

Are We There Yet: Assessing Trajectories of Two Restored Prairies
to Target Native Prairies over a Decadal Time Frame

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ABSTRACT

Tallgrass prairie restoration aims to increase biodiversity, reinstate natural ecosystem functioning, and increase wildlife habitat in lands that have been degraded by human activity. Ecological restoration often involves identifying intact target communities that can be used as a reference for what a successfully restored community looks and functions like. The purpose of this study was to use the International Society for Ecological Restoration standards for ecosystem restoration to assess the compositional and functional similarities and differences between two restorations established under contrasting climate conditions to two nearby native prairie targets. We leveraged a sequential restoration experiment initiated in 2010 at the Konza Prairie Biological Station to compare trajectories of plant community development and ecosystem functioning in restorations established under different planting-year climate conditions in relation to nearby native prairie targets. Plant species composition, functional group cover based on plant life history traits, and aboveground net primary productivity (ANPP) were measured at the same scales in the restored and native prairies. Indicator species analysis was performed to identify species-level dissimilarities between the composition of the plant communities. The restoration sequences, while distinct from one another due to the effects of planting-year precipitation, were more similar to one another than they were to either target in terms of species and functional group composition. Functionally, the restorations differed from one another in their response to precipitation, with the prairie established in a drought year being less sensitive to interannual variability in precipitation than the prairie established in an average rainfall year. The two targets were quite dissimilar from one another. The reference target closest to the restorations and on the most similar soil was more like the restorations than the other native prairie target in terms of species composition, functional composition, diversity, and

evenness. Species diversity and evenness was higher in this closest target, while species richness was highest in the further target. Both reference systems had higher species richness than the restorations, with the prairie established in the average rainfall year having a significantly lower total species richness. Indicator species for the restorations were all species planted during restoration, whereas the native prairie communities had a larger number of unique species not present in the restorations. In conclusion, even with a small sown species pool, the development of restored prairie approached native prairies on a decadal time scale to contain higher diversity than functionally similar native prairie, but targets can be dissimilar from one another even in the same region and under the same management regime. Knowledge of plant composition in targets, compared to restored prairies, can inform management decisions by revealing satellite species that could be overseeded to steer restoration trajectories closer to native communities.

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INTRODUCTION

Tallgrass prairie is a floristically diverse grassland ecosystem found only in North America (Freeman 1998) characterized by tall grasses and maintained by frequent fire and large native grazers (Risser et al. 1981). Much of the historic range of the prairie has been converted to agriculture due to the deep, rich, and fertile Mollisol soils that develop in grasslands. Today, the tallgrass prairie is one of the most degraded ecosystems in the world, with an estimated 82-99% of its historic range lost primarily to agriculture (Sampson & Knopf 1994, Sampson et al. 2004), and the unplowed remnants mostly exist in small, fragmented parcels of land embedded in a larger matrix of agriculture and development (Cully et al. 2003, Taft 2016). This reduced and fragmented area leaves unplowed prairie vulnerable to edge effects and small population sizes, which makes the rare and endangered species within this ecosystem vulnerable to extirpation. The small amount of tallgrass prairie that remains continues to be threatened by urban development, continued expansion of row crop agriculture (Lark et al. 2015), and woody encroachment brought about by fire suppression (Heisler et al. 2003). While conservation efforts to preserve what little of the unplowed tallgrass prairie remains are vitally important, prairie restoration is the primary means to increase the extent of this endangered ecosystem. Few studies have demonstrated full restoration to predetermined benchmarks because defining and identifying appropriate targets to assess recovery can be difficult and they may be absent on the landscape (White & Walker 1997), or evaluations of restored communities are based on a snapshot in time. Documenting the composition of plants and functioning of restoration as they develop under different environmental conditions, and in comparison to restoration targets, is needed to understand factors influencing trajectories of ecosystem recovery from long-term disturbance (Bradshaw 1987).

The practice of restoring tallgrass prairie dates to the 1930s. The Curtis Prairie restoration, first conceived by Aldo Leopold, was initiated in 1936 at the University of Wisconsin Arboretum under the direction of Theodore Sperry (Sperry 1994). Since then, prairie restoration has expanded throughout the Midwest US through activities such as purchasing of land and reconstruction of prairie communities by non-profit groups. For example, as of 2013 The Nature Conservancy had restored more than 9000 hectares of prairie from croplands (Rowe et al. 2013). In addition, many small-scale experimental restorations are active areas of ecological inquiry into factors influencing diversity and productivity (Foster et al. 2007, Gibson et al. 2013, Grman et al. 2013, Jaksetic et al. 2017, Zirbel et al. 2017, Baer et al. 2020).

Restorations commonly aim to achieve specific goals including improvement in ecosystem services, increasing pollinator resources, or increasing biodiversity (Hobbs & Harris 2001). One of the most frequently stated goals of prairie restoration is to re-establish a diverse native plant community representative of a historic, or extant, target (Kinscher & Tieszen 1998, Polley et al. 2005, Newbold et al. 2019). While guidelines exist for identifying a target community (Society for Ecological Restoration International 2016, McDonald et al. 2016), targets can be difficult to define and even harder to replicate (Wodika & Baer 2015). For example, many tallgrass prairie restorations tend to have lower species richness and biodiversity when compared to nearby unplowed native prairie (Kindscher & Tieszen 1998, Polley et al. 2005, McLachlan & Knispel 2005). One factor in these dynamics is the concept of core and satellite species, the distribution of species in an ecosystem is bimodal between a group of abundant core species and rare satellite species (Hanski 1982). The higher species richness in native prairies can be attributed to the presence of rare satellite species which may be absent in restorations due to a variety of factors (Gotelli & Simberloff 1987). A difficulty in these

assessments is that composition in restored grasslands is dynamic over time, so a single-time comparison is not adequate to predict community recovery relative to benchmarks (Baer et al. 2003, Camill et al. 2005, Manning & Baer 2018). Restoration success can also vary with assessment metrics. For example, ecosystem functioning can recover without a similar recovery in composition.

Restoration targets are generally assemblages of species and ecosystem attributes chosen as goals for the functioning and structure of a restored community. The qualities of reference sites used to define benchmarks to assess restoration progress include biodiversity, community structure, and ecosystem functioning metrics (White & Walker 1997, SER International Standards 2016). However, determining an appropriate target is difficult because nature is inherently variable over both time and space. Where and when plant community structure is measured can result in compositionally different target communities (White & Walker 1997) because ecosystems can be spatially and temporally heterogeneous on the landscape scale. Tallgrass prairie, in particular, is temporally and spatially heterogeneous because plant communities change in response to topographic position and variation in ecological drivers such as fire and grazing (Collins et al. 2012). Due to the possibility of distinct community, structural, and functional differences on a small geographic scale, using more than one reference site, where possible, is important to determining a range of appropriate target qualities for a restoration (Ruiz-Jaen & Mitchell Aide 2005, SER International Standards 2016). A local ecosystem may simply no longer exist due to historic land use habits such as fire suppression, conversion to agriculture, or urbanization (Turner et al. 1993, Higgs 1997). In such contexts, historical records and regional ecosystems may be the only reference available for determining restoration targets. Even intact ecosystems can undergo change over time, climactic events can create a variety of

disturbances that change and alter ecosystems composition, structure, and function (White & Walker 1997, Higgs 1997, Higgs et al. 2014). For example, fire suppression in tallgrass prairie can lead to woody encroachment and development of feedbacks that prevent future fire and sustain shrub and forest species (Ratajczak et al. 2011, Ratajczak et al. 2016, Collins et al. 2021).

Drought is a topic of particular concern for grassland restoration. Due to climate change, drought risk is projected to increase in mid-continental regions by the late 21st century (Meehl et al. 2007, Polley et al. 2013). Extreme drought events are also projected to increase in frequency over the course of the next 30 years (Strzepek et al. 2010). Extreme climate events can have a significant effect on vegetation structure with intense drought events having a larger effect on productivity and vigor in C₄ grasslands than sustained moderate drought (Weltzin et al. 2003, Carroll et al. 2020). Drought that is both severe and chronic can change the plant community over time with prolonged drought able to change the dominant species within a community and having the change persist over a time following the alleviation of drought conditions (Albertson & Weaver 1942, Albertson & Weaver 1944, Hoover et al. 2004). Drought creates disturbance within an ecosystem that can leave it vulnerable to invasion by exotic species (Elton 1958), and restorations can be more vulnerable to invasion by exotic species than never-cultivated native habitat fragments (Blumenthal et al. 2005). For example, post-drought conditions led to a boom in the proportion of exotic species within a restored community (Carter & Blair 2012). Additionally, drought conditions at the onset of restoration can alter the initial trajectory of plant community assembly and ecosystem functioning (Manning & Baer 2018, Eckhoff et al. *in press*).

