Received: 22 January 2024 | Revised: 22 July 2024 | Accepted: 16 August 2024

DOI: 10.1002/ecs2.70141

ECOSPHERE
AN ESA OPEN ACCESS JOURNAL

ARTICLE

Climate Ecology

Nitrogen enrichment drives accelerative effect of soil heterogeneity on the flowering phenology of a dominant grass

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Funding information
National Science Foundation,
Grant/Award Number: DEB-1922915

Handling Editor: Dawn M. Browning

Abstract

Plant phenology is affected by both abiotic conditions (i.e., temperature, nitrogen enrichment, and drought) and biotic conditions (i.e., species diversity). The degree of spatial heterogeneity in soil resources is known to influence community assembly and dynamics, but the relationship between resource heterogeneity and phenology or the potentially interactive effects of soil resources on phenology are less understood. We leveraged a tallgrass prairie restoration experiment that has manipulated soil nitrogen availability and soil depth over 20 years to test the effects of environmental heterogeneity, nutrient enrichment, and potentially interactive effects of global change drivers (nutrient enrichment and a drought manipulation) on the phenology of a highly dominant prairie grass (*Andropogon gerardii*). We recorded the timing of major developmental stages of *A. gerardii* in plots containing four soil heterogeneity treatments (control, soil depth heterogeneity, nutrient/depth heterogeneity, and nutrient/precipitation heterogeneity). We found that the boot, first spikelet, and emerged spikelet stages of *A. gerardii* occurred earlier in treatments with greater heterogeneity of soil nitrogen, and this effect was driven by the accelerative effect of nitrogen enrichment on phenology. Reduced precipitation increased the flowering length of *A. gerardii* but did not otherwise affect developmental phenology. There were no interactive effects among any soil resource treatments on phenology. These results advance our understanding of the relationship between plant phenology and global change drivers, which is important for understanding and predicting the timing of plant resource use and the provision of resources to higher trophic levels by plants under varying levels of resource availability.

KEYWORDS

Andropogon gerardii, big bluestem, drought, fertilization, grassland, nitrogen, restoration, tallgrass prairie

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INTRODUCTION

Plant phenology is an important indicator of the timing of resource availability and consumption in an ecosystem, and a critical area of inquiry for understanding how species and ecosystems are responding to global change. As plants transition through different stages of growth and reproduction, their demand for soil resources changes, as indicated by varying nutrient concentrations in biomass over a growing season (Gibson et al., 2016; Griffin & Jung, 1983). As a result, plant phenology can control dynamics of soil resources such as water and available nitrogen at the landscape scale (reviewed in Nord & Lynch, 2009). Further, differential productivity can mediate carbon cycling, evapotranspiration rates can affect hydrologic processes and potential for water runoff, and senescence affects nutrient translocation from above to belowground transformations via decomposition and mineralization (Gu et al., 2003). Plant development is responsive to environmental conditions. Rising average global temperatures and increased atmospheric CO_2 have shifted germination and flowering to occur earlier in the growing season for many species, extending the length of the growing season at scales ranging from one species to entire landscapes (Cleland et al., 2006; Hoover et al., 2012; Linderholm, 2006; Reed et al., 2019). Drought has been shown to advance flowering in some species while delaying it in others, and the effect of nitrogen enrichment similarly varies by species, with no consensus on single or interactive effects of these global change drivers (Biederman et al., 2017; Cleland et al., 2006; Jentsch et al., 2009; Nord & Lynch, 2009; Wolf et al., 2017). In addition to responding to abiotic conditions, changes in phenology have also been linked to levels of species diversity, where some species exhibit delayed flowering times in treatments of greater species diversity relative to monoculture (Wolf et al., 2017). The relationship between species diversity and phenology is poorly understood, but diversity could affect phenology if the presence of more species results in greater resource acquisition and/or use through niche complementarity (Loreau, 1998; Palmborg et al., 2005; Tilman et al., 1997). Though plant phenology is closely tied to soil resources, few studies have investigated the effect of heterogeneity in the distribution of soil resources or the potentially interactive effects of nitrogen availability and other soil resources on phenology (Cleland et al., 2006; Jentsch et al., 2009; Wolf et al., 2017). Moreover, knowledge of how global change drivers affect the phenology of foundation species is important because reproductive success and population dynamics of dominant species can determine diversity and ecosystem productivity (Collins & Calabrese, 2012; Grime, 1998; Hillebrand et al., 2008).

Andropogon gerardii (big bluestem) is a dominant perennial C_4 grass that can comprise the majority of aboveground biomass in the tallgrass prairie (Epstein et al., 1997). The initiation of flowering in *A. gerardii* marks a switch in resource allocation from vegetative growth, including the production of asexually reproductive belowground buds, to sexual reproduction ending in the production of seeds (Ott & Hartnett, 2011). Rates of establishment and growth of *A. gerardii* differ between asexual and sexual methods of reproduction (Willand et al., 2013). Understanding the timing of these distinct modes of reproduction under varying resource heterogeneity and availability regimes (including drought that is predicted to become more frequent in the central United States with future climate change; Sheffield & Wood, 2008) is relevant to predicting forage quality in rangelands (Gibson et al., 2016) and population dynamics and resilience of the tallgrass prairie ecosystem (Ott & Hartnett, 2011) in the face of global change.

