Interannual variability in climate effects on community assembly and ecosystem functioning in restored prairie

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Abstract. Community assembly theory attempts to explain factors influencing the composition of communities, which can be governed by deterministic and/or stochastic processes. We used a sequential restoration approach to gain insights into how interannual variation in climate influences community assembly in an agriculture field restored to tallgrass prairie. Species composition and aboveground net primary production (ANPP) were followed for three years in each of three sequentially restored communities, which were established in different years, and sown with the same suite of species using the same live seeding rate for each species. There was a sequence-by-age interaction for sown, volunteer, and total species composition (P = 0.001), cover (P < 0.009), diversity (P < 0.024), and richness (P < 0.025). Annual net primary production had a sequence-by-age interaction for total, sown, and volunteer species (P < 0.05). In general, species diversity and richness increased over time. We attributed different starting compositions and trajectories in the developing composition of communities and ANPP among sequences to variation in precipitation. Sequences II and III were sown under drought conditions and became dominated by a drought-resistant agricultural weed that corresponded with delayed establishment and lower ANPP of sown species in those sequences. This study suggests that the effects of drought on community composition vary depending on restoration year, with younger restorations exhibiting greater sensitivity to drought than those that are more established.

Key words: deterministic processes; diversity; prairie; productivity; restoration; stochastic processes.

INTRODUCTION

Community assembly theory attempts to explain factors influencing the richness and relative abundance of interacting species (Keddy 1992, Young et al. 2001, Heil 2004, Fukami 2010). If the local community is predictable under certain physical (environmental) and biotic conditions, community assembly is considered governed by deterministic processes. Alternatively, community assembly is considered governed by stochastic processes if species composition largely results from random processes influencing the dispersal and order in which species arrive (Heil 2004). One approach to elucidating deterministic vs. stochastic influences on community assembly is to follow community development subsequent to the introduction of the same species pool into sites under similar or varying environmental conditions in time or space (Bakker et al. 2003, Trowbridge 2007). An important application of knowing the relative influence of these processes on community assembly is predictability in achieving a target composition of species when restoring degraded environments.

Deterministic processes have been proposed to drive community assembly in harsh environments, where only a subset of species from the regional species pool can persist, whereas stochastic processes are proposed to play a larger role in...
community assembly where the majority of the regional species pool could theoretically persist (Chase 2007). Unpredictable events such as interannual variation in climate may change the relative influence of deterministic and stochastic processes on community assembly, particularly if they alter dispersal, arrival, and niche availability. Once species arrive, deterministic processes are presumed to influence germination, seedling establishment, and survivorship (Bakker et al. 2003), although priority effects can play a significant role in determining the trajectory of a developing community (Hobbs and Norton 2004, Young et al. 2015). Stochastic events like interannual variability in precipitation can complicate our ability to understand community assembly processes, as they can affect dispersal and conditions conducive to survival. This is particularly important in tallgrass prairie, an ecosystem that has been largely lost due to conversion to agriculture and as such is the focus of many restoration efforts in the U.S. Midwest, where climate is predicted to become more variable (Polley et al. 2013).

Extreme climatic conditions are stochastic events that influence community assembly processes (Thibault and Brown 2008) and ecosystem functioning, for example, aboveground net primary production (ANPP; Nippert et al. 2006). The Intergovernmental Panel on Climate Change (IPCC) has made predictions of longer dry periods in between precipitation events for many grassland ecosystems (IPCC 2007). More variable rainfall can change the composition of grassland communities in part by reducing soil moisture (Harper et al. 2005, Polley et al. 2013). This could represent a critical abiotic filter in communities establishing from seed like initial stages of prairie restoration (Harris et al. 2006) via differential seed emergence and survival (Walck et al. 2011). Tallgrass prairie exhibits resilience to drought through mostly vegetative reproduction and the presence of drought-adapted genotypes of dominant grasses (Avolio and Smith 2013). Because subordinate species contribute most to diversity, these species tend to be a focus of ecological restorations.

