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Heterogeneity promotes resilience in restored prairie: implications for the 'environmental heterogeneity hypothesis'

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Abstract

Enhancing resilience in formerly degraded ecosystems is an important goal of restoration ecology. However, evidence for the recovery of resilience and its underlying mechanisms requires long-term experiments and comparison to reference ecosystems. We used data from an experimental prairie restoration that featured long-term soil heterogeneity manipulations and data from comparable remnant (reference) prairie to (1) quantify the recovery of ecosystem functioning (i.e., productivity) relative to remnant prairie, (2) compare resilience of restored and remnant prairies to a natural drought, and (3) test whether soil heterogeneity enhances resilience of restored prairie. We compared sensitivity and legacy effects between prairie types (remnant and restored) and among four prairie sites that included two remnant prairie sites and prairie restored under homogeneous and heterogeneous soil conditions. We measured sensitivity and resilience as the proportional change in aboveground net primary productivity (ANPP) during and following drought (sensitivity and legacy effects, respectively) relative to average ANPP based on four pre-drought years (2014-2017). In non-drought years, total ANPP was similar between remnant and restored prairie, but remnant prairie had higher grass productivity and lower forb productivity compared to restored prairie. These ANPP patterns generally persisted during drought. Sensitivity of total ANPP to drought was similar between restored and remnant prairie, but grasses in restored prairie were more sensitive to drought. Post-drought legacy effects were more positive in restored prairie, and we attributed this to the more positive and less variable legacy response of forb ANPP in restored prairie, especially in the heterogeneous soil treatment. Our results suggest that productivity recovers in restored prairie and exhibits similar sensitivity to drought as remnant prairie. Furthermore, creating heterogeneity promotes forb productivity and enhances prairie resilience to drought.

Keywords: drought legacy effects; drought sensitivity; ecological restoration; grasslands; productivity; resiliency; soil heterogeneity; tallgrass prairie

INTRODUCTION

Ecological restoration aims to steer recovery of ecosystems degraded by human activity to attain components and functions representative of a reference ecosystem, including resilience to periodic stress or disturbance (Gann et al. 2019). Ecosystem resilience is the capacity to absorb or bounce back from disturbance that causes change in the environment, indicated by retaining or returning to a similar identity, composition, and functioning (Holling 1963, McDonald et al. 2016, Gann et al. 2019). In this way, ecological restoration can buffer the impacts of interannual variability in climate and climate extremes by reestablishing species and complexity that promote resilience to future disturbances (Zabin et al. 2022). For example, improved river-flood plain connectivity can mitigate flood impacts (Opperman et al. 2010) and restoring coastal foundation species can protect shorelines from disturbance (Gedan et al. 2011). Knowledge of conditions that will enhance resilience of restored ecosystems under increasingly variable and more extreme climates is needed to guide ecological restoration, and ecological theory should robustly inform factors influencing functioning, sensitivity, and resilience of restored ecosystems (Bradshaw 1987, Smith 2011, Maurer et al. 2020).

The 'environmental heterogeneity hypothesis' predicts that greater variability in resources enables more species to coexist (Ricklefs 1977, Huston 1979), and higher biodiversity can increase ecosystem functioning and resilience to drought and climate extremes (Tilman and Downing 1994, Isbell et al. 2015). Ecosystem resistance (or insensitivity) to drought is indicated by negligible change in functioning relative to average during drought, whereas resilience reflects rate of recovery to average or higher than average functioning following drought (i.e., positive legacy effect) (Tilman and Downing 1994, Yahdjian and Sala 2006, Hoover et al. 2014, Griffin-Nolan et al. 2018). Aboveground net primary productivity (ANPP) is a common measure of ecosystem functioning used to assess sensitivity and resilience to perturbations such as drought (Gann et al. 2019). Grassland ecosystems, such as the tallgrass prairie, have been shown to be both sensistive and resilient to drought as demonstrated by reductions in ANPP during drought and increased ANPP following drought (Griffin-Nolan et al. 2018, Luo et al. 2023).

The productivity of tallgrass prairie is spatially and temporally heterogeneous (Knapp and Smith 2001). Spatial heterogeneity in ANPP is created in part by variation in fire frequency (Knapp and Seastedt 1986, Blair 1997) and grazing by megaherbivores (Knapp et al. 1999, Collins and Smith 2006, Elson and Hartnett 2017). Long-term studies in the Flint Hills region of the North American Great Plains have shown that soil depth, which varies with topography, and nitrogen (N) availability are also deterministic drivers of ANPP in tallgrass prairie (Briggs and Knapp 1995, Turner et al. 1997, Collins et al. 2018). Typically, ANPP is lower in shallow upland soils overlaying limestone rock compared to deep lowland soil (Briggs and Knapp 1995), and ANPP is higher in N fertilized soils (Blair 1997, Turner et al. 1997, Nieland et al. 2021). Temporal heterogeneity of ANPP in tallgrass prairie results from climate variability and extremes, including droughts (Knapp and Smith 2001, Hoover et al. 2014, Griffin-Nolan et al. 2018, Zambreski et al. 2018, Ratajczak et al. 2019). In contrast to remnant prairie in the Flint Hills, restored prairies are often located on deep, formerly cultivated soils. ANPP in prairie restored on deep and homogeneous cultivated soils is less spatially heterogeneous than ANPP of prairie restored in soil where rooting depth and nutrient availability were manipulated to promote soil heterogeneity (Baer et al. 2016).