The objective of this study was to quantify the effect of manipulated spatial heterogeneity in soil resources and two global change drivers (nitrogen and precipitation) on the phenology of *A. gerardii*. Phenology was measured in a long-term prairie restoration experiment containing four levels of soil heterogeneity (nutrient heterogeneity, depth heterogeneity, nutrient/depth heterogeneity, and control plots) that have been maintained since 1998. Heterogeneity treatments have effectively increased spatial variation in plant rooting depth, inorganic nitrogen availability, and aboveground productivity relative to plots without soil manipulations for more than two decades (Baer et al., 2003, 2016, 2020). Long-term monitoring has also revealed reduced dominance of *A. gerardii* and a corresponding increase in species diversity in nitrogen-enriched subplots of the nitrogen/depth heterogeneity after 20 years of treatment (Baer et al., 2016, 2020; Figure 1), a pattern maintained in the 2021 growing season (A. Wojciechowski and S. Baer, *unpublished data*). A rainfall interception treatment was added to the nutrient heterogeneity plots in 2020 to assess the interactive effects of two global change drivers, nitrogen availability and precipitation, on restored grassland communities. This long-term experimental restoration was used to test the following hypotheses: (1) the start dates of *A. gerardii* life stages would occur later where increased soil resource heterogeneity has increased species diversity (i.e., Wolf et al., 2017); (2) nitrogen enrichment and reduced precipitation would advance *A. gerardii* flowering (Biederman et al., 2017; Jentsch et al., 2009; Power et al., 2006); and (3) reduced precipitation would dampen the effect of nitrogen enrichment in combination, lessening the accelerative effect on flowering (Bloor et al., 2010).

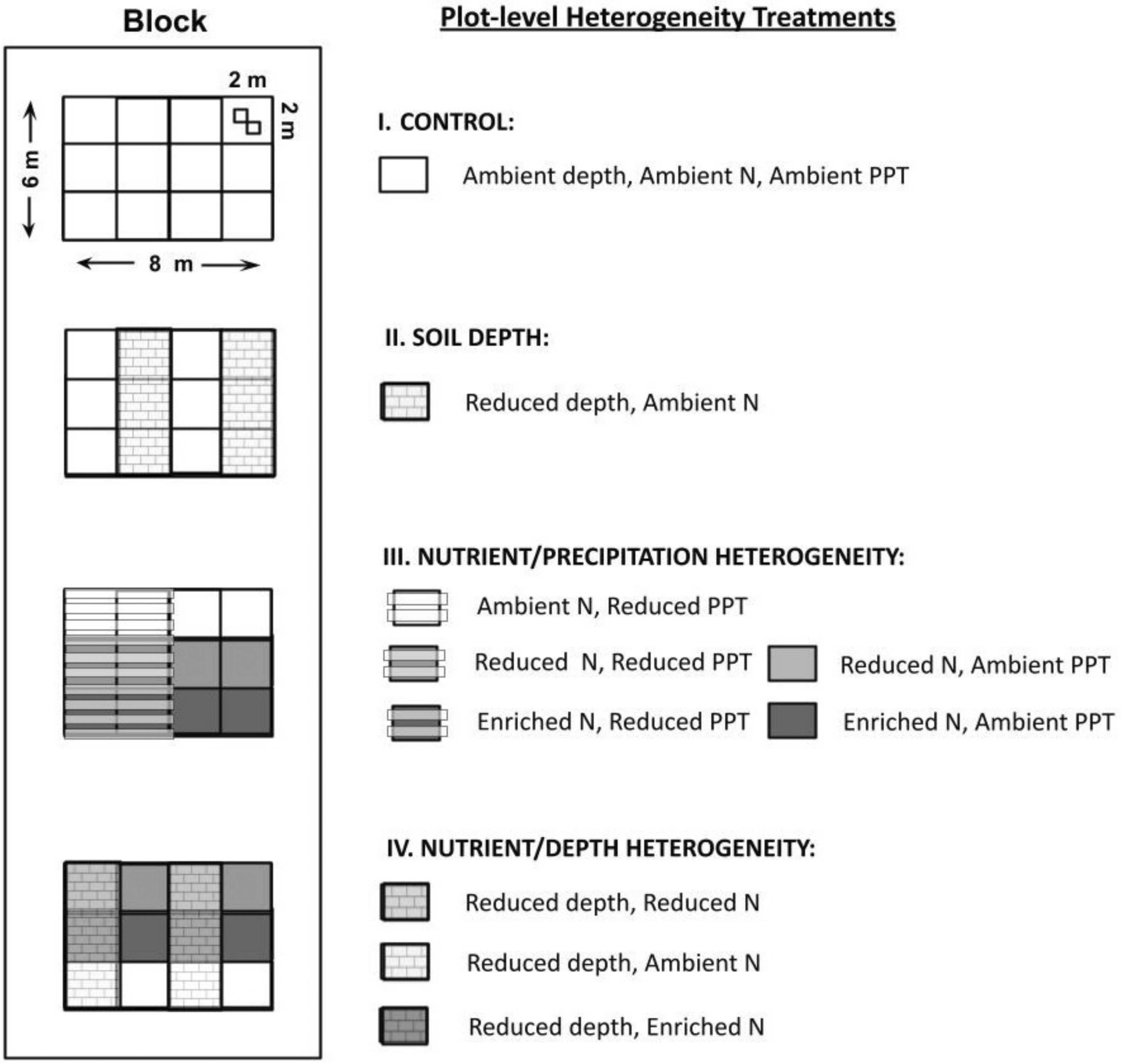

FIGURE 1 Plot and subplot-level experimental treatments. Each plot was divided into twelve 2 m × 2 m subplots for sampling, with each subplot containing two 0.25-m^2 quadrats for sampling. Subplot-level treatments consisted of three 2 m × 8 m strips assigned to reduced, ambient, or enriched N, alternating 2 m × 6 m strips assigned to deep or shallow soil, and a half-plot (4 m × 6 m) reduced or ambient precipitation treatment. Plot-level heterogeneity treatments of nutrient/depth, nutrient/precipitation, soil depth, and control were randomly assigned within each of four blocks ($n = 4$ per treatment, 16 plots total). Nutrient/depth heterogeneity treatment contained subplot-level manipulations of soil nitrogen and soil depth, nutrient/precipitation heterogeneity treatment contained subplot-level manipulations of soil nitrogen and precipitation, and soil depth heterogeneity treatment contained subplot-level manipulations of soil depth.