Ecological restorations have been used to reveal community assembly processes in grasslands (Bakker et al. 2003), abandoned agricultural land (Fukami et al. 2005), floodplain (Trowbridge 2007), lotic (Lepori and Malmqvist 2009), and lentic (Chase 2010) systems. We initiated three restoration sequences using the same methods at the same site, but in different years. We sampled plant communities for species composition and aboveground net primary productivity in each sequence for three consecutive years (resulting in a 7-yr study) to elucidate the influence of interannual climate variability on community assembly and ecosystem functioning. Because we relied on natural variation in environmental conditions, we developed hypotheses based on four possible scenarios. (1) If environmental conditions are similar over time, there are two potential outcomes: (i) If similar communities developed under these conditions, this would reveal the deterministic nature of community assembly; and (ii) if similar different communities develop, this would indicate stochastic processes (e.g., dispersal from the regional species pool) are largely influencing community assembly. (2) If different communities develop under similar environmental conditions, this would indicate stochastic processes (e.g., soil water availability, seed bank) largely influence community assembly. (3) If environmental conditions varied among years that communities were established, two possible outcomes would reveal different assembly rules: (i) Community development along similar trajectories despite different initial conditions would reveal the importance of deterministic processes, and (ii) community development along different trajectories would demonstrate sensitivity of community development to stochastic events (e.g., drought) and potential for different states to arise in response to variation to an ecological driver. In the latter case, deterministic processes (seed mix and site conditions) could still cause convergence over the longer term. (4) Lastly, we hypothesized that stochastic processes (interannual climate variability) can change the trajectory of community development, at least temporarily, by overriding deterministic influences (seed mix, soil type, and land-use history) to result in varying species composition and aboveground productivity.

**METHODS**

**Study site**

The sequential restoration experiment was initiated in 2010 at the Konza Prairie Biological Station (KBPS) and Long-Term Ecological Research
(LTER) site located 9 km south of Manhattan, Kansas, USA. Prior to cultivation, the field was representative of lowland native tallgrass prairie, dominated by warm-season (C₄) grasses (*Andropogon gerardii*, *Bouteloua curtipendula*, *Schizachyrium scoparium*, and *Sorghastrum nutans*) and interspersed with a diversity of forbs and other grasses (Abrams and Hulbert 1987). Soil at the restoration site is classified as a Reading silt loam, with 0–1% slope formed from alluvial and colluvial deposits. The region has a mean annual temperature of 12.7°C and receives 835 mm of precipitation annually on average.

The field used for all restoration sequences (sequence I: 2010; sequence II: 2012; and sequence III: 2014) was in conventional agriculture (primarily rotation between corn and soybeans, with occasional wheat and milo plantings) for >70 yr up to the time each sequence was installed. Prior to restoration, the soil in each sequence was shallowly disturbed with a field cultivator. In early June, four 20 x 20 m plots separated by a 5-m buffer were delineated in each sequence. Each 20 x 20 m plot was divided into four 10 x 10 m subplots for sampling purposes (A–D; Fig. 1). The last plot in sequence I was truncated to contain only two subplots due to shade imposed by a gallery forest.

### Restoration approach

Seed was hand-collected from Konza Prairie and other areas of native prairie in Riley County, Kansas. Locally collected seed was cleaned to remove large stems, leaves, and non-seed-containing flower parts. All seed was kept in dry storage. A subsample of each species was sent to the Illinois Crop Association to determine percent live seed calculated from purity, germination, and dormancy (% purity x [% germination + % dormancy]).

