAC</td>
<td>—</td>
<td>5.0%</td>
<td>40.0%</td>
</tr>
<tr>
<td><em>Ambrosia grayi</em></td>
<td>Asteraceae</td>
<td>Native</td>
<td>FAC</td>
<td>FACW</td>
<td>0.0%</td>
<td>65.0%</td>
</tr>
<tr>
<td><em>Ambrosia trifida</em></td>
<td>Asteraceae</td>
<td>Native</td>
<td>FAC</td>
<td>FAC</td>
<td>0.0%</td>
<td>0.0%</td>
</tr>
<tr>
<td><em>Coreopsis tinctoria</em></td>
<td>Asteraceae</td>
<td>Native</td>
<td>FAC</td>
<td>FAC</td>
<td>30.0%</td>
<td>10.0%</td>
</tr>
<tr>
<td><em>Erigeron canadensis</em></td>
<td>Asteraceae</td>
<td>Native</td>
<td>FAC</td>
<td>UPL</td>
<td>0.0%</td>
<td>0.0%</td>
</tr>
<tr>
<td><em>Symphyotrichum subulatum</em></td>
<td>Asteraceae</td>
<td>Native</td>
<td>OBL</td>
<td>OBL</td>
<td>0.0%</td>
<td>0.0%</td>
</tr>
<tr>
<td><em>Xanthium strumarium</em></td>
<td>Asteraceae</td>
<td>Native</td>
<td>FAC</td>
<td>FAC</td>
<td>5.0%</td>
<td>0.0%</td>
</tr>
<tr>
<td><em>Rorippa sinuate</em></td>
<td>Brassicaceae</td>
<td>Native</td>
<td>FACW</td>
<td>FACW</td>
<td>0.0%</td>
<td>0.0%</td>
</tr>
<tr>
<td><em>Bassia scoparia</em></td>
<td>Chenopodiaceae</td>
<td>Exotic</td>
<td>FACU</td>
<td>FACU</td>
<td>0.0%</td>
<td>0.0%</td>
</tr>
<tr>
<td><em>Chenopodium album</em></td>
<td>Chenopodiaceae</td>
<td>Native</td>
<td>FACU</td>
<td>FAC</td>
<td>0.0%</td>
<td>0.0%</td>
</tr>
<tr>
<td><em>Chenopodium leptophyllum</em></td>
<td>Chenopodiaceae</td>
<td>Native</td>
<td>FACU</td>
<td>FAC</td>
<td>0.0%</td>
<td>35.0%</td>
</tr>
<tr>
<td><em>Cyperus esculentus</em></td>
<td>Cyperaceae</td>
<td>Native</td>
<td>FACW</td>
<td>FACW</td>
<td>0.0%</td>
<td>15.0%</td>
</tr>
<tr>
<td>Species</td>
<td>Family</td>
<td>Native/Exotic</td>
<td>Distribution</td>
<td>Cover</td>
<td>Spread</td>
<td>Abundance</td>
</tr>
<tr>
<td>---------------------------------</td>
<td>----------------</td>
<td>---------------</td>
<td>--------------</td>
<td>-------</td>
<td>--------</td>
<td>-----------</td>
</tr>
<tr>
<td><em>Eleocharis palustris</em></td>
<td>Cyperaceae</td>
<td>Native</td>
<td>OBL</td>
<td>FACW</td>
<td>25.0%</td>
<td>10.0%</td>
</tr>
<tr>
<td><em>Schoenoplectus tabernaemontani</em></td>
<td>Cyperaceae</td>
<td>Native</td>
<td>OBL</td>
<td>OBL</td>
<td>0.0%</td>
<td>0.0%</td>
</tr>
<tr>
<td><em>Euphorbia prostrata</em></td>
<td>Euphorbiaceae</td>
<td>Native</td>
<td>UPL</td>
<td>—</td>
<td>0.0%</td>
<td>10.0%</td>
</tr>
<tr>
<td><em>Lythrum californicum</em></td>
<td>Lythraceae</td>
<td>Native</td>
<td>OBL</td>
<td>OBL</td>
<td>0.0%</td>
<td>5.0%</td>
</tr>
<tr>
<td><em>Malvella leprosa</em></td>
<td>Malvaceae</td>
<td>Native</td>
<td>FAC</td>
<td>FAC</td>
<td>15.0%</td>
<td>0.0%</td>
</tr>
<tr>
<td><em>Marsilea vestita</em></td>
<td>Marsileaceae</td>
<td>Native</td>
<td>OBL</td>
<td>OBL</td>
<td>5.0%</td>
<td>15.0%</td>
</tr>
<tr>
<td><em>Alopecurus carolinianus</em></td>
<td>Poaceae</td>
<td>Native</td>
<td>FACW</td>
<td>FACW</td>
<td>0.0%</td>
<td>0.0%</td>
</tr>
<tr>
<td><em>Bouteloua dactyloides</em></td>
<td>Poaceae</td>
<td>Native</td>
<td>FACU</td>
<td>FACU</td>
<td>0.0%</td>
<td>0.0%</td>
</tr>
<tr>
<td><em>Bromus arvensis</em></td>
<td>Poaceae</td>
<td>Exotic</td>
<td>FACU</td>
<td>FACU</td>
<td>0.0%</td>
<td>0.0%</td>
</tr>
<tr>
<td><em>Digitaria sanguinalis</em></td>
<td>Poaceae</td>
<td>Exotic</td>
<td>FAC</td>
<td>—</td>
<td>0.0%</td>
<td>5.0%</td>
</tr>
<tr>
<td><em>Echinochloa crusgalli</em></td>
<td>Poaceae</td>
<td>Exotic</td>
<td>FAC</td>
<td>FACW</td>
<td>40.0%</td>
<td>50.0%</td>
</tr>
<tr>
<td><em>Eriochloa contracta</em></td>
<td>Poaceae</td>
<td>Native</td>
<td>FAC</td>