MATERIALS AND METHODS

Study site

The restoration experiment is located in a former agricultural field within the Konza Prairie Biological Station (KPBS) in the Flint Hills of northeastern Kansas, USA (39°05′ N, 96°35′ W). Annually burned lowland plant communities at KPBS are dominated by four C_4 grass species (*A. gerardii*, *Sorghastrum nutans*, *Panicum virgatum*, and *Schizachyrium scoparium*), and most diversity is contributed by the >300 subordinate forb species occurring throughout the site. Prior to restoration, the field was cropped continuously for over 50 years. The soil in the restoration site is classified as Reading silt loam (mesic Typic Argiudoll). KPBS has a 30-year average (1989–2019) annual precipitation of 835 mm and an average annual temperature of 13°C (Nippert, 2024a, 2024b). Mean average precipitation in 2021 was 632 mm, of which 424 mm was received during the growing season (April through September).

In 1998, all plots were sown with 42 native prairie species using a log-normal distribution of dominant grasses and subordinate forbs to resemble never-cultivated tallgrass prairie. In 2005, seeds of 15 additional forb species were sown into all plots at a rate of 25 live seeds/m^2 (Baer et al., 2016). Beginning in 2013, seeds of 17 additional species (14 forbs, 2 grasses, and 1 sedge) that occur at KPBS were added to all plots for five consecutive years. The experimental area has been burned almost annually in the early spring since 2003 (Baer et al., 2020), a common management practice in this region especially for suppressing the growth of woody species (Briggs et al., 2005; Collins et al., 2021).

Experimental design

In 2021, a phenology survey of *A. gerardii* was conducted across four soil heterogeneity treatments ($n = 4$ each) assigned to plots according to a randomized complete block design. A total of 16 plots (6 m × 8 m) were assigned to four blocks. Within each block, plots were randomly assigned to one of four heterogeneity treatments: soil depth heterogeneity, nutrient/depth heterogeneity, nutrient/precipitation heterogeneity, or control treatment. All plots were further divided into twelve 2 m × 2 m subplots, each containing two 0.5 m × 0.5 m permanent sampling quadrats. Heterogeneity treatments were produced by combinations of up to two subplot-level treatments. Plots assigned to the soil depth heterogeneity treatment contained alternating 2 m × 6 m strips of deep and shallow soil (three subplots/strip). The shallow soil subplot treatment was achieved by excavating soil to a depth of 20–25 cm and burying pieces of rough-cut limestone slabs prior to the initial planting in 1998. Plots assigned to the nutrient/depth heterogeneity treatment contained 2 m × 8 m strips of reduced nitrogen, ambient nitrogen, and enriched nitrogen soil (four subplots/strip) assigned perpendicular to 2 m × 6 m strips of deep and shallow soil (three subplots/strip). This produced a 2 × 3 factorial combination of soil depth and nutrient availability, resulting in two subplot replicates for each of the six nitrogen and depth treatment combinations. Reduced N was achieved by initially adding sawdust to reduce N availability and effectively immobilized N. Starting in 2005, reduced N treatment has been maintained by applying 84.2 g C/m^2 (sucrose-C) three times per growing season. Elevated-N was achieved by adding 5 g N/m^2 in the form of NH_4-NO_3 in early June every year since 1998. Plots assigned to the nutrient/precipitation heterogeneity treatment consisted of 2 m × 8 m strips of reduced nitrogen, ambient nitrogen, and enriched nitrogen soil (four subplots/strip) assigned perpendicular to 4 m × 6 m strips of ambient precipitation and reduced precipitation (six subplots/strip), resulting in two subplot replicates of each nitrogen and precipitation treatment combination. Reduced precipitation was achieved using rainout shelters. Rainout shelter roofs were made of clear polycarbonate slats spaced to exclude 66% of incoming precipitation and minimally shade. Similarly constructed rainout shelters reduce photosynthetically active radiation (PAR) by less than 10% (Yahdjian & Sala, 2002). Rainout shelters were erected in May and removed in October in 2020 and 2021. Rainout shelter effect on PAR was measured above and below shelters in June 2021 using a 50-cm ceptometer (Decagon Devices, Pullman, Washington, USA). The presence of rainout shelters reduced yearly average light availability by 12.4%.

Resource heterogeneity

Efficacy of the subplot treatments was assessed by measuring inorganic soil nitrogen availability in all subplots and soil moisture in subplots of the nutrient/precipitation heterogeneity treatment. Gravimetric water content was measured in nutrient/precipitation heterogeneity treatments every 2–3 weeks after rainout shelter installation. One 2-cm diameter soil core was taken to a depth of 20 cm between the two replicate subplots of each treatment combination in each plot. Soil cores were homogenized through a 4-mm sieve. A 20-g sample of soil was weighed, dried at 105°C for at least 48 h, and reweighed. Inorganic nitrogen availability in the form of nitrate was measured using buried ion exchange resins (Binkley & Matson, 1983). Nylon bags containing 10 g of strongly basic anion exchange resins (Dowex 1X8-100) were buried in the top 10-cm of soil in May and harvested in September of 2021. Following retrieval, resin bags were washed with deionized water then extracted with 75-mL of 2N KCl on an orbital shaker at 200-rpm for one hour (Baer & Blair, 2008). Each extraction was filtered through a 0.4-m polycarbonate membrane filter. Extracts were analyzed for NO_3-N concentration on an OI Analytical FS3700 Automated Flow Solution Analyzer using diazotization of sulfanilamide after reduction of nitrate to nitrite through a cadmium coil (Keeney & Nelson, 1982).