Species included in the seed mix and live seeding rates for each species were determined by amount and live seed collected in 2009, with the intention of sowing a 60:40 live seed ratio of forbs to dominant grasses. The same suite of species and live seeding rates for each species was used subsequently in each restoration sequence (Table 1). Due to very low germination and dormancy of

### Table 1. Species, life-form, and live seed amounts used in each sequential restoration.

| Species                        | Life-form | Live seeds per 20 m² |
|--------------------------------|-----------|----------------------|
| *Andropogon gerardii* Vitman. C₄ grass | 320       |
| *Andropogon gerardii* Vitman. var. KAW C₄ grass | 620       |
| *Bouteloua curtipendula* (Michx.) C₄ grass | 1100      |
| *Elymus canadensis* L. C₃ grass | 300       |
| *Panicum virgatum* L. C₃ grass | 200       |
| *Schizachyrium scoparium* (Michx.) Nash. C₄ grass | 20        |
| *Sorghastrum nutans* (L.) Nash. C₄ grass | 160       |
| *Amorpha canescens* Pursh. Subshrub legume | 440       |
| *Baptisia australis* (L.) R.Br. Legume | 60        |
| *Dalea candida* (Michx.) Willd. Subshrub legume | 440       |
| *Dalea multiflora* (Nutt) Shinn. Subshrub legume | 300       |
| *Dalea purpurea* Vent. Subshrub legume | 300       |
| *Desmanthus illinoensis* (Michx.) MacM. Subshrub legume | 500       |
| *Echinacea angustifolia* DC. C₃ forb | 40        |
| *Helianthus pauciflorus* (Nutt) C₃ forb | 220       |
| *Lespedeza capitata* Michx. Legume | 480       |
| *Liatris punctata* Michx. C₃ forb | 8         |
| *Oenothera macrocarpa* Nutt. C₃ Forb | 60        |
| *Oligomerum rigidum* (L.) Small var. rigidum C₃ forb | 40        |
| *Rosa arkansana* Porter. Subshrub | 120       |
| *Silphium integrifolium* Michx. C₃ forb | 420       |

Note: Nomenclature and life-form follow plants.USDA.gov.
A. gerardii collected in 2009, we supplemented the seed mix with a cultivar (var. KAW) and the same ratio of live hand-collected to purchased seed of A. gerardii was used in all subsequent restorations. Prior to sowing, each plot was hand-raked. Seed was applied by hand-broadcasting and then compacted (by lightly walking over) to promote soil–seed contact. Our restorations received no management during the first three years. Although fire is widely used to assist the establishment of restorations, there was not enough fuel in sequence I to carry a fire for the first three years, which determined the course of management for the subsequent sequences.

Plant composition, ANPP, and climate measurements
Species composition was recorded in August of each installation year and in June and August for two subsequent years in each sequence. Percent cover of each plant species was visually estimated in permanently located 10-m² circular areas in the center of each subplot. Percent cover was converted to modified Daubenmire categories (Carter and Blair 2012), and mid-range values and maximum cover in these categories for each species were used to calculate diversity (Simpson’s equitability: E) and analyze change in species composition over time. Tree seedlings were hand-pulled after being recorded.

Annual ANPP was determined by clipping all plants from two randomly placed 0.1-m² quadrats in each subplot at peak biomass (early September). Biomass was sorted into sown and volunteer forbs and grasses. Litter was sorted into current- and previous-year biomass. Biomass was dried (60°C) and weighed. Precipitation data were acquired for each year (2010–2016) from Konza Prairie retrieved from the National Centers for Environmental Information (NCDC 2016).

Data analysis
The composition of total species, volunteer species, and sown species was compared among sequence (SEQ) installation (A. SEQ I: 2010; B. SEQ II: 2012; C. SEQ III: 2014). Black bars indicate growing season months (May–August).

(Fig. 2. Continued)
sequences of the same age (established in different years) and over time within a sequence using permutational multivariate analysis of variance (PERMANOVA ver. 1.0.6, Primer-E, Aukland, New Zealand) in Primer (6.1.16; Clarke and Gorley 2006). PERMANOVA was chosen because of its power in detecting changes in community structure (Anderson and Walsh 2001). Convergence and divergence in community composition over time among sequences was indicated by lack or presence of interaction between sequence age and time, respectively. Community change over time was visually depicted using non-metric multidimensional scaling based on Bray–Curtis dissimilarities.

