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ARTICLE

Climate Ecology

Grassland management actions influence soil conditions and plant community responses to winter climate change

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Abstract

Restoring ecosystems in a changing climate requires understanding how management interventions interact with climate conditions. In tallgrass prairies, disturbance through fire, mowing, or grazing is a critical force in maintaining herbaceous plant diversity. However, unlike historical fire regimes that occurred throughout the growing season, management actions like prescribed fire and mowing are commonly limited to the spring or fall seasons. Warming winters are resulting in less snow, causing overwintering plants to experience reduced insulation from snow and these more extreme winter conditions may be exacerbated or ameliorated depending on the timing of management actions. Understanding this novel interaction between the timing of management actions and snow depth is critical for managing and restoring grassland ecosystems. Here, we applied experimental management treatments (spring and fall burn and fall mow) in combination with snow depth manipulations to test whether the type and timing of commonly implemented disturbances interact with snow depth to affect restored prairie plant diversity and composition. Overall, snow manipulations and management actions influenced soil temperature while only management actions influenced spring thaw timing. Burning in the fall, which removes litter prior to winter resulted in colder soils and earlier spring thaw timing. However, plant communities were mostly resistant to these effects. Instead, plants responded to management actions such that burning and mowing, regardless of timing, increased plant diversity and spring burning increased flowering structure cover while reducing weedy cool season grass cover. Together these results suggest that grassland plant communities are resistant to winter climate change over the short term and that burning or mowing is critical to promoting plant diversity in tallgrass prairies.

KEYWORDS
disturbance regime, grassland restoration, management actions, plant diversity, prescribed fire, snow manipulation, soil temperature, tallgrass prairie, winter climate change

INTRODUCTION

Effective conservation and restoration rely on appropriate management actions that support outcomes of interest such as plant community diversity and composition (Grman et al., 2013). Yet, the impacts management actions like implementing disturbance can be altered by a changing climate, generating novel interactions between climate and management (Brambila et al., 2022). Indeed, in many systems, the impacts of management actions like seeding, applying disturbances such as prescribed fire, mowing, or grazing, and removing unwanted vegetation depend on the climate context and weather patterns following the management intervention (Groves et al., 2020). However, we know little about how management decisions like disturbance type and timing might interact with the effects of climate change to determine plant community responses in restored grasslands.

Grassland restoration is widely practiced around the world, as grasslands and especially prairies in North America have been severely degraded or lost due to land use change (Samson & Knopf, 1994). Reestablishing historically common disturbance regimes, such as frequent, low-intensity fire or grazing through management actions, is critical to the restoration of grassland plant diversity and function. Both fire and grazing promote diversity by removing biomass and litter; increasing plant establishment, space for plant growth, and flowering (Hulbert, 1988; Knapp et al., 1999; Old, 1969); and altering nutrient cycling (Hobbs et al., 1991; Ojima et al., 1994). Fire in tallgrass prairies in eastern and central North America is also known to promote growth of herbaceous species, increase flowering amount and synchrony (Wagenius et al., 2020), and suppress woody species. Increased flowering after fire also provides resources for wild pollinators (Carbone et al., 2019; Mola & Williams, 2018), an important service provided by grasslands (Van Nuland et al., 2013). Mowing is often used as a replacement of grazing or fire because it can be easier to implement (Davison & Kindscher, 1999), but can have different effects due to the lack of biomass removal and presence of heat and smoke (Kitchen et al., 2009; Randa & Yunger, 2001). For example, while mowing and burning tend to have similar effects on species composition, burning tends to increase biomass production while mowing tends to decrease biomass (Randa & Yunger, 2001), likely because of the buildup of litter (Knapp & Seastedt, 1986). Yet, while it is clear that routine disturbance is critical for maintaining grassland diversity, the mechanisms linking particular aspects of disturbance regimes (i.e., frequency, timing, duration, and intensity) to community change are not well understood (Foster et al., 2018).

Historically, tallgrass prairies likely experienced fire every 2–5 years (Allen & Palmer, 2011; Collins & Wallace, 1990) until European colonization and conversion of grassland to agriculture. These fires are thought to have occurred throughout the growing season (spring, summer, and fall) as fires were ignited both by lightning and Indigenous Americans managing the landscape for game and forage (Collins & Wallace, 1990). Today, prescribed fire is applied in the spring, which tends to promote the success of late-flowering C4 grasses (Copeland et al., 2002; Howe, 1995), a competitively dominant feature of restored prairies (Grman et al., 2021), while fire during the fall tends to promote small forbs and cool season grasses (Vermeire & Russell, 2018; Weir & Derek Scasta, 2017). In addition, the timing of fire plays an underappreciated role in determining when plant litter is present, influencing plant productivity, seed establishment (Knapp & Seastedt, 1986), seed predation (Anderegg et al., 2022), and seasonal soil temperatures (Lubbe & Henry, 2019). Thus, the fire disturbance regime, especially related to fire timing, is a critical force in shaping tallgrass plant communities.

In temperate climates, the winter season changes faster than any other season, with various ecological consequences (Kreyling, 2010; Williams et al., 2015). Warming winter temperatures tend to result in a loss of snow cover and warmer, more variable air temperatures (Kreyling et al., 2019). Snow acts as an effective insulator, so despite the warmer air temperatures, soil temperatures tend to decrease when snow is not present during the winter (Brown & DeGaetano, 2011). This can have extensive impacts on plants and animals that rely on the subnivium, the zone of thermal stability under the snow, for survival during cold winter conditions (Pauli et al., 2013; Thompson et al., 2021). Additionally, the presence of dead plant litter during the winter might play an important role in acting as insulation for the soil in the absence of snow (Lubbe & Henry, 2019). Snow and litter presence also influence soil moisture as melting snow produces moisture in the spring and litter can reduce evaporative water loss from the soil surface (Facelli & Pickett, 1991). On the other hand, when snow or litter is not present, soils can thaw sooner, potentially generating a longer growing season (Slatyer et al., 2022). Earlier spring thaw timing also, however, results in greater potential for false spring events where plants activate growth before the last damaging frost occurs (Marino et al., 2011; Wipf et al., 2009). On the other hand, while reduced snow is expected for the future, annual snow accumulation is highly variable and future extremes could result in periods of increased snow accumulation. This would reverse the effects described above. Various plant functional types are likely to be differentially affected by winter-related changes like earlier snowmelt or less snow depending on emergence phenology, growth rates, and cold tolerance (Henn et al., 2022). For example, the dominant C4 grasses tend to start growing later in the spring (Benning & Bragg, 1993; Towne & Craine, 2014) and thus are unlikely to be damaged by false springs while C3 grasses and some forbs capitalize on the cool, early spring, and may be more sensitive to earlier spring timing to either increase their growing season length or sprout before damaging frosts.

The interaction between management actions like disturbance timing and climate change like winter snow conditions will likely influence plant community outcomes of interest in restoration projects. However, we know little about how plant communities in restored tallgrass prairies are likely to respond to the combination of disturbance timing and snow loss. For example, it is possible that removing litter prior to winter through fall management actions exposes overwintering plants to damaging cold conditions (Lubbe & Henry, 2020), but also provides a longer growing season (Lubbe & Henry, 2019). Thus, understanding how disturbance timing and snow conditions interact could be critical for determining which management actions support restoration outcomes like plant diversity, composition, and flowering under varying climate conditions (Figure 1).

