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ARTICLE

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Persistent decadal differences in plant communities assembled under contrasting climate conditions

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Abstract

Plant community assembly outcomes can be contingent upon establishment year (year effects) due to variations in the environment. Stochastic events such as interannual variability in climate, particularly in the first year of community assembly, contribute to unpredictable community outcomes over the short term, but less is known about whether year effects produce transient or persistent states on a decadal timescale. To test for short-term (5-year) and persistent (decadal) effects of establishment year climate on community assembly outcomes, we restored prairie in an agricultural field using the same methods in four different years (2010, 2012, 2014, and 2016) that captured a wide range of initial (planting) year climate conditions. Species composition was measured for 5 years in all four restored prairies and for 9 and 11 years in the two oldest restored prairies established under average precipitation and extreme drought conditions. The composition of the four assembled communities showed large and significant differences in the first year of restoration, followed by dynamic change over time along a similar trajectory due to a temporary flush of annual volunteer species. Sown perennial species eventually came to dominate all communities, but communities remained distinct from each other in year five. Precipitation in June and July of the establishment year explained short-term coarse community metrics (i.e., species richness and grass/forb cover), with wet establishment years resulting in a higher cover of grasses and dry establishment years resulting in a higher cover of forbs in restored communities. Short-term differences in community composition, species richness, and grass/forb cover in restorations established under average precipitation and drought conditions persisted for 9–11 years, with low interannual variability in the composition of each prairie over the long term, indicating persistently different states on a decadal timescale. Thus, year effects resulting from stochastic variation in climate can have decadal effects on community assembly outcomes.

KEYWORDS
climate variability, community assembly, deterministic processes, priority effects, restoration, stochastic processes, tallgrass prairie, year effects

INTRODUCTION

Community assembly outcomes are notoriously difficult to predict (Fukami & Nakajima, 2011; Heil, 2004; Kraft & Ackerly, 2014), including the composition of plant communities established through ecological restoration (Brudvig et al., 2017). Uncertainty in community outcomes is expected if community assembly is governed by stochastic (neutral) processes or when stochastic variation in ecological drivers interrupts deterministic (niche-based) processes (Heil, 2004). Understanding the role of spatial and temporal variation in environmental conditions on community assembly is needed to better predict short-term restoration outcomes and understand whether short-term variation in communities is transient or persists over the longer term. Spatial variation in the environment at the start of community development is known to influence diversity decades following restoration (Baer et al., 2020). Plant communities sown in different years, corresponding to temporal (stochastic) variation in the environment, can also result in compositionally different communities, a phenomenon known as "year effects" (Werner et al., 2020). Furthermore, variation among restored communities has been related to planting year weather, suggesting that year effects can persist on a decadal timescale (Groves et al., 2020). No studies, however, have followed the composition of communities established in different years beyond a few establishment years (Manning & Baer, 2018), which is needed to document whether year effects are transient or persist over time and to understand the extent to which stochastic events have deterministic and predictable effects on community assembly.

Community assembly studies aiming to reveal the degree to which communities are structured by stochastic or deterministic processes (Chase & Myers, 2011; Yang et al., 2013) can be complicated by stochastic events such as interannual variation in climate (Wilsey, 2021). One approach to revealing the stochastic or deterministic nature of community assembly is to follow the development of communities assembled with the same species pool in different sites that contain known (spatial) variations in the environment (Bakker et al., 2003; Trowbridge, 2007). To understand the role of temporal variation in the environment (year effects) on community assembly, communities need to be established (e.g., sown) in the same site with the same species pool over different years (Werner et al., 2020). Despite the fact that year effects can be larger than experimental treatment effects (Stuble, Fick, & Young, 2017), markedly few ecological studies are repeated over time to test for temporal contingencies in community outcomes (Vaughn & Young, 2010; Werner et al., 2020). Year effects can also create historical contingencies (order and timing of initial events have lasting consequences) based on environmental factors that vary year to year (Fukami, 2015; Stuble, Fick, & Young, 2017). Historical legacies of climate variation on community assembly outcomes have been documented immediately following restoration when annual volunteer species are abundant (Groves & Brudvig, 2019; Manning & Baer, 2018; Stuble, Fick, & Young, 2017), but less is known about whether those initial community differences persist over longer (decadal) timescales, when sown perennial species dominate communities.