Cover, diversity, richness, and ANPP of all, sown, and volunteer species were analyzed for main effects and interaction between sequence and age using the mixed-model procedure in SAS (SAS Inst. 9.4). Plot was assigned as a random effect and year (response within a sequence over time) was treated as a repeated measure (α = 0.05). Log and square root transformations were applied where appropriate.

**RESULTS**

Precipitation received in the year when each sequence was installed (sequence I: 2010; sequence II: 2012; and sequence III: 2014) varied among and within years. In 2010, the annual precipitation approximated the long-term average (835 mm). Annual precipitation in 2012 and 2014 was 39% and 20% below that received in 2010. June precipitation was relatively similar in 2010 and 2014 (191 and 185 mm) and higher than that received in 2012 (116 mm). Further, June + July precipitation in 2012 and 2014 was 60% and 40% below that of 2010 (Fig. 2).

From 2010 to 2016, 140 species were identified in the sequences, of which 121 were volunteer species. *Liatris punctata* was the only sown species not to appear. In sequence I, 17 of the 20 (85%) sown species were recorded across all years, and 15 of the 20 (75%) sown species remained at the end of year 3. In sequence II, 18 of the 20 (90%) sown species were recorded across all years, and by the end of the third year, 18 of the 20 sown species remained. In sequence III, 14 of the 20 (70%) sown species were recorded across all years, and at the end of year 3, 14 of the 20 (70%) sown species remained.

There was a significant sequence-by-age interaction that affected total ($F_{4.24} = 15.40; P < 0.0001$), sown ($F_{4.24} = 32.00; P < 0.0001$), and volunteer ($F_{4.24} = 4.37; P = 0.009$) species cover (Table 2). *Sorghastrum nutans* was the dominant sown species in sequences I and III (20.6 and 54.5% cover, respectively), whereas *Helianthus pauciflorus* (10.6% cover) was the dominant sown species in sequence II three years post-sowing. *Eragrostis* spp. (91.7% cover) and *Abutilon theophrasti* (13.8% cover) were the dominant volunteer species in the initial restoration year for all sequences. *Conyza canadensis* was the dominant species in sequence I, sequence II, and sequence III (16.1, 25.9, and 72.2% cover, respectively) in the second year, but the amount of cover varied among the sequences.

The composition of communities varied among sequences over time. There was a

![Table 2. Total and proportional cover of total, sown, and volunteer species (± SE) in each sequence for three years.](image)

| Sequence | Age | Total cover ± SE | Sown cover ± SE | Volunteer cover ± SE | % Sown | % Volunteer |
|----------|-----|------------------|----------------|---------------------|--------|------------|
| I        | 1   | 84.25 ± 15.41 (a,x) | 12.32 ± 1.66 (a,x) | 71.94 ± 15.78 (a,x) | 14.62  | 85.38      |
| I        | 2   | 63.50 ± 8.41 (a,x)  | 36.47 ± 3.23 (b,x) | 27.03 ± 5.96 (b,x) | 57.43  | 42.57      |
| I        | 3   | 94.25 ± 4.88 (a,x)  | 78.88 ± 2.94 (c,x) | 15.38 ± 6.58 (b,x) | 83.69  | 16.31      |
| II       | 1   | 111.66 ± 8.13 (a,x) | 6.66 ± 0.11 (a,x)  | 111.00 ± 8.19 (a,y) | 0.59   | 99.41      |
| II       | 2   | 65.56 ± 15.50 (b,x) | 4.35 ± 0.74 (a,y)  | 61.22 ± 15.14 (b,y) | 6.64   | 93.36      |
| II       | 3   | 112.29 ± 8.09 (a,x) | 51.35 ± 4.31 (b,y) | 60.94 ± 10.07 (b,y) | 45.73  | 54.27      |
| III      | 1   | 107.94 ± 7.72 (a,x) | 3.97 ± 0.68 (a,x)  | 103.97 ± 7.48 (a,y) | 3.68   | 96.32      |
| III      | 2   | 237.07 ± 19.84 (b,y) | 134.85 ± 18.84 (b,z) | 102.22 ± 4.56 (a,z) | 56.88  | 43.12      |
| III      | 3   | 189.88 ± 8.47 (c,y) | 165.88 ± 7.39 (c,z) | 24.00 ± 6.38 (a,x) | 87.56  | 12.44      |