Plant community composition is commonly measured to quantify diversity metrics and floristic quality indices (FQI) and to perform direct community comparisons between restorations and reference systems (Baer et al. 2005, Sluis et al. 2017, Manning et al. 2018, Bach

& Kleiman 2021). In a meta-analysis of papers submitted to the journal *Restoration Ecology* that measured restoration success, plant richness was used in 79% of studies as the preferred measurement of restored diversity, whereas plant cover was used in 62% of studies in reference to structure and composition of restored sites (Ruiz-Jaen & Mitchell Aide 2005). Indeed, for some restoration activities, like remediation following intensive mining, using plant community composition to assess the progress of restoration is a legal requirement (Allen 1992). For example, the Surface mining Control and Reclamation Act of 1977 requires all assessments made at former mine locations to look at plant community diversity, seasonal variety, and resilience and specifically refers to community level measurements when requiring a diverse vegetative structure (Allen 1992).

Using functional groupings is another way to assess the progression of a community towards restoration targets (Funk 2021, Zirbel & Brudvig 2020). Many species overlap in life history, resource use, and physiological traits. Using functional guilds can decrease the variance in a dataset and provide information about a community response to fluctuation in resources more than plant species composition (Kindscher & Wells 1995). For example, variation in life history, resource use, and physiological traits can increase the likelihood of survival and compensatory growth when resources become limited (Perez-Ramos et al. 2017). Functional diversity within a plant community relates to increased ecosystem resilience and resistance to drought (Tilman et al. 1997, Isbell et al. 2015). To this end, restoring a diverse assemblage of life history traits is important to attain one of the primary restoration goals of recreating communities that can withstand periodic stress (SERI 2019) and persist in the face of future climate change.

Ecosystem functioning is another important element in determining restoration success relative to targets (Gann et al. 2019). Aboveground net primary productivity (ANPP) is an

important measure of ecosystem functioning in grassland systems and it has relationships to other ecosystem traits relating to forage and animal carrying capacity on the landscape (Sala et al. 1988). In grasslands ANPP varies temporally due to climatic factors such as precipitation or temperature, as well as spatially due to topographic differences and from disturbances like fire and grazing (Briggs & Knapp 1995, Knap et al. 1998). ANPP has also been shown to interact positively with species diversity producing ‘transgressive overyielding,’ where a high diversity community often generates greater biomass than a monoculture of the most productive species within that community (Tilman et al. 1996, Isbell et al. 2015). Total ANPP can recover rapidly in prairies restored from bare soil and even exceed that found in comparable native targets (Baer et al. 2002, Baer et al. 2003). These factors make ANPP an important measurement to consider when assessing restoration success. Currently, we lack solid knowledge of when ANPP in restorations begin to track that in native prairies, and to what extent these dynamics in restored prairies are related to precipitation, which explains between 30 to 39% of temporal variation within native grassland systems (Laurenroth & Sala 1992, Heisler-White et al. 2008).

QUESTIONS, OBJECTIVES, AND HYPOTHESES

To assess trajectories of community development in the context of recovery toward target/benchmark native prairie requires measurement of community composition over time in both native (never-cultivated, similarly managed, extant target) and restored prairies. This research leveraged long-term data collected from two prairies sown into a former agricultural field in two different years under average and drought conditions, as well as data collected using the same methods over the same time frame from nearby native prairie to address the following questions. (1) Do restored plant communities resemble those of native, never cultivated, target prairies on a decadal time scale, and how does drought during the restoration establishment

change the trajectories of plant community recovery in relationship to target communities (2)

When does the aboveground net primary productivity (ANPP) in restored prairie recover to the extent that temporal dynamics track native prairie in response to interannual variability in precipitation?

To inform the questions motivating this research I leveraged and contributed to long-term data collection spanning a decade in two prairies restored under contrasting initial climate conditions at the Konza prairie Biological Station where data could be compared to a native, never cultivated, prairie. The objectives of this research were to (1) assess recovery of plant communities and the extent to which drought changes the trajectories or delays recovery by comparing plant species composition, diversity, and functional group composition in prairies restored under average rainfall and drought conditions to similarly managed native prairie, and (2) evaluate when ecosystem functioning in restored prairie begins to track native prairie and becomes similarly sensitive to annual rainfall by comparing ANPP dynamics in restored and native prairie for 10 years. These objectives aimed to test the corresponding hypotheses:

(H_{1a}) Species composition of the restored prairie will approach but not represent never-cultivated prairie that is similarly managed on a decadal time scale due to the absence of many “satellite” species.

(H_{1b}) Drought occurring in the establishment year acts as a filter on community assembly, altering the trajectory community recovery and alters the recovery trajectory away from the target.

(H₂) Functional composition of the restored prairie will represent that of nearby never-cultivated prairie that is similarly managed on a decadal time because coarse-scale measurements of

communities are predicted to recover sooner than fine scale measurements of species composition (Brudvig 2017).

(H_{3a}) The relationship between precipitation and ANPP in restorations will develop over time and become similar to that in native unplowed prairies as the restorations grow older.

(H_{3b}) Drought occurring in the establishment year will delay the development of ANPP sensitivity (correlation) with precipitation.

METHODS

Study Site

Prairies were restored in a former agricultural field in 2010 and 2012 at the Konza Prairie Biological Station (KPBS, 39°05'N, 96°35'W), located 9 km south of Manhattan, Kansas. The site had been cultivated for soy, wheat, and milo for over 70 years prior to restoration. Before cultivation, the site would have been representative of native lowland tallgrass prairie, dominated by the warm season C₄ grasses (*Andropogon gerardii*, *Bouteloua curtipendula*, *Schizachyrium scoparium*, and *Sorghastrum nutans*) combined with a variety of forbs and other grasses (Abrams & Hulbert 1987). The soil at site is classified as Reading silt loam, with 0-1% slope (USGS soil survey web map). The mean annual temperature in the region is 12.8° C and the average yearly precipitation is 851 mm.

Restoration Approach

To establish the restored prairies, seeds from 20 native prairie species (Table 1) were hand-collected from KPBS and the surrounding environs. Collected seed was cleaned to remove large pieces of stem, leaf, and other non-seed containing vegetative matter. Seeds were kept in dry

storage until the time at which they were planted. A sample of each species was sent to the Illinois Crop Association to determine the percent live seed (PLS) based on seed purity, percent germination, and percent dormancy. The seeding mix for all sequences was determined by the amount of live seed collected in 2009 and was planned such that the final sown mix would be a 60:40 ratio of forbs to dominant prairie grasses. Due to the low PLS of *Andropogon gerardii* seed, the mix was supplemented with a purchased cultivar (var. KAW), with germplasm originating from the same region as this study. Each plot was hand-raked prior to planting. Seed was then hand-broadcast and manually compacted to establish good seed-soil contact. Each restoration sequence received no management for the first three years after establishment because there was not enough fuel to carry fire through the plots. Each sequence was burned annually in the spring following the third growing season since establishment.

Sequential Restoration Study design

This study used two prairies restored in different years (restoration sequences) to compare recovery of plant community structure and ecosystem functioning in restorations established under contrasting precipitation conditions relative to that of native (never-cultivated) prairie targets (Figure 1). In early June 2010, four 20 m x 20 m plots were delineated in sequence I (SEQ I) with a 5 m buffer strips between each plot. Plots were further divided into four 10 x 10 m subplots with a permanent 10 m² circular sampling quadrats for species composition (A-D, Fig. 2). The last plot in the SEQ I was truncated to contain only two subplots due to shade from a nearby forest, the remaining two subplots were installed in a nearby area with the same agricultural history (Manning & Baer 2018). A similar design, with all four 20 m x 20 m plots located in one linear sequence was used to reconstruct prairie in 2012 (SEQ II) within the same agricultural field that remained cultivated until sowing.

Never-cultivated “Native” Prairie Comparisons

Restored prairies were compared to native prairies located in two other native prairie areas at KPBS. Native prairies were selected based on similar topographic position (lowland areas) and management history. Species composition and ANPP were compared to native prairie 1D (2010-2020) as one “target” community located 4.1 km from the restorations. Community composition and ANPP were also quantified in 2020 from a lowland area located 0.75 km from the restorations (headquarters B: HQB). Two additional native prairie sites were used to compare recovery of ANPP using the “control” treatments in two long-running experiments within the headquarters areas (HQA and HQC), located 0.9 km and 0.87 km from the restorations. Both prairie locations (1D and HQ) had an identical management regimen to the restored sequences (ungrazed and burned annually in the spring). The headquarters areas (HQA, HQB, and HQC) are on Reading silt loam soil and the lowland area of 1D is on Tully silty clay loam soil.

