FINAL REPORT

Title: The interactive effects of prescribed fire timing and climate change on Midwestern tallgrass prairie communities

JFSP PROJECT ID: 16-2-01-26

August 2020

Jonathan J. Henn

University of Wisconsin-Madison, Department of Integrative Biology

Ellen I. Damschen

University of Wisconsin-Madison, Department of Integrative Biology

Table of Contents

Figures:

Tables:

Abstract:

In this study we examined how the season of fire, combined with snow manipulation to simulate winter climate change, affect tallgrass prairie plant responses. Managers often apply prescribed fire in tallgrass prairie in the spring, but historically, fire likely occurred throughout the year. The timing of fire is known to affect plant responses, so continual spring burning may favor certain plants over others. In addition, due to the potential for dead litter to insulate the soil over cold winter conditions, the timing of fire could interact with winter conditions to negatively impact plants and animals. We aimed to test whether burning in the fall vs. the spring, along with removing or adding snow during the winter affect winter soil temperature dynamics, prairie plant performance, seed establishment, and plant community composition and diversity. We did this by installing a replicated field experiment for three years where plots were burned annually in either the spring or fall and subplots had snow manipulation applied during the winter. We found that soil temperatures get much colder when snow depth is reduced and dead litter is removed before the winter by burning or mowing. However, snow reduction and fall burn/mow also resulted in earlier thaw timing, increasing the length of the growing season. Plants emerged earlier in fall burn treatments and flowered earlier in both spring and fall burn treatments while mowing did not affect plant responses. Seed establishment was almost negligible in all treatments, but seed predation was high during the time when we added seeds. Removing litter while seed predation was otherwise high reduced seed predation substantially. Finally, all fire and mowing treatments increased species diversity and richness compared to control plots. Overall, this indicates the importance of managing prairies with disturbance. However, the timing of that disturbance does not have strong positive or negative effects on plant responses, so a mixture of disturbance timing is likely to promote the highest plant diversity. Winter conditions had strong effects on winter soil temperatures, but minimal effects on plant responses, indicating that prairie plants can tolerate extreme winter conditions.

Objectives:

Our objectives were to determine How fire timing, snow depth, and their interaction affect prairie (1) plant growth and fecundity, (2) phenology, and (3) seedling establishment? In addition, we aimed to assess how prairie plant (4) community diversity responds to fire timing, snow depth, and their interaction.

We hypothesized that fire timing and snow depth would interact to affect all four responses of interest. More specifically, we expected that fire in the fall would promote growth and fecundity in early-flowering forbs and C3 grasses while spring burns would favor C4 grasses. However, snow reduction would create more stressful winter conditions, favoring more stress-tolerant species but providing the potential for advanced emergence and flowering phenology due to earlier spring thaw timing. Seedling establishment would be enhanced in plots with fire due to the removal of litter that can block seed access to the soil. We expected greater community diversity following fire treatments during any time, but that snow reduction could interact with fall fire to negatively impact diversity by causing freezing damage to some species.

These objectives align closely with the details of a Graduate Research Innovation grant call, as

they were complementary to Jonathan Henn's PhD dissertation, titled "Plant community and environmental change: building links through functional traits". The experiment funded by this grant expanded upon other research on prairie plant growth and phenology in the greenhouse and enabled several undergraduate-led parallel projects.

We were able to achieve all objectives. We made measurements of all responses to our experimental treatments. However, related to objective three, we added many seeds of several species during the first two years, but observed almost no successful establishment of these species. This result motivated an undergraduate side-project to investigate how seed predation varied between our treatments and through time.

Background:

The nature of climate change and its effects on natural communities often depend on the geographical, biotic and abiotic context in which a community is found (Gilman et al., 2010; IPCC, 2014; Parmesan, 2006; Stuble et al., 2007). For example, disturbance regimes (i.e., frequency, timing, and intensity of disturbance) are well known to affect species distributions and community composition (Archibald et al., 2013; White and Jentsch, 2001). Disturbance regimes might also "set the stage" for community responses to climate change by establishing a legacy of species and conditions that are more or less resilient to changing climate conditions (Johnstone et al., 2016; Ladwig et al., 2018; Seidl et al., 2014). Understanding these interactions will provide guidance for better management of disturbance for conservation under future climate conditions.

Tallgrass prairies are fire-dependent grasslands of eastern North America that have been extensively lost due primarily to land use change and fire suppression (Samson and Knopf, 1994). Historically, prairies are thought to have been burned every 1-3 years (Anderson, 1990). This frequent, low intensity fire is critical for maintaining high herbaceous plant diversity (Bowles and Jones, 2013; Brye et al., 2002; Peterson et al., 2007) and preventing encroachment by woody species (Ratajczak et al., 2016). Historically, fire likely occurred throughout the growing season. Today, land managers primarily use prescribed fire in the early spring and, to a lesser extent, in the fall. The timing of fire affects prairie plant growth, phenology, and community composition (Henderson, Richard, 1990; Howe, 1994; Towne and Craine, 2014). Burning in the fall, for example, promotes forb and cool season grass cover while burning in the spring promotes warm season C4 grass cover (Towne and Craine, 2014). Fire, in either season, also increases the quantity and synchrony of flowering, modifies the quantity of underground buds, and reduces litter cover to encourage plant recruitment (Dalgleish and Hartnett, 2008; Pavlovic et al., 2011; Wagenius et al., 2020). The feedbacks between fire, vegetation, and climate are important regulators of the prairie ecosystem and temperate grasslands worldwide. Global climate change, therefore, has the potential to alter these feedbacks with consequences for plant community composition, diversity, and structure.

Fire, however, is not the only way of managing prairie vegetation and grazing or mowing might also provide effective means of maintaining plant diversity. While grazing or mowing have been shown to have similar effects as burning, including litter removal to open space for seedling establishment, nutrient cycling, and removing woody species (Ojima,' et al., 1994). However,

the effectiveness of mowing compared to fire remains a common question of land managers.

The climate is changing fastest in winter compared to any other season for many temperate grasslands, including tallgrass prairie (IPCC, 2014). Compared to changes during the growing season, winter climate change is poorly understood (Kreyling, 2010). Winter climate changes, including increased precipitation falling as rain, lower snow cover and depth, and changing timing of fall freezing and spring thawing events, can have substantial effects on ecosystem function and structure (Kreyling et al., 2019; Ladwig et al., 2016; Williams et al., 2015). These effects are primarily caused by two mechanisms. First, the loss of snow results in colder and more variable soil temperature conditions due to the insulative properties of snow (Groffman et al., 2001a; Pauli et al., 2013). These temperature effects change soil nutrient availability and increase fine root turnover by causing freezing damage to microbes and fine roots (Kreyling et al., 2019; Schaberg et al., 2011). Cold soil temperatures can also have sublethal effects that hinder growth, reproduction, and survival following stressful winter conditions (Guiden et al., 2018; Malyshev and Henry, 2012). The second mechanism is due to changes to spring thaw dates and the frequency of freeze-thaw cycles, resulting in "false springs" (Augspurger, 2013; Chamberlain et al., 2019) and modifying the timing of plant phenological events such as emergence, flowering, and fruiting (Ladwig et al., 2019; Tedla et al., 2020). The ultimate effects of these two winter-related changes are likely to depend on species emergence cues, tolerance of cold, and response to fire timing.