*Note: The first letter represents differences within a sequence at different ages, and the second letter represents differences among sequences at the same age.*
sequence-by-age interaction that affected sown (PERMANOVA: pseudo-F = 13.539; $P = 0.001$), volunteer (PERMANOVA: pseudo-F = 7.962; $P = 0.001$), and total (PERMANOVA: pseudo-F = 10.119; $P = 0.001$) species composition. PERMANOVA results for sown, volunteer, and total species composition showed differences among sequences of the same age and over time within a sequence (Fig. 3A–C). Each sequence had different initial total, sown, and volunteer species compositions, which contributed to each restoration traveling along different compositional trajectories through the third year. The restoration treatment trajectories progressed similarly but never completely converge or diverge.

There was a sequence-by-age interaction that affected total species diversity ($F_{4,24} = 31.36; P < 0.0001$) and richness ($F_{4,24} = 6.72; P = 0.0009$). When broken down into sown and volunteer species, there were also sequence-by-age interactions for diversity (sown: $F_{4,24} = 13.31; P < 0.0001$; volunteer: $F_{4,24} = 9.81; P = 0.0001$) and richness (sown: $F_{4,24} = 6.92; P < 0.0007$; volunteer: $F_{4,24} = 3.36; P < 0.0254$; Fig. 4A–F).

There was also a significant sequence-by-age interaction that affected total ($F_{4,18} = 13.47; P < 0.05$), sown ($F_{4,18} = 13.47; P < 0.0001$), and volunteer species ($F_{4,18} = 10.82; P = 0.0001$) ANPP. The temporal ANPP dynamics in sequence II resulted from a single volunteer species (Conyza canadensis [Canadian horseweed]) coming to dominance in the second year, then its subsequent decline during the third year. Sown ANPP for all sequences was highest during the third year. Furthermore, sown ANPP for sequences I and III was significantly higher than for sequence II during the third year (Fig. 5A). Volunteer ANPP peaked prior to the third year and was lowest during the third year in all sequences. The ANPP of volunteer species was highest in the first year following restoration in sequences I and III. However, the highest

![Fig. 3. Non-metric multidimensional scaling depiction of (A) sown, (B) volunteer, and (C) total species composition in the sequential restorations over time. Ellipses indicate significantly different composition between sequences of the same age (solid lines: age = 1; dashed lines: age = 3; ellipse not drawn for age = 2 for clarity). Different colors (gray, black, and white) represent the three sequences (I, II, and III), and the different shapes (triangle, square, and circle) represent the three ages (1, 2, and 3).](image-url)
Assembly rules are defined as general principles that influence membership of species occurrence in a community. To reveal whether community assembly is deterministic or stochastic or results in alternative stable states (Heil 2004), we supplied identical seed mixes to a site with similar soil conditions and land-use history over time. We relied on interannual climate variability to determine its role in the composition, trajectories of change, diversity, and functioning of developing tallgrass prairie. If community assembly is deterministic, then we expected subsequent restorations established under similar conditions to show similar composition and change in composition over time. The communities that established during this study, however, experienced varying environmental conditions during their establishment year, which enabled us to examine the effect of variation in precipitation on developing community structure and function, with implications for revealing the role of drought during establishment in the development of alternate stable states.