The majority of the tallgrass prairie ecosystem has been converted row-crop agriculture (Samson and Knopf 1994, Comer et al. 2018) and restoring grassland reverses many ecosystem disservices caused by cultivating soil, including resilience of ecosystem functioning (Birgé et al. 2016). Although ANPP can increase rapidly following grassland restoration on formerly cultivated soil (Baer et al. 2002, 2003), there are knowledge gaps about the extent to which productivity dynamics in restored grassland reflect never cultivated prairie over the long term, and whether restored grassland is resilient to perturbations such as drought. Sensitivity to drought might develop as restorations age. For example, prairies restored for less than a decade showed no reduction in ANPP (lack of sensitivity) response to natural (Manning and Baer 2018) and experimental drought (Carter and Blair 2012). In contrast, a much older restored prairie (>65 years) exhibited comparable reductions in productivity (sensitivity) as similarly managed remnant prairie during years with water stress (Kucharik et al. 2006). The discrepancy in restored grassland ANPP response to drought might be explained by the development of resilience over time in ecosystems recovering from disturbance (Odum 1969, Kominoski et al. 2018).

Here, we leveraged ANPP data from a multi-decadal prairie restoration experiment and two long-term experiments in remnant (never cultivated) prairie collected prior to, during, and after a severe growing season drought to ascertain (1) whether multi-decadal restored grassland functions similar to remnant prairie and (2) whether environmental heterogeneity in multi-decadal restored prairie increases ecosystem functioning and resilience to drought. The experimental restoration was established in 1997 on formerly cultivated soil to test the applicability of the ‘environmental heterogeneity hypothesis’ to restoring biodiversity. The restoration experiment contained homogeneous and heterogeneous soil treatments (Baer et al. 1999, 2003, 2016), and after 20 years of restoration the heterogeneous soils supported higher plant diversity and richness than prairie restored on homogeneous soil (Baer et al. 2020). For comparison to remnant prairie, we obtained ANPP data from unmanipulated control plots in two nearby long-term experiments in remnant prairie under the same management regime as the restored prairie. In all experiments, ANPP was collected using the same methods and in the same years prior to drought, during drought, and following drought. These datasets enabled us to determine whether ecosystem functioning before, during, and after drought (including drought sensitivity and legacy effect) in multi-decadal restored prairie is similar to remnant prairie, and test the hypothesis that greater resource heterogeneity (corresponding with higher plant diversity) increases ecosystem functioning and resilience to drought.

METHODS

Study Site

All experiments were located at the Konza Prairie Biological Station (KPBS) and Long-Term Ecological Research site in Riley County, KS ($39^{o}05^{o}$ N, $96^{o}35^{o}$ W). The remnant (never cultivated) prairie is dominated by perennial C_4 grasses (*Andropogon gerardii, Sorghastrum nutans, Panicum virgatum* and *Schizachyrium scoparium*) and includes some of the >300 subordinate forb species that occur throughout the site. The climate is characterized by warm, dry summers and wet, cool winters. From 1989-2019, mean annual precipitation was 832 mm and a mean annual temperature was 13°C (Konza Data Catalog data sets APT01 and AWE01 [Nippert 2024a, 2024b]). Across the six study years (2014-2019), Riley County experienced a locally severe-to-extreme drought in the growing season months of April to September in 2018 (Appendix S1: Figure S1), described as reaching a Palmer Drought Severity Index of -2 to -4.9 (Palmer 1965).

The restored and remnant prairie experiments were located 0.75 km from one another, on similar soils, in similar topographic positions (lowland), and included treatments with similar management history. The restoration experiment was established on a former agricultural field that had been continuously cropped for >50 years. The soil at the restoration site is classified as Reading silt loam (fine-silty, mixed, superactive, mesic typic Pachic Argiudoll). The two remnant prairie experiments used in this study were located on Irwin silty clay loam (fine, mixed, superactive, mesic Pachic Argiustolls) soil (Knapp et al. 2001, Carson and Zeglin 2018). Both remnant prairie experiments included control plots managed similar to the restored prairie: not grazed by cattle or bison and burned annually each spring. Annual burning is a common practice in the region to prevent woody encroachment (Briggs et al. 2005, Collins et al. 2021).

Experimental Design

We used a subset of whole plots in the restoration prairie experiment representing the most homogeneous (RES_{HOM}) and most heterogeneous (RES_{HET}) soil treatments for this study. Each whole-plot heterogeneity treatment was assigned to a 6 m x 8 m plot in each of four blocks according to a randomized complete block design (Baer et al. 1999). The RES_{HET} plots contained a 2 x 3 factorial combination of soil depth and nutrient availability assigned to vertical and horizontal strips according to a split block design. Soil depth (two levels: shallow or deep) was assigned to two of four alternating 2 m x 6 m strips (Fig. 1). Prior to the initial planting, shallow soil depth was achieved by excavating the soil to a depth of 20-25 cm, burying pieces of rough-cut limestone slabs in the maximum heterogeneity treatments to mimic the uplands of the Flint Hills, and returning the topsoil to the plots. All plots were excavated to control for disturbance prior to burying the limestone slabs (Baer et al. 1999). Soil nutrient availability (three levels: reduced-N, ambient-N, and enriched-N) was assigned to one of three 2 m x 8 m strips (perpendicular to depth treatments). Reduced-N strips were created by incorporating 5.5 kg dry sawdust/m^2 prior to planting in 1998 and have received 84.2 g C/m^2 (~200 g sucrose/m^2) three times during the growing season since 2003 to maintain microbial demand and immobilization of N (Baer et al. 2003). Enriched-N treatments have received 5 g N/m^2 in June of every year since 1998 by hand-broadcasting ammonium-nitrate pellets (Baer et al. 2003). The deep ambient-N strips never received experimental manipulations (Fig. 1). Baer et al. (2016, 2020) demonstrate that the heterogeneous treatment increased variation in soil depth and available inorganic nitrogen (Appendix S1: Table S1). RES_{HOM} plots receive no soil manipulations.