Species composition and phenology

Phenology life stage observations of *A. gerardii* were conducted weekly during the growing season of 2021 from May through November. Start date (Julian day) was the date of the first observation of each life stage within two 0.25-m^2 permanent sampling quadrats in each

2 m × 2 m subplot ($n = 24$ per plot). Four stages of perennial grass phenology defined by Moore et al. (1991) were used to categorize *A. gerardii* phenology: boot (flowering structure begins to develop, marking the start of reproduction), first spikelet (first full emergence of flowering structure), emerged spikelet (all flowering structures fully emerged), and anthesis (anther emergence). Observations of first leaf, caryopsis (production of seed), and senescence stages were also noted but analyses were not performed because these stages were observed on the same Julian day for all plants. Flowering length was calculated as (Julian date of anthesis–Julian date of first spikelet) in order to capture entire flowering length from the emergence of the first spikelet through the last date of spikelet persistence (González-Suárez et al., 2020). The maximum percent cover of *A. gerardii* was observed in each subplot during early September 2021.

Statistical analyses

Mean start date (Julian day), flowering length, resin-collected NO_3-N, soil moisture, and percent grass cover were analyzed for both heterogeneity treatment and subplot-level treatment main effects and interactions. Shapiro's test for normality was performed for each variable, and data were log-transformed if not normally distributed before statistical analysis. We used mixed models, with block assigned as a random effect, to determine whether plot-level heterogeneity treatment affected timing and variation for each of the four phenology stages, flowering length, and grass cover, followed by the least squares mean comparison procedure. Main effects and interactions of the subplot treatments were analyzed separately within each heterogeneity treatment. The soil depth heterogeneity treatment was analyzed as a strip-plot design, with strips assigned to each depth level treated as a random effect. The nutrient/precipitation heterogeneity treatment was analyzed according to a split-block design, with nutrient levels assigned to horizontal strips and precipitation levels assigned to adjacent vertical strips treated as random effects. The nutrient/depth heterogeneity treatment was also analyzed as a split-block design, with nutrient levels assigned to horizontal strips and depth assigned to alternating vertical strips treated as random effects (Baer et al., 2003). Satterthwaite's method of calculating degrees of freedom was used for all subplot treatment analyses. All mixed model tests were performed using the lmerTest package in R and post hoc tests were performed using the emmeans package in R (v4.2.1, Lenth, 2017; R Core Team, 2022). Significance was assigned at $\alpha = 0.05$.

RESULTS

Treatment effectiveness

Heterogeneity treatment at the plot level effectively increased heterogeneity in soil resources. Heterogeneity in soil nitrogen availability, measured as the coefficient of variation in resin-collected soil nitrate (NO_3-N), was greater in nutrient/depth heterogeneity and nutrient/precipitation heterogeneity treatments than in the control treatment (Appendix S1: Table S1). Subplot-level treatments also effectively altered resource availability. Nitrogen-enriched subplots had higher average resin-collected NO_3-N than ambient and reduced nitrogen subplots (Appendix S1: Table S1). Average percent soil moisture was significantly lower under the rainout shelters for 7 of 11 sampling dates (Appendix S1: Figure S1).

Focal species cover

A. gerardii was present in 99% of subplots and all plots. No significant differences in grass percent cover were detected among heterogeneity treatments (plot level) or between nitrogen or precipitation treatments (subplot-level) (Appendix S1: Table S2).

Plot-level heterogeneity effects on phenology

Heterogeneity treatment affected the timing of reproductive phenology. Average start date of the boot ($F_{3,9} = 5.6$, $p = 0.019$), first spikelet ($F_{3,9} = 6.5$, $p = 0.013$), and emerged spikelet ($F_{3,12} = 4.1$, $p = 0.033$) stages was earlier in the nitrogen/precipitation heterogeneity treatment than control treatment (Figure 2). The nitrogen/precipitation heterogeneity treatment accelerated the average start date of the boot stage by 3.0 days relative to the control treatment and by 2.8 days relative to the nitrogen/depth heterogeneity treatment. The nitrogen/precipitation heterogeneity treatment also accelerated the average start date of the first spikelet stage by 4.9 days and the average start date of the emerged spikelet stage by 4.5 days relative to control (Figure 2). The soil depth and nitrogen/depth treatments were not significantly different from the control treatment for any life stage. Heterogeneity treatment had no effect on flowering length (Figure 2).

Subplot-level nutrient, soil depth, and drought effects

There was a main effect of nitrogen within the nitrogen/depth heterogeneity treatment (Figure 3). Across both