Year effects in developing grassland communities (undergoing secondary succession or restoration) can result from a variety of factors such as the amount and timing of precipitation, temperature, and biotic interactions (Groves et al., 2020). In California annual grasslands, climate determines "forb years" (dominated by herbaceous nongrass species) versus "grass years" when initial seeding conditions are dry versus wet, respectively (Pitt & Heady, 1978; Stuble, Fick, & Young, 2017). In tallgrass prairie, precipitation and temperature in the establishment year can delay the germination and establishment of sown species, resulting in different compositions of communities in the first year of restoration (Groves & Brudvig, 2019). Variation in composition among restored prairie communities sampled over a broad spatial scale and across a range of restoration ages (up to 19 years restored) showed that the richness and cover of sown and nonsown species were related to variation in planting year weather (Groves et al., 2020). No studies, however, have followed community composition over time in communities restored using the same species pool in the same site to reveal the role of temporal variation in climate on trajectories of compositional change and persistence of year effects on community composition. In tallgrass prairie, forbs contribute most to richness and diversity so knowledge of initial climate effects on the richness and forb cover may be key to achieving biodiversity goals of ecological restoration.

Once widespread, the majority of the North American tallgrass prairie ecosystem has been lost due to its conversion to row-crop agriculture (Sampson & Knopf, 1994). Ceasing cultivation and sowing seeds of native species are practices widely used to restore tallgrass prairie communities and reverse many ecosystem disservices by agriculture. In tallgrass prairie, diversity is largely determined by the presence and relative abundance of forb species, and attaining high forb abundance and diversity are common goals of prairie restoration. However, plant species diversity in many restored prairies often falls short of remnant grasslands (Baer et al., 2005; Benayas et al., 2009; Newbold et al., 2020; Sluis, 2002) and community outcomes are often highly variable (Brudvig et al., 2017). Difficulty in predicting restoration outcomes is likely to correspond to whether structural aspects used to characterize communities are coarse or fine community metrics. The "hierarchy of predictability hypothesis" surmises that coarse community metrics such as species richness and forb cover are more predictable measures of restoration outcomes compared to fine measurements such as the relative abundance of species (Brudvig et al., 2017; Laughlin et al., 2017).

To understand the influence of interannual variability in climate occurring in the establishment (planting) year on developing communities, we sequentially restored prairie in an agricultural field using the same restoration methods every other year (Manning & Baer, 2018). Trajectories of plant community development were compared among four restorations over their first five establishment years to reveal the role of initial year climate on short-term community outcomes. In addition, we followed community trajectories in two restorations established in average precipitation and extreme drought conditions for 11 and 9 years, respectively, to evaluate whether year effects are transient or persist on a decadal timescale. We hypothesized: (1) variation in initial year climate would explain variation in trajectories of community development and coarse metrics of community outcomes would correspond to planting year climate over the short-term; and (2) different community states achieved over the short term in restorations established under highly contrasting initial climate conditions would persist over the longer term.

METHODS

Prairie communities were sequentially restored in a lowland agricultural field at the Konza Prairie Biological Station and Long Term Ecological Research site in northeastern Kansas (39°06′09″ N, 96°36′07″ W). The 30-year mean annual temperature is 12.7°C with a mean annual precipitation of 835 mm. The site was historically dominated by C_4 grasses with a large diversity of forbs (Abrams & Hulbert, 1987). The soil type at the study site is a Reading silt loam (mesic Pachic Argiudoll) and the field was cultivated for conventional row-crop agriculture for over 50 years, rotating between winter wheat and soybeans. The field remained cultivated prior to the installation of each restoration sequence.

Each restoration sequence (SEQ) was established in a 30 × 110-m strip of the agricultural field. Sequences were installed in 2010 (SEQ I), 2012 (SEQ II), 2014 (SEQ III), and 2016 (SEQ IV) (Appendix S1: Figure S1, Manning & Baer, 2018). In each planting year, four 20 × 20-m plots were independently restored in that seed mixtures were created separately for each plot and hand-broadcasted separately by plot. Each plot was divided into four 10 × 10-m subplots (A–D) for sampling. Plots and sequences were separated by 5-m buffer strips. Due to space constraints, plot 4 of SEQ I was divided into two 20 × 10-m plots, with one located in an adjacent and historically similarly managed agriculture field. Sequence II contained deer exclosures (1.5 m tall, 5 × 10 cm mesh metal fencing) randomly assigned to half the subplots. We used all subplots in this study because plant species composition and cover of forbs and grasses (variables measured here) were similar between control and exclosure subplots and lower richness in the exclosures in some years (unpublished analyses), when averaged with control subplots, would underestimate the positive effect of drought on richness in the presence of deer (estimated at 6.6 individuals km^{-2}).