Here, we implemented experimental management actions (fall and spring burn and fall mow) and snow depth manipulations to assess the effects of management type and timing, along with snow depth on grassland plant community diversity and composition over three years in restored tallgrass prairie. Specifically, we ask the following questions: (1) How do managed disturbance techniques (fire and mowing) and snow depth manipulations, simulating potential future winter conditions, affect soil temperatures? (2) How do these treatments affect species diversity, plant functional group cover, and flowering structure abundance in restored prairies? (3) Does snow manipulation influence the outcome of different management treatments? We expected that (1) the loss of snow combined with the removal of litter before winter from either fall fire or fall mowing will result in colder winter soil conditions and earlier spring thaw timing; (2) management treatments will promote overall diversity while fire (but not mowing) will promote flower production; (3) fall fire will promote forb and cool season (C3) grass species cover while spring fire will promote warm season (C4) grass cover; (4) the cold temperatures resulting from plots experiencing fall burns and less snow will reduce species diversity and cover. We focus on plant community diversity and functional group cover as these factors are the defining features of grassland plant community structure and increasing plant diversity while promoting forb growth and flowering are primary goals of tallgrass prairie restoration (Barak et al., 2021). Ultimately, we aim to provide guidance on management actions for achieving prairie restoration goals.

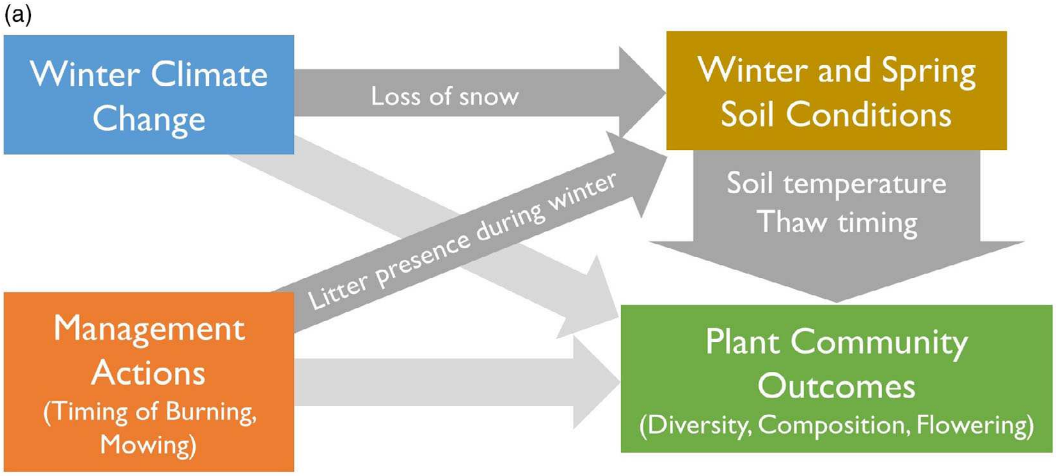
METHODS

Study site

To test our predictions, we established a field experiment in 2016 that examined the interactive effects of management actions and snow depth manipulations on prairie plant communities at Mounds View Grassland, approximately 231-ha property owned and managed by The Prairie Enthusiasts (https://www.theprairieenthusiasts.org) in Iowa County, Wisconsin, USA (42.95807 N, 89.86454 W). We established experimental blocks in areas that were restored to tallgrass prairie in 2011 from corn–soy rotation agriculture using the same seed mix and seeding technique. Seeding was done by broadcasting 77 native species of grasses and forbs during the late fall of 2010 into corn stubble to allow natural cold stratification during the winter. Following seeding, all sites were burned every 2–3 years in the spring prior to the start of our experiment. We acknowledge that the study site is a relatively recent restoration and is unlikely to reach an equilibrium state; however, many of the characteristic tallgrass prairie species were present and the site has typical tallgrass prairie structure. During this study, dominant species included C4 grasses such as *Andropogon gerardii* and *Sorghastrum nutans*, C3 grasses such as *Elymus repens* and *Bromus inermis*, and forbs such as *Ratibida pinnata*, *Monarda fistulosa*, *Silphium integrifolium*, *Symphyotrichum* spp., and *Parthenium integrifolium*. The common C4 grasses reached heights of 2–3 m and most forbs were 1–2 m tall and there was less than 5% bare ground cover. Many of the forbs and C3 grasses initiated growth in early spring while C4 grasses did not begin to grow until later spring and some species like *M. fistulosa* often overwintered above ground.

Experimental setup

We established eight experimental blocks in September 2016 (Figure 2). Each experimental block contained four treatment levels that were randomly assigned to one of four 10 × 20 m plots (fall burn, spring burn, fall mow, and control). Within each treatment plot, we established six 2 × 2 m subplots arranged in a grid with 2 m separating each plot where snow depth manipulation



(b)

Management Action	Litter presence during winter	Fire presence	Season of intervention
Fall Mow	Modified	No	Fall
Fall Burn	No	Yes	Fall
Spring Burn	Yes	Yes	Spring
Control	Yes	No	N/A

FIGURE 1 (a) Hypothesized connections between management actions, winter climate change, and soil conditions with plant community outcomes. We expect that the effects of management actions will depend on their timing, which removes plant litter either before or after winter, affecting winter and spring soil conditions. The loss of snow due to winter climate change will also affect winter and spring soil conditions, ultimately influencing plant community outcomes through variation in soil temperature and thaw timing. Dark gray arrows show focal connections while light gray arrows show other likely connections. (b) The effects of each of the management actions that we test. N/A, not applicable.

occurred. These subplots had a randomly assigned snow treatment level (snow reduction, snow addition, and no manipulation [control]) with two replicate snow treatment-level subplots within each fire treatment plot, for a total of 192 subplots. We measured vegetation (individual plants and community composition) in the middle 1 × 1 m section of each plot to avoid edge effects. For additional details on experimental setup, see Henn (2020).

Treatment applications

Fall-mow treatments were applied annually in October and fall-burn treatments were applied between November and December from 2016 to 2018 (Appendix S1: Table S1). Spring-burn treatments were applied between March and April from 2017 to 2019 (Appendix S1: Table S1). All burn treatments resulted in more than 90% of litter consumption and mow treatments cut litter at 10 cm above the ground using a large tractor with a pull-behind trail mower. We did not remove cut aboveground biomass from the plots in mow treatments. Snow depth in snow-removal subplots was reduced to 2 cm above the soil by shoveling, being careful not to disturb the soil or existing vegetation. Biomass in mowed plots was quickly packed down by the weight of snow, so there was no biomass that was exposed during snow removal. Snow that was removed from snow-reduction subplots was added to the snow-addition subplots. Snow-control plots were left untouched. By moving snow from snow-reduction to snow-addition plots, we also likely redistributed moisture in addition to temperature-related effects, but do not have documentation of this. In addition, snow-addition treatments likely influenced snow density and, therefore, insulation capacity (Rixen et al., 2008). Snow depth treatments were applied each time that more than 10 cm of snow accumulated, so the number of snow depth manipulation treatments per year depended on the number of days with greater than 10 cm snow accumulation (Appendix S1: Table S1). Total snow accumulation as of 15 March for the years