The occurrence and timing of fire may affect how plant growth and the timing of key life history events respond to winter climate change. For example, the seasonality of fire might alter how winter climate change acts on plant communities by removing litter before or after winter. Litter in tallgrass prairies controls productivity and plant emergence timing (Knapp and Seastedt, 1986; Old, 1969), insulates the soil, and traps snow (Lubbe and Henry, 2019). Litter removal before winter might, therefore, exacerbate effects of winter climate change by increasing temperature variability and extreme freezing events while favoring species adapted to fire and cold-related stresses. Similarly, reduced snow depth coupled with litter removal before winter may result in substantially earlier spring thaws, extending the growing season but potentially exposing young tissues to freezing temperatures. The degree to which future plant community composition and diversity will shift under winter climate change may depend on interactions of climate with fire as well as species-specific life history traits associated with how individuals will respond. Ultimately, this project aimed to provide insight for managers effectively make prescribed fire decisions to manage grasslands under changing winter climate conditions by determining the overall effects of fire timing, snow depth, and their interaction on prairie plant growth and diversity.

Materials and Methods:

Study Site
We established a field experiment in 2016 that tested the interactive effects of disturbance and winter climate change (snow depth) on restored prairie plant communities at Mounds View Grassland, a 572-acre 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 restored to tallgrass prairie in 2011 from corn-

soy rotation agriculture using the same species and seeding technique. All sites were burned every 2-3 years in the spring prior to the start of our experiment. All of our blocks were established in vegetation consisting of herbaceous perennial plants characteristic of tallgrass prairie including warm-season grasses such as *Andropogon gerardii, Sorghastrum nutans, Panicum virginicum,* cool-season grasses such as *Poa pratensis, Boutiloua curtipendula, Bromus inermis,* and forbs such as *Silphium integrifolium, Solidago rigida, Monarda fistulosa, Tadescantia ohioense, Asclepias syriaca, Symphyotrichum laevis, Echinacea pallida*, and *Parthenium integrifolium.*

Experiment
We established eight experimental blocks in September, 2016 (Figure 1). Each experimental block contained four treatment levels that were randomly assigned to one of four 10x20 m plots (fall burn, spring burn, fall mow, and control). Within each treatment plot we established six 2x2 m subplots arranged in a grid with 3 m separating each plot where snow manipulation occurred. These subplots had a randomly assigned snow treatment level (snow reduction, snow addition, no manipulation (control)) with two replicate snow treatment level subplots within each disturbance treatment plot, for a total of 192 plots. We measured vegetation (individual plants and community composition) in the middle 1x1m section of each plot to avoid edge effects.

Treatment applications
Fall mow treatments were applied annually in October, and fall burn treatments were applied between November and December from 2016-2018 (Table 1). Spring burn treatments were applied between March and April from 2017-2019 (Table 1). Snow depth in snow removal subplots was reduced to 2cm by shoveling, being careful not to disturb the soil or existing vegetation. Snow that was removed from snow reduction subplots was added to the snow addition subplots. Snow control plots were left untouched. Snow treatments were applied each time that more than 10cm of snow accumulated, and thus varied from year to year (Table 1).

Soil temperature measurements
Each year following the fall burn, 124 iButton (DS1921G-F5# Thermochron, 4K, iButtonLink Technology) dataloggers were placed in a random subset of vegetation plots stratified by treatment level to capture as much variation in treatment effects on soil temperature. Soil temperature iButtons were waterproofed using small (5 x 10 cm) zip-top plastic bags and placed at 2cm below the soil surface in the center of each subplot. We also measured air temperature at each experimental block by mounting one iButton at 2m above ground under a radiation shield. Temperature data were recorded every two hours from after the fall burn (~December) until April each year.

Table 1: Timing of disturbance treatments and number of snow manipulations from each season of the study.

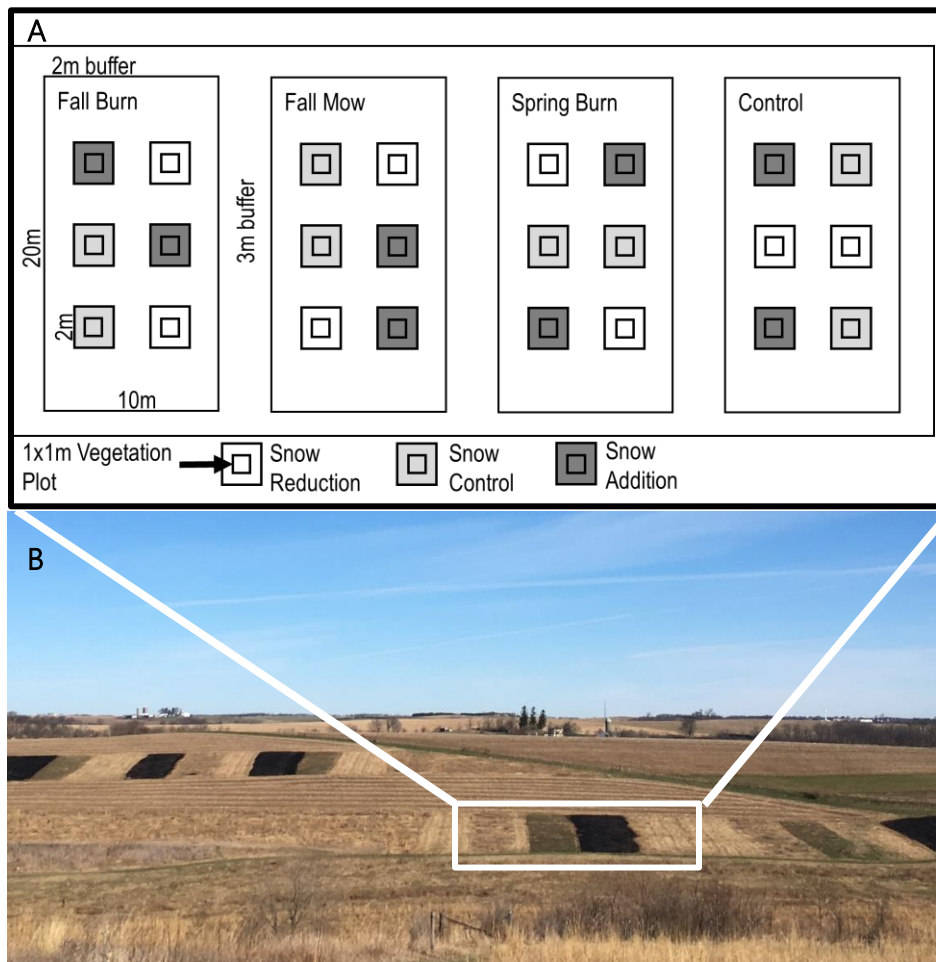| Season	Mowing	Fall Burn	Spring Burn	Number Snow Manipulations
2016-2017	10/22/2016	11/27/2016	4/10/2017	3
2017-2018	10/25/2017	11/20/2017	4/23/2018	3
2018-2019	10/29/2018	12/16/2018	4/15/2019	6

Figure 1: Experimental design. A) One experimental block with randomly assigned plot treatment levels (fall burn, fall mow, spring burn, control) and subplot snow depth treatment levels (snow reduction, snow control, snow addition). B) Photograph of half of the experimental blocks in 2019 following spring burns.