In 2020, plots were delineated in HQB for sampling species composition and ANPP, whereas long-term species composition and ANPP data were obtained for comparison from HQB, HQC and 1D. Plots of similar dimensions as the sequential restoration (20 m x 20 m subdivided into four 10 m x 10 m subplots [A-D] with 10 m² circular sampling areas for species composition in the center of each subplot) were established in HQB (n=8). To assure independence, each plot was positioned such that any edge was at least 15 m away from the edge of another plot. The permanent sampling areas in 1D were established in 1983 and consist of four 50-m long transect with five permanent 10-m² circular plots spaced equidistantly along the length of the transect (n=4), ANPP estimates were obtained along the transect outside of the species composition sampling areas. Long-term ANPP estimates were obtained from 1D and two experiments in the HQ watershed. I used independent control treatment plots from the

belowground plot experiment (BGP, n=4) containing a factorial combination of nutrient addition, prescribed fire regime, and mowing (experimental design described in detail: Blair & Zeiglin), and the irrigation transects (IT, n=6) containing water additions and control plots (experimental design described in detail: Broderick et al., 2022).

Plant Species Composition

Species composition in the restoration sequences, HQB, and 1D were measured using the same methodology. Species composition was recorded from each subplot within each plot in August of each restoration installation year (SEQ I: 2010 and SEQ II: 2012) and in each June and August in subsequent years (through 2020), with the exception of 2016 in SEQ I (species composition not measured). Starting in each restoration's sixth growing season (2017 in SEQ I and 2018 in SEQ II), species composition was measured from two randomly chosen subplots in each plot, and those same subplots were measured in subsequent years. Species composition surveys were conducted twice a year in spring (May/ June) and a late summer survey (August/September) in 1D (2010-2020) and HQB (measured in plots delineated in 2020).

In all restoration sequences and native prairies, species composition was measured by visually estimating the percent cover of each species in 10 m² circular quadrats in the center of each subplot. Percent cover estimates were assigned to modified Daubenmire scale (1 = 0-1%, 2 = 1-5%, 3 = 5-25%, 4=25-50%, 5 = 50-75%, 6 = 75-95%, 7 = 95-100%, Bailey & Poulton 1968, as used by Carter & Blair 2012). The maximum cover of each species from the spring and summer surveys were converted to the mid-range values of each category and used to analyze the change in species composition, richness, and diversity over time. Maximum cover was used to compute the relative cover of each species and compute Shannon's diversity, Pielou's

evenness, and total species richness in each 10 m² sampling area in restored sequence and native prairies. Species were assigned to functional groups based on a combination of life history, photosynthetic pathway, leguminous or not, and life form (Table 2).

Ecosystem Functioning: ANPP

Aboveground net primary productivity (ANPP) was estimated annually at peak biomass (late summer to early fall) from 2010-2020 in the restored prairies, 1D, and long-term experiments in HQA and HQC. All plant biomass was harvested from two randomly placed 0.1-m² quadrats in the same years, plots, and subplots species composition was measured in the restored prairie. In 1D, four quadrats were placed adjacent to, and at least 3-meters away from, the species composition plots in the lowland transects, the side of the transect that was clipped alternated between years (n=20). In HQA, six 0.1 m² quadrats were clipped in each plot (n=6) within the irrigation transect experiment. In HQC, two 0.1 m² quadrats were clipped from each of the control plots (n=4) in the belowground plot experiment.

For all ANPP samples, live biomass was separated from litter. In the restored prairies, each quadrat was placed within the borders of the subplot and outside the 10 m² permanent species composition quadrat. Biomass was clipped and sorted into sown and volunteer forbs and grasses. Litter was sorted into prior-year and current-year biomass. In native prairies, biomass was sorted into grasses, forbs, woody plants, this year's litter, and previous years' litter. In the LTER watersheds, ANPP was collected annually at the end of the growing season (August to October). All biomass was dried (60°C), weighed, and converted into g/m² by multiplying the dry weight by 10. Annual ANPP was related to precipitation data acquired from the Konza data catalog (<http://lter.konza.ksu.edu/>).

Statistical Analysis

Trajectories of plant community development in the restorations (SEQs I and II) were visualized with the remnant prairies (HQB and 1D) using non-metric multidimensional scaling (NMDS) based on Bray-Curtis dissimilarities. In 2020, community composition was compared among all restored and remnant prairies using a permutational multivariate analysis of variance (PERMANOVA). PERMANOVA was used for its power in detection of changes in community structure (Anderson and Walsh 2001). These analyses were performed in R version 4.0.2 (R Core team 2020) using the vegan package (Jari Oksanen et al. 2019). Indicator Species Analysis was performed to identify the species driving differences in the community composition among the sites. Indicator species analysis was performed using the Indicspecies package in R (De Caceres M, Legendre P. 2009). Shannon's diversity, richness, and evenness were calculated using functions from the vegan package (Jari Oksanen et al. 2019) and the plotrix package (Lemon, J. 2006)

Functional groups were determined using an agglomerative cluster analysis approach (Fukami et al. 2005) using life history traits of each species (Table 2). Ward's Method was used due to this method having the strongest agglomerative coefficient out of the possible clustering methods and 13 clusters were chosen to define the functional trait groups. This number of clusters was chosen because a larger number resulted in groups composed of only one or two species. This clustering was performed in R using the cluster package (v2.1.1, Maechler et al. 2019) and clusters were visualized for selection using the factoextra package (v1.0.7, Kassambara & Mundt 2020)

The relationship between ANPP and precipitation in each site and sequence was examined using Pearson's correlation procedure in R. To assess whether sensitivity to precipitation develops as restorations age, correlations were performed using all years of growth and from ages 4-11 in SEQ I and 4-9 in SEQ II. Statistical similarity between the last 5 years of ANPP were calculated using Anova and similarities between groups were determined with a post-hoc Fishers LSD test in R using the PMCMRplus package (Thorsten Pohlert 2022).

RESULTS

Species and Functional Composition

Of 226 species recorded from the restored and native prairies during the extent of the study, 139 were unique to the restorations, and 49 were unique to the remnants. In the 2020 study year, there were 25 species found only in the restorations and 55 species found only in the native prairies. These numbers include counts of taxa that were only identified to the genus level or never completely identified.

The trajectory of community development in the decadal visualization showed change in species composition occurring over time in the two restored communities (SEQs I and II), approaching that of the remnant prairie (HQB) in closest proximity to the restored prairies, and to a lesser extent, the other remnant prairie located farther from the restored prairies (1D) (Figure 1). Although the restored communities changed along the same trajectory in the NMDS ordination space, the composition of species in the restored prairies (SEQ I & SEQ II) remained different from each other into 2020 and distinctly different from both native remnant prairies, which were also different from one another (PERMANOVA: $F = 10.86$, $P < 0.01$, $R^2 = 0.67$).

Indicator species were determined for each restored prairie, target native prairie, and for each combination of units (Table 3). For the restored prairies *Dalea multiflora* was found to be an indicator for SEQ I, whereas *Liatris punctata* and *Desmodium illinoense* were indicators for SEQ II. Indicator species common to both restorations were *Baptisia australis*, *Dalea purpurea*, *Silphium integrifolium*, *Desmanthus illinoensis*, *Oligoneuron rigidum*, and *Oenothera macrocarpa*. In the native prairie, indicator species in 1D included *Ruellia humilis*, *Vernonia baldwinii*, *Carex meadii*, *Asclepias viridis*, *Physalis virginiana*, *Asclepias verticillate*, *Eragrostis spectabilis*, *Baptisia bracteate*, *Brickellia eupatoroides*, and *Dichantheium oligosanthes*. Indicator species for HQB were *Carex brevior*, *Silphium laciniatum*, *Psoraleum tenuiflorum*, and *Carex bicknellii*. Indicator species common to 1D and HQB were *Sporobolus compositus*, *Ambrosia psilostachya*, and *Solidago altissima*. (Appendix/Table 4).

Diversity, evenness, and richness in the restorations changed more dynamically over time compared to the native prairie measured over the same decadal period (Fig. 3). After a decade of restoration, diversity and evenness the restored prairies were similar to the nearest native prairie site (HQB) and significantly higher than 1D (diversity: $F_{(3,16)} = 7.514$, $P = 0.002$, evenness: $F_{(3,16)} = 22.4$, $P < 0.001$). In many years, the drought established sequence (SEQ II) had higher diversity than SEQ I. Species richness in the two remnants were similar to each other and SEQ II, but richness in SEQ I was lower than the remnant prairies ($F_{(3,16)} = 4.14$, $P = 0.024$, Fig. 3),

The trajectory of change in functional group composition in the decadal visualization shows less compositional change over time relative to species composition, and the two restored communities (SEQs I and II) move in the same direction through the ordination space of the closest remnant prairie (HQB), and (Figure 4). The location in ordination space for the restored communities in 2020 were driven largely by the abundance of legumes and perennial C₃ forbs,

while the nearest reference site (HQB) was characterized by more perennial C₃ graminoids, woody plants, and annual C₃ forbs and the further reference site (1D) had a high abundance of C₄ graminoids (Figure 5).

ANPP Relationship with Precipitation

Total precipitation varied between 2010-2020. The maximum annual precipitation that occurred during this interval was 1097.4 mm (2019). The least amount of annual precipitation occurred in 2012 with only 571.3 mm. Precipitation during the growing season also varied widely, making up between 48-75% of the total annual precipitation depending on the year (Fig 6).