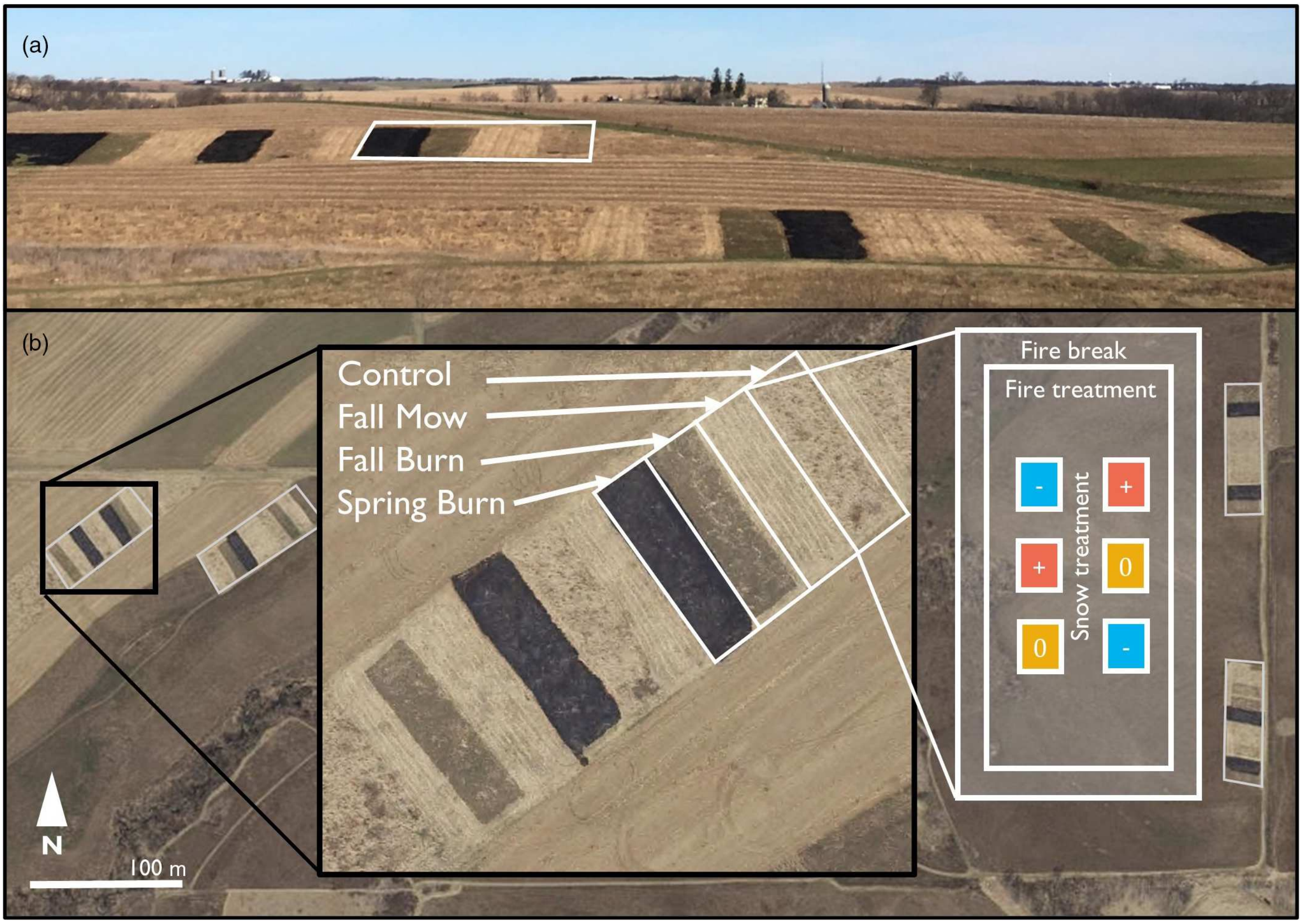


FIGURE 2 Experimental design. (a) View from the ground of four, westernmost experimental blocks. (b) Aerial photograph of the experimental blocks in 2018 following spring burns. Two experimental blocks are zoomed in and labeled by fire treatment with an example of snow depth manipulation and vegetation plot placement in each fire treatment plot.

included in this study was 112 cm (2016–2017 winter), 79 cm (2017–2018 winter), 140 cm (2018–2019 winter), and 106 cm is the 1981–2010 average (Wisconsin State Climatology Office). The growing seasons for each year were close to average temperatures (6–8°C mean annual temperature; 8°C is the 1981–2010 average) and wetter (1000–1300 mm/year; 860 mm is 1981–2010 average) than the 1981–2010 averages (Wisconsin State Climatology Office).

Soil temperature measurements

To capture treatment effects on soil temperature, 124 iButton (DS1921G-F5# Thermochron, 4K, iButtonLink Technology) dataloggers were placed in a subset of vegetation plots stratified by treatment level each year following the fall burn (plots were chosen randomly within stratified groups). Soil temperature iButtons were waterproofed using small (5 × 10 cm) zip-top plastic bags and placed at 2 cm below the soil surface in the center of each subplot. We also measured air temperature at each experimental block by mounting one iButton at 2 m above ground under a radiation shield. Temperature data were recorded every 2 h after the fall burn (November/December) until April (prior to each spring burn) each year.

Plant responses

To assess how the whole plant community responds to management actions and snow manipulation, we measured the plant community composition twice annually from 2017 to 2019 by visually estimating the percent aerial cover at 1 m of each species rooted in the 1 × 1 m vegetation subplots. We conducted surveys in July and September of each year to capture early- and late-flowering species. In each subplot, we estimated vegetative cover to the nearest percent during the community surveys in 2019. In 2017 and 2018, we used

Daubenmire cover classes: 0%–1%, 1%–5%, 6%–25%, 26%–50%, 51%–75%, 76%–95%, and 96%–100% cover (Daubenmire, 1959). To analyze community change over all years, we categorized all observations (including percent cover estimates from 2019) into the midpoints of each Daubenmire cover class. We counted any vegetation that intersected with any part of the plot and allowed species to overlap, so the total cover could exceed 100%. In addition to vegetative cover, we also quantified the percent cover of all flowering structures for each species to the nearest percent cover in 2019 and into Daubenmire cover classes in 2017 and 2018 (hereafter referred to as "flowering structure cover").

Data analyses

We assessed how our treatments affected soil temperature by calculating two metrics. First, we calculated the minimum temperature reached by each datalogger to determine how cold the soil became during each winter in each treatment. Second, we calculated the spring thaw date by determining the first day when the rolling mean temperature for the next 24 h was greater than 0.5°C. To allow for easier comparison between years, we relativized the thaw date within each year so that the mean is zero and negative values indicate earlier thaw while positive values indicate later thaw. In addition, we also calculated freezing degree days and thawing degree days as the sum of the daily mean temperatures for all days between 21 December and 15 March for each year with a mean temperature less than 1 and greater than 1, respectively. We compare the freezing degree day and thawing degree day values for each plot (temperature at 2 cm below the soil surface) to air temperatures at 2 m.

For the plant community responses, we analyzed all surveys (a summer and fall survey from each year). We used nonmetric multidimensional scaling (NMDS) in three dimensions to visualize the influence of our treatments on overall community composition and we assessed differences between our plots using permutational multivariate analysis of variance (PERMANOVA) and permutational multivariate analysis of dispersion (PERMDISP) while accounting for the blocked, repeated measures structure of our data in the permutations. These multivariate analyses were performed using the "vegan" package (Oksanen et al., 2020) in R.

We assessed the extent to which our management treatments, snow treatments, and their interactions affected winter soil and plant community metrics using linear mixed effect models. We analyzed minimum soil temperature and spring thaw date along with several plant community metrics of interest to prairie restoration practitioners including species richness, diversity (Shannon index), percent cover of forbs, C4 grasses, C3 grasses, and legumes, and percent cover of forb flowering structures and C4 grass flowering structures. We fit a model for each response of interest where the fixed predictor variables included our management treatment level, our snow treatment level, and their interaction. Random effects in each model included random intercepts for each plot nested in each management treatment plot, nested in each block to account for the repeated measures and split plot design of our experiment. We treated year as a random intercept in the soil temperature models and both year and season of survey as random intercepts in the plant community models, as we were most interested in the overall effects of our treatments while accounting for year-to-year and seasonal differences. In all cases, the year variable was treated as a factor without order because we did not expect our responses to change linearly through time. Linear mixed effects models were run using the lmerTest package (Kuznetsova et al., 2017) and post hoc comparisons were calculated using the emmeans package (Lenth, 2021) in R (R Core Team, 2021).