All plots were initially sown and later over-seeded with the same species. Each restored prairie plot was originally sown with 42 prairie species in late fall of 1997 using a log-normal distribution of dominant grasses and subordinate forbs to resemble the distribution of species in never-cultivated tallgrass prairie. All plots received supplemental seed additions of 15 new forb species in 2005 and 17 new species (2 grasses and 15 forbs) repeatedly sown from 2013 to 2017 (Baer et al. 2020). The experimental area was fenced in 1998 to prevent deer browsing and has been burned annually in the early spring since 1998, except in 2000 and 2003.

The remnant prairie experiments used in this study have historically been referred to as the "irrigation transect" and the "belowground plot" experiments at KPBS, referred to here as REM_{IRT} and REM_{BGP}, respectively. The irrigation transect experiment has manipulated water availability by irrigation since 1991 (described in detail by Knapp et al. [2001]). We used ANPP data from six non-irrigated control plots (10 m^2) for comparison with the restoration experiment (Fig. 1). REM_{BGP} has manipulated fire frequency, mowing, and nutrient availability since 1986 (described in detail by Carson and Zeglin [2018]). We used ANPP data from four annually burned, unmowed, and unfertilized control plots (12.5 m^2) for additional comparison with the restoration experiment (Fig.1).

Data Sources and Measurements

Daily precipitation totals from 2014 to 2019 were obtained from the Konza LTER Data Catalog data set APT01 (Nippert 2024a) and used to calculate cumulative precipitation patterns. The 30-year average cumulative precipitation pattern was calculated using daily precipitation totals from 1989 to 2019.

The ANPP data from the restored and remnant prairie experiments were accessed from the Konza LTER Data Catalog data sets PRP01 (Baer et al. 2024), WAT01 (Blair 2023) and PBB01 (Blair and Zeglin 2023). Total, grass, and forb ANPP were determined for the same time period (2014-2019) using the same methods in remnant and restored prairie experiments. In all experiments, plant material was harvested from 0.1 m^2 quadrats at peak biomass. Biomass was sorted into grasses, forbs, and litter produced in the sampling year. All biomass was dried at 60°C and weighed to estimate ANPP (Briggs and Knapp 1991). In the restoration experiment, we harvested biomass from twelve quadrats in each plot (n = 4 per heterogeneity treatment). In REM_{IRT}, ANPP was estimated from six quadrats in each of 6 control plots. In REM_{BGP}, ANPP was estimated from two quadrats in each of 4 control plots.

Statistical Analysis

Prior to statistical analyses, ANPP estimates from multiple quadrats within a plot were averaged for each plot for each year (2014-2019) and then averaged across years to calculate average ANPP for each plot in each experiment. Average, drought year (2018), and post-drought year (2019) ANPP were used to calculate drought sensitivity and drought legacy effect relative to their pre-drought ANPP average (2014-2017) according to Griffin-Nolan et al. (2018), where:

drought sensitivity = $|(ANPP_{2018} – ANPP_{Avg})/ ANPP_{Avg})|$ and drought legacy effect = $(ANPP_{2019} – ANPP_{Avg})/ANPP_{Avg}$.

We analyzed ecosystem functioning (average, drought year, and post drought year ANPP) and resilience (sensitivity and legacy effect) in two ways: by prairie type (restored vs. remnant prairie) and among prairie sites (REM_{IRT} vs REM_{BGP} vs RES_{HOM} vs RES_{HET}). We compared the functioning and resilience of restored to remnant prairie type by assigning all plots from REM_{IRT} and REM_{BGP} to remnant prairie (n = 10) and all plots from RES_{HOM} and RES_{HET} treatments to restored prairie (n = 8). Restored prairie ANPP was compared to remnant prairie ANPP using ANOVA ($\alpha = 0.05$). For the second set of analyses, we tested whether heterogeneity explained differences in functioning and resilience between restored and remnant prairie sites. We compared responses among all prairie experiments (sites) using independent plots as the replicate in each remnant and restored prairie (REM_{IRT}, REM_{BGP}, RES_{HOM}, and RES_{HET}); data were analyzed using a one-way analysis of variance (ANOVA, $\alpha = 0.05$) followed by post-hoc least squares means comparisons (Lenth 2016). All variables were normally distributed based on the Shapiro-Wilks normality test. All statistical analyses were performed in R (R Core Team 2020).

RESULTS

Total precipitation across the six years of observation (2014-2019) ranged from 706 mm to 1003 mm at KPBS (Fig. 2). The cumulative precipitation in each of these six years shows the growing season drought in 2018 (Fig. 2). In April and June of 2018, KPBS received only 52% and 30% of the 30-year cumulative monthly average, which resulted in the 2018 growing season receiving the lowest cumulative precipitation during the six years of observation (Fig. 2). Conversely, KPBS received +119% and +117% of the 30-year growing season and annual average cumulative precipitation, making 2019 one of the wettest growing seasons and years in the six years of observation (Fig. 2).

Across years and growing seasons with average precipitation (2014-2017), total ANPP was similar between remnant and restored prairie ($F_{1,16} = 2.34$, $P = 0.146$, Fig. 3A) and among all sites and heterogeneity treatments ($F_{3,14} = 1.15$, $P = 0.362$, Fig. 3B). Total ANPP during the drought year was less similar between restored and remnant prairie ($F_{1,16} = 3.68$, $P = 0.073$, Fig. 3A) but the site analysis revealed no significant differences among the remnant prairie experiments or heterogeneity treatments in restored prairie ($F_{3,14} = 1.25$, $P = 0.330$, Fig. 3B). Post-drought (2019) total ANPP was 27% higher in restored prairie than remnant prairie ($F_{1,16} = 6.93$, $P = 0.018$, Fig. 3A). Total ANPP in the RES_{HOM} treatment was similar to both remnant prairie sites, whereas total ANPP in the RES_{HET} treatment was 35% to 64% higher compared to other prairie sites and treatments in 2019 ($F_{3,14} = 9.12$, $P = 0.001$, Fig. 3B).