Total ANPP ranged from 148 – 1,937 g/m² in the restorations and 212 – 1008 g/m² in the native prairies (Fig 6). Sown species comprised the majority (85-99%) of ANPP after three years in SEQ I and after four years in SEQ II. Volunteer ANPP became negligible (<5%) after three years since restorations were established (Fig. 6). Total ANPP averaged over the last 6 years (2015-2020), when sown species dominated the restoration, varied among the sites ($F_{(4,17)} = 4.727$, $p = 0.01$). Total ANPP in 1D was highest and higher than all other native (HQA and HQB) and restored prairies, and restored SEQ I was higher than HQC. Restored SEQs I and II were not different from each other in this period (Fig. 7).

Over the decadal study period, there were no consistent patterns in the strength of correlations between total ANPP and precipitation among native prairie sites or between the restored sites. There was a strong positive correlation between total ANPP and total precipitation ($r = 0.73$, $P < 0.001$) and growing season precipitation ($r = 0.73$, $P < 0.001$) in 1D. These relationships were less strong in HQA (total PPT: $r = 0.45$, $P < 0.001$, growing season PPT: $r = 0.46$, $P = 0.011$) and HQC (total PPT: $r = 0.30$, $P = 0.004$, growing season PPT ($r = 0.33$, $P =$

0.004). Total ANPP in SEQ I was correlated with annual precipitation over all years (1-11: $r = 0.48$, $P < 0.002$) and after sown species dominated (4-11y: $r = 0.62$, $P < 0.001$). Total ANPP was also correlated with growing season precipitation in each time period (1-11 y: $r = 0.44$, $P < 0.005$, 4-11y: $r = 0.62$, $P < 0.001$). In both cases the strength of correlation increased as SEQ I aged. Unlike SEQ I, the strength of the correlation between total ANPP and annual precipitation in SEQ II did not increase as the restored prairie aged (1-11y: $r = 0.70$, $P < 0.001$, 4-11y: $r = 0.59$, $P = 0.003$). The same pattern was observed for growing season precipitation in SEQ II (1-9 y: $r = 0.63$, $P < 0.001$, 4-9 y: $r = 0.52$, $P = 0.011$).

DISCUSSION

The goal of this research was to utilize the Society of Ecological Restoration International Standards (Gan et al. 2019) to assess restoration progress compared to native prairie targets across a decadal time scale. The guidelines stress the importance of determining an appropriate reference ecosystem to inform the target for restoration and the identification of the key ecosystem attributes of a target that can be used to inform restoration goals and assess progress towards those goals. Restoration targets can rely on historical information, which may not be directly comparable due to vague (non-quantitative) descriptive reports of prairie prior to cultivation (Betz 2011). Alternatively, extant nearby remnants may be used as targets, but may have different soil characteristics and hydrology than the restoration site (Sluis et al. 2002, Meyer et al. 2004, Wodika & Baer 2015, Bach & Kleiman 2022). The latter is especially likely because factors responsible for the existence of the never-cultivated native tallgrass prairie (e.g., Flint Hills of Kansas) are often related to the land's poor suitability for conventional row crop agriculture (Samson & Knopf 1994). Thus, prairie restorations often may only be comparable to a limited number of sites (Kindscher & Tieszen 1998) that may not represent the range of plant

composition and diversity of tallgrass prairie (Collins & Calabrese 2012). The presence of a long-term restoration experiment embedded in a long-term ecological research site in the Flint Hills of Kansas provides a unique opportunity to evaluate recovery of restored prairie relative to multiple never cultivated prairie targets, and the occurrence of drought during one sequence of restorations offers inference to assess the resilience of restored prairie.

Tallgrass prairie plant communities vary in structure and function over space and time in response to varying ecological drivers such as fire frequency and grazing regimes. Consequently, there is a wide range of potential plant community targets depending on the particular management regime of a site. This study is unique in that the watershed-scale fire and grazing experiment spanning upland and lowland areas at the Konza Prairie Biological Station provided the opportunity to evaluate community and ecosystem recovery in the context of native prairie targets in the surrounding landscape managed in the same way as the restored prairies. Despite the similar topographic position and management regime, the native prairies communities were different from one another due to higher prevalence of C₄ grasses in 1D than HQA. The variation in composition between the two targets was likely due to subtle differences in soil or a legacy of some historic and undocumented management of the land prior to the establishment of the KPBS experimental treatments over 40 years ago.

Following a decade of restoration, species composition in the reconstructed prairies remained distinct from one another and from the native prairies. Community composition in the restorations changed over time along a trajectory toward the native prairie located in closest proximity to the restorations (HQA). This native prairie also shared most similarity in soil classification to the restoration site. The restoration established in the average precipitation year became closer in ordination space to both of the target sites over time than did the prairie

restored in a drought year. This experiment previously showed that community composition of restored prairie is affected by drought occurring in the establishment year on short (Manning & Baer 2018) and decade-long time scales (Eckhoff et al. 2023), with higher presence of forbs in the drought-restored prairie driving compositional differences. As the restorations aged, plant community change between years within a restoration became smaller after the 4th or 5th year of growth, following implementation of the annual fire regime. Thus, a decade of restoration is a reasonable timeframe to compare to native prairie targets. Annual fire, in the absence of grazing, is known to stabilize the native prairie communities (Ratajczak et al. 2022), so continued annual fire regime will likely result in persistent differences in composition between restored to native prairie. Further, the annual fire regime will likely be more beneficial to the dominant C₄ grasses than the forb species planted in the restorations, which may eventually cause convergence in community structure. These restorations were deliberately planted with a high forb to grass ratio so that the grasses would not immediately dominate the restorations, a strategy that may allow more forb species to persist over time in these communities (Klopf et al. 2014).

Prairie restorations often have lower levels of species richness than native prairie remnants (Kindscher & Tienzen 1998, Sluis 2002, Mclaughlin & Knispel 2005, Baer et al. 2005, Barak et al. 2017, Sluis et al. 2018, Bach & Kleiman 2022). It follows that two contemporaneous prairie targets located the same place and managed under the same treatment regimen would be more diverse and contain more species richness than restored prairies within that same region. In 2020, diversity and evenness in the decadal-restored prairies approximated the closest native prairie target watersheds (HQB) and exceeded the other prairie target (1D). Despite different species composition, richness was similar between the two native prairie targets and the drought established restoration (Eckhoff et al. 2023) that contained higher species richness than prairie

restored in an average precipitation year. Both native reference prairies contained higher species richness than SEQI, suggesting that drought in the establishment year has decadal effects on similarity in richness to native prairie. The high richness and low diversity and evenness in 1D conforms to the ‘core-satellite hypothesis’ (Hanski 1982), with this community having a large number of species, but primarily dominated by a few prolific species, in this instance being C₄ prairie tallgrasses and most species being far less abundant on the landscape. However, the core-satellite distribution of species was not consistent between the remnants, demonstrated by higher evenness in HQB. The core-satellite distribution of species was also not a characteristic of either restored prairie, both of which contained higher evenness than 1D.

Unique and indicator species in the restored prairie show greater turnover in the restorations as they develop to reflect the sown species pool. More unique species in the restorations across the decadal time scale compared to the native prairie (1D) over the same time frame was predominately due to the colonization of volunteer annual C₃ forbs and grasses in the first several years since restoration, many of which dropped out during succession to communities dominated by sown perennial species (Manning & Baer 2016). Considering only data from 2020, the native watersheds contained more than twice as many species unique to these watersheds compared to the restorations, demonstrating that unplowed native prairie harbors a larger pool of species than the prairie restorations. All but one of the indicator species in the restored prairies were forbs sown into the former agricultural soil. This suggests that the seed mix and seeding rates have a strong influence on membership in restored communities and supports an in-depth survey of restorations and outcomes in prairies (Rowe et al. 2010). While many of the species sown in the restorations were found in the native targets, the abundance of many forbs in the restorations was generally higher.

The trajectory of change in functional group composition in the restorations shows that the functional structure of restored prairie plant communities stabilizes as they age regardless of different planting-year climate conditions and targets can vary widely in functional composition. In the early years of restoration, the communities were composed primarily of annual C₃ forbs and annual C₃ grasses. The largest difference in functional composition in the decadal-restored prairies was the higher relative cover of legumes and perennial C₃ forbs in compared to the native prairies. Functional group composition of similarly managed native prairie varied widely within a small distance from one another. The individual plots within HQB were highly variable. Several plots in HQB had functional overlap with 1D and others were compositionally similar to some restored plots. Variation in historical utilization by grazers and in fire frequencies might be partially responsible for the differences between the functional composition of the two prairie targets that resulted from variation in grass dominance. This historical legacy may also play a role regarding the within site variation observed, where the difference between plots in 1D was relatively small while the difference between plots in HQB was much more pronounced.