Growth and phenology measurements

To determine how differences in disturbance and snow depth affect plant performance (Table 2), we measured the growth and phenology of six species that occurred in a majority of treatment plots and that span a range of life history characteristics (Table 3, grass vs. forb, early- vs. late-flowering, maximum height). We marked 38-121 individual stems of each species across the experiment with metal numbered tags each year. To measure emergence and growth, we measured the height of the stem apex on each stem every two to four weeks between May and September. To measure phenological stage, we recorded which of five phenological stages each individual was in: stem extending (no reproductive structures present), flowers developing, flowers open, fruit developing, and fruit dispersing approximately each week. To account for differences in plant age and size, we measured the length of the longest axis and perpendicular axis of the clump to which each marked stem belonged and counted the number of reproductive stems in each clump at the end of the growing season. Assuming an elliptical shape, we

calculated the area covered by each plant to use as a covariate in analyses. To measure seed production and seed mass, we placed mesh bags on all flowers of all marked individuals after flowers were no longer open for pollination. We then collected these bags at the end of the growing season to count all seeds and weigh a subset of up to 30 of those seeds.

Plant Community Measurements
To assess how the whole plant community responded to disturbance and climate change, we measured plant community composition twice annually from 2017 to 2019 by visually estimating the percent areal cover of each species rooted in the 1x1m vegetation subplots. We measured the community composition in July and September in each year. To measure composition, 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%, 96-100% cover (Daubenmire, 1959). We also measured the cover of reproductive material during each survey. We took the middle of each Daubenmire cover class to standardize the data between years.

Seed predation measurements
To assess the amount of seed predation that occurred in our experimental plots, we deployed seed predation depots 10 times during the 2018-2019 season starting in June and ending in May. We deployed seed predation depots approximately each month and filled the depots with sand and 40 *Sorghastrum nutans* seeds, as those seeds were readily available in the local environment. We allowed seed predation to happen for 3-5 days before collecting the contents of each depot to count the number of remaining seeds. We deployed three depots in random corners (one in each corner) of the fire treatment plots. We did not test whether snow manipulation affects seed predation. Seed depots were made of Tupperware containers measuring 24.13 x 15.75 x 13.46cm.

Analysis
Soil Temperature responses
To assess how soil temperature dynamics vary during the winter by each treatment, we calculated two metrics that characterize changes to winter soil conditions that relate to potential cold damage and changing spring timing. These include the minimum temperature reached in each plot during each winter (Table 2, "Minimum Temperature") and the first day when the two-day rolling mean temperature was above 1°C (Table 2, "Relative Thaw Date"). To allow for inter-year comparisons of thaw date, we relativized the thaw date in each year by z-transforming the day of year within each year so that earlier dates are negative values and later dates are positive values.

Plant growth and phenology response
To quantify plant responses to our treatments, we calculated plant growth and phenology metrics (Table 2). We used height at first measurement as a proxy for emergence timing and early spring growth (Table 2, "First Height"), the mean growth rate across the season (Table 2, "Mean Growth"), the date of first flowering structure (Table 2, "Flowering Phenology"), and the number of flowering stems on each individual (Table 2, "Flower Production"). Like the date of first thaw, the first height and date of first flowering measurements were relativized for each year to facilitate comparisons of treatment effects between years. To assess differences in seed

production (Table 2, "Seed Production") between treatments, we calculated the total number of seeds produced per individual by multiplying the number of seeds counted on a single stem times the number of reproductive stems produced by an individual plant. We also quantified average seed mass (Table 2, "Seed Mass") by weighing up to 30 of the seeds that we collected from each individual and dividing that number by the number of seeds that we weighed.

Table 2. Descriptions of soil characteristic and plant response metrics used for analysis. The definition column includes information about how the metric was calculated and how to interpret each metric.

Metric	Response	Definition
Minimum Temperature	Soil	The minimum temperature reached during the winter each year for each temperature datalogger
Relative Thaw Date	Soil	First day of year when the mean soil temperature for the following 24 hours remained above 0.5°C. Relativized within years to enable cross-year comparisons. Negative values indicate earlier dates, positive values indicate later dates.
First Height	Plant	Height from first measurement in spring. Relativized within years to enable cross-year comparisons. Negative values indicate shorter plants (later emergence), positive values indicate taller plants (earlier emergence).
Mean Growth Rate	Plant	Average of growth rate (cm/day) between each plant height measurement during each year.
Flowering Timing	Plant	Number of days between soil thaw and the appearance of the first reproductive structure. Relativized within years to enable cross-year comparisons. Negative values indicate earlier flowering, positive values indicate later flowering.
Flower Production	Plant	Number of flowering stems for each marked individual. Values are log transformed with 0.1 added to all values to account for the number of zero observations.
Seed Production	Plant	Number of seeds produced on the sampled reproductive stem multiplied by the number of reproductive stems on that individual. Log-transformed for model fitting.
See Mass	Plant	Mass of all measured seeds (up to 30 seeds) divided by the number of seeds measured to obtain a per-seed mass estimate. Log-transformed for model fitting.

Table 3. Target species and their characteristics. Flower timing and maximum height are determined based on our data. Early flower timing is defined as negative relative flower timing values while maximum height is measured as the mean of the maximum height measured for each species in each block across all years.

Species	Abbreviation	Family	Growth Form	Flower Timing	Maximum Height (cm)
Andropogon gerardii	ANDGER	Poaceae	Grass	Late	239
Sorghastrum nutans	SORNUT	Poaceae	Grass	Late	199
Silphium integrifolium	SILINT	Asteraceae	Forb	Early	194
Ratibida pinnata	RATPIN	Asteraceae	Forb	Early	140
Monarda fistulosa	MONFIS	Lamiaceae	Forb	Early	134
Symphyotrichum laevis	SYMLAE	Asteraceae	Forb	Late	143

Plant community response

To assess whether our treatments affected plant community diversity and composition, we calculated species richness (number of species), and species diversity (Shannon diversity index) for both vegetative and flower cover, along with the cover of predominant functional groups in temperate grasslands: C4 grasses, C3 grasses, legumes, and non-leguminous forbs (Kindscher and Wells, 1995). We analyzed flower cover of C4 grasses and forbs, as they are dominant cover types and forb flowers often provide resources for pollinators.