Seeds of the same 20 native plant species collected from the surrounding native prairie and county (Appendix S1: Table S1) were used in all restoration sequences. One grass species was supplemented with a locally-sourced cultivar. Seeds were collected for 2 years prior to the installation of each sequence. Seeds of each species collected each year were combined with seed collections of each species from prior years. All seed was cleaned, and a subsample of each species was sent to the Illinois Crop Association to determine the percent live seed (PLS; based on purity, germination, and dormancy) prior to each sequence installation. The species mix was based on the amount and identity of species collected in 2009, with a seeding rate of 141 live grass seed/m^2 and 172 live forb seed/m^2 representing a 45:55 grass:forb live seed ratio.

All sequences were installed the last week of May/first week of June (Julian dates 144–153) in each establishment year. The soil in each sequence was field cultivated and hand raked prior to sowing. Seeds of each species were combined, mixed with damp sand, and hand broadcast separately for each plot to foster independence between plots. After sowing, seeds were manually compacted by foot in each plot to promote contact with soil. Buffer areas were sown with seed mixes that contained similar total live seed amounts but with species in different proportions relative to the study plots based on the remaining seed. There was insufficient biomass to carry fire following the first three growing seasons of SEQ I. To keep management consistent among sequences, an annual spring fire regime was initiated in each sequence after the third growing season. Annual burning is a common practice used to prevent woody encroachment in tallgrass prairie (Briggs et al., 2005).

Percent cover of each plant species was visually estimated in permanent 10 m^2 circular sampling areas in the center of each subplot in each plot in May and September each year (2010–2020), but only in September in a sequence's installation year. The cover estimate for each species was assigned to a modified Daubenmire cover class (1 = 0%–1%, 2 = 2%–5%, 3 = 6%–25%, 4 = 26%–50%, 5 = 51%–75%, 6 = 76%–95%, 7 = 96%–100%) to minimize observer bias (Carter & Blair, 2012; Daubenmire, 1968). The percent cover corresponding to the midpoint of the Daubenmire cover class was recorded and the maximum percent cover from the seasonal surveys was used to calculate community metrics in each subplot each year. Species richness was determined by totaling the number of unique species from all subplots within each plot. Due to increased sampling effort after the installation of each sequence, species composition was measured in two of four subplots in each plot after five growing seasons.

Local climate data were downloaded from the Konza LTER website for all years of the study. The amount of precipitation in the 2 months following sowing (June/July) was calculated for each sequence and used to relate precipitation to community composition.

Statistical analyses

Short-term community response to establishment year

Each plot in each sequence was treated as an independent experimental unit (field replicate) within each sequence ($n = 4$ per sequence), which was geo-statistically supported by Scott and Baer (2019). To compare trajectories of community development over time among sequences, the effects of AGE (years since seeding) and SEQ (corresponding with planting year) and their interaction on species composition were analyzed using repeated measures permutational multivariate analysis of variance (PERMANOVA) with 1000 permutations using the "adonis" function in the *vegan* package of R (vegan: Oksanen et al., 2020). Community composition was visualized using nonmetric multidimensional scaling (NMDS) with the "metaMDS" function in the *vegan* package of R. To reveal the strength and direction of age and initial precipitation on plant composition, vector analysis was executed by the "envfit" function in the *vegan* package of R.

Species richness, relative grass cover, and relative forb cover were analyzed for main effects and interaction between SEQ and AGE (years restored) with linear mixed models using the "lmer" function in the *lme4* package of R (Bates et al., 2018). AGE was treated as a repeated measure and plot was assigned as a random effect. Data were log-transformed to adhere to assumptions of homoscedasticity and normal distribution of residuals.

Decadal community response to average and drought conditions in the establishment year

To examine community change in the two oldest sequences (SEQs I & II) we used similar statistical methods as the analysis of four sequences over 5 years (community composition: repeated measures PERMANOVA, visualized with NMDS; coarse measurements: linear mixed models). We also assessed the persistence of community states over the longer term by plotting the distance between community centroids between years (e.g., Y1–Y2, Y2–Y3, etc.) in each sequence. Distances between centroids were calculated based on a Bray–Curtis dissimilarity matrix using the "usedist" function of the *usedist* package in R (Bittinger, 2020). Because dissimilarity between communities is likely to be correlated with richness, differences between richness should be considered when interpreting dissimilarity patterns.

All statistical analyses were performed on the average community metric for each plot within each sequence using R statistical software (R Core Team, 2020), $\alpha = 0.05$.

RESULTS

The climate was highly variable among the four sequence installation years (Table 1). From 2010 to 2016 annual precipitation ranged from 571 mm to 998 mm, including an extreme drought during the establishment year of SEQ II in 2012 (Rippey, 2015). The 2012 drought reduced annual precipitation (571 mm, 68% long-term average) and precipitation in the critical months following sequence installation (June/July: 138 mm, 69% long-term average).