RESULTS

Winter and spring soil temperatures

Our management and snow manipulation treatments influenced winter minimum soil temperature while only the management treatments influenced spring thaw timing (Figure 3). Both management ($F = 16.43$, df = 3, 25, $p < 0.01$) and snow manipulation ($F = 21.6$, df = 2, 49, $p < 0.01$) had substantial effects on soil minimum temperature where fall-burn treatments and snow reductions both tended to reduce soil temperatures. Fall-mow treatments resulted in intermediate reductions in soil temperature relative to control and spring-burn treatments. Like soil temperature, the management treatment significantly affected thaw timing ($F = 24.6$, df = 3, 21, $p < 0.01$) where fall-burn treatment resulted in earlier thaw timing and the fall-mow treatment had intermediate effects compared with the other management treatments in all years. The effect of snow did not have a consistent effect on soil thaw timing ($F = 0.11$, df = 2, 51, $p = 0.9$); snow reduction resulted in relatively earlier thaw timing in spring-burn plots but later thaw timing in fall-burn plots. On average, the earliest and latest thawing plots differed in thaw timing by 7 days. There were no significant interactions between management and snow manipulation on minimum temperature ($F = 1.84$, df = 6, 45, $p = 0.11$) or soil thaw timing

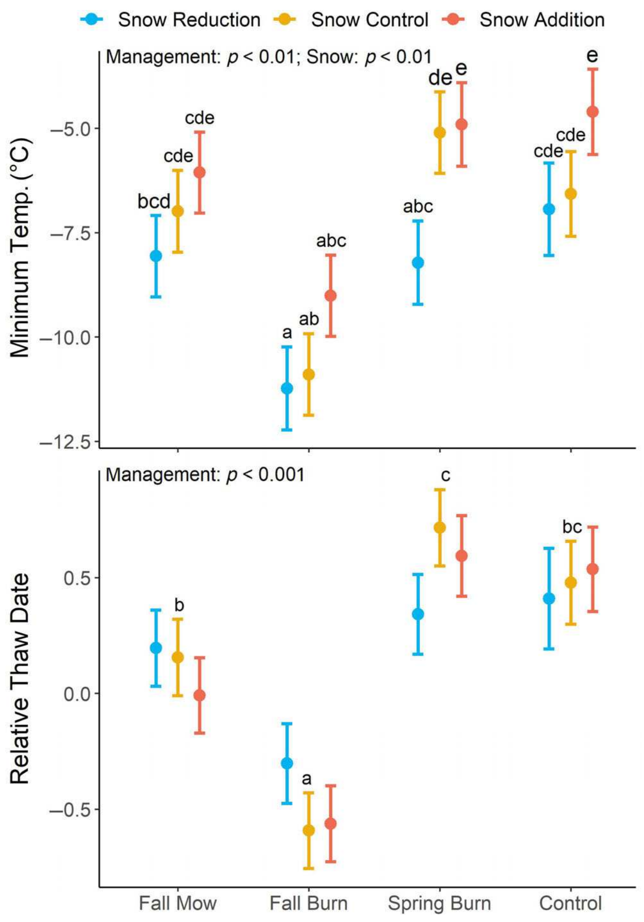


FIGURE 3 Mean soil minimum temperature and relative thaw date (negative numbers indicate earlier thaw timing) responses to experimental treatments (error bars indicate 1 standard error). Text in each panel indicates the highest order significant effect for that response and letters in each plot indicate significant pairwise differences. Where there is only one letter for each management action, it indicates differences between management actions averaged across snow treatments.

($F = 1.1$, df = 6, 50, $p = 0.38$). On average, fall-burn treatment plots experienced more thawing degree days than the spring-burn and control treatment plots, while snow did not matter. On the other hand, snow-reduction plots experienced the most freezing degree days, regardless of management treatment (Appendix S1: Figure S1).

Community composition responses

There were significant differences in community composition between our treatments where there was a significant interaction between management and snow manipulation in determining the position (PERMANOVA management:snow effect, $F = 2.7$, df = 6, 556, $p < 0.001$) and dispersion (PERMDISP, $F = 2.05$, df = 11, 564, $p = 0.02$) of our plots in community composition space. However, our treatments explained little of the variation in community composition (management $R^2 = 0.022$, snow $R^2 = 0.004$, management:snow $R^2 = 0.017$). The first NMDS axis corresponded mostly to differences in community composition between our experimental blocks (Appendix S1: Figure S2), while the second and third axes display differences between plots that are more related to our treatments (Figure 4). Overall, there is little difference in the centroid of each treatment group, but fall-burn treatments tended to result in smaller variation in community composition while spring-burn treatments tended to increase variability in community composition. In fall-burn plots, snow addition tended to reduce the variation in community composition while snow reduction had the same effect in no management (control) plots (Figure 4).

Community diversity and functional group responses

Management treatment levels influenced species diversity ($F = 6.85$, df = 3, 21, $p < 0.01$), richness ($F = 3.19$, df = 3, 21, $p = 0.04$), and flowering species richness ($F = 3.15$, df = 3, 21, $p = 0.05$) relative to control plots, while snow manipulation and the interaction between management and snow manipulation had no significant impact on any community diversity metrics (Figure 5; Appendix S1: Figure S3). Plant functional group cover responses to treatments were only marginally significant and varied by functional group. There was an interaction between management treatment and snow where forb cover tended to be higher in spring-burn plots with reduced snow, while forb cover was lower in fire control plots with additional or control levels of snow ($F = 2.18$, df = 6, 56, $p = 0.06$; Figure 6). Burning in spring tended to promote forb flowering compared with other management treatments ($F = 2.59$, df = 3, 21, $p = 0.08$; Appendix S1: Figure S4). C3 grass cover tended to be promoted in no management (control) plots ($F = 3.15$, df = 3, 21, $p = 0.05$) while legume cover and C4 grass cover and flowering were not affected by the treatments or the interaction between management and snow manipulation.

DISCUSSION

While snow manipulation influenced soil temperatures, only management type and timing strongly influenced plant species composition, functional group cover, and diversity. These results highlight the importance of

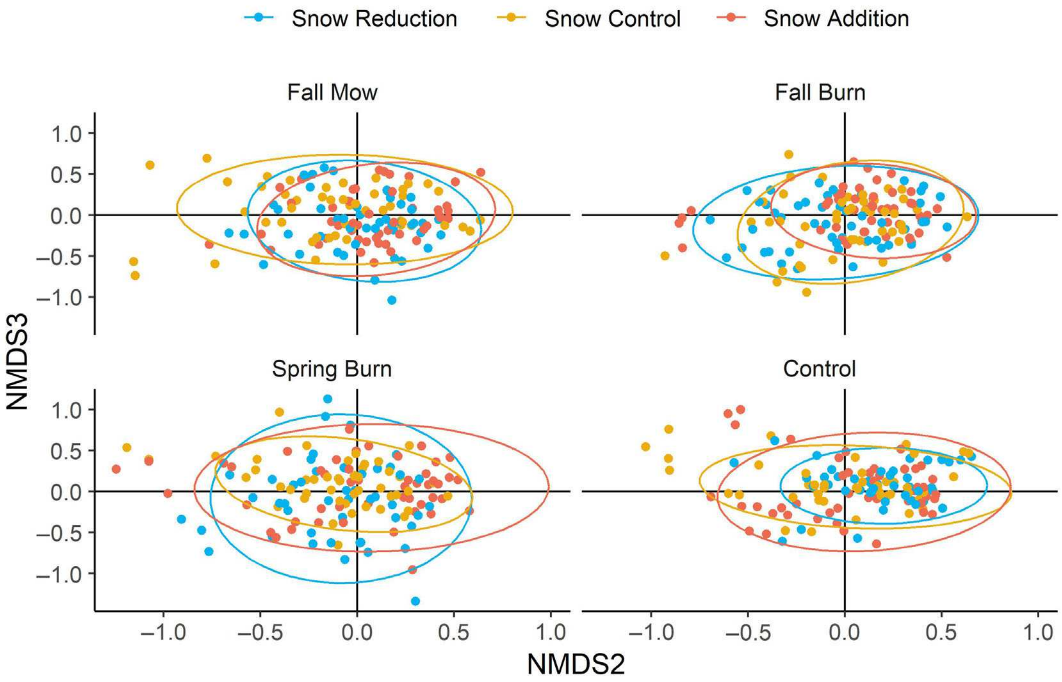


FIGURE 4 Nonmetric multidimensional scaling (NMDS) scores along the second and third axes for our study plots grouped by experimental treatments. Colors indicate snow treatments and ellipses represent the normal 95% ellipse for each treatment combination.