Model

We used linear mixed effect models to assess differences in soil temperature, plant growth, phenology, and fecundity, along with plant community responses between treatments. For all models, we included a random effect of block with disturbance treatment nested in block along with the individual plot id to account for the split-plot experimental design. Prior to analysis of soil temperature and community responses, we took the average of the two replicate subplots in each plot to avoid pseudoreplication. All models were run using R 3.6.1 (RCoreTeam, 2017) with the lmerTest package (Kuznetsova et al., 2017). Significance testing was based on Satterthwaite degrees of freedom.

For soil temperature responses, we modeled the minimum temperature and relative thaw date as a function of fire treatment, snow treatment, and year along with all interactions between them.

For plant responses, we modelled each response as a function of disturbance treatment, snow treatment, and their interaction, along with log-transformed plant size as a covariate to control for differences due to plant size. For species growth and phenology measures, we also allowed random intercepts for year to account for differences between year in average response due to unmeasured factors that may have varied between years. We also included random intercepts for species to account for different responses due to differences in species life history strategies.

Community responses were assessed using the same linear mixed effect model. We modelled each survey (twice per year) as separate surveys, but included random terms for year and season to account for innate differences between seasons and years in the surveys. We modelled the responses of each plant functional group separately because we measured each species independently, allowing total cover in each plot to exceed 100%, which decreases the

dependence of one group on another. Additionally, we expected different functional groups to respond to different treatment effects, so separate models allowed us to assess whether functional groups responded more to minimum soil temperature or relative thaw date.

Results and Discussion:

Soil temperature
Differences between snow addition and snow control were minor compared to the effect of snow reduction in all winters. Soil temperatures were significantly colder in snow reduction plots in the first (2016-17) and third (2018-19) winters but did not in the middle (2017-18) winter (Figure 2, Table 4). The winter of 2017-2018 did not experience expected patterns in soil temperature dynamics, which is likely due to the very low snow fall during that winter (snow accumulation as of March 15 for 2016-2017 winter: 112cm, 2017-2018 winter: 79cm, 2018-2019 winter: 140cm, 1981-2010 average: 106cm, WI state climatology office). Fall burn treatments tended to have the coldest temperatures in all winters, but to a lesser degree in the middle winter. The timing of spring thaw varied by 8 days in in the springs of 2017 and 2019 and by 4 days in the spring of 2018. Relative thaw date was most strongly affected by fire treatment, where burning in the fall resulted in earlier soil thaw dates. Snow addition had variable effects on relative thaw date where it advanced soil thaw dates in the first year, but delay them in the second year. Snow reduction tended to delay soil thaw dates in the third year.
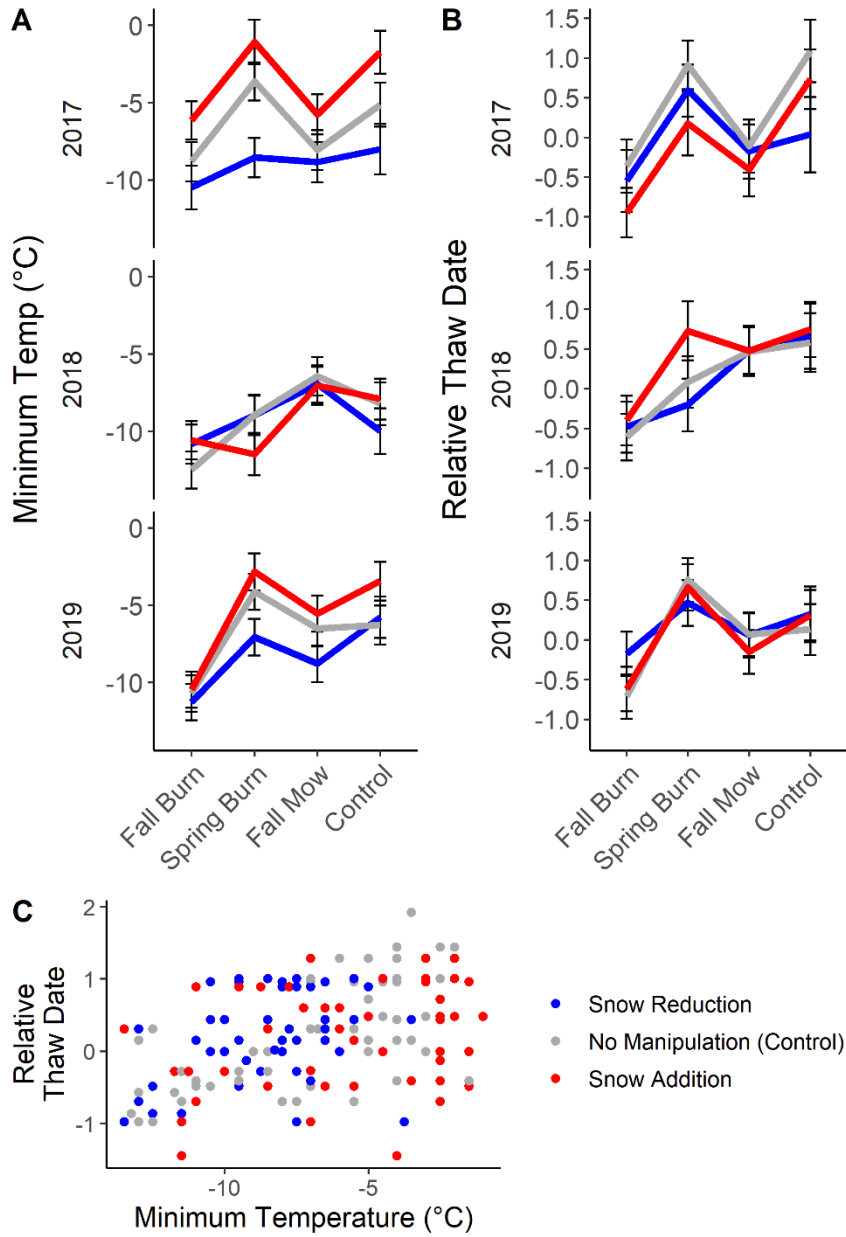
Figure 2: Soil temperature responses to fire and snow treatments between years. A) Mean soil minimum temperature and B) relative thaw date (+/- 95% confidence interval) for each disturbance and snow treatment combination each year. C) Relationshp between soil minimum temperature and relatve thaw date for each plot across all years.