Despite similar total ANPP prior to and during drought, the grass and forb components of ANPP differed among the restored and remnant prairies. Remnant prairie had 23% higher grass ANPP than restored prairie in the years used to calculate average precipitation ($F_{1,16} = 7.47$, $P = 0.015$, Fig. 3C), which was attributed to moderately lower grass ANPP in RES_{HOM} ($F_{3,14} = 2.74$, $P = 0.083$, Fig. 3D). During the 2018 drought, remnant prairie had 57% higher grass ANPP than restored prairie ($F_{1,16} = 11.72$, $P = 0.003$, Fig. 3C), largely due to higher grass ANPP in one of the remnant prairies (REM_{IRT}) relative to the homogeneous restoration ($F_{3,14} = 3.85$, $P = 0.034$, Fig. 3D). Post drought grass ANPP, however, was similar between remnant and restored prairie types ($F_{1,16} = 0.15$, $P = 0.708$, Fig. 3C) and among prairie sites ($F_{3,14} = 2.52$, $P = 0.100$, Fig. 3D).

Forb ANPP was consistently higher in the restored prairie than remnant prairie prior to, during, and after the 2018 growing season drought. In the period used to calculate average productivity, restored prairie had 69% higher forb ANPP than remnant prairie ($F_{1,16} = 5.29$, P = 0.035, Fig. 3E), and forb ANPP did not differ between the homogeneous and heterogeneous treatments ($F_{3,14} = 2.48$, $P = 0.103$, Fig. 3F). During drought, forb ANPP in restored prairie was nearly twice that in remnant prairie ($F_{1,16} = 4.27$, $P = 0.055$, Fig. 3E), resulting from the combined response of prairies within type that was not attributed to a particular site ($F_{3,14} = 2.03$, $P = 0.157$, Fig. 3F). The year following drought, restored prairie had 3.8 times more forb ANPP than remnant prairie ($F_{1,16} = 27.88$, $P < 0.001$, Fig. 3E). Forb ANPP was 3.5 to 5.3 times higher in the RES_{HET} than in both remnant prairie sites, while the RES_{HOM} had 3.8 times higher forb ANPP than one of the remnant prairie sites ($F_{3,14} = 11.07$, $P < 0.001$, Fig. 3F).

Differences between restored and remnant prairie in sensitivity of ANPP response to drought varied with ANPP category. Sensitivity of total ANPP to drought was similar between prairie types ($F_{1,16} = 0.51$, P = 0. 485, Fig. 4A) and among prairie sites ($F_{3,14} = 0.38$, $P = 0.768$, Fig. 4B). However, sensitivity of grass ANPP to drought was 70% greater in restored prairie than in remnant prairie ($F_{1,16} = 5.10$, P = 0. 038, Fig. 4A), and did not differ between heterogeneity treatments due to high variation and low statistical power ($F_{3,14} = 1.72$, $P = 0.208$, Fig. 4A). Forb ANPP sensitivity to drought was highly variable and did not differ between remnant and restored prairie types ($F_{1,16} = 0.02$, $P = 0.886$, Fig. 4A) or among prairie sites ($F_{3,14} = 0.22$, $P = 0.883$, Fig.4B).

Drought legacy effects were positive in both prairie types. Restored prairie, however, exhibited 70% more positive drought legacy effect for total ANPP than did remnant prairie ($F_{1,16} = 11.34$, $P = 0.004$, Fig. 4C). The higher drought legacy effect in restored prairie resulted from the RP_{HET} having a 30-40% higher drought legacy effect relative to the remnant prairie sites ($F_{3,14} = 5.55$, $P = 0.010$, Fig. 4D). Grass ANPP drought legacy effects were not different between remnant and restored prairie types ($F_{1,16}$ = 1.73, P = 0.207, Fig. 4C) or among prairie sites ($F_{3,14}$ = 1.78, P = 0.197, Fig. 4D). Forb ANPP drought legacy effects were highly variable in all prairies, resulting in no differences between prairie types ($F_{1,16}$ = 2.15, P = 0.162 , Fig. 4C) or among prairie sites ($F_{3,14}$ = 0.86, P = 0. 485, Fig. 4D). Although not significant, average forb drought legacy effects were 2.1 times higher in the restored prairie compared to remnant prairie due to the extremely high productivity of forb species that were not distributed evenly within and among plots (Fig. 4C).

Discussion

A core question in restoration ecology is whether ecological theory can be applied to restoring ecosystem functioning and promoting resilience to periodic stress (Bradshaw 1987). We addressed this question by comparing productivity and resilience to drought in remnant prairie to a multi-decadal restored prairie that, uniquely, contained contrasting environmental soil heterogeneity treatments. Most studies of temporal ANPP dynamics in restored prairie capture only the first decade of restoration, often the establishment years (Baer et al. 2003, 2014, Polley et al. 2007, Carter and Blair 2012, Willand et al. 2013, Manning and Baer 2018), when there is large variation in community composition among volunteer and sown species. Ours is the first study to demonstrate that in terms of ANPP, long-term restored prairie functions similarly to remnant prairie and exhibits similar or greater resilience to drought than remnant prairie when restored under higher environmental heterogeneity. However, when the productivity of grasses and forbs were considered separately, restored and remnant prairies differed during average precipitation years and during the 2018 drought regardless of heterogeneity treatment, suggesting mechanisms of resilience may vary between restored and remnant prairie.