Disturbance plays a critical role in the community assembly process (Menninger and Palmer 2006). If all species have access to the community, then assembly trajectories should converge under similar environmental conditions (Chase 2003). However, during the course of this study, each restoration treatment experienced different environmental conditions (i.e., initial precipitation) following the addition of propagules. Most notable was the drought of 2012, which was reported by the USDA Economic Research Service as one of the most devastating and costly natural disasters in U.S. history (Mallya et al. 2013). The 2012 growing season was the warmest and driest growing season on record since 1936 and the Dust Bowl.
This resulted in varying establishment and initial composition of plant communities and their changing trajectories over time. We attributed this response to receiving sufficient precipitation for seed germination, as evidenced by similar ANPP at age 1 in each sequence, but differential establishment of species with varying tolerances to drought. For example, a drought tolerant volunteer species (C. canadensis) became dominant in SEQs II and III, which received 14% of July rainfall relative to July rainfall in SEQ I.

Whole community composition change over time suggests that the sequences follow a convergence-progression trajectory, which suggests that the community trajectories are becoming more similar over time (Matthews and Spyreas 2010). However, the composition of sown species exhibited a divergence-progression trajectory, which suggests that the communities of planted species are developing toward unique target communities with respect to the relative abundance of sown species (Matthews and Spyreas 2010). Thus, stochastic events can result in development of more than one compositional makeup of target species when the same composition of propagules is supplied. Although the trajectories of community development were different, diversity and richness converged, which could indicate increasingly similar niche dimensionality over time (Harpole and Tilman 2007).

Deterministic succession has been assumed to occur under similar abiotic conditions, and stochastic succession ensues when extreme or some other unpredictable event occurs, leading to alternate community development trajectories (Turner et al. 1998, Kreyling et al. 2011). Climate extremes have been shown to initiate stochastic succession lasting several years (Kreyling et al. 2011), which is further evidenced by the dissimilarity among the restored communities in response to average precipitation vs. drought total ANPP, (B) sown ANPP, and (C) volunteer ANPP. Shapes (triangle, square, and circle) represent different sequences (I–III). Differences among sequences within an age are indicated by a–c (vertically), and differences within a sequence among ages are indicated by x–z (horizontally). Means accompanied by the same letter were not significantly different ($\alpha = 0.05$).

Fig. 5. Main effects (mean ± standard error) for annual net primary productivity (ANPP) by age for (A)
conditions in this study. Furthermore, even disturbances that are relatively short-lived can leave a long-term legacy in an ecosystem and drive it toward alternate states (Scheffer and Carpenter 2003). If climate changes in the U.S. Midwest according to IPCC predictions, restoration outcomes could become even less predictable.

The results from this study suggest that the effects of drought on community composition during the early years of community establishment vary with community age. For example, younger communities exhibited greater sensitivity to drought than more established restored prairie. In fact, drought conditions in 2012 had no negative effect on species composition, diversity, richness, or ANPP in the oldest restored community, which was established in 2010. This stochastic event, however, likely contributed to the trajectories of community development in SEQs II and III that were divergent from that of SEQ I. Thus, establishment of more late successional (in this case, sown species) species in the first year increases the probability that a restoration treatment will develop on a desirable trajectory. When the establishment of later successional or sown species is prevented or delayed as the result of a stochastic event (e.g., drought), niches open for the establishment of volunteer species and can result in development of less desirable communities in the short term. We hypothesize that these states will be transient (unstable) as communities age and cumulatively share more of the same climate conditions and if the initially different conditions do not result in priority effects (Fukami 2010), which are difficult to document if not experimentally manipulated, or experience chronic disturbances (e.g., multiyear drought). Long-term studies that include more sequences initiated under contrasting precipitation conditions or a gradient of precipitation will ultimately reveal the predictability of the effect of stochastic events on community assembly and ecosystem functioning.

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