Table 4: ANOVA results for soil temperature responses to experimental treatments and years. Values reported indicate the F-value with numerator and denominator Satterthwaite degress of freedom and p-value. Terms include treatment levels as follows: Disturbance ("Dist") = fall burn, spring burn, fall mow, and control; Snow = snow reduction, no manipulation (control); and snow addition, Year = 2017, 2018, 2019.

Term	Minimum temp		Relative Thaw Date	
	F(df)	**p**	**F(df)**	**p**
Disturbance	**17 (3,27)**	**<0.001**	**7 (3,28)**	**<0.001**
Snow	**114(2,127)**	**<0.001**	**6 (2,152)**	**<0.01**
Year	**225 (2,387)**	**<0.001**	1 (2,285)	0.33
Dist:Snow	**4.3 (6,126)**	**<0.001**	2 (6,147)	0.11
Dist:Year	**56 (6,386)**	**<0.001**	**5 (6,283)**	**<0.001**
Snow:Year	**51 (4,387)**	**<0.001**	**12 (4,286)**	**<0.001**
Dist:Snow:Year	**6 (12,386)**	**<0.001**	**3 (12,283)**	**<0.001**

Plant growth and phenology
Only fire treatments had significant effects on plant responses (figure 3). Plants emerging in fall burn plots were larger, indicating earlier emergence timing compared to other treatments. Growth rate was not affected by the treatments while individuals in spring burn plots tended to flower earlier compared to the other treatments. Flower production was not affected by fire, but there was a trend toward snow impacts where snow manipulation tended to decrease flower production except in fall burn treatments where flower production was somewhat larger in snow addition plots. Seed production had a trend toward an increase in seed production in fall burn plots with snow added. Otherwise, fall mow plots tended to produce more seeds when no snow manipulation occurred. Finally, seed mass was marginally greater
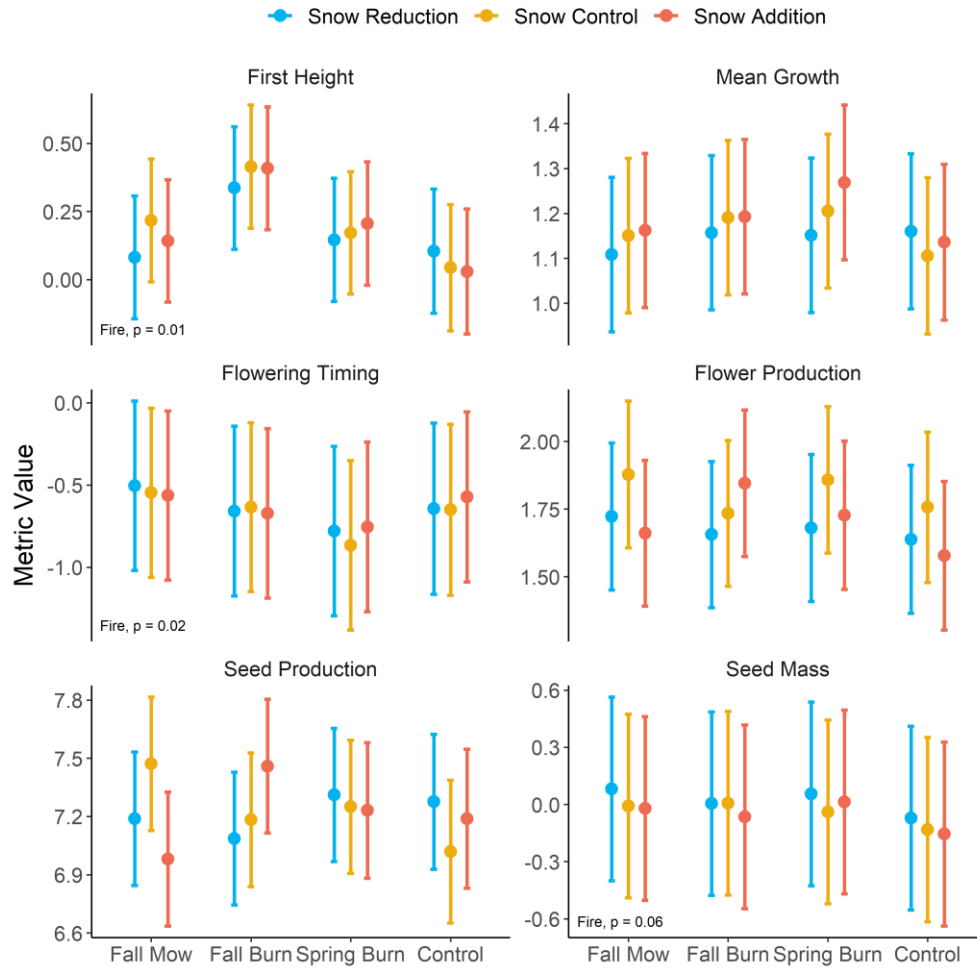
Figure 3: Mean values (+/- Standard Error) for plant growth, phenology, and fecundity responses to fire and snow treatments (colors). These are values averaged for all species studied over all years. Significant model effects are included as text in lower-left corner of panels. Descriptions of each response are included in table 2 and for more detailed statistics see table 5.

Table 5: Anova table containing model results for each plant response. Response variable column indicates the selected response and Effect indicates the predictor variables. F-values are followed by numerator and denominator degrees of freedom and significant p-values are indicated in bold.

Response Variable	Effect	F (df)	p
First Height	Fire	4.91 (3, 20)	**0.01**
First Height	Snow	0.28 (2, 127)	0.76
First Height	log(Plant Size)	142.29 (1, 1438)	**<0.01**
First Height	Fire:Snow	0.3 (6, 126)	0.94
Mean Growth	Fire	0.93 (3, 23)	0.44
Mean Growth	Snow	1.3 (2, 123)	0.28
Mean Growth	log(Plant Size)	229.56 (1, 1420)	**<0.01**
Mean Growth	Fire:Snow	0.63 (6, 121)	0.71
Flower Production	Fire	0.34 (3, 25)	0.8
Flower Production	Snow	2.17 (2, 134)	0.12
Flower Production	log(Plant Size)	1955.86 (1, 1442)	**<0.01**
Flower Production	Fire:Snow	0.76 (6, 131)	0.6
Flowering Timing	Fire	4.15 (3, 27)	**0.02**
Flowering Timing	Snow	0.3 (2, 724)	0.74
Flowering Timing	log(Plant Size)	26.89 (1, 784)	**<0.01**
Flowering Timing	Fire:Snow	0.43 (6, 745)	0.86
Seed Production	Fire	0.1 (3, 29)	0.96
Seed Production	Snow	0.01 (2, 124)	0.99
Seed Production	log(Plant Size)	301.4 (1, 554)	**<0.01**
Seed Production	Fire:Snow	1.58 (6, 120)	0.16
Seed Mass	Fire	2.95 (3, 17)	**0.06**
Seed Mass	Snow	2.49 (2, 588)	**0.08**
Seed Mass	log(Plant Size)	0.54 (1, 583)	0.46
Seed Mass	Fire:Snow	0.36 (6, 585)	0.91