The restored prairie was functionally similar to remnant prairie in terms of total ANPP prior to and during drought, but not in the post-drought year. Following drought, restored prairie exhibited greater ANPP than remnant prairie due to higher ANPP in prairie restored on heterogeneous soil. Higher ANPP in the heterogeneous soil was driven by higher ANPP of forbs following drought, which has been shown to explain recovery of ANPP from drought in other grasslands (Xu et al. 2017). Contrary to our hypothesis, ANPP in prairie restored under heterogeneous soil conditions was not higher than ANPP in the homogeneous soil in average and drought conditions despite that the heterogeneity treatment supported higher plant diversity in timeframe of this study (Baer et al. 2020 and A. Wojciechowski *unpublished data*). However, the heterogeneous soil treatment did have higher ANPP than the homogeneous soil treatment in the post-drought year, supporting the notion that diversity increases recovery of ecosystem functioning from disturbance (Isbell et al. 2009, Tilman et al. 2012, 2014), including resilience to drought (Isbell et al. 2015).

Resilience can be assessed by examining the sensitivity of productivity during drought and the recovery of productivity following drought (Tilman and Downing 1994, Hoover et al. 2014, Griffin-Nolan et al. 2018). Here, restored and remnant prairies were similarly sensitive to drought in terms of total ANPP, but grass ANPP was more sensitive to drought (across both heterogeneity treatments) in restored prairie than remnant prairie. A previous rainfall manipulation experiment at KPBS found that resilience of remnant prairie to size and frequency of rain events (Knapp et al. 2002) was related to drought-adapted genotypes of *A. gerardii* (Avolio and Smith 2013). Although we did not assess genotypic differences between remnant and restored prairies, the cultivar seed source of *A. gerardii* used in the restoration lacked the 9X cytotype that is more tolerant to drier conditions (Keeler 2004, McAllister et al. 2015). The potential absence of drought tolerant genotypes could result in greater sensitivity of restored prairie to drought than remnant prairie. Although sensitivity to the amount and variability of rainfall is driven by grasses that primarily use water from relatively shallow soil depths (Knapp et al. 2001, Nippert et al. 2006), remnant prairie may contain plants with deeper roots accessing deeper soil water (Nippert and Knapp 2007, Kitchen et al. 2009, Ebeling et al. 2014). We did not assess the depth distribution of roots in our restored prairie, but remnant prairie contain more roots deeper in the soil profile than restored prairie that have been established for decades on formerly cultivated soil (Matamala et al. 2008).

Drought legacy effects can be highly variable (Hoover et al. 2014, Yahdjian and Sala 2006, Griffin-Nolan et al. 2018) but are generally negative across grasslands and forest ecosystems (Sala et al. 2012, Anderegg et al. 2015), which likely reflects response to greater drought severity in arid or dryland systems (Yahdjian and Sala 2006, Anderagg et al. 2015). Contrary to the global trend, mesic grassland tends to show positive (higher ANPP than expected following drought) or no drought legacy effects (Hoover et al. 2014, Wagg et al. 2017, Griffin-Nolan et al. 2018). Consistent with other studies in tallgrass prairie, all but one remnant prairie plot and all restored prairie plots exhibited a positive drought legacy effect. A positive post-drought productivity legacy effect could result from accumulation of available nitrogen during drought with less plant uptake of nitrogen (Seastedt and Knapp 1993), supported by greater recovery of ANPP following drought under chronic nutrient enrichment (Bharath et al. 2020). Alternatively, positive legacy effects have been observed in grasslands resulting from community functional dispersion due to mortality or senescence of dominant species and corresponding fast growth rate of drought avoiding/escaping forbs (Griffin-Nolan et al. 2019). Here, drought legacy effects were more positive in restored prairie than remnant prairie, which we attributed to the strong post-drought growth response of forbs, less variability in the positive legacy effect observed in forbs among plots in heterogeneous soil, and overall higher ANPP of forbs in the restored prairie on heterogeneous soil.

Nearby comparable non-disturbed ecosystems are often used to assess recovery of ecosystem processes in response to human intervention that aims to reverse environmental degradation (Aronson et al. 2017). Here, we demonstrate that restored prairie can attain productivity levels comparable to remnant prairie and respond similarly to drought, though grass productivity was more sensitive to drought in restored prairie. Our results also show that prairie restored on heterogeneous soil can exhibit (1) higher productivity than remnant prairie and prairie restored on homogeneous soil following drought and (2) a more positive drought legacy effect than remnant prairie. These results demonstrate that prairie restored on heterogeneous soil can be more resilient to drought than remnant prairie, and equally or more resilient to drought than prairie restored on homogeneous soil. Restoring prairie can also achieve higher ecosystem functioning than remnant prairie following drought due to higher forb productivity. Thus, sowing a high ratio of forbs:grasses or over-seeding restored prairie with forbs to increase floristic diversity (Deever et al. 2023, Dickson and Busby 2009, Klopf et al. 2014, Baer et al. 2020, Drobney et al. 2020) may also increase resilience to drought and promote multi-functionality of restored grasslands (Zavaleta et al. 2010).