<td>FAC</td>
<td>0.0%</td>
<td>5.0%</td>
</tr>
<tr>
<td><em>Hordeum jubatum</em></td>
<td>Poaceae</td>
<td>Native</td>
<td>FACW</td>
<td>FAC</td>
<td>0.0%</td>
<td>0.0%</td>
</tr>
<tr>
<td><em>Leptochloa fusca</em></td>
<td>Poaceae</td>
<td>Native</td>
<td>FACW</td>
<td>FACW</td>
<td>40.0%</td>
<td>0.0%</td>
</tr>
<tr>
<td><em>Panicum dichotomiflorum</em></td>
<td>Poaceae</td>
<td>Native</td>
<td>FAC</td>
<td>FACW</td>
<td>15.0%</td>
<td>5.0%</td>
</tr>
<tr>
<td><em>Setaria magna</em></td>
<td>Poaceae</td>
<td>Native</td>
<td>FACW</td>
<td>—</td>
<td>0.0%</td>
<td>0.0%</td>
</tr>
<tr>
<td><em>Setaria pumila</em></td>
<td>Poaceae</td>
<td>Exotic</td>
<td>FAC</td>
<td>FAC</td>
<td>0.0%</td>
<td>0.0%</td>
</tr>
<tr>
<td><em>Setaria verticillata</em></td>
<td>Poaceae</td>
<td>Exotic</td>
<td>FAC</td>
<td>FAC</td>
<td>15.0%</td>
<td>0.0%</td>
</tr>
<tr>
<td><em>Polygonum amphibium</em></td>
<td>Polygonaceae</td>
<td>Native</td>
<td>OBL</td>
<td>OBL</td>
<td>0.0%</td>
<td>20.0%</td>
</tr>
<tr>
<td><em>Polygonum lapathifolium</em></td>
<td>Polygonaceae</td>
<td>Native</td>
<td>OBL</td>
<td>FACW</td>
<td>10.0%</td>
<td>0.0%</td>
</tr>
<tr>
<td><em>Polygonum pensylvanicum</em></td>
<td>Polygonaceae</td>
<td>Native</td>
<td>OBL</td>
<td>FACW</td>
<td>5.0%</td>
<td>0.0%</td>
</tr>
<tr>
<td><em>Polygonum persicaria</em></td>
<td>Polygonaceae</td>
<td>Native</td>
<td>OBL</td>
<td>FACW</td>
<td>25.0%</td>
<td>0.0%</td>
</tr>
<tr>
<td><em>Rumex crispus</em></td>
<td>Polygonaceae</td>
<td>Exotic</td>
<td>OBL</td>
<td>FACW</td>
<td>20.0%</td>
<td>0.0%</td>
</tr>
<tr>
<td><em>Portulaca oleracea</em></td>
<td>Portulacaceae</td>
<td>Native</td>
<td>FAC</td>
<td>FAC</td>
<td>0.0%</td>
<td>20.0%</td>
</tr>
<tr>
<td><em>Verbascum thapsus</em></td>
<td>Scrophulariaceae</td>
<td>Exotic</td>
<td>UPL</td>
<td>—</td>
<td>5.0%</td>
<td>0.0%</td>
</tr>
<tr>
<td><em>Solanum interius</em></td>
<td>Solanaceae</td>
<td>Native</td>
<td>—</td>
<td>—</td>
<td>15.0%</td>
<td>0.0%</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Note</th>
</tr>
</thead>
<tbody>
<tr>
<td>aFederal Geographic Data Committee (2013); bHaukos et al. (1997); cUSDA (2019)</td>
</tr>
</tbody>
</table>
Figure A3.1. Total biomass (a), above-ground biomass (b), and below-ground biomass (c) as a function of average soil temperature between germination day (Table 3.2) and day 28 for Texas samples. Biomass was significantly influenced by climate scenario, but soil moisture and seed bank density were not significant main effects. Regression model significance levels denoted at $p < 0.05$ (*) and $p < 0.01$ (**) and regression equations are listed in Table 3.3.
VITA

Rachel Kazmiera Owen was born and raised in central Iowa. She graduated from Ankeny High School in Ankeny, IA in 2009. After high school, she attended Iowa State University in Ames, IA from 2009-2013 where she received dual bachelor’s degrees in Agronomy and Global Resource Systems and a minor in Economics. She received a master’s of science degree at South Dakota State University from the Department of Plant Science in 2015. Her master’s thesis was titled “Spatial variability of saline and sodic soils in the black glaciated region of the northern Great Plains, USA”.

Rachel began her dissertation work at the University of Missouri in 2015 in the School of Natural Resources with an emphasis on Soil, Environmental and Atmospheric Sciences. Her doctoral research titled, “Playa wetland plant and soil response to predicted climate and land use change in the southern Great Plains,” was completed from 2015-2019.