In total, 198 species were identified in all plots from 2010 to 2020, with all 20 sown species observed within 5 years. All sequences were dominated by early successional annuals for the first 2 years of assembly. A common agricultural weed, *Conyza canadensis* (L.) Cronquist (horseweed), dominated communities in the second establishment year in all four sequences but persisted for a third year in SEQ II that was established in a drought year (2012; Appendix S1: Table S2). Perennial sown species comprised the majority of composition in the third year in SEQs I, III, and IV, but not until year four in SEQ II.

Short-term community response to establishment year and age

Over the course of their first five growing seasons, community composition in SEQs I-IV exhibited a SEQ-by-AGE interaction (PERMANOVA $F_{12,60} = 5.97$, $p = 0.001$;

TABLE 1 Annual precipitation, June/July precipitation (mm), and percent of average precipitation during the study period at the Konza Prairie Biological Station.

Year	SEQ	Annual (mm)	Annual percent avg.	June + July (mm)	June + July percent avg.
2010	**I**	**848**	**101%**	**347**	**172%**
2011		813	97%	156	77%
2012	**II**	**571**	**68%**	**138**	**69%**
2013		804	96%	254	126%
2014	**III**	**681**	**81%**	**209**	**104%**
2015		998	119%	270	134%
2016	**IV**	**981**	**117%**	**161**	**80%**
2017		751	90%	109	54%
2018		830	99%	119	59%
2019		1097	131%	249	124%
2020		840	100%	293	145%

Note: Bold indicates sequence (SEQ) installation year.

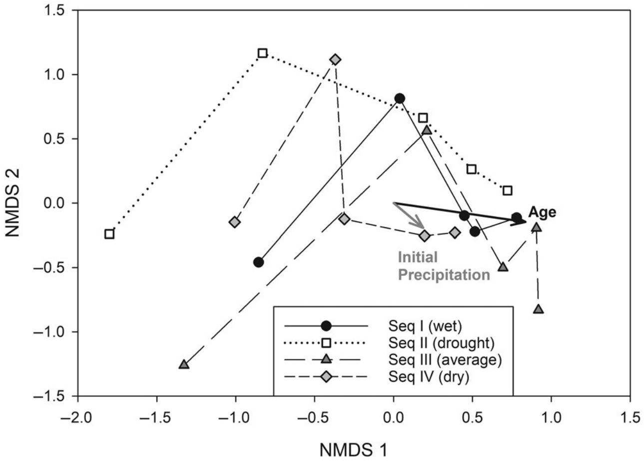

FIGURE 1 Nonmetric multidimensional (NMDS) ordination showing compositional change in each sequence over time. Vectors indicate strength and direction of effects age of restoration and initial precipitation. Ordination axes 1 and 2 are shown. Legend includes precipitation conditions in the initial year in parentheses.

Figure 1). This interaction resulted from differences in community composition among all sequences in their first year, followed by communities becoming more similar in their second growing season, then separating from each other in their third growing season. To increase the visibility of the trajectories of each sequence, centroids of all plots in a sequence over time are shown in the NMDS ordination (plot-level community data are displayed in Appendix S1: Figure S1). The final ordination resulted in a three-dimensional solution (stress = 0.13). Although composition tended to converge in the NMDS ordination space (Figure 1), communities remained distinct among sequences at age = 5 ($p < 0.04$). Age ($r^2 = 0.72$, $p = 0.001$) and initial precipitation was correlated with community change ($r^2 = 0.073$, $p = 0.05$).

Although communities changed over time within each sequence, variation among sequences in most years was greater than variation within a sequence. During the first 5 years of community development in all four sequences, there was a strong interaction between SEQ and AGE on species richness ($F_{12,60} = 7.75$, $p < 0.001$) and relative forb and grass cover ($F_{12,60} = 4.53$, $p < 0.001$; Figure 2). In sequences restored under lower-than-average June/July precipitation (SEQs II and IV), richness increased to levels higher than sequences established under average or higher levels of precipitation (SEQs I and III). In year 2 of all sequences, there was a decrease in grass cover and an increase in forb cover due to the dominance of *Conyza canadensis*. After 5 years of restoration, communities that were established in average or higher June/July precipitation had lower forb cover and higher grass cover compared with drier establishment year conditions.