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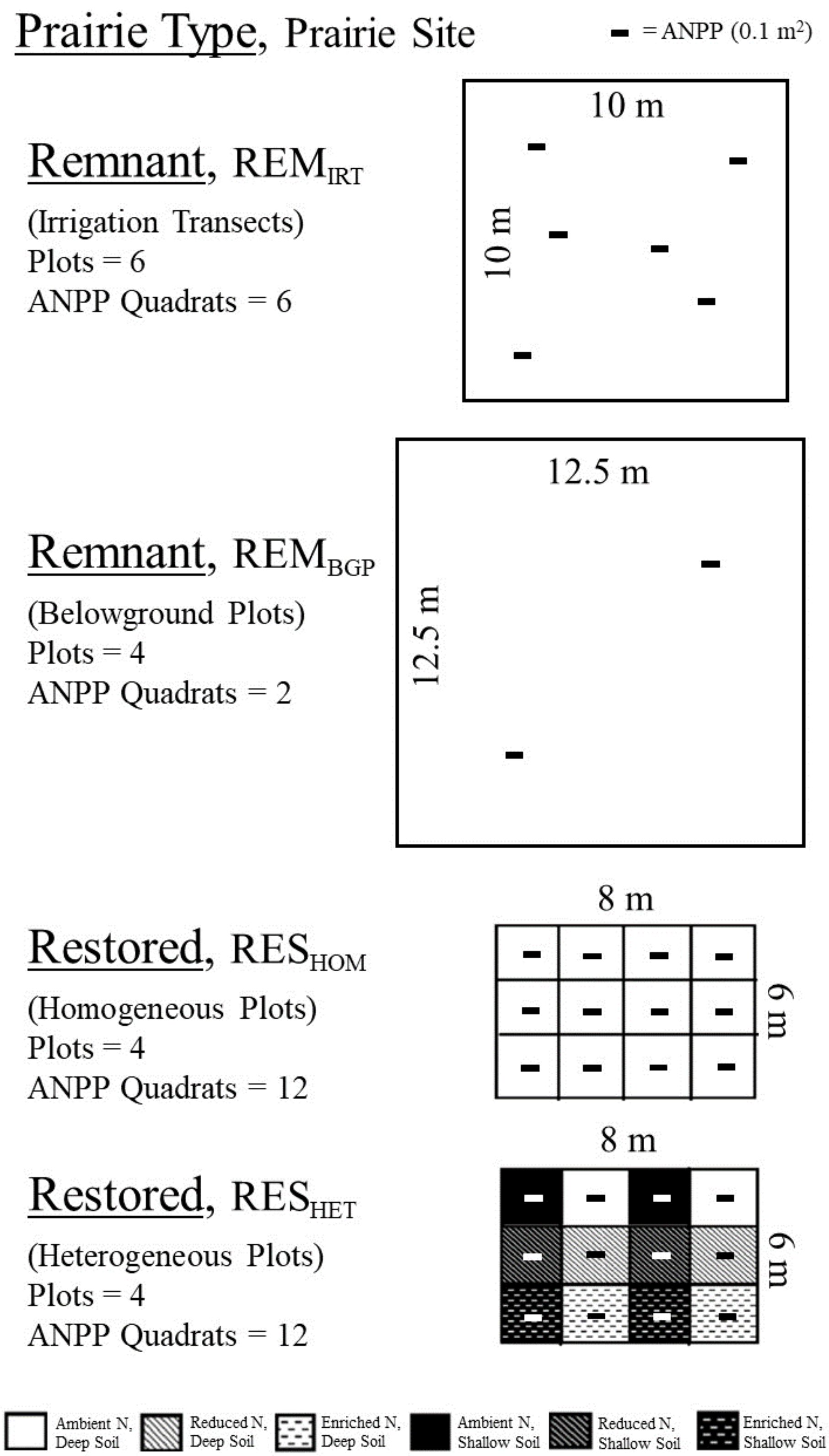
Figure Legends

Figure 1. Dimensions and number of ANPP quadrats in each experimental unit (plot) within each of the remnant prairies (REM_{IRT} = irrigation transects; REM_{BGP} =belowground plots) and restored prairie experiment containing homogeneous (RES_{HOM}) and heterogeneous (RES_{HET}) treatments used in this study.

Figure 2. Daily cumulative precipitation each year of this study from 2014 to 2019 and the 30-year average (30YR) at KPBS. The dashed box indicates the growing season (April-September).

Figure 3. Mean ($\pm$ standard error) total, grass, and forb ANPP from 2014 to 2017 prior to drought (= average ANPP), ANPP during the drought of 2018, and in the post-drought year of 2019 (A, C, E) between prairie types [remnant vs. restored] and (B, D, F) among prairie sites [REM_{IRT} vs REM_{BGP} vs RES_{HOM} vs RES_{HET}]. Comparisons between prairie types and among prairie sites were performed by average, drought, and post-drought period. Means accompanied by the same letter were not signficantaly different ($\alpha = 0.05$).

Figure 4. Mean ($\pm$ standard error) drought sensitivities of total, grass, and forb ANPP (A) between prairie types and (B) among prairie sites. Mean ($\pm$ standard error) drought legacy effects of total, grass, and forb ANPP (C) between prairie types and (D) among prairie sites. Means accompanied by the same letter within a ANPP type were not signficantaly different ($\alpha = 0.05$).



Prairie Type, Prairie Site
= ANPP (0.1 m2)
Remnant, REMIRT
(Irrigation Transects)
Plots = 6
ANPP Quadrats = 6
10 m
10 m
Remnant, REMBGP
(Belowground Plots)
Plots = 4
ANPP Quadrats = 2
12.5 m
12.5 m
Restored, RESHOM
(Homogeneous Plots)
Plots = 4
ANPP Quadrats = 12
8 m
6 m
Restored, RESHET
(Heterogeneous Plots)
Plots = 4
ANPP Quadrats = 12
8 m
6 m
Ambient N, Deep Soil
Reduced N, Deep Soil
Enriched N, Deep Soil
Ambient N, Shallow Soil
Reduced N, Shallow Soil
Enriched N, Shallow Soil