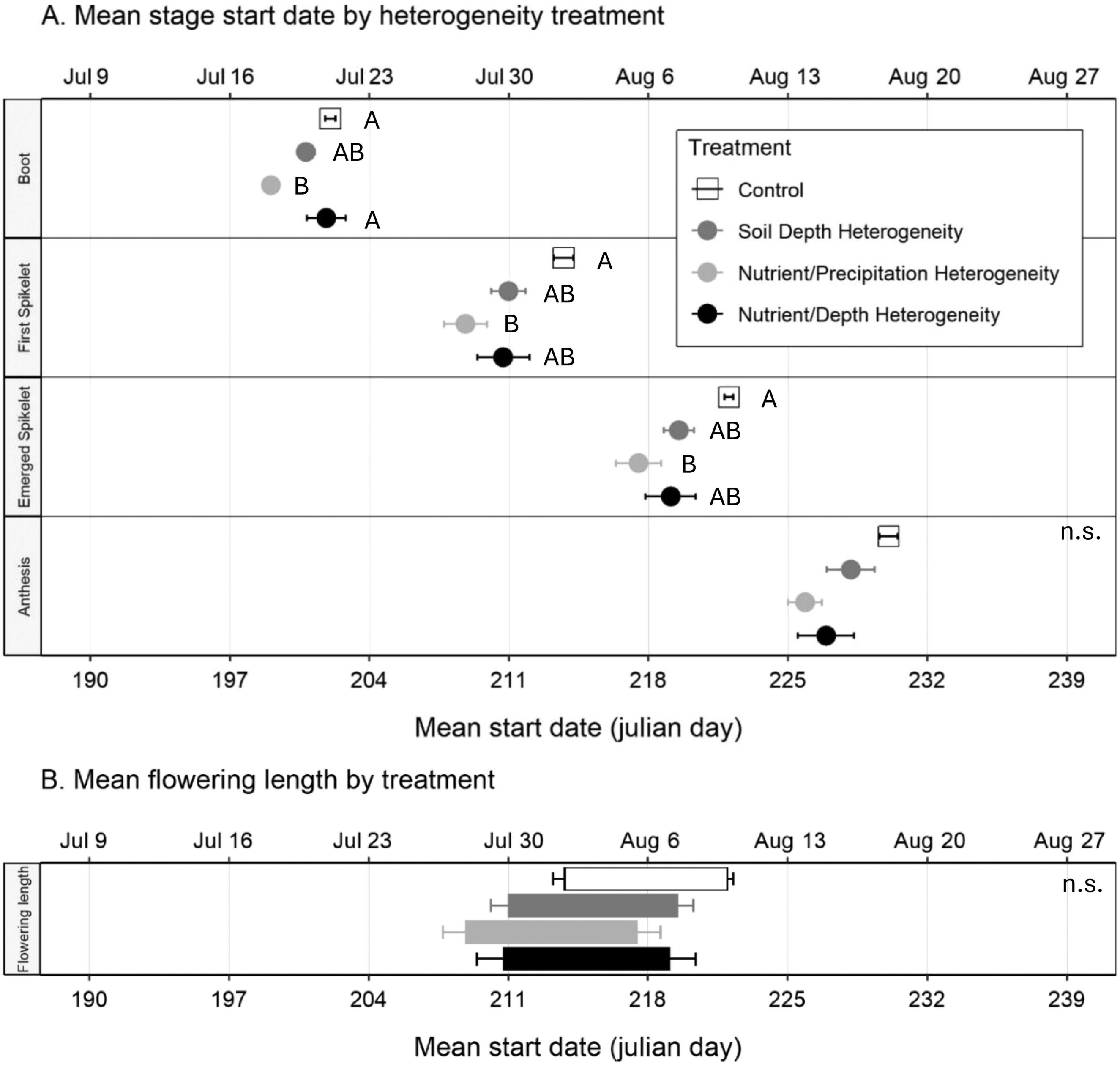

FIGURE 2 Effects of plot-level heterogeneity treatment on (A) start date (Julian day, mean ± SE) of four phenology stages and (B) average flowering length (days, mean ± SE).

levels of soil depth, nitrogen enrichment accelerated the average start date of the boot ($F_{2,22} = 5.2$, $p = 0.014$), first spikelet ($F_{2,26} = 11.1$, $p < 0.001$), emerged spikelet ($F_{2,26} = 13.2$, $p < 0.001$), and anthesis ($F_{2,24} = 14.3$, $p < 0.001$) stages. Nitrogen enrichment accelerated the average start of the emerged spikelet and anthesis stages by 7.2 and 7.8 days, respectively, relative to soil with ambient nitrogen. Nitrogen enrichment accelerated the boot, first spikelet, emerged spikelet, and anthesis stages by 4.0, 8.0, 8.7, and 9.7 days, respectively, relative to soil with reduced nitrogen (Figure 3). There were no significant differences in phenology between the ambient and reduced nitrogen treatments. Notably, nitrogen availability was also not significantly different between these treatments (Appendix S1: Table S1). There were no significant interactions between nitrogen and depth on the phenology of *A. gerardii* in the nutrient/depth heterogeneity treatment, nor was there an effect of depth in the nitrogen/depth heterogeneity or soil depth heterogeneity treatments.

Precipitation regime had no effect on the timing of any life stages of *A. gerardii*; however, reduced precipitation