Total ANPP in restored prairies began to track interannual variation in the native prairies following 3-4 years of restoration but the relationship with precipitation varied among restored prairies. In SEQ I (restored under average precipitation), the correlation between precipitation and ANPP became more strongly positive as the sequence aged. In the fourth growing season, biomass was composed mostly of sown species, and was the first growing season following the introduction of an annual fire regime and diversity and richness of the restoration peaked before slowly declining, then leveling out. In contrast, the correlation between ANPP and annual precipitation in SEQ II, established in a drought year, started out significant, but became less significant as the sequence aged. The correlation between ANPP and April - August growing

season precipitation in SEQ II, however, remained significant for all intervals examined, and the correlation was strongest after the 4th year of growth. The difference in the strength of correlations between the sequences suggests that the drought during the establishment may influence responsiveness to annual precipitation over the long term. Notably it seems that, much like native grasslands, the two restored communities varied in their sensitivity to precipitation (Griffan-Nolan et al. 2018). This variation could be due to the higher forb cover found in SEQ II. Forb ANPP has been found to be less responsive to drought than grasses in tallgrass prairie systems (Nippert et al. 2006). Both restorations were more responsive to extreme precipitation events than the native prairies. In 2019, an above average rainfall year, mean ANPP in both sequences exceeded ANPP in the native prairies. In 2020, while both sequences showed a decrease in mean ANPP, the reduction was more pronounced in SEQ I than in SEQ II. This suggests that a restored community that is established in a drought year may be more resilient to variation in climate than one which is established in an average precipitation year.

Aboveground productivity is an important metric of ecosystem recovery in restorations because this is the energy base for higher trophic levels within the ecosystem. The difference in average ANPP among the native prairies over a 6-year period shows that ecosystem functioning can vary greatly between different targets within the same ecosystem. This range of possible ecosystem functioning for restoration targets suggests that it is reasonable to expect a restoration to differ from a chosen target since subtle changes across the landscape can potentially cause large differences in the ecosystem functioning of a prairie community. Restorations can exhibit a higher ANPP than comparable native grasslands (Baer et al. 2004), but in this case the restored prairies, both fell with the range of the native prairie targets, despite differences in ANPP early in the restoration process and in response to planting-year precipitation.

Conclusions

It is important to consider the wide range of reasons behind ecological restoration in order to determine appropriate targets. While ecological factors like increasing local biodiversity, wildlife habitat, and ecosystem services are frequently the primary reasons behind ecosystem restoration, they are not the only factors that need to be taken into consideration when determining if a restoration meets its goals, and how appropriate fidelity to a reference ecosystem is to achieving restoration targets. Financial, political, human use, and societal motivations are frequently involved in restoration decision making and are important factors to weigh when determining restoration targets (Higgs 1997). With all this to consider, determining a target can be quite difficult, ideally a reference system would fulfil the ecosystem attributes restoration should aim to achieve according to the SER guidelines (Gann et al. 2019). Knowledge of species diversity, vegetation structure, and ecological processes are needed to create targets and facilitate restoration goals (Ruiz-Jaen & Mitchell Aide 2005). All of this points to one ideal target for a specific ecosystem based on the restoration goals, but the range of differences between the two targets studied here was unexpected, but not unprecedented (Wodika & Baer 2015). Either native prairie studied could be considered an appropriate reference system for the restorations but due to the large effect that relatively small changes in spatial dynamics can have on communities within the same ecosystem these targets were quite different from one another. To this end, a restoration which develops into a healthy ecosystem of the intended type may in fact not end up resembling the chosen target.

The restored prairies followed similar recovery trajectories despite the fact that communities restored under differing precipitation conditions remained distinct from one another. While drought induces persistent differences in the restored communities (Eckhoff et al.

2023), they were far more similar to one another structurally and functionally than the native prairie sites were to each other. This shows a strong effect that the initial species pool has on the community structure of prairie restorations and the role of planting-year climate on creating communities that persists despite differences in establishment year conditions. Limitations of the seed mix used were noticeable in both the community composition and the indicator species analysis, suggesting that dispersal into these restored communities is limited and a slow process that should not be relied upon to for regeneration of highly diverse restored communities. Thus, comparison of restored communities to potential targets can reveal species that are missing and could be overseeded to either increase diversity or steer restored communities toward restoration targets.

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APPENDIX A: TABLES

Table 1. Seeding rates (live seed/m²), life history, photosynthesis pathway, and life form of species sown in the sequentially restored prairies. Nomenclature follows the USDA plants database.

Species	Seeding rate live seed/m ²	Life History	Photosynthesi c Pathway	Life Form
<i>Andropogon gerardii</i> Vitman	16	Perennial	C4	Graminoid
<i>Andropogon gerardii</i> KAW	31	Perennial	C4	Graminoid
<i>Bouteloua curtipendula</i> (Michx.) Torr.	10	Perennial	C4	Graminoid
<i>Elymus canadensis</i> L.	8	Perennial	C3	Graminoid
<i>Panicum virgatum</i> L.	1	Perennial	C4	Graminoid
<i>Schizachyrium scoparium</i> (Michx.) Nash	18	Perennial	C4	Graminoid
<i>Sorghastrum nutans</i> (L.) Nash	55	Perennial	C4	Graminoid
<i>Amorpha canescens</i> Pursh	22	Perennial	C3	Woody shrub
<i>Baptisia australis</i> (L.) R. Br.	3	Perennial	C3	Legume
<i>Dalea candida</i> Michx. ex Willd.*	15	Perennial	C3	Legume
<i>Dalea multiflora</i> (Nutt.) Shinnners*	15	Perennial	C3	Legume
<i>Dalea purpurea</i> Vent.	23	Perennial	C3	Legume
<i>Desmanthus illinoensis</i> (Michx.) MacMill. Ex B.L. Rob. & Fernald	15	Perennial	C3	Legume
<i>Echinacea pallida</i> (Nutt.) Nutt.	2	Perennial	C3	Forb
<i>Helianthus pauciflorus</i> Nutt.	11	Perennial	C3	Forb

<i>Lespedeza capitata</i> Michx.	24	Perennial	C3	Forb
<i>Liatris pycnostachya</i> Michx.	1	Perennial	C3	Forb
<i>Oenothera macrocarpa</i> Nutt.	3	Perennial	C3	Forb
<i>Oligoneuron rigidum</i> (L.) Small	31	Perennial	C3	Forb
<i>Rosa arkansana</i> Porter	2	Perennial	C3	Woody sub- shrub
<i>Silphium integrifolium</i> Michx.	6	Perennial	C3	Forb

**Seed of *Dalea candida* and *Dalea multiflora* were mixed in the initial seeding year and a 50/50 split of the two species was used for seeding rates in all subsequent years

Table 2. Functional group assignments were determined through agglomerative cluster analysis. These groups were determined using a collection of life history traits: life history (annual, perennial, biennial, unknown), photosynthetic pathway (C₃,C₄, or unknown), life-form (forb, graminoid, shrub, sub-shrub, tree, unknown), cotyledons (monocot, dicot, unknown), and general traits (wood, legume, unknown). Traits for each species were found using the USDA plants database.

Functional Groups	
1	Annual C ₃ forb
2	Perennial C ₃ forb
3	Perennial C ₄ Forb
4	Woody shrub or sub-shrub
5	C ₄ Grass
6	Unknown Forb
7	Legume
8	Annual C ₃ Graminoid
9	Perennial C ₃ Graminoid
10	Biennial C ₃ Forb
11	Annual C ₄ Graminoid
12	Unknown
13	Non-Graminoid Monocot

Table 3. Table of Pearson's product moment correlations between total ANPP and annual precipitation and growing season precipitation for Sequences I and II for both the entire span of restoration and from 4 years of age up. *Significant p-value, **Marginally Significant p-value

		SEQ I		SEQ II	
Rainfall Regime	Time Frame	r	p	r	p
Total PPT	0-11(9)	0.494	0.002*	0.697	<0.001*
	4-11(9)	0.589	<0.001*	0.386	0.062**
April/August PPT	0-11(9)	0.438	0.005*	0.626	<0.001*
	4-11(9)	0.618	<0.001*	0.410	0.046*

Table 5. Indicator species analysis of restored prairies compared to native watersheds (each unit and combination of units. Species that are indicators of multiple sites are noted in the combinations (1 = species was found exclusively at that site, <1=). species was present in other sites, but the abundance was significantly greater in the site where the species is listed as an indicator. (* p < 0.05, ** 0.001 < p < 0.05, *** p < 0.001)

Species	Both Restored (Seq I + II)	Seq I	Seq II	Both Targets (1D + HQB)	1D	HQB
<i>Baptisia australis</i>	1***	-	-	-	-	-
<i>Dalea purpurea</i>	1***	-	-	-	-	-
<i>Silphium integrifolium</i>	1***	-	-	-	-	-
<i>Desmanthus illinoiense</i>	0.996***	-	-	-	-	-
<i>Oligoneuron rigidum</i>	0.935***	-	-	-	-	-
<i>Oenothera macrocarpa</i>	0.866***	-	-	-	-	-
<i>Dalea multiflora</i>	-	0.954***	-	-	-	-
<i>Liatris punctata</i>	-	-	0.879**	-	-	-
<i>Desmodium illinoiense</i>	-	-	0.866*	-	-	-
<i>Sporobolus compositus</i>	-	-	-	1***	-	-
<i>Ambrosia psilostachya</i>	-	-	-	0.972**	-	-
<i>Solidago altissima</i>	-	-	-	0.945**	-	-
<i>Ruellia humilis</i>	-	-	-	-	1***	-