Fig. 1

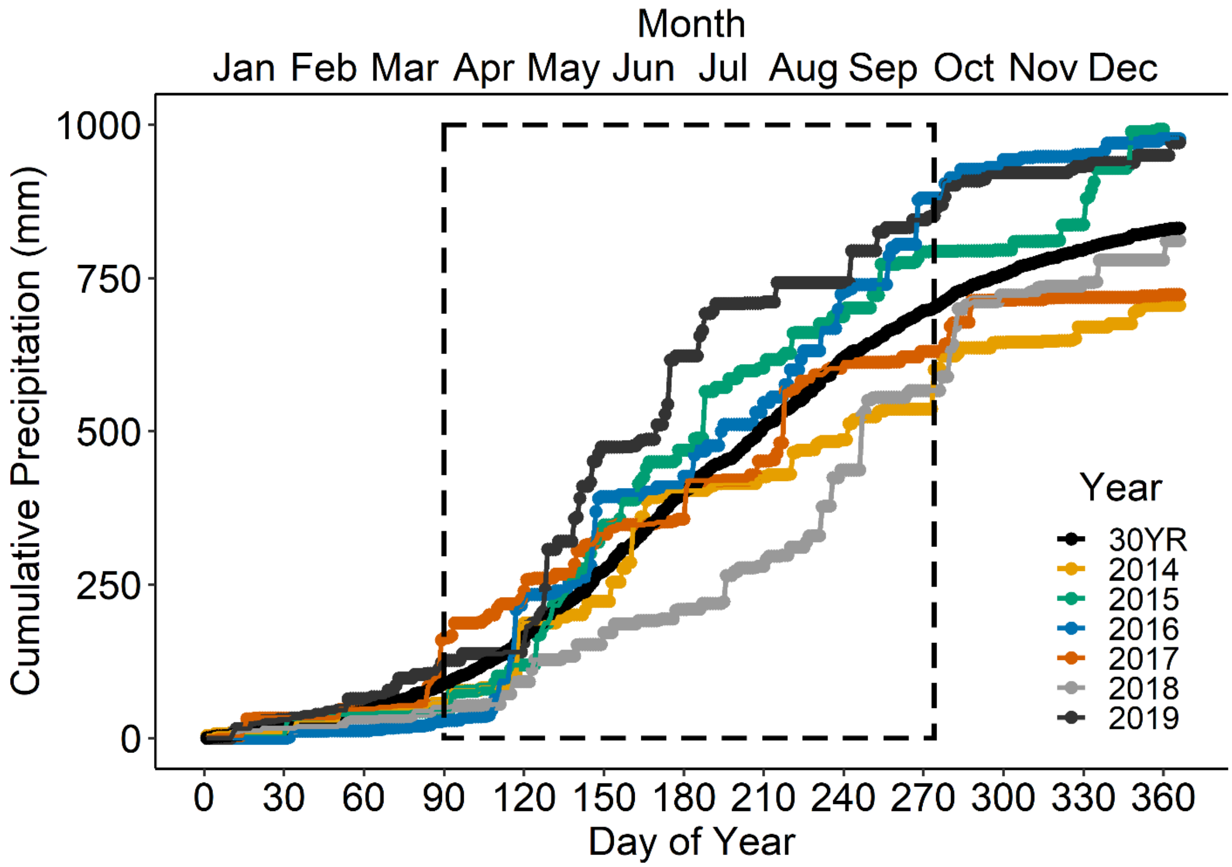

Month
Jan Feb Mar Apr May Jun Jul Aug Sep Oct Nov Dec
Cumulative Precipitation (mm)
1000
750
500
250
0
Year
30YR
2014
2015
2016
2017
2018
2019
0 30 60 90 120 150 180 210 240 270 300 330 360
Day of Year