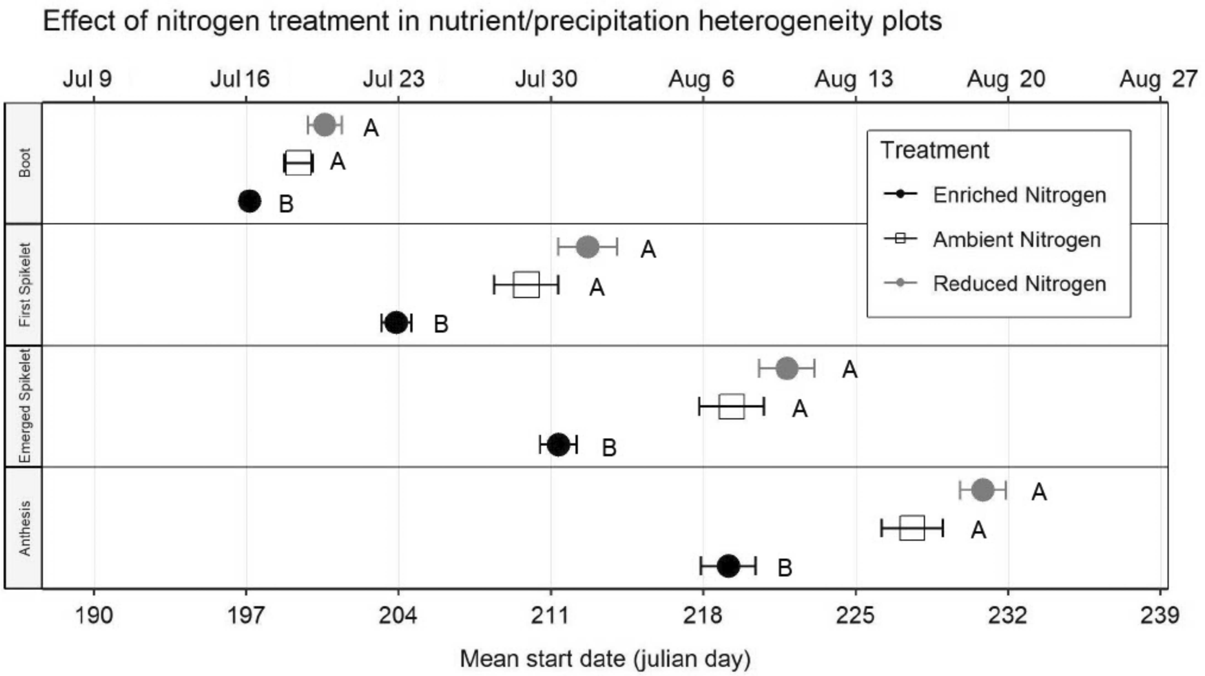

FIGURE 3 Effects of soil nitrogen subplot treatment on start date (mean ± SE) of four phenology stages within nutrient/precipitation heterogeneity plots. Means accompanied by the same letter were not significantly different (α = 0.05; n.s., no significant difference among all comparisons).

increased average flowering length by 4.5 days compared with the ambient precipitation treatment ($F_{1,42} = 16$, $p < 0.001$; Figure 4). Within the nitrogen/precipitation heterogeneity treatment, nitrogen enrichment accelerated the average start date of the boot ($F_{2,9} = 8.3$, $p = 0.009$), first spikelet ($F_{2,9} = 11.7$, $p = 0.003$), emerged spikelet ($F_{2,6.7} = 14.1$, $p = 0.004$), and anthesis ($F_{2,9} = 19.3$, $p = 0.001$) stages for both ambient and reduced precipitation treatments. Nitrogen enrichment accelerated the average start date of the boot stage, first spikelet, emerged spikelet, and anthesis stages by 2.2, 6.0, 8.0, and 8.5 days relative to soil with ambient nitrogen, respectively, and 3.5, 8.8, 11.0, and 12.0 days relative to the reduced nitrogen treatment, respectively (Figure 5). Similarly to the nitrogen/depth heterogeneity treatment, nitrogen availability was not significantly different between reduced and ambient nitrogen treatments, and there were no significant differences in phenology between the ambient and reduced nitrogen treatments (Appendix S1: Table S1). There were no significant interactive effects of nitrogen and precipitation on the phenology of *A. gerardii* in the nitrogen/precipitation heterogeneity treatment.

DISCUSSION

This study explored the phenology of a dominant grass species in response to variation in the environment. We examined the effect of spatial heterogeneity in two global change drivers, nitrogen enrichment and drought, and soil depth on the phenology of the flagship species of tallgrass prairie. We observed an effect of heterogeneity on the development of *A. gerardii*, but only where heterogeneity resulted from variation in soil nitrogen availability. Heterogeneity induced by varying nitrogen availability produced an overall accelerative effect on *A. gerardii* phenology, driven by the consistent accelerative effect of nitrogen enrichment on phenology. Consistent with our predictions, phenology of *A. gerardii* was accelerated in response to nitrogen enrichment and inducing drought increased the length of flowering. In contrast to our predictions, inducing drought did not advance phenology, and the observed effect of soil nitrogen had no interaction with precipitation.

Spatial heterogeneity in soil resources affected the phenology of *A. gerardii*, but not consistently across heterogeneity treatments. We hypothesized that development of *A. gerardii* in the nutrient/depth heterogeneity treatment would be delayed compared with homogeneous control plots because peak flowering dates can occur later in more diverse species assemblages (Cleland et al., 2006; Wolf et al., 2017). Despite that the nutrient/depth heterogeneity treatment has been observed to contain higher plant species diversity than the control treatment (Baer et al., 2020, A. Wojciechowski, *unpublished data*), there was no difference in phenology in this treatment