Decadal community response to average and drought conditions in establishment year

On a decadal timescale, community composition in the two oldest sequences restored in average precipitation and drought conditions exhibited a SEQ-by-AGE interaction (PERMANOVA $F_{7,57} = 5.80$, $p = 0.001$; Figure 3a). The final ordination resulted in a two-dimensional solution (stress = 0.13) and shows the centroids of all plots in a sequence for each age (plot-level community data are displayed in Appendix S1: Figure S2). Years since establishment ($r^2 = 0.66$, $p = 0.001$) and initial precipitation

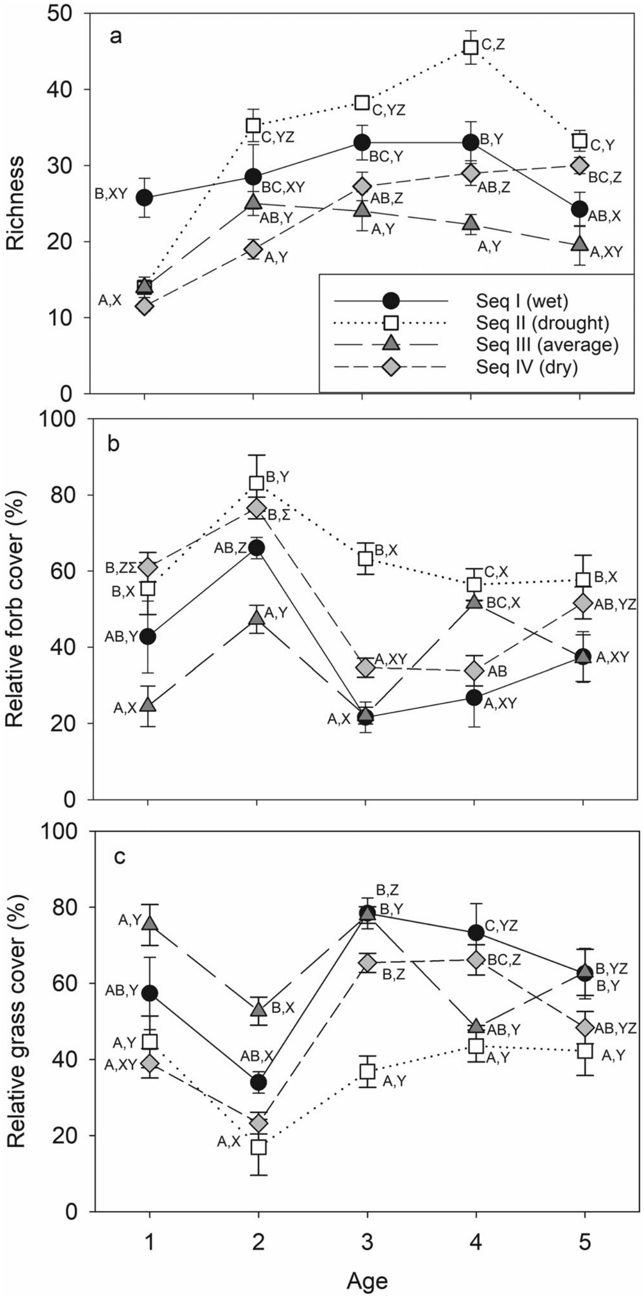

FIGURE 2 Average (±standard error) of (a) species richness, (b) relative forb cover, and (c) relative grass cover by sequence over the first 5 years of community assembly. Symbol and line type represent different sequences (I–IV). Differences between sequences within an age are indicated by A–C (vertically), and differences within a sequence across time are indicated by X–Z (horizontally). Means accompanied by the same letter were not significantly different.