<i>Vernonia baldwinii</i>	-	-	-	-	1***	-
<i>Carex meadii</i>	-	-	-	-	1***	-
<i>Asclepias viridis</i>	-	-	-	-	1***	-
<i>Pysalis virginiana</i>	-	-	-	-	1***	-
<i>Asclepias verticillata</i>	-	-	-	-	1**	-
<i>Eragrostis spectabilis</i>	-	-	-	-	0.932**	-
<i>Baptisia bracteata</i>	-	-	-	-	0.866**	-
<i>Brickellia eupatoroides</i>	-	-	-	-	0.866*	-
<i>Dichantherium oligosanthes</i>	-	-	-	-	0.844*	-
<i>Carex brevior</i>	-	-	-	-	-	0.921**
<i>Silphium laciniatum</i>	-	-	-	-	-	0.866**
<i>Psoraleidum tenuiflorum</i>	-	-	-	-	-	0.791**
<i>Carex bicknellii</i>	-	-	-	-	-	0.791**

APPENDIX B: FIGURES

Figure 1. Map of the Konza Prairie Biological Station watersheds (WS) with locations of the restored prairies (orange) and remnant prairies (1D =yellow, HQA, HQB, and HQC = purple) used to assess restoration recovery trajectories.

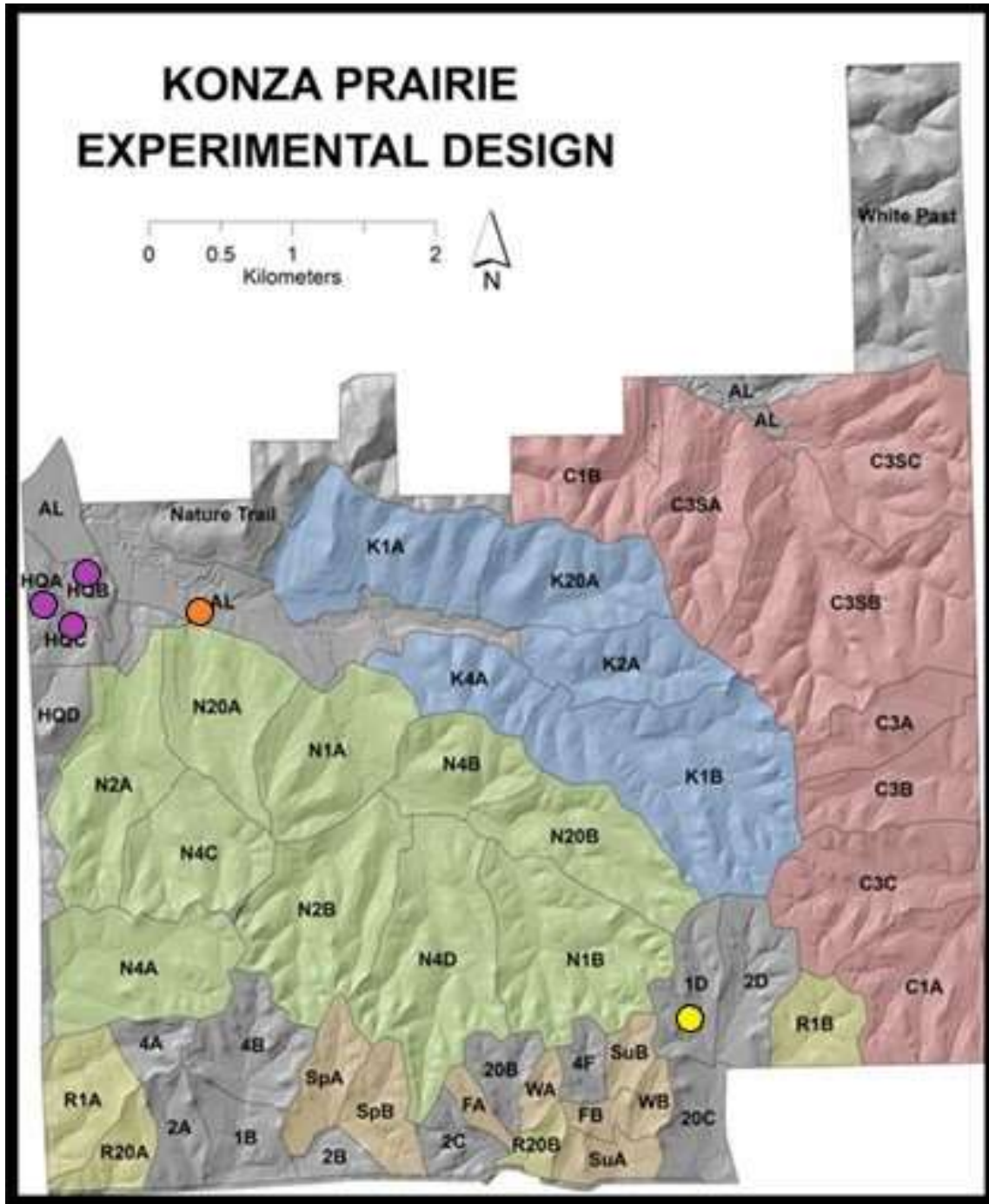


Figure 2. Change in plant community composition of restored prairies (SEQ I and SEQ II) over a decadal timeframe compared to two native prairie communities (HQB and WD1d). Sequence I was established in an average precipitation year while SEQ II was established in a drought year. Ellipses show the 95% confidence interval around the centroid of each community in 2020, arrows show temporal trajectories of change in centroid over from 2010-2020 for SEQ I, 2012-2020 in SEQ II, and 2010-2020 for 1D, HQB was only sampled in 2020.

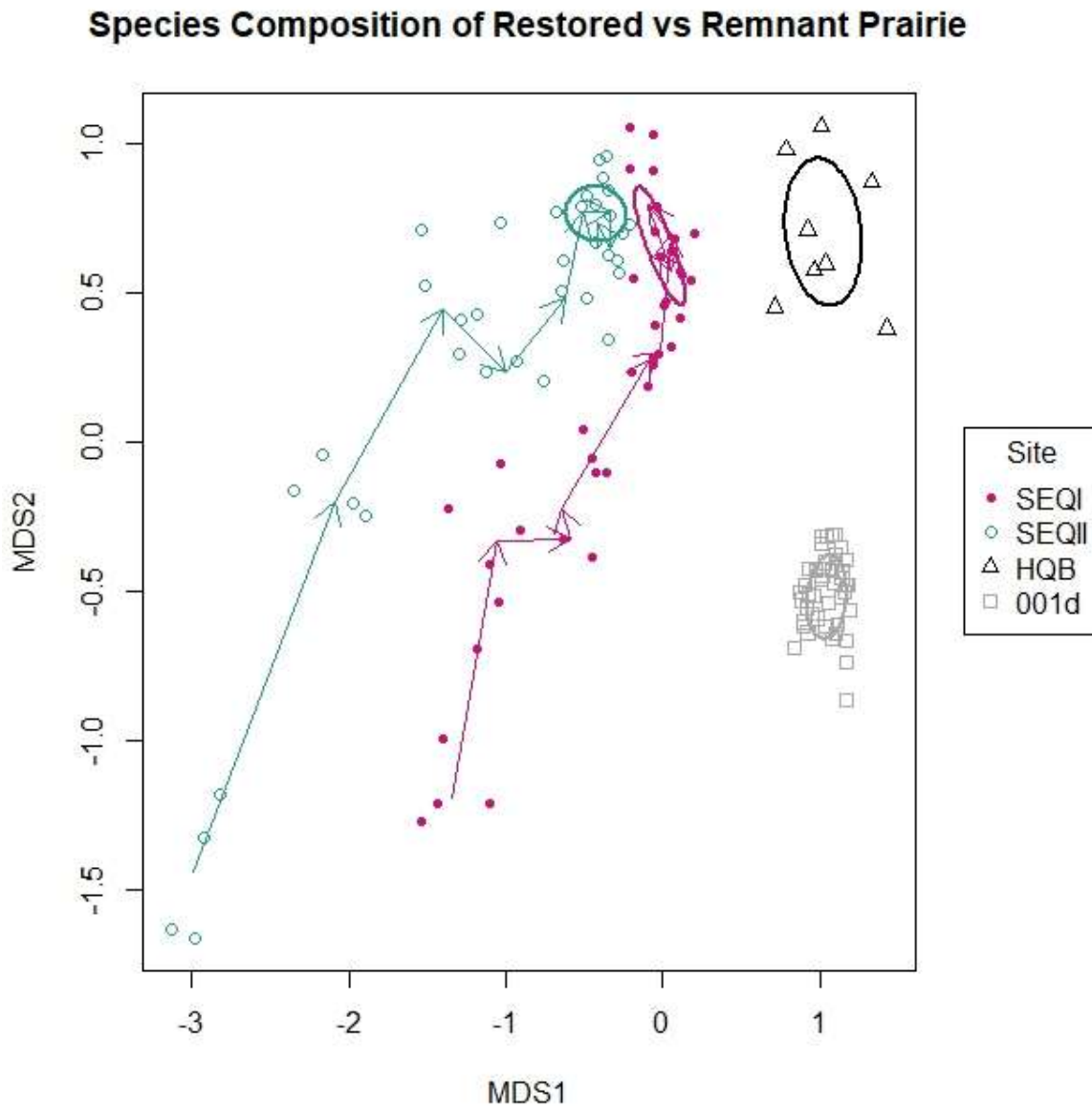


Figure 3. Mean (\pm standard error) of Shannon's diversity, Pielou's evenness index, and richness (per 10 m²) of plant communities (A, C, E) each year sampled from 2010-2020 in SEQI (pink), SEQII (teal), 1D (gray) and WS HQB (black), and (B, D, F) compared among all restored and native communities in 2020. Differences among communities in 2020 were determined using Fisher's LSD post-hoc testing, means accompanied by the same letter were not significantly different ($\alpha = 0.05$).