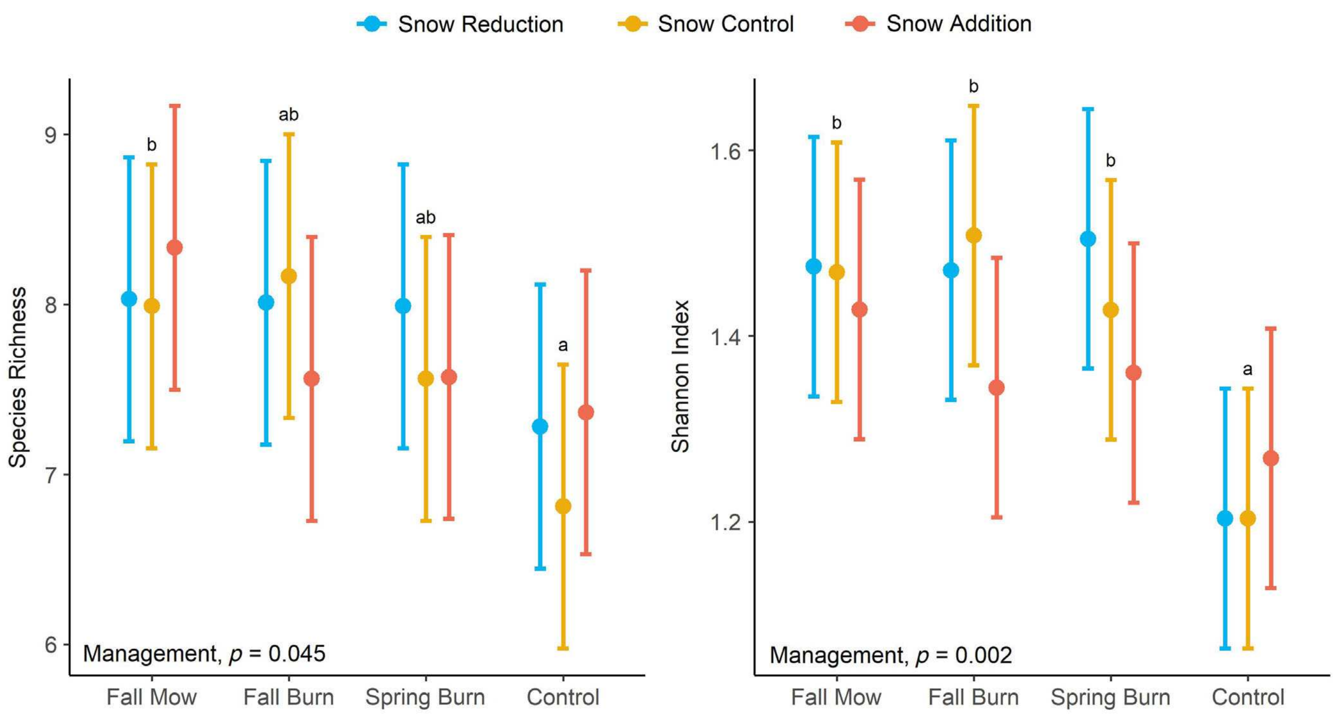


FIGURE 5 Plant community diversity and richness for vegetative cover responses to experimental treatments. Points are the mean value for each response in each treatment category. Error bars represent 1 standard error. Text in each panel indicates the highest order significant effect for that response and letters in each plot indicate significant pairwise differences. Where there is only one letter for each management action, it indicates differences between management actions averaged across snow treatments.

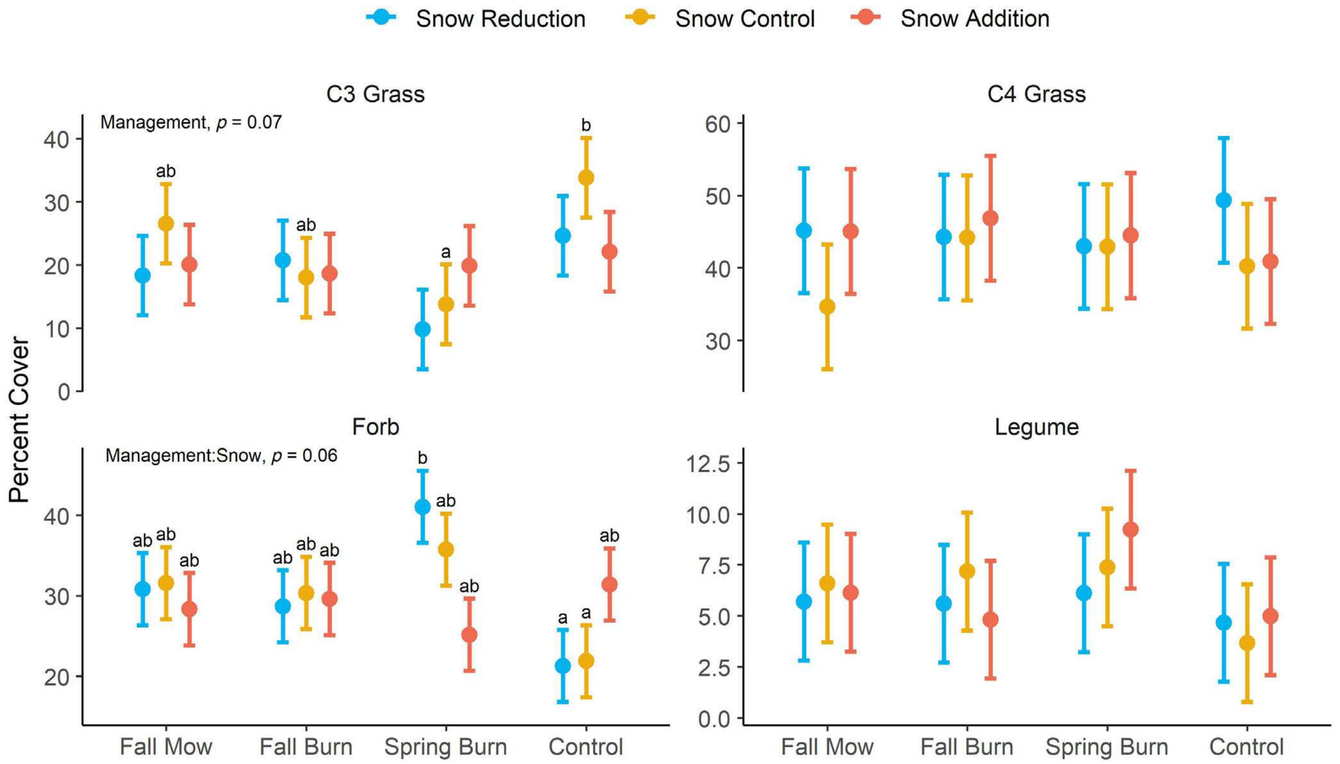


FIGURE 6 Plant functional group cover responses to experimental treatments. Points are the mean value for each response in each treatment category. Error bars represent 1 standard error. Text in each panel indicates the highest order significant effect for that response and letters in each plot indicate significant pairwise differences. Where there is only one letter for each management action, it indicates differences between management actions averaged across snow treatments.

frequent disturbance in promoting plant species diversity in tallgrass prairies while plant communities tend to be resistant to changes in snow depth manipulation over the short term. Since temperate grasslands are often dominated by long-lived perennial species, it may take years or decades before widespread impacts in the plant community composition are evident.

Soil temperature dynamics

Winter snow depth reductions led to expected influences on soil temperature dynamics by reducing minimum temperatures (Lubbe & Henry, 2019). Overall, soil minimum temperatures were cold enough where damage to underground plant organs could occur, as plant roots tend to tolerate temperatures between −5 and −15°C during winter (Ambroise et al., 2020; Schaberg et al., 2011). Indeed, the loss of snow depth tended to increase plant mortality and damage in a review of snow manipulation effects (Slatyer et al., 2022). In addition to roots, the temperatures reached near the soil surface could damage the stem-based underground perennating structures that determine aboveground growth (Lubbe et al., 2021; Ott et al., 2019).