Community response

Fire alone primarily affected plant community responses where all disturbance treatments tended to increase plant diversity (Figure 4) while fall disturbances tended to increase species richness. No disturbance increased the prevalence of C3 grasses while burning in either the spring or fall increased forb flowers (Figure 5). Forb cover was the only response that showed a significant interaction with snow depth where snow reduction in spring burn plots tended to promote forb cover.
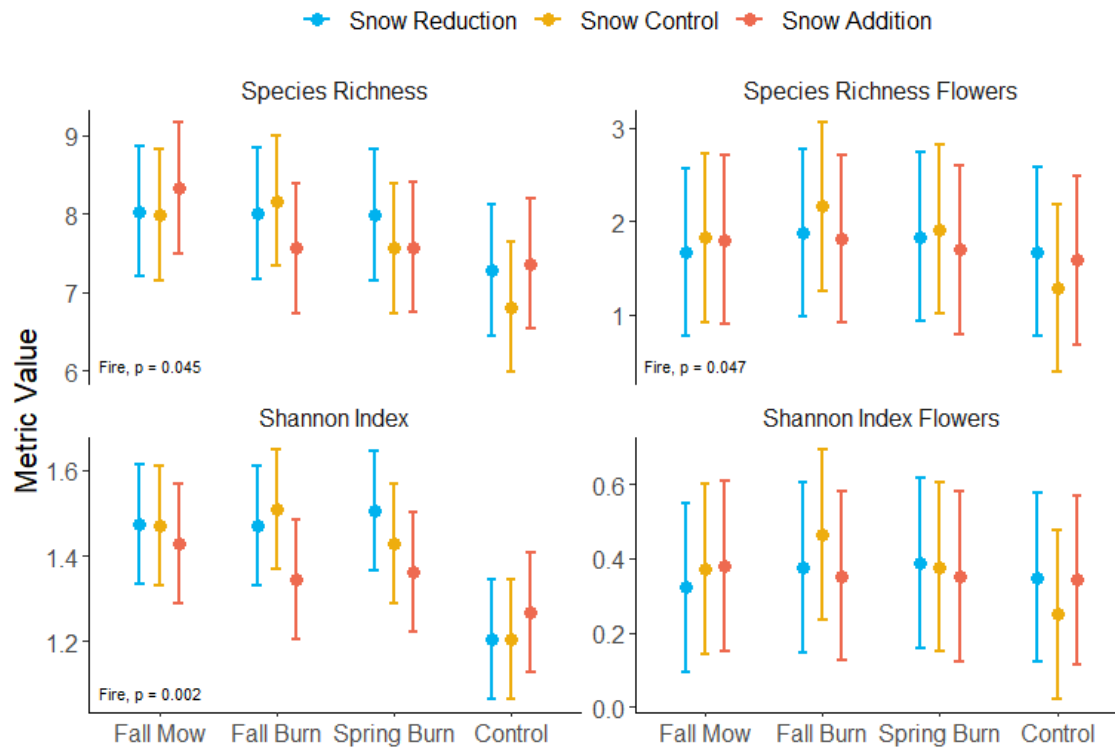
Figure 4: Mean values (+/- Standard Error) for community richness and diversity responses to fire and snow treatments (colors) for vegetation and flowering species. These are values averaged over all years. Significant model effects are included as text in lower-left corner of panels. For more detailed statistics see table 6.
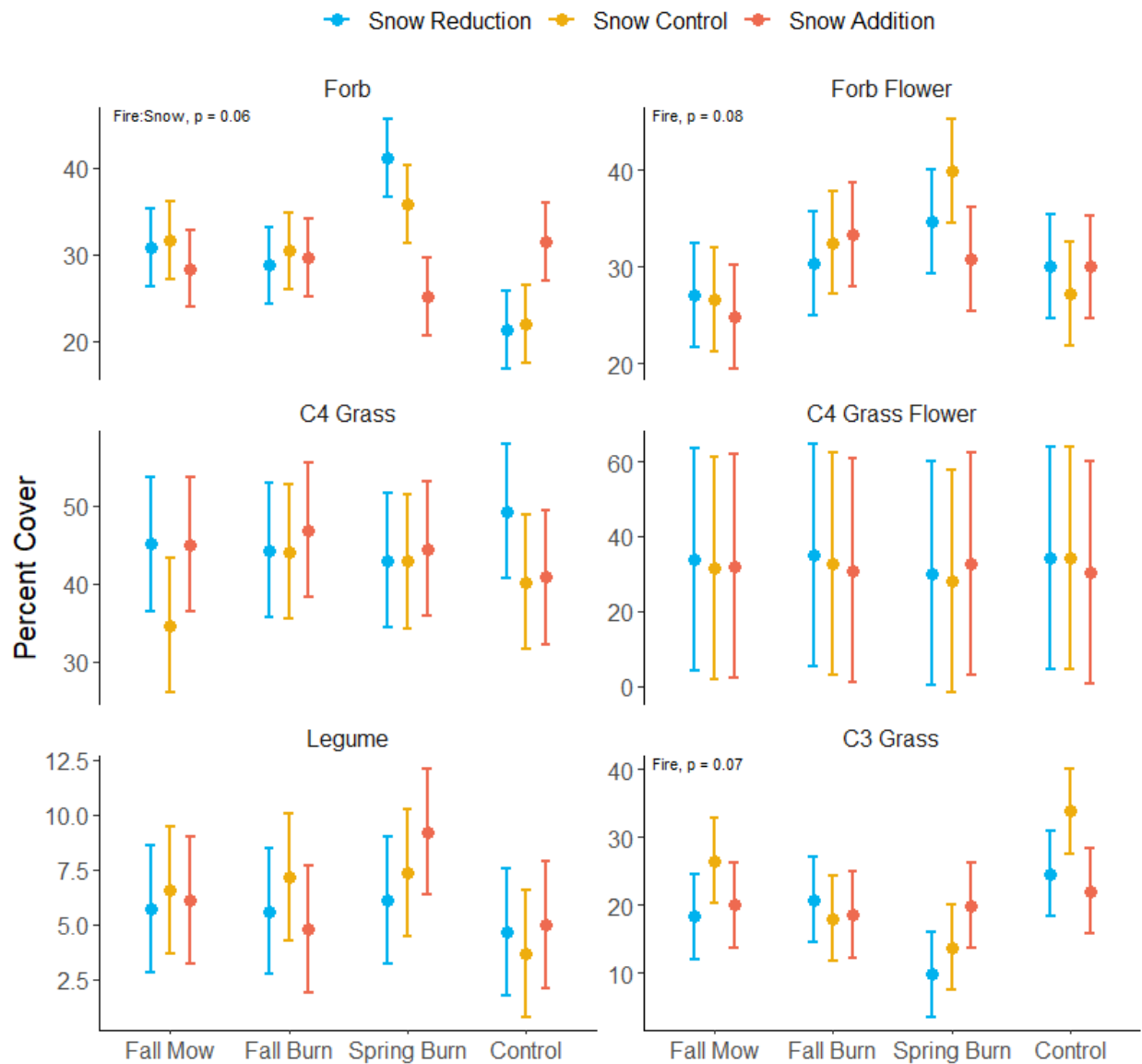
Figure 5: Mean values (+/- Standard Error) of functional group cover in response to fire and snow treatments (colors). These are values averaged over all years. Significant model effects are included as text in upper-right corner of panels. For more detailed statistics see table 6.