Fig. 2

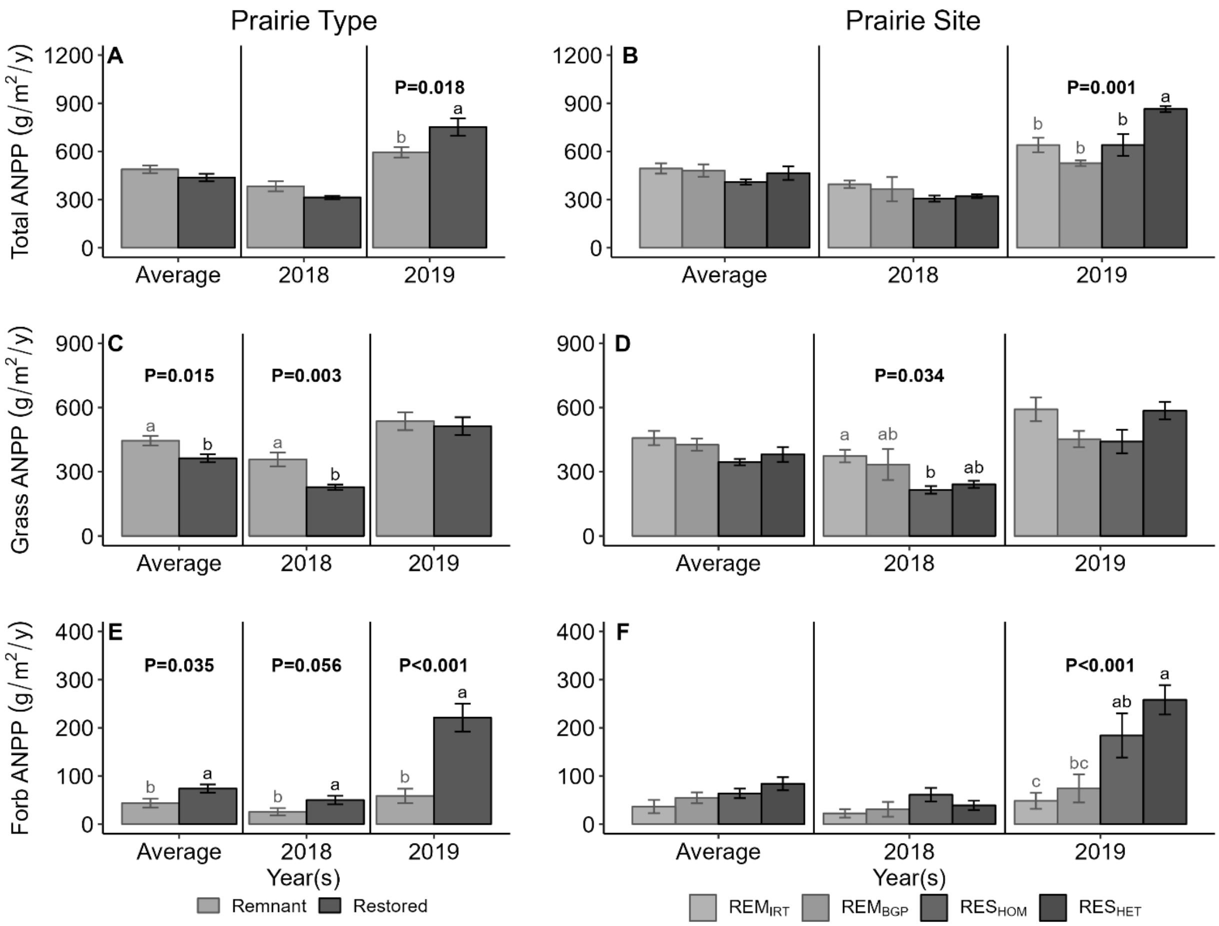
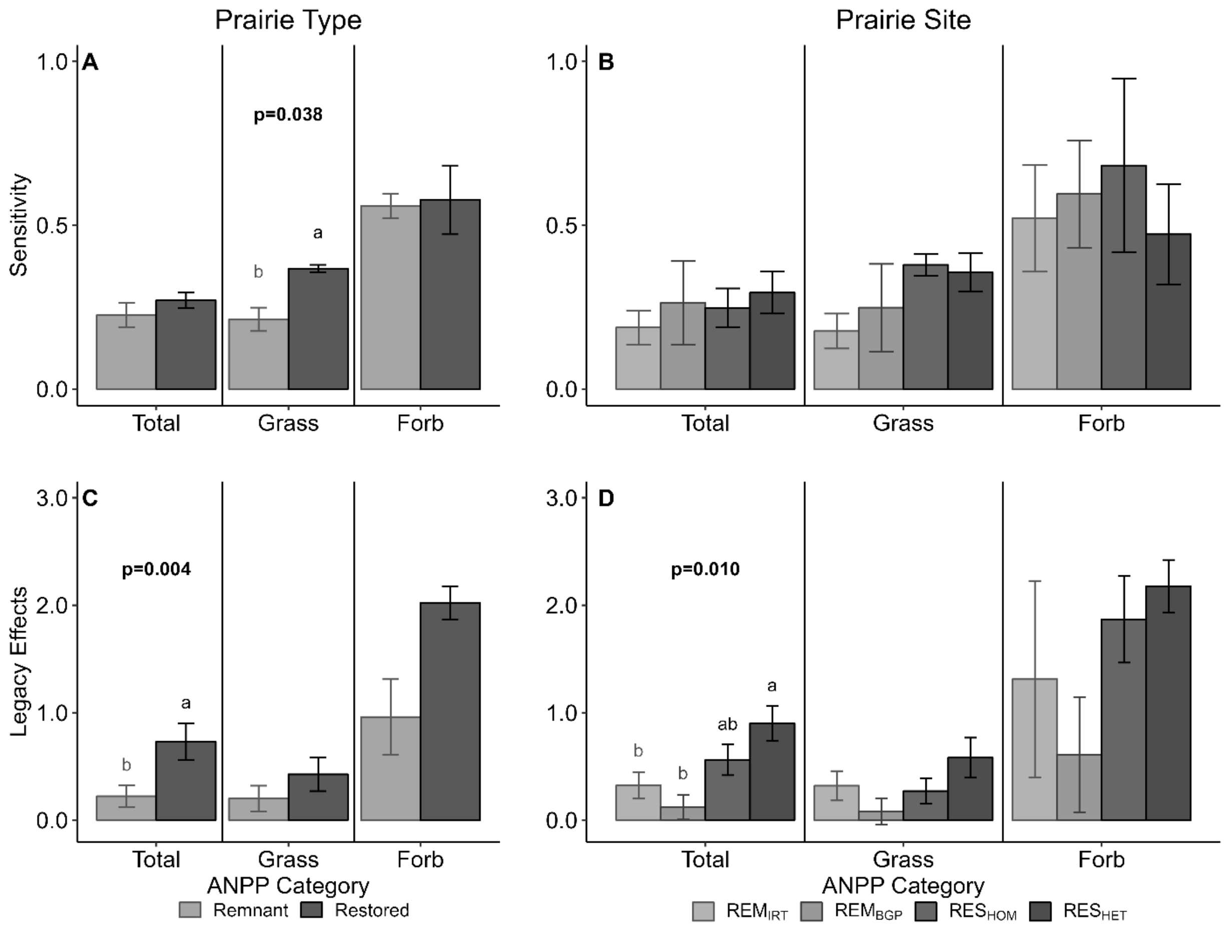

Prairie Type
Prairie Site
Total ANPP (g/m2/y)
Grass ANPP (g/m2/y)
Forb ANPP (g/m2/y)
A
B
C
D
E
F
P=0.018
P=0.001
P=0.015
P=0.003
P=0.034
P=0.035
P=0.056
P<0.001
P<0.001
Average
2018
2019
Year(s)
Remnant
Restored
REM IRT
REM BGP
RES HOM
RES HET

Fig. 3

617


Prairie Type
Prairie Site
A
B
C
D
p=0.038
p=0.004
p=0.010
a
b
ab
Sensitivity
Legacy Effects
Total
Grass
Forb
ANPP Category
Remnant
Restored
REM_IRT
REM_BGP
RES_HOM
RES_HET

618 Fig. 4