While spring thaw timing did not significantly respond to snow manipulations, management actions changed when the growing season started. These results highlight the importance of litter during the winter for determining spring thaw timing, as complete litter removal in the fall (fall-burn treatment) resulted in the earliest spring thaw timing while litter manipulation due to fall mowing also resulted in earlier spring thaw timing, but this effect was much weaker. In addition, while not significant, the interaction between snow manipulation and management actions produced interesting effects. For example, the earliest thawing in spring-burn plots occurred when snow was reduced, likely because less snow allowed for early snowmelt dates while the litter during the winter prevented the soil from freezing deeply. On the other hand, thawing in fall-burn plots was latest when snow was reduced, likely because the lack of both litter and snow promoted deeper soil freezing. Deeper soil freezing could result in delayed spring thaw despite the lack of snow cover in the spring. Changes in the timing of when soils thaw can influence plant emergence and flowering phenology (Assmann et al., 2019; Prevéy et al., 2017), with potentially cascading impacts on other species interactions like herbivory and pollination.

Earlier soil thawing may directly influence plants in both positive and negative ways. A longer growing season might increase the potential carbon gain during the growing season, but there is evidence that some plants may not be able to capitalize on longer growing seasons (Zani et al., 2020). In addition, earlier bud burst associated with earlier thaw timing might increase the risk of damage from false springs (Chamberlain et al., 2021), but the relatively sheltered position of herbaceous plant buds near the soil surface and potentially under litter may reduce this risk, depending on whether buds are located below ground and when they start growing (Lubbe & Henry, 2019). The interplay between longer growing seasons and potential exposure to early spring frosts warrants further investigation, as the effects on plant success likely depend on plant overwintering and sprouting strategies (Henn et al., 2022) and cues (Chandler & Travers, 2022).

Plant community responses

The strongest plant community response that we observed in this study was that management actions, regardless of type or timing, favor increased plant richness and diversity (Figure 5). This corroborates extensive evidence that disturbance by fire promotes plant diversity in tallgrass prairies by reducing litter and opening space for seed establishment and plant emergence (Alstad et al., 2016; Bowles & Jones, 2013; Collins & Smith, 2006; Nerlekar & Veldman, 2020). On the other hand, the lack of strong diversity and richness responses to snow conditions could be the result of several factors. First, our results might be the consequence of frequent fire-promoting species that are both tolerant of fire and to other stresses like cold temperatures (Ladwig et al., 2018). Stress co-tolerance (Vinebrooke et al., 2004) could play a role both because our plots were burned regularly prior to the experiment and because our management treatments may have further promoted stress-tolerant species and individuals. If plant species in our system are tolerant to routine, low-intensity fires, they may also be tolerant of lower or more variable temperatures associated with changes in snow depth because they have been repeatedly exposed to low-insulation conditions following fires. Second, the species in our plots tended to be long-lived perennial species that have evolved under variable winter and spring conditions for millennia (Veldman et al., 2015), and so may be resistant to winter-related changes (Lubbe & Henry, 2019, 2020; Suzuki, 2014). While changes in snow depth have led to little change in a perennial plant community, we do not know the timescale of the observed resistance. Sublethal effects on plants generated by changing snow conditions (Guiden et al., 2018) are likely to accumulate, especially if seeds or seedlings are more sensitive to cold temperatures than large adult plants. This could lead to slow, long-term community change or even eventual thresholds where wholesale community change may occur (Gibson & Newman, 2019).

Plant functional group responses to management actions and snow manipulations were weaker and less consistent than overall plant community diversity responses. Forb species were more likely to flower in burned plots, regardless of burn season (Appendix S1: Figure S3), which is consistent with research showing that burning promotes forb flower production (Hartnett, 1991; Wagenius et al., 2020). Increased forb flowering in spring-burn plots and flower richness in fall-burn plots indicate the importance of burning in providing pollinator habitat in restored grasslands. This appears to be the main difference in the effect of mowing compared with burning, as the fall-mow treatment did not have the same effect on flower production.

Burning in the spring tended to reduce C3 grass cover compared with increased C3 grass cover in control plots. This is likely because C3 grasses emerge and develop earlier in the season than most other plant guilds, as they specialize on cool conditions in early spring and summer to complete most of their life cycle. As many of the C3 grass species in this study were non-native species such as *B. inermis* and *Poa pratensis*, the reduction in C3 grass cover could be seen as a substantial benefit of burning in the spring compared with burning in the fall.

Burning in the spring promoted forb cover when snow depth was reduced. Snow reduction tended to reduce soil temperatures in spring-burn plots and cause earlier thaw timing. Thus, chilling requirements for seed germination and emergence could have been met earlier in the colder snow-reduction plots than in plots with deeper snow and warmer temperatures. Testing this and other potential mechanisms for species responses under reduced snow depth and earlier thaw timing will require further investigation, especially since this phenomenon was only observed in forbs and is counter to previous studies in alpine systems that showed that forb productivity was increased by delayed snow melt timing (Wipf & Rixen, 2010).

Implications for management and conclusions

Our study demonstrates how disturbance is not only critical for maintaining plant community diversity but might also set the stage for plant responses to climate change in ways that influence important tallgrass prairie management outcomes like C3 grass cover, forb cover, and flower availability. Both disturbance-mediated litter cover during winter and snow manipulation affected minimum soil temperatures and soil thaw dates in spring. Plant communities primarily responded to management actions, but not changes in snow depth. Both mowing and burning increased overall species richness and diversity along with flowering species richness. Weedy C3 grasses were reduced while forb flowering was increased by spring burning. Interactions between forb species cover and winter conditions in spring-burn plots indicate that the effects of management decisions might depend on how winter conditions change in the future. Overall, spring burning is likely to have the most positive influence in developing a diverse native tallgrass prairie community under future winter conditions because it resulted in reduced C3 grasses, increased forb flowering, and forb cover.

Overall, considering how changing climate conditions will influence the restoration outcomes of management decisions will be critical for effectively managing ecosystems in the future. As climate and other global changes rapidly modify the context in which restoration and conservation measures are implemented, it is important to consider how the effects of management interventions will change. Specifically, testing scenarios to generate actionable recommendations (Heller & Zavaleta, 2009) will increase our ability to efficiently and effectively manage systems for biodiversity. Here we provide a model for understanding interactions between potential future climate conditions and common grassland management actions, which reveals that the timing of and type of managed disturbance (prescribed fire and mowing) and changes in snow depth lead to immediate and dramatic impacts on soil temperature dynamics. The cascading impacts of these two interacting drivers have not yet resulted in large changes to the extant plant community. Management actions of any type (mowing and fire) and in any season (fall and spring) have positive impacts on plant community diversity regardless of changes in snow depth. In the short term, it seems that prairie plants can cope with winter climate change, but longer term plant responses for this perennial-dominated ecosystem seem likely and will be critically important to evaluate to improve predictability of management outcomes and restoration efforts.

AUTHOR CONTRIBUTIONS

Jonathan J. Henn and Ellen I. Damschen conceived the study and designed the experiment. Jonathan J. Henn collected data, performed analyses, and wrote the manuscript with the assistance of Ellen I. Damschen. Both authors approved the submission of this manuscript.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data and code (Henn & Damschen, 2022) are available from Open Science Framework: https://osf.io/tfq9g/.

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REFERENCES

Allen, M. S., and M. W. Palmer. 2011. "Fire History of a Prairie/Forest Boundary: More than 250 Years of Frequent Fire in a North American Tallgrass Prairie." *Journal of Vegetation Science* 22: 436–44.