Table 6: Anova table containing model results for each community response. Response variable column indicates the selected response and Effect indicates the predictor variables. F-values are followed by numerator and denominator degrees of freedom and significant p-values are indicated in bold.

Response Variable	Effect	F (df)	p
Shannon Index	Fire	6.85 (3, 21)	**<0.01**
Shannon Index	Snow	1.52 (2, 56)	0.23
Shannon Index	Fire:Snow	1.13 (6, 56)	0.36
Shannon Index Flowers	Fire	3.19 (3, 21)	**0.04**
Shannon Index Flowers	Snow	0.41 (2, 56)	0.67
Shannon Index Flowers	Fire:Snow	0.85 (6, 56)	0.54
Species Richness	Fire	1.59 (3, 21)	0.22
Species Richness	Snow	0.05 (2, 56)	0.95
Species Richness	Fire:Snow	1.49 (6, 56)	0.2
Species Richness Flowers	Fire	3.15 (3, 21)	**0.05**
Species Richness Flowers	Snow	0.26 (2, 56)	0.77
Species Richness Flowers	Fire:Snow	1.46 (6, 56)	0.21
Forb	Fire	2.65 (3, 21)	**0.08**
Forb	Snow	0.24 (2, 56)	0.79
Forb	Fire:Snow	2.18 (6, 56)	**0.06**
Forb Flower	Fire	2.59 (3, 21)	**0.08**
Forb Flower	Snow	0.26 (2, 56)	0.77
Forb Flower	Fire:Snow	0.61 (6, 56)	0.72
C4 Grass	Fire	0.19 (3, 21)	0.9
C4 Grass	Snow	1.77 (2, 56)	0.18
C4 Grass	Fire:Snow	0.84 (6, 56)	0.54
C4 Grass Flower	Fire	0.37 (3, 21)	0.77
C4 Grass Flower	Snow	0.43 (2, 56)	0.65
C4 Grass Flower	Fire:Snow	0.41 (6, 56)	0.87
Legume	Fire	1.15 (3, 21)	0.35
Legume	Snow	0.71 (2, 56)	0.5
Legume	Fire:Snow	1.3 (6, 56)	0.27
C3 Grass	Fire	2.71 (3, 21)	**0.07**
C3 Grass	Snow	1.71 (2, 56)	0.19
C3 Grass	Fire:Snow	1.61 (6, 56)	0.16

Seed predation

Seed predation was generally low during the spring and summer, increasing greatly during the late fall and early winter (November to January), corresponding to times when seeds are readily available and when we conducted our seed additions. However, treatments where litter had been removed experienced significantly less seed predation after the treatments were applied (see

Figure 6, fall mow treatment in November along with fall mow and fall burn treatments in December). The spring burn treatment had little effect on seed predation.
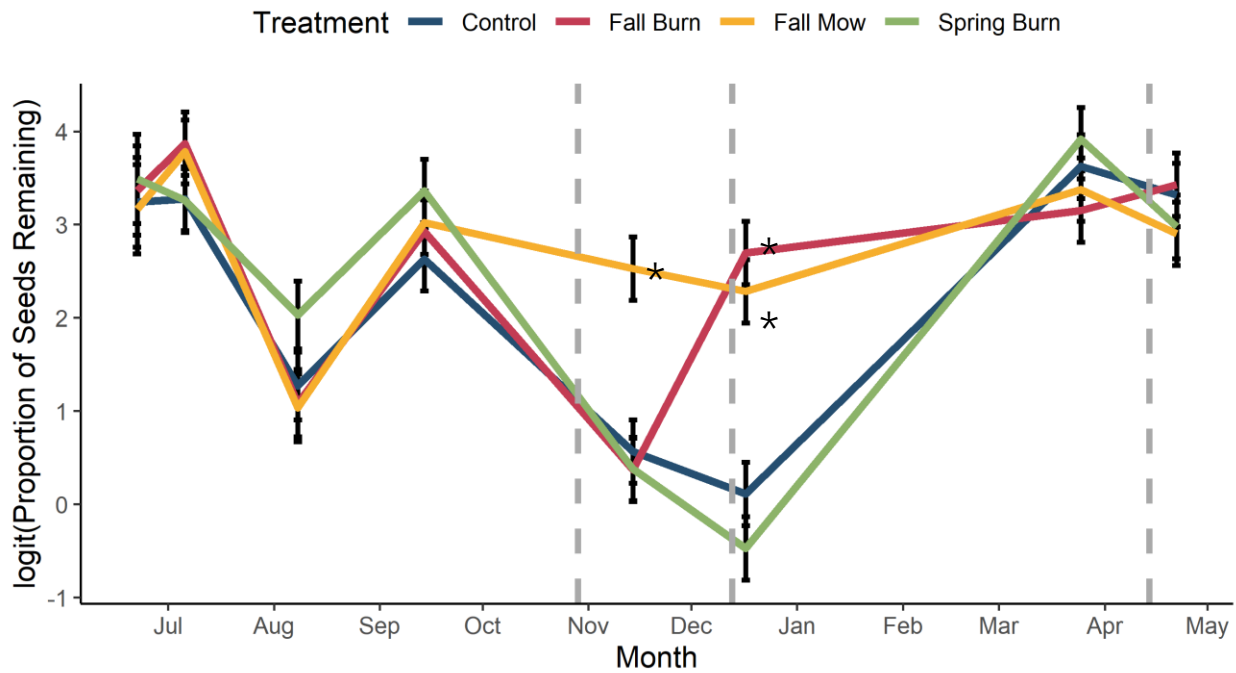

Figure 6: Seed predation through the year from June 2018 to May 2019. Lines indicate average, logit-transformed, proportions of seeds remaining after 3-5 days for each fire treatment. Lower numbers indicate more seeds eaten. Vertical dotted lines indicate treatment applications where the line prior to November is the fall mow treatment, the line after December indicates the fall burn treatment, and the line after April indicates the spring burn treatment. Asterisks indicate times when the treatment was significantly different from the control treatment ($p < 0.05$).

Discussion

Our experiment demonstrates that both disturbance timing and type interact with winter climate to affect winter soil temperature dynamics. However, disturbance timing and type affect plant performance and community diversity much more strongly than winter climate conditions.