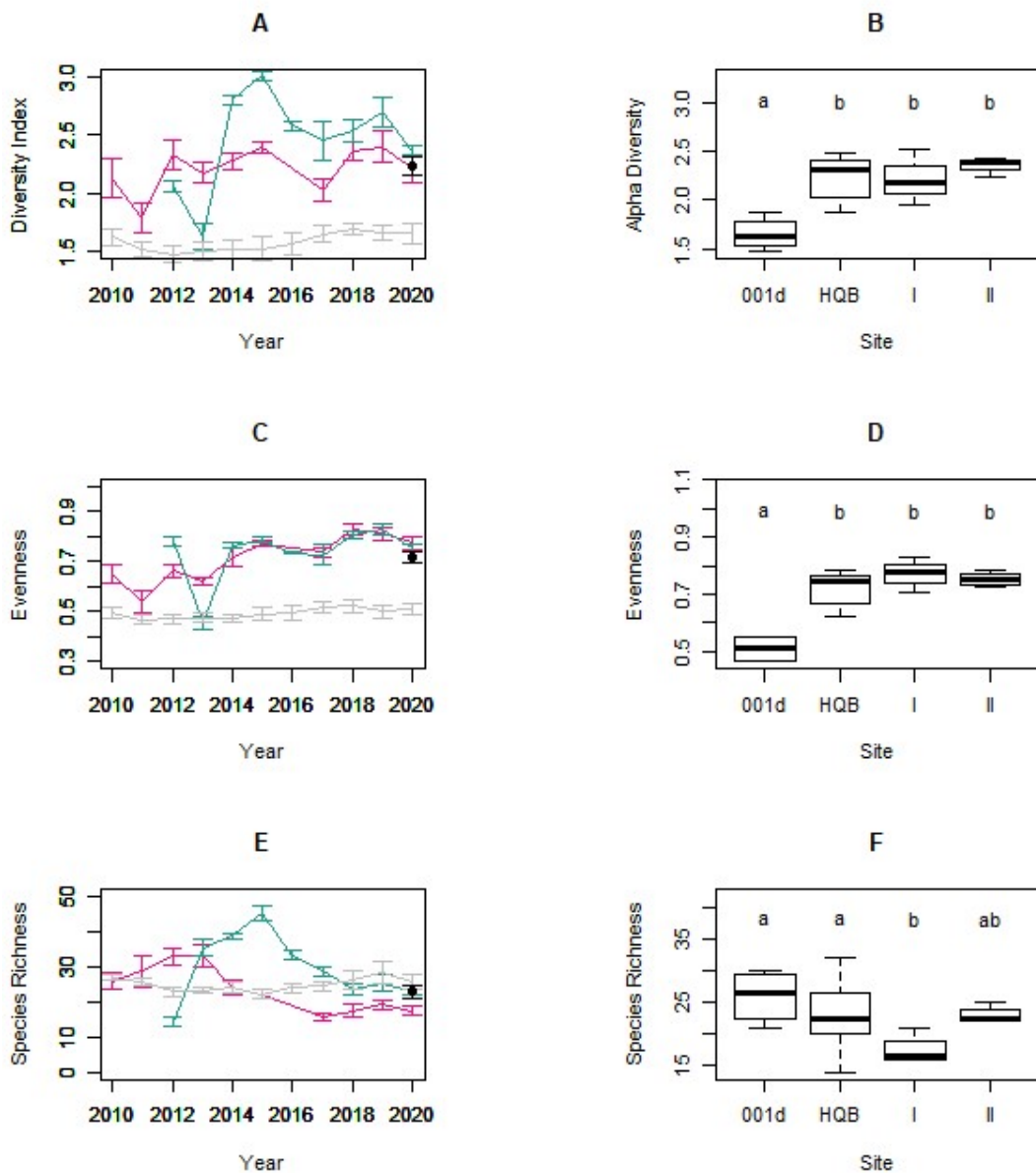


Figure 4. Ordination of functional composition over time. Arrows track directional change of centroids in the ordination space over time in SEQ I (2010-2020, pink), SEQ II (2012-2020, teal). Ellipses show the 95% confidence interval around the centroid each restored prairie and native prairie targets (HQB and 1D) in 2020.

Functional Group Composition of Restored vs Remnant Prairie

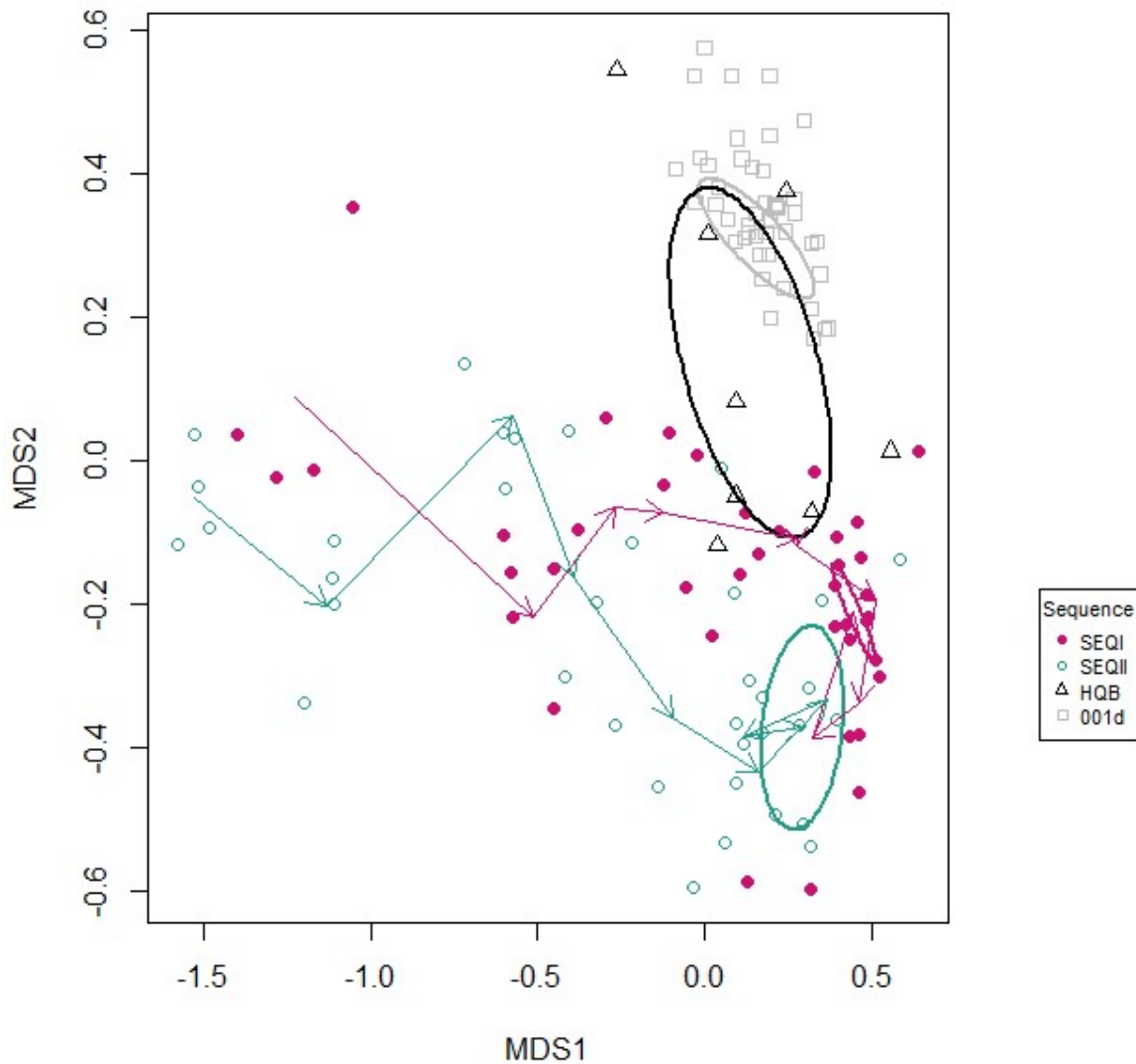


Figure 5. Ordination of functional group composition of SEQI, SEQII, HQB, and 1D in 2020 determined through hierarchical cluster analysis. Arrows indicate the directional influence of the most abundant functional groups present in the communities. Ellipses show the 95% confidence interval from the centroid of each community for the 2020 sampling year.