Alstad, A. O., E. I. Damschen, T. J. Givnish, J. A. Harrington, M. K. Leach, D. A. Rogers, and D. M. Waller. 2016. "The Pace of Plant Community Change Is Accelerating in Remnant Prairies." *Science Advances* 2: e1500975.

Ambroise, V., S. Legay, G. Guerriero, J.-F. Hausman, A. Cuypers, and K. Sergeant. 2020. "The Roots of Plant Frost Hardiness and Tolerance." *Plant & Cell Physiology* 61: 3–20.

Anderegg, G. C., J. J. Henn, J. L. Orrock, and E. I. Damschen. 2022. "Litter Removal Reduces Seed Predation in Restored Prairies during Times when Seed Predation Would Otherwise Be High." *Restoration Ecology* 30: e13550.

Assmann, J. J., I. H. Myers-Smith, A. B. Phillimore, A. D. Bjorkman, R. E. Ennos, J. S. Prevéy, G. H. R. Henry, N. M. Schmidt, and R. D. Hollister. 2019. "Local Snow Melt and Temperature—But Not Regional Sea Ice-Explain Variation in Spring Phenology in Coastal Arctic Tundra." *Global Change Biology* 25: 2258–74.

Barak, R. S., Z. Ma, L. A. Brudvig, and K. Havens. 2021. "Factors Influencing Seed Mix Design for Prairie Restoration." *Restoration Ecology* 30(5): e13581.

Benning, T. L., and T. B. Bragg. 1993. "Response of Big Bluestem (*Andropogon gerardii* Vitman) to Timing of Spring Burning." *The American Midland Naturalist* 130: 127.

Bowles, M. L., and M. D. Jones. 2013. "Repeated Burning of Eastern Tallgrass Prairie Increases Richness and Diversity, Stabilizing Late Successional Vegetation." *Ecological Applications* 23: 464–78.

Brambila, A., P. B. Reed, S. D. Bridgham, B. A. Roy, B. R. Johnson, L. Pfeifer-Meister, and L. M. Hallett. 2022. "Disturbance: A Double-Edged Sword for Restoration in a Changing Climate." *Restoration Ecology* e13675.

Brown, P. J., and A. T. DeGaetano. 2011. "A Paradox of Cooling Winter Soil Surface Temperatures in a Warming Northeastern United States." *Agricultural and Forest Meteorology* 151: 947–56.

Carbone, L. M., J. Tavella, J. G. Pausas, and R. Aguilar. 2019. "A Global Synthesis of Fire Effects on Pollinators." *Global Ecology and Biogeography* 28: 1487–98.

Chamberlain, C. J., B. I. Cook, I. Morales-Castilla, and E. M. Wolkovich. 2021. "Climate Change Reshapes the Drivers of False Spring Risk across European Trees." *The New Phytologist* 229: 323–34.

Chandler, E. K., and S. E. Travers. 2022. "The Timing of Snowmelt and Amount of Winter Precipitation Have Limited Influence on Flowering Phenology in a Tallgrass Prairie." *Botany* 100: 301–11.

Collins, S. L., and M. D. Smith. 2006. "Scale-Dependent Interaction of Fire and Grazing on Community Heterogeneity in Tallgrass Prairie." *Ecology* 87: 2058–67.

Collins, S. L., and L. L. Wallace. 1990. *Fire in North American Tallgrass Prairies*. Norman, OK: University of Oklahoma Press.

Copeland, T. E., W. Sluis, and H. F. Howe. 2002. "Fire Season and Dominance in an Illinois Tallgrass Prairie Restoration." *Restoration Ecology* 10: 315–23.

Daubenmire, R. 1959. "Canopy Coverege Method of Vegetation Analysis." *Northwest Science* 33: 39–64.

Davison, C., and K. Kindscher. 1999. "Tools for Diversity: Fire, Grazing and Mowing on Tallgrass Prairies." *Ecological Restoration* 17: 136–43.

Facelli, J. M., and S. T. A. Pickett. 1991. "Plant Litter: Its Dynamics and Effects on Plant Community Structure." *The Botanical Review* 57: 1–32.

Foster, C. N., P. S. Barton, C. I. MacGregor, J. A. Catford, W. Blanchard, and D. B. Lindenmayer. 2018. "Effects of Fire Regime on Plant Species Richness and Composition Differ among Forest, Woodland and Heath Vegetation." *Applied Vegetation Science* 21: 132–43.

Gibson, D. J., and J. A. Newman. 2019. *Grasslands and Climate Change*. Cambridge: Cambridge University Press.

Grman, E., T. Bassett, and L. A. Brudvig. 2013. "Confronting Contingency in Restoration: Management and Site History Determine Outcomes of Assembling Prairies, but Site Characteristics and Landscape Context Have Little Effect." *Journal of Applied Ecology* 50: 1234–43.

Grman, E., C. R. Zirbel, J. T. Bauer, A. M. Groves, T. Bassett, and L. A. Brudvig. 2021. "Super-Abundant C 4 Grasses Are a Mixed Blessing in Restored Prairies." *Restoration Ecology* 29: e13281.

Groves, A. M., J. T. Bauer, and L. A. Brudvig. 2020. "Lasting Signature of Planting Year Weather on Restored Grasslands." *Scientific Reports* 10: 5953.

Guiden, P. W., B. M. Connolly, and J. L. Orrock. 2018. "Extreme Cold Consistently Reduces Seedling Growth but Has Species-Specific Effects on Browse Tolerance in Summer." *American Journal of Botany* 105: 2075–80.

Hartnett, D. C. 1991. "Effects of Fire in Tallgrass Prairie on Growth and Reproduction of Prairie Coneflower (*Ratibida columnifera*: Asteraceae)." *American Journal of Botany* 78: 429–35.

Heller, N. E., and E. S. Zavaleta. 2009. "Biodiversity Management in the Face of Climate Change: A Review of 22 Years of Recommendations." *Biological Conservation* 142: 14–32.

Henn, J. J. 2020. *Plant Community and Environmental Change: Building Links through Functional Traits*. Madison, WI: The University of Wisconsin-Madison.

Henn, J., and E. Damschen. 2022. "Data and Code from 'Grassland Management Actions Influence Soil Conditions and Plant Community Responses to Winter Climate Change.'" OSF. https://doi.org/10.17605/OSF.IO/TFQ9G.

Henn, J. J., L. M. Ladwig, and E. I. Damschen. 2022. "Disturbance Type and Timing Affect Growth and Tolerance Strategies in Grassland Plant Leaves." *Rangeland Ecology & Management* 80: 18–25.

Hobbs, N. T., N. Thompson Hobbs, D. S. Schimel, C. E. Owensby, and D. S. Ojima. 1991. "Fire and Grazing in the Tallgrass Prairie: Contingent Effects on Nitrogen Budgets." *Ecology* 72: 1374–82.

Howe, H. F. 1995. "Succession and Fire Season in Experimental Prairie Plantings." *Ecology* 76: 1917–25.

Hulbert, L. C. 1988. "Causes of Fire Effects in Tallgrass Prairie." *Ecology* 69: 46–58.

Kitchen, D. J., J. M. Blair, and M. A. Callaham. 2009. "Annual Fire and Mowing Alter Biomass, Depth Distribution, and C and N Content of Roots and Soil in Tallgrass Prairie." *Plant and Soil* 323: 235–47.

Knapp, A. K., J. M. Blair, J. M. Briggs, S. L. Collins, D. C. Hartnett, L. C. Johnson, and E. Gene Towne. 1999. "The Keystone Role of Bison in North American Tallgrass Prairie." *BioScience* 49: 39.

Knapp, A. K., and T. R. Seastedt. 1986. "Detritus Accumulation Limits Productivity of Tallgrass Prairie." *BioScience* 36: 662–8.

Kreyling, J. 2010. "Winter Climate Change: A Critical Factor for Temperate Vegetation Performance." *Ecology* 91: 1939–48.