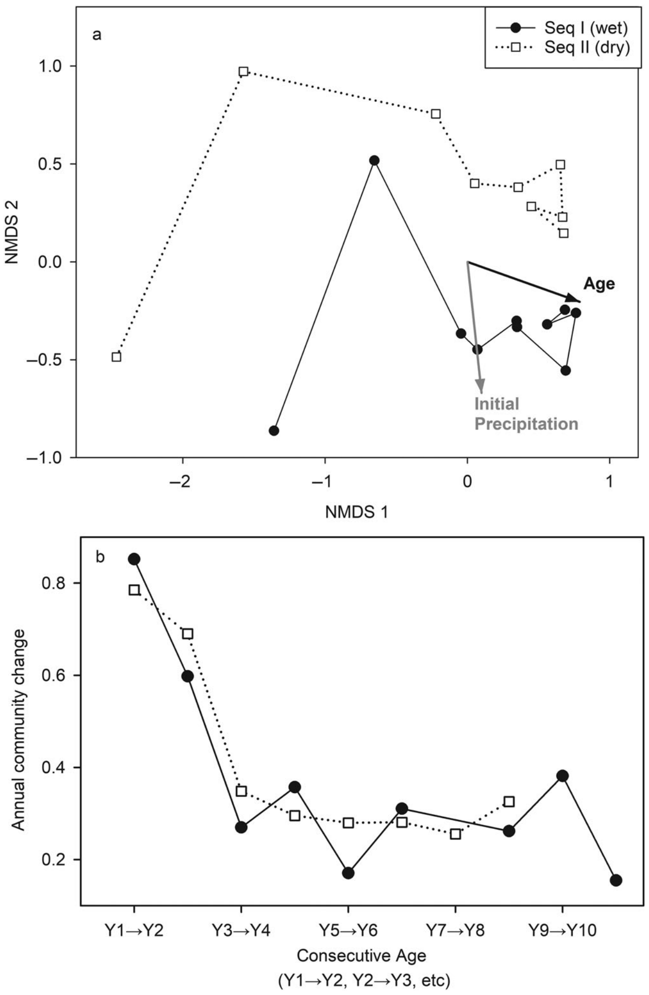

FIGURE 3 Ordination of (a) the two oldest sequences (SEQ I & II) over time. Vectors indicate strength and direction of effects of age and June/July precipitation of establishment year. (b) Distance between community centroids between consecutive years (Y1–Y2, Y2–Y3, etc.) based on community dissimilarity matrix.

(corresponding with initiation year) ($r^2 = 0.456$, $p = 0.001$) were significant vectors in the community ordination, with initiation year explaining the separation in composition between the two sequences throughout their development. Communities in each sequence experienced large year-to-year changes until approximately the 6th growing season (Figure 3b), after which communities showed little change in the ordination space.

Coarse-scale plant community metrics differed on a decadal timescale between sequences restored in average versus dry precipitation conditions. Species richness was affected by an interaction between AGE and SEQ ($F_{1,72} = 5.68$, $p = 0.02$; Figure 4a), resulting from initially low species richness in the first year of SEQ II increasing to levels higher than SEQ I after the second growing season. Relative grass and forb cover exhibited main effects of SEQ, corresponding to variation between planting years ($F_{1,72} = 9.95$, $p < 0.0001$; Figure 4), where grass cover was higher in SEQ I than SEQ II and forb cover was higher in SEQ II than SEQ I across all years.

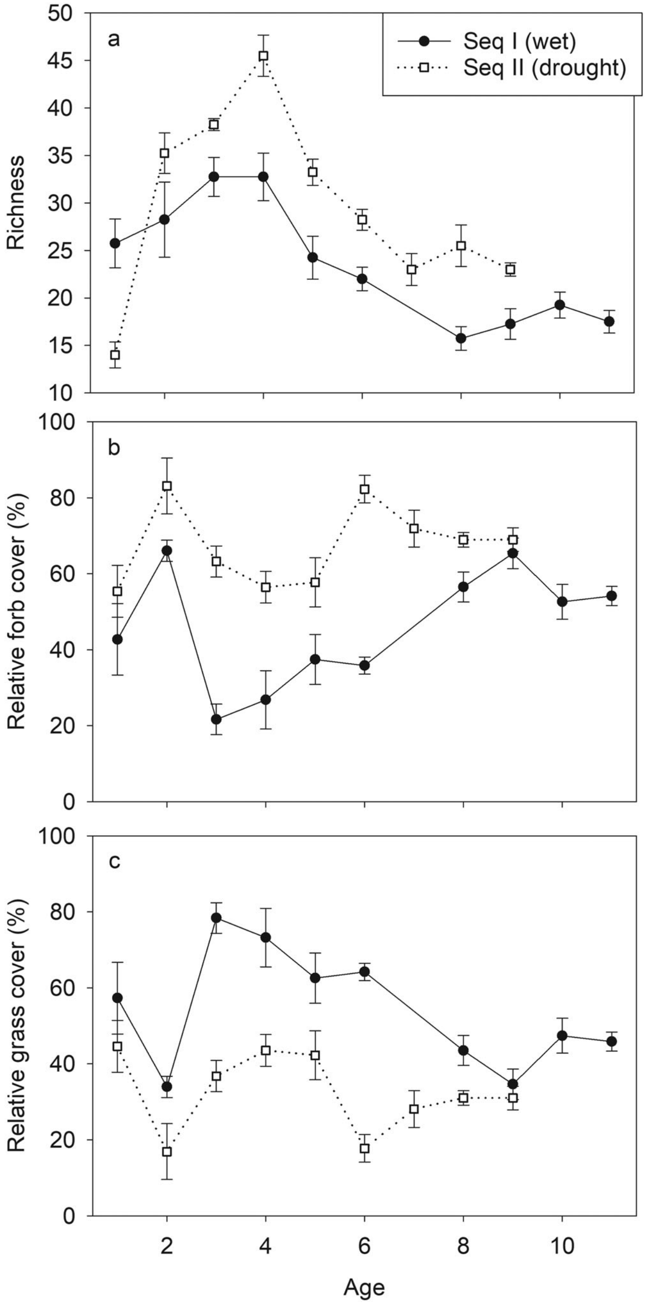

FIGURE 4 Average (±standard error) of (a) species richness, (b) relative forb cover, and (c) relative grass cover by sequence over time. Shape and line type represent different sequences (I & II).