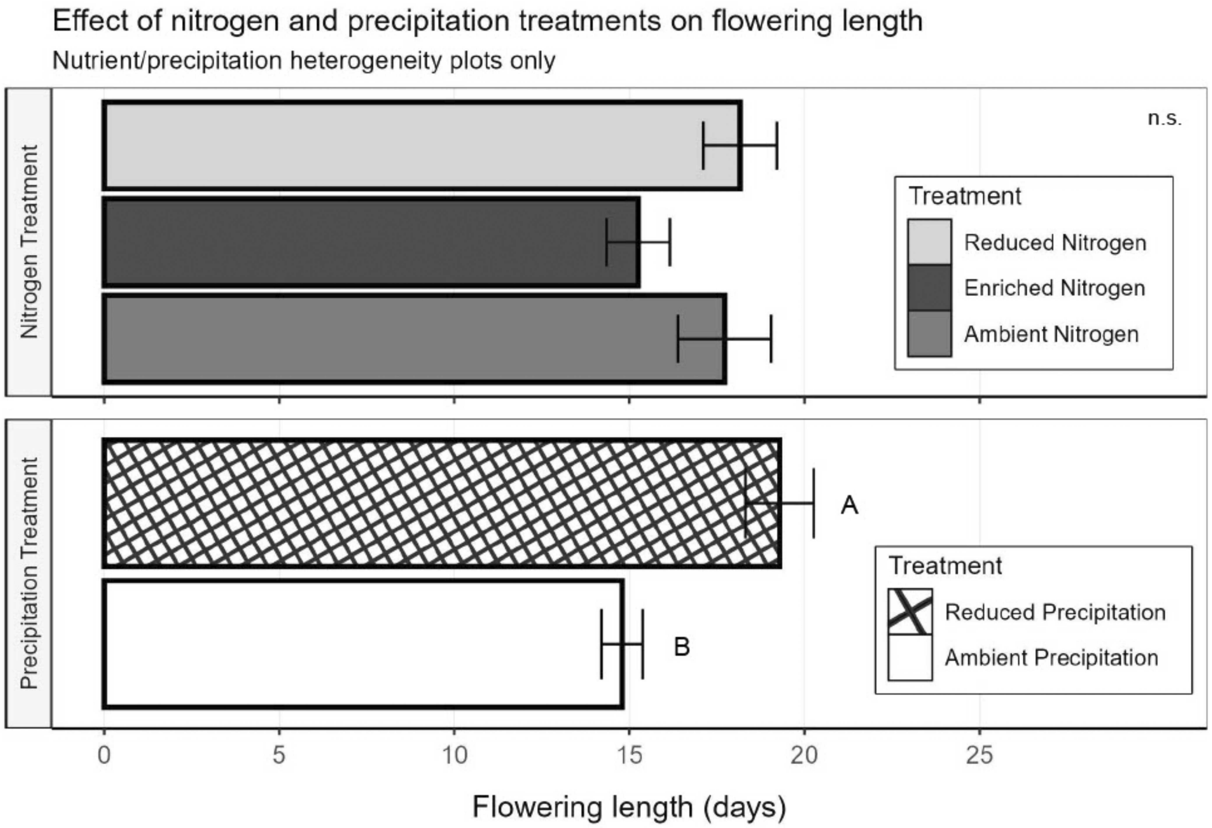

FIGURE 4 Effects of soil nitrogen treatment and reduced precipitation treatment on flowering length within nutrient/precipitation heterogeneity plots. Means accompanied by the same letter were not significantly different (α = 0.05; n.s., no significant difference among all comparisons).

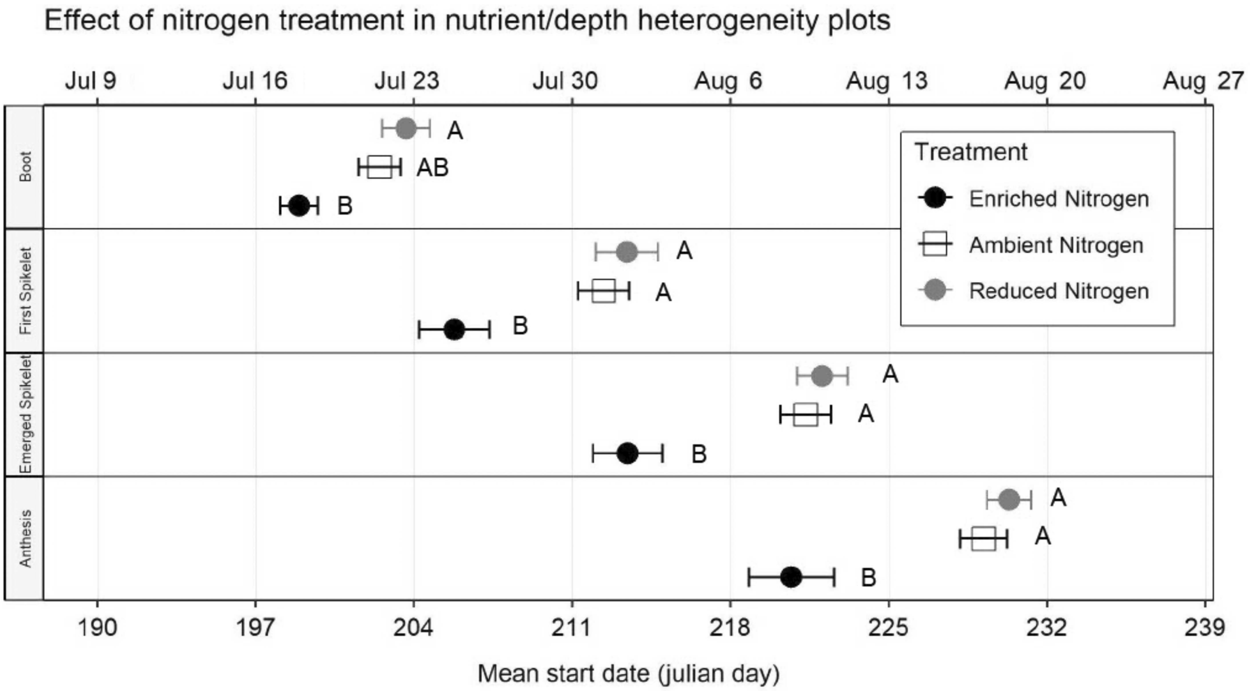

FIGURE 5 Effects of soil nitrogen treatment on start date (mean ± SE) of four phenology stages within nutrient/depth heterogeneity plots. Means accompanied by the same letter are not significantly different (α = 0.05; n.s., no significant difference among all comparisons).

compared with homogeneous soil. Nitrogen enrichment has been shown to advance phenology in grassland communities (Biederman et al., 2017), and phenology was indeed accelerated in the nutrient/precipitation heterogeneity treatment, driven by the accelerative effect of nitrogen enrichment in deep soil. However, this effect was not seen in the nutrient/depth treatment. We conclude that heterogeneity in soil nitrogen and soil depth begets greater heterogeneity in phenology without a directional effect on the timing of growth and reproduction.