Functional Group Composition of Restored vs Remnant Prairie

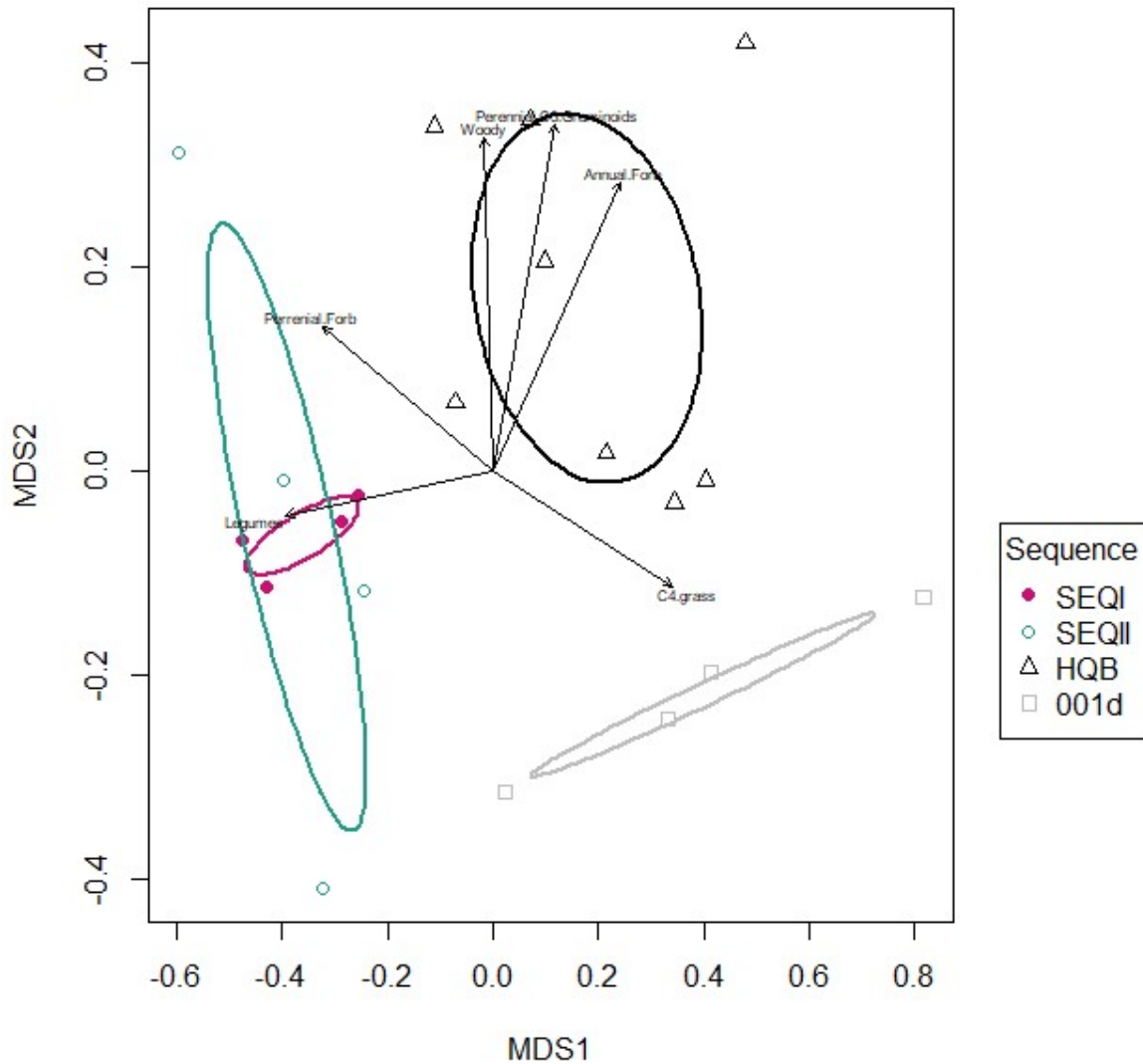


Figure 6. From 2010-2021, (A) total and growing season (June-July) precipitation by year, corresponding (B) total ANPP in restored SEQ I and SEQ II and native prairies in 1D, HQA, and HQC, and (C) proportion of sown and volunteer ANPP in the restorations.

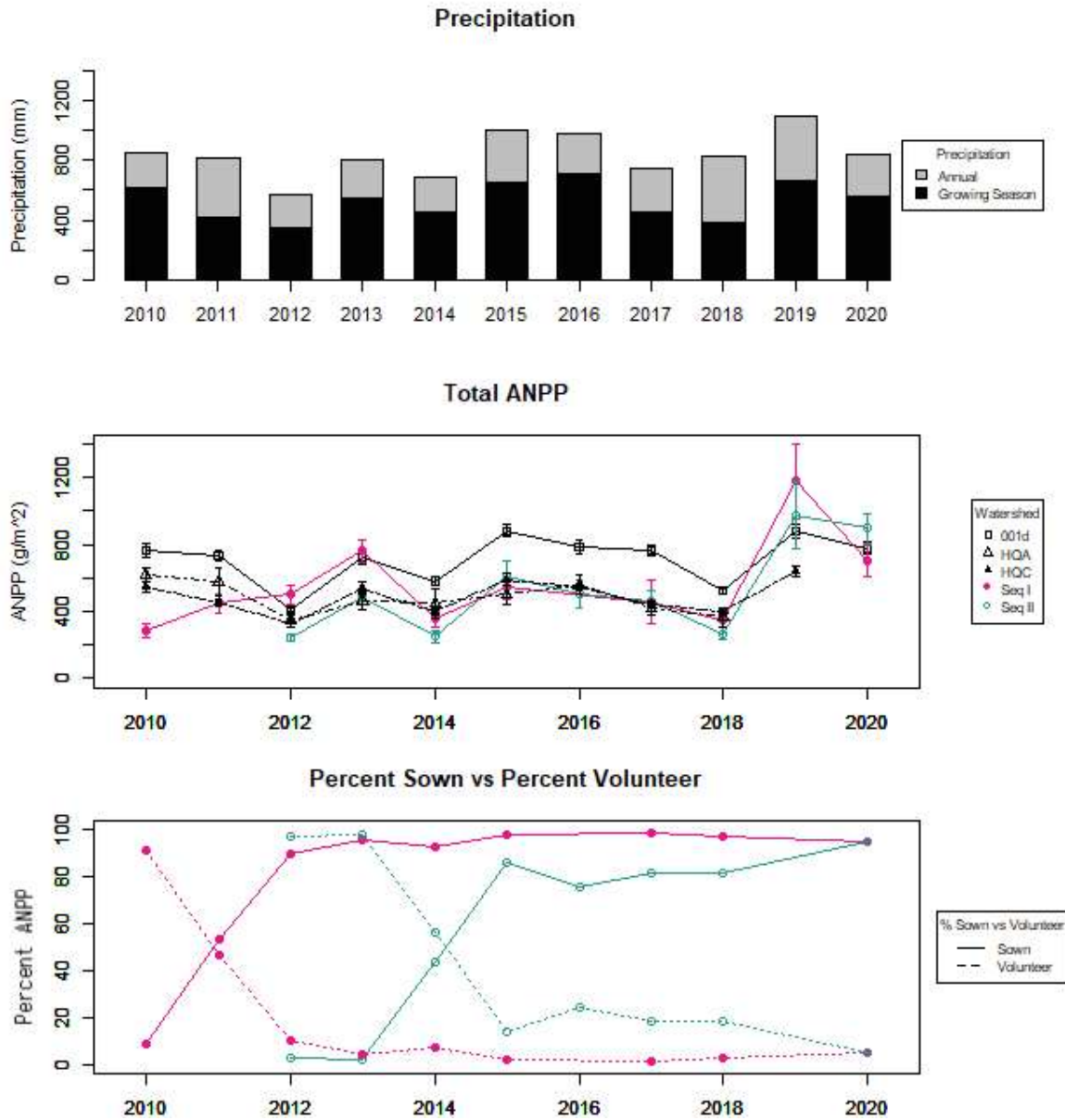


Figure 7. Mean (\pm standard error) of total ANPP in each native prairie target and restored sequence from 2015-2020, when restorations were dominated by sown species. Letters a-c were assigned through a post-hoc LSD test, means accompanied by the same letter were not significantly different.