DISCUSSION

Plant community assembly experiments demonstrating year effects are generally not initiated over enough years to relate year effects to variation in an environmental factor, or followed long enough to ascertain whether community differences observed in short-term studies are transient or persist over time (Vaughn & Young, 2010; Werner et al., 2020). Moreover, some tests of year effects on community assembly have weeded volunteer species (Stuble, Fick, & Young, 2017; Young et al., 2017), resulting in less relevance to predicting restoration outcomes. This study is the first to establish communities using identical seed mixes over more than three planting years and to follow these communities for 5 years. This study is also the first to follow communities restored in average precipitation versus extreme drought year on a decadal timescale. In support of our hypotheses, we found evidence for year effects, and that planting year June/July precipitation was related to community composition. Coarse community metrics also corresponded to wet or dry establishment years in the 5th growing season. Community development over the longer term in prairies constructed under highly contrasting climate conditions corroborates results from the 5th restoration year and illuminates persistent outcomes of interannual variability in climate on restored plant communities.

Plant community composition changed dynamically in all sequences over 5 years. Despite differences in community development trajectories among sequences, the early compositional change in each sequence resulted from a shift in dominance from annual agricultural weeds to native sown perennial species. Most restored grasslands follow this general trajectory, with native perennials coming to dominate communities after the third growing season (Baer et al., 2003; Camill et al., 2004; Foster et al., 2011; Manning & Baer, 2018). The proliferation of one species, *Conyza canadensis*, in the second growing season caused community composition in all sequences to shift in a similar direction in the ordination space. Dominance by *C. canadensis* continued through the third growing season in the sequence restored during the drought of 2012, characterized by the hottest temperatures recorded since the Dustbowl of the 1930s (Rippey, 2015). Drought occurring at the onset of community assembly has been shown to delay the establishment of sown species and result in communities with distinct compositions (Groves & Brudvig, 2019; Manning & Baer, 2018). By including more planting years that spanned a wide range of establishment conditions, this study shows that distinct communities established among planting years (year effects) and composition is partly explained by planting year precipitation.

Consistent with our first hypothesis, compositional differences among sequences were attributed to variations in climate that occurred among planting years (Kreyling et al., 2011; Stuble, Fick, & Young, 2017; Stuble, Zefferman et al., 2017). Previously in this experiment, year effects were evident into the third year of community assembly, when communities were predominantly in the “weedy” successional state (Manning & Baer, 2018). Here, those initial compositional differences continued for 5 years, when communities were dominated by sown perennial species, indicating that variation in initial composition affects future composition. Furthermore, planting year precipitation was associated with coarse differences among communities. Specifically, communities assembled during drought contained higher forb cover than those assembled in wetter conditions. This suggests that stochastic events, such as interannual variability in planting year precipitation, may result in predictable outcomes for community assembly. While we attribute strong community differences to the variation in initial year conditions, interactions between stochastic and deterministic processes are likely to also play a role in the assembly of different communities (Chase & Myers, 2011; Yang et al., 2013). For example, the arrival of nonsown species from the regional species pool represents a stochastic process that was uncontrolled in this experiment and the early dominance of these volunteer species could impose priority effects (Fukami, 2015). While we demonstrate that climate explains a small amount of community variation, the inclusion of more planting years, longer term monitoring, and consideration of additional predictor variables will be necessary to predict the effect of planting year climate on community outcomes with greater certainty.

High levels of species richness have been shown to increase grassland resilience to drought (Isbell et al., 2015; Tilman et al., 2014), so knowledge of consequences of planting year climate on richness in subsequent years may aid in predicting future resilience of restored communities. Here, multiple communities established in years of low precipitation initially contained lower species richness that increased to levels higher than communities established in average or wet conditions. Drought in the establishment year also resulted in higher relative forb cover. In tallgrass prairie, forbs exploit water from deeper in the soil profile relative to grasses (Nippert & Knapp, 2007), which could promote community resistance to drought in the future. Although there has been descriptive evidence of climate-induced “forb years” and “grass years” in assembled communities (e.g., Pitt & Heady, 1978; Zavaleta et al., 2003), few controlled studies demonstrate this phenomenon. Wetter establishment conditions have been shown to favor grasses over forbs in California (Stuble, Fick, & Young, 2017), which can result in a priority effect that creates a historical contingency in community assembly (Werner et al., 2016; Young et al., 2017). Thus, understanding how climate alters the balance between the establishment of grasses and forbs will help to predict future coarse outcomes of community assembly.