Though only the nutrient/precipitation heterogeneity treatment had distinct phenology from the control treatment at the plot level, the accelerative effect of nitrogen enrichment at the subplot level was consistent across the nutrient/precipitation heterogeneity and nutrient/depth heterogeneity treatments. In both heterogeneity treatments containing altered nitrogen, enrichment accelerated the start dates of four reproductive stages: the boot, first spikelet, emerged spikelet, and anthesis stages. Throughout the growing season, the extent of acceleration increased with each successive life history stage. Results among plant phenology experiments that manipulate soil nitrogen vary widely among ecosystems and species, and few studies of the phenological response to nutrient enrichment have been conducted in tallgrass prairie. Our finding that nitrogen enrichment advances *A. gerardii* phenology supports previous work showing that nitrogen enrichment advances community-level prairie phenology by increasing relative cover of early (May–June) flowering species and decreasing that of late (September–October) flowering species (Biederman et al., 2017).

The observed accelerative effect of nitrogen enrichment on phenology here contrasts with a previous finding that nitrogen enrichment delayed flowering in grasses in a Mediterranean grassland (Cleland et al., 2006). This suggests that the relationship between soil nitrogen and phenology must be considered within the context of limiting nutrients in the ecosystem, and of species' nitrogen use. Grasslands in the central United States are nitrogen-limited (Blair, 1997), whereas Mediterranean grasslands are limited by water availability. Furthermore, central United States grasslands are dominated by C_4 grass species, including *A. gerardii*, which are characterized by more efficient nitrogen and water use than the C_3 species that dominate Mediterranean grasslands. In an ecosystem context of nitrogen limitation, we observed that abundant nitrogen caused accelerated flowering in a species characterized by efficient nitrogen use, perhaps suggesting an acceleration of overall development. In contrast, in a grassland in which nitrogen is not typically limiting, and in low nitrogen use efficiency species, abundant nitrogen caused species to delay the switch from vegetative to reproductive growth (Cleland et al., 2006).

In contrast to our prediction that drought would advance development of *A. gerardii*, reduced precipitation had no effect on the average start date of life stages. Instead, reduced precipitation, coinciding with lower soil moisture, increased overall flowering length. Early reproduction is considered part of the dehydration escape strategy (Volaire, 2018), and drought has been found to advance the flowering period of grassland species by an average of four days and increase flowering length by the same amount of time (Cleland et al., 2007; Jentsch et al., 2009). Mid-summer (mid-June) drought has been observed to advance the phenology of the population as a whole and reduce the rate of late-season flowering up to 94% (Dietrich & Smith, 2016). In considering potential interactive effects between nitrogen and drought, we expected that reduction in soil moisture would reduce mineralization and passive delivery of nitrogen to plants, dampening the effect of nitrogen addition on phenology. Further, we predicted that drought and lower soil nitrogen availability would serve as co-limiting resources to exaggerate the advance in *A. gerardii* reproduction. However, there was no interactive effect of precipitation and nitrogen treatment on the flowering length or timing of *A. gerardii* phenology.

In the context of differences in asexual and sexual methods of population regeneration (Willand et al., 2013), the observed advance in *A. gerardii* phenology in response to nitrogen enrichment could explain reduced dominance observed in this population after 16–20 years following nitrogen enrichment in combination with addition of propagule of new species (Baer et al., 2020). *A. gerardii* primarily reproduces through asexual, vegetative buds (Dalgleish & Hartnett, 2009). Only some tillers make the transition to aboveground sexual reproduction, or flowering (boot, first spikelet, emerged spikelet, and anthesis stages), at which point individuals cease to produce belowground buds, and some of these asexually produced buds initiate growth. While reproductive tillers of *A. gerardii* produce buds that are more successful at establishing new growth, vegetative tillers produce asexual buds for a longer proportion of the growing season and contribute more to the dormant bud bank from year to year (Ott & Hartnett, 2011). The dormant bud bank ensures resilience of *A. gerardii* to regular disturbance such as fire. If nitrogen enrichments advanced transition of some tillers to sexual reproduction, the resulting reduction of the dormant bud bank over time, in combination with regular (annual) fire disturbance, may have produced the observed reduced dominance of *A. gerardii* in the enriched nitrogen treatments (Baer et al., 2016, 2020). Further and more direct study is needed to link *A. gerardii* physiology to phenology, and patterns of dominance. Nonetheless, this observation illustrates the potential role of phenology in connecting physiology to community-scale processes.

Ultimately, our findings demonstrate a link between spatial and temporal dimensions of resource management in tallgrass prairie restoration. The effect of nitrogen enrichment in advancing the phenology and reduced precipitation in increasing flowering length of this dominant C_4 grass in tallgrass prairie can inform management strategies for optimizing forage production (Gibson et al., 2016). Importantly, better understanding of the effects of global change drivers on soil nitrogen and moisture contributes to understanding of grassland dynamics as the global climate changes (Zhou et al., 2022).

ACKNOWLEDGMENTS

This research was conducted in partial fulfillment of an undergraduate Honors thesis in the Department of Ecology & Evolutionary Biology at the University of Kansas and supported by a grant from the National Science Foundation (DEB-1922915). We thank Nathaniel Weickert for his assistance with seedling identification. This study took place on the unceded ancestral territory of Indigenous peoples who stewarded the land since time immemorial.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Krause et al., 2024) are available from Dryad: https://doi.org/10.5061/dryad.rn8pk0pn7.

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SUPPORTING INFORMATION

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

How to cite this article: Krause, Anna G., Ashley A. Wojciechowski, and Sara G. Baer. 2025. "Nitrogen Enrichment Drives Accelerative Effect of Soil Heterogeneity on the Flowering Phenology of a Dominant Grass." *Ecosphere* 16(1): e70141. https://doi.org/10.1002/ecs2.70141