Kreyling, J., K. Grant, V. Hammerl, M. A. S. Arfin-Khan, A. V. Malyshev, J. Peñuelas, K. Pritsch, et al. 2019. "Winter Warming Is Ecologically More Relevant than Summer Warming in a Cool-Temperate Grassland." *Scientific Reports* 9: 14632.

Kuznetsova, A., P. B. Brockhoff, and R. H. B. Christensen. 2017. "lmerTest Package: Tests in Linear Mixed Effects Models." *Journal of Statistical Software* 82: 1–26.

Ladwig, L. M., E. I. Damschen, S. Martin-Blangy, and A. O. Alstad. 2018. "Grasslands Maintained with Frequent Fire Promote Cold-Tolerant Species." *Journal of Vegetation Science* 29: 541–9.

Lenth, R. V. 2021. emmeans: Estimated Marginal Means, aka Leas-Squares Means.

Lubbe, F. C., and H. A. L. Henry. 2019. "Plant Rhizome Positioning in the Soil and under Litter: Trade-offs of Frost Avoidance

Versus Growth." *Perspectives in Plant Ecology, Evolution and Systematics* 41: 125500.

Lubbe, F. C., and H. A. L. Henry. 2020. "The Role of Perennation Traits in Plant Community Soil Frost Stress Responses." *Annals of Botany* 126: 873–81.

Lubbe, F. C., J. Klimešová, and H. A. L. Henry. 2021. "Winter Belowground: Changing Winters and the Perennating Organs of Herbaceous Plants." *Functional Ecology* 35: 1627–39.

Marino, G. P., D. P. Kaiser, L. Gu, and D. M. Ricciuto. 2011. "Reconstruction of False Spring Occurrences over the Southeastern United States, 1901–2007: An Increasing Risk of Spring Freeze Damage?" *Environmental Research Letters* 6: 024015.

Mola, J. M., and N. M. Williams. 2018. "Fire-Induced Change in Floral Abundance, Density, and Phenology Benefits Bumble Bee Foragers." *Ecosphere* 9: e02056.

Nerlekar, A. N., and J. W. Veldman. 2020. "High Plant Diversity and Slow Assembly of Old-Growth Grasslands." *Proceedings of the National Academy of Sciences of the United States of America* 117: 18550–6.

Ojima, D. S., D. S. Schimel, W. J. Parton, and C. E. Owensby. 1994. "Long- and Short-Term Effects of Fire on Nitrogen Cycling in Tallgrass Prairie." *Biogeochemistry* 24: 67–84.

Oksanen, J., F. Guillaume Blanchet, M. Friendly, R. Kindt, P. Legendre, D. McGlinn, P. R. Minchin, et al. 2020. "vegan: Community Ecology Package." R package version 2.5-7. https://CRAN.R-project.org/package=vegan.

Old, S. M. 1969. "Microclimate, Fire, and Plant Production in an Illinois Prairie." *Ecological Monographs* 39: 355–84.

Ott, J. P., J. Klimešová, and D. C. Hartnett. 2019. "The Ecology and Significance of below-Ground Bud Banks in Plants." *Annals of Botany* 123: 1099–118.

Pauli, J. N., B. Zuckerberg, J. P. Whiteman, and W. Porter. 2013. "The Subnivium: A Deteriorating Seasonal Refugium." *Frontiers in Ecology and the Environment* 11: 260–7.

Prevéy, J., M. Vellend, N. Rüger, R. D. Hollister, A. D. Bjorkman, I. H. Myers-Smith, S. C. Elmendorf, et al. 2017. "Greater Temperature Sensitivity of Plant Phenology at Colder Sites: Implications for Convergence across Northern Latitudes." *Global Change Biology* 23: 2660–71.

R Core Team. 2021. *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing.

Randa, L. A., and J. A. Yunger. 2001. "A Comparison of Management Techniques on Plant Species Composition and Biomass in a Tallgrass Prairie Restoration." *Proceedings of the 17th North American Prairie Conference* 17: 92–7.

Rixen, C., M. Freppaz, V. Stoeckli, C. Huovinen, K. Huovinen, and S. Wipf. 2008. "Altered Snow Density and Chemistry Change Soil Nitrogen Mineralization and Plant Growth." *Arctic, Antarctic, and Alpine Research* 40: 568–75.

Samson, F., and F. Knopf. 1994. "Prairie Conservation in North America." *Bioscience* 44: 418–21.

Schaberg, P. G., D. V. D'Amore, P. E. Hennon, J. M. Halman, and G. J. Hawley. 2011. "Do Limited Cold Tolerance and Shallow Depth of Roots Contribute to Yellow-Cedar Decline?" *Forest Ecology and Management* 262: 2142–50.

Slatyer, R. A., K. D. L. Umbers, and P. A. Arnold. 2022. "Ecological Responses to Variation in Seasonal Snow Cover." *Conservation Biology* 36: e13727.

Suzuki, R. O. 2014. "Combined Effects of Warming, Snowmelt Timing, and Soil Disturbance on Vegetative Development in a Grassland Community." *Plant Ecology* 215: 1399–408.

Thompson, K. L., B. Zuckerberg, W. P. Porter, and J. N. Pauli. 2021. "The Decline of a Hidden and Expansive Microhabitat: The Subnivium." *Frontiers in Ecology and the Environment* 19: 268–73.

Towne, E. G., and J. M. Craine. 2014. "Ecological Consequences of Shifting the Timing of Burning Tallgrass Prairie." *PLoS One* 9: e103423.

Van Nuland, M. E., E. N. Haag, J. A. M. Bryant, Q. D. Read, R. N. Klein, M. J. Douglas, C. E. Gorman, et al. 2013. "Fire Promotes Pollinator Visitation: Implications for Ameliorating Declines of Pollination Services." *PLoS One* 8: e79853.

Veldman, J. W., E. Buisson, G. Durigan, G. W. Fernandes, S. Le Stradic, G. Mahy, D. Negreiros, et al. 2015. "Toward an Old-Growth Concept for Grasslands, Savannas, and Woodlands." *Frontiers in Ecology and the Environment* 13: 154–62.

Vermeire, L. T., and M. L. Russell. 2018. "Seasonal Timing of Fire Alters Biomass and Species Composition of Northern Mixed Prairie." *Rangeland Ecology & Management* 71: 714–20.

Vinebrooke, R. D., K. L. Cottingham, N. M. S. Jon, S. I. Dodson, S. C. Maberly, and U. Sommer. 2004. "Impacts of Multiple Stressors on Biodiversity and Ecosystem Functioning: The Role of Species Co-Tolerance." *Oikos* 104: 451–7.

Wagenius, S., J. Beck, and G. Kiefer. 2020. "Fire Synchronizes Flowering and Boosts Reproduction in a Widespread but Declining Prairie Species." *Proceedings of the National Academy of Sciences of the United States of America* 117: 3000–5.

Weir, J. R., and J. Derek Scasta. 2017. "Vegetation Responses to Season of Fire in Tallgrass Prairie: A 13-Year Case Study." *Fire Ecology* 13: 137–42.

Williams, C. M., H. A. L. Henry, and B. J. Sinclair. 2015. "Cold Truths: How Winter Drives Responses of Terrestrial Organisms to Climate Change." *Biological Reviews* 90: 214–35.

Wipf, S., and C. Rixen. 2010. "A Review of Snow Manipulation Experiments in Arctic and Alpine Tundra Ecosystems." *Polar Research* 29: 95–109.

Wipf, S., V. Stoeckli, and P. Bebi. 2009. "Winter Climate Change in Alpine Tundra: Plant Responses to Changes in Snow Depth and Snowmelt Timing." *Climatic Change* 94: 105–21.

Zani, D., T. W. Crowther, L. Mo, S. S. Renner, and C. M. Zohner. 2020. "Increased Growing-Season Productivity Drives Earlier Autumn Leaf Senescence in Temperate Trees." *Science* 370: 1066–71.

SUPPORTING INFORMATION

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

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