In accordance with our second hypothesis, differences between communities assembled in average precipitation and drought conditions over the short term persisted on a decadal timescale. After the sixth growing season, communities established in 2010 (average precipitation) and 2012 (extreme drought) showed relatively little change in their respective ordination space, similar to the minor year-to-year variation observed in ungrazed, annually burned remnant grasslands (Fay et al., 2011; Nippert et al., 2006; Petrie et al., 2018). The small change in plant community structure after 6 years of establishment suggests that differences in plant communities due to initial precipitation are not transient and may persist for longer than a decade. In native grasslands, changes in ecological drivers (e.g., reduced fire frequency) can result in state changes that take decades to emerge (Baer et al., 2020; Gaiser et al., 2020; Ratajczak et al., 2014; Zinnert et al., 2021). This study suggests that state changes may emerge faster in response to variations in ecological drivers that occur at the onset of community development. Demonstrating long-term effects of variation in establishment year climate on communities suggests that stochastic events in the early stages of community assembly have deterministic outcomes for communities.

Despite using a different approach, our results corroborate findings from Groves et al. (2020) that showed planting year weather was related to coarse community outcomes. Groves et al. (2020) surveyed >80 restorations varying in age but sampled all restorations only at one time. Using repeated sampling, our study demonstrates that severe drought conditions during the establishment year created differences in coarse community metrics that persisted for most years of a decade. After the first year of restoration, species richness was consistently higher in the drought-established community. In both sequences, richness was highest in years 2–4, when both annual and perennial species were present, then declined to different levels in each sequence. In the absence of over-seeding, species richness has frequently been shown to decrease on a decadal scale as restored communities develop, a phenomenon attributed to an increase in C_4 grasses that outcompete less-abundant forb species (Baer et al., 2016; Camill et al., 2004; Sluis, 2002). In contrast with other restored prairies (Baer et al., 2016; Camill et al., 2004; Klopf et al., 2014), relative grass cover did not increase consistently over time in this study, probably due to the low ratio of grasses to forbs in the sown species pool reducing the potential for grass dominance. Instead, the decrease in species richness after 4 years of restoration resulted from the loss of many annual agricultural weeds as perennial species came to dominate (Willand et al., 2013). Despite the dynamic change in richness over time, prairie established during drought resulted in higher relative forb cover for most years in the first decade of community assembly. This study supports the counterintuitive suggestion that planting during drier years may help restore native (sown) species (Groves et al., 2020) and achieve the conservation goals of increasing biodiversity and ecosystem services promoted by biodiversity.

CONCLUSION

This study contributes to a growing body of inquiry about how interannual variability in climate influences grassland plant communities, with application to achieving conservation goals. Temporal variability in grassland community composition is often attributed to variability in climate (Adler & Levine, 2007; Bakker et al., 2003; Gherardi & Sala, 2015; Haddad et al., 2002; Ren et al., 2012), but the effects of initial (planting year) climate on developing communities is often neglected as a significant driver of community composition (Werner et al., 2020). As interannual variability in precipitation increases in the United States Midwest and beyond (IPCC 2019), knowledge of how establishment year conditions shape communities is applicable to achieving restoration goals. Our results indicate that short-term community composition is explained in part by planting year precipitation, and initial differences in community composition are not transient, indicated by decadal differences in assembled community states. We also found that drought promotes decade-long higher species richness and forb cover, two important components of biodiversity that can promote grassland resilience to drought (Isbell et al., 2015). One application of our findings is that general climate patterns (i.e., El Niño and La Niña events) might be used to anticipate restoration outcomes and adapt restoration methods to achieve different goals, for example, incorporating more forb seed under wet establishment conditions to suppress grass dominance and promote diversity (Klopf et al., 2014). Results from this study also suggest that staggering plantings over time (and space) could promote heterogeneity in a restored landscape, which is a unique attribute of remnant tallgrass prairie (Collins et al., 2018). Ultimately, this study demonstrates that establishment year climate influences the development of different community states over the short and long term, and suggests that (without human intervention) stochastic events at the onset of community establishment following long-term disturbance may have deterministic effects on community assembly.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

All data (Baer et al., 2022) are available in the Environmental Data Initiative (EDI) Data Portal at https://doi.org/10.6073/pasta/4e5864da4f6b28acb218b0c05d7bd1f7.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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