Soil temperature dynamics

Lowering winter snow depth reduced minimum soil temperatures and accelerated spring thaw timing (Lubbe and Henry, 2019). As hypothesized, the lack of litter in fall burn and mowing treatments led to lower minimum soil temperatures and earlier thaws (Lubbe and Henry, 2019). The variation in these patterns between years, however, illustrates how seasonal snow depth, air temperature, and the presence of litter interact to determine winter soil conditions. Low snow accumulation during the 2017-2018 winter resulted in minimal impacts of snow manipulations, resulting in increased importance of litter cover. Interestingly, mowed plots had higher soil temperatures than fall burn plots during this middle winter, possibly due to decomposition of compressed litter generating additional heat (Khvorostyanov et al., 2008). Additionally, the effect of litter and snow as insulators of the soil varied from year to year where snow manipulation generated larger variation in minimum temperature during the first winter

compared to later winters. Overall, soil minimum temperatures were cold enough where damage to underground plant organs might be expected, as plant roots tend to tolerate temperatures between -5°C and -15°C during winter (Ambroise et al., 2020; Schaberg et al., 2011).

Spring thaw timing was mostly determined by disturbance treatments. There were some cases where snow manipulation resulted in variation in thaw timing where snow reduction advanced spring thaw in spring burn plots but delayed spring thaw in fall burn plots in 2019. This is likely because fall burn plots led to a deeper layer of frozen soil when snow was reduced, so they took longer to thaw. Spring burn plots did not experience deeper freezing more when snow was reduced, so lower snow accumulation resulted in earlier exposure to warm temperatures. A similar dynamic occurred in the first winter where snow control plots experienced the latest thaw timing, possibly because snow reduction resulted in faster exposure to warm air temperatures while snow addition prevented freezing in the soil.

Plant responses
Our treatments affected three of our measured plant responses, indicating that fire influences plant performance. Emergence was earlier in fall burn treatments. This suggests that earlier thaw timing promotes earlier emergence. Plant emergence and reproductive phenology were not significantly impacted by snow depth, unlike previous studies (Pardee et al., 2019; Sherwood et al., 2017; Wang et al., 2018).

Earlier emergence can result in damage if freezing temperatures occur after emergence (Augspurger, 2013). For example, seeds emerging after earlier snow melt tend to have lower survival, but higher establishment (Wang et al., 2018). Additionally, Pardee et al., (2019) found that early-flowering species were more sensitive to early spring melt and exposure to frost events. However, earlier emergence can also come with advantages to growth, as plants may have greater access to space and nutrients if they emerge earlier (Muffler et al., 2016). This is what we observed in our study as individuals that emerged earlier grew faster. This response may likely be due to the fact that burn plots were the plots most likely to promote growth and establishment potentially through providing space and nutrients (Maret and Wilson, 2000; Old, 1969).

Flowering-related responses, like growth-related responses, were most related to fire timing. Generally, flowering occurred earlier when fires occurred, regardless of fire timing. There was some evidence that snow depth might affect flower production. Other studies have found that early-flowering species are especially sensitive to snow reduction (Wipf, 2010) and climate change (Sherry et al., 2007), so larger responses from species that flower earlier than our study species might be expected. A shorter time between soil thaw and flowering could mean that plants can produce fewer flowers. The prevalence of this pattern in fall burn plots with snow reduction, regardless of species identity, indicates that responses to reduced litter (Knapp and Seastedt, 1986; Lubbe and Henry, 2019) in the spring has especially important effects on reproductive output.

Seed production had a tendency to be affected by snow depth only when disturbance occurred in the fall, mirroring flower production trends. This indicates the potential importance of winter conditions in determining plant fitness after disturbance occurs. Seeds were smaller in control

plots, indicating that a lack of available nutrients, space, or delayed emergence could result in smaller seeds.

Community responses
Several of the plant community metrics of interest were affected by experimental treatments. Most notably, species diversity remained constant through the experiment except for a decline in diversity in control plots. This indicates the importance of frequent fire in maintaining prairie plant species diversity (Bowles and Jones, 2013). Richness, on the other hand, tended to be highest in fall disturbance treatment plots. Since most prairie plants are long-lived perennials, we are likely only seeing changes in rare, small, or annual species in each plot as large plants are unlikely to die in a few years (Veldman et al., 2015). In burn plots, the snow addition plots resulted in lower species richness and diversity. This seems to indicate one of two things. First, it is possible that cold winter soil temperatures favor a larger array of species by promoting tolerant species while controlling sensitive species that are likely to grow quickly. On the other hand, a shorter growing season may disfavor some species. Flowering species richness generally followed similar trends as all species richness. However, fall burn tended to produce more flowering species compared to spring burn, which was not expected.

Of the plant guilds, forbs and C3 grasses responded most strongly to the treatments. C3 grasses increased in control plots. Unexpectedly, C4 grasses did not respond. Previous research would suggest that the greatest increases in C4 grass cover should occur in spring burn plots while forb and C3 grass cover should increase in fall burn plots (Henderson, Richard, 1990; Howe, 1994; Towne and Craine, 2014). We did not see these patterns, potentially because this experiment was conducted in a relatively young prairie restoration where communities are still assembling and C4 grass cover tends to be dominant in early prairie restorations (McCain et al., 2010). Forb cover was only promoted in spring burn plots where snow had been removed. This could be the ideal conditions for forb growth, as there is fire to promote growth and lower snow may have allowed for a longer spring growing season. As expected, fire promoted forb flowering, which is also likely to promote pollinator communities.

Seed predation
Our results mirror other results suggesting that seed predation decreases substantially when cover is absent. This is likely because the rodents that are primarily consuming the seeds lack cover from their predators (Orrock et al., 2004); or could rather the trend could be a result of restricted foraging movement and lower ability of rodents to find seeds (Reed et al., 2004). This trend suggests that it may be worthwhile adding seeds to restored prairies in the fall only after mowing or burning has occurred to minimize seed predation.

Outreach activities
We shared the results of this experiment at six conferences. One was a local conference (Midwest Ecology and Evolution Conference, Henn et al. 2019, Anderegg et al. 2019), two were Ecological Society of America conferences (Anderegg et al. 2019, Henn et al. 2019, Henn et al. 2020), two were international conferences (International Association for Landscape Ecology, Henn et al. 2019, New Phytologist Next Generation Scientists, Henn et al. 2019), and one was a graduate student conference (Graduate Climate Conference, Henn et al. 2018). We have plans to publish six paper based on this work (see Appendix B). Two of these papers will focus explicitly

on restoration and management of prairie communities and one will be published open access. The other four will focus on testing ecological theory while providing insight for management. Once these papers are published, we will be preparing press releases and research briefs to disseminate their results amongst managers and researchers.

We also included education activities in this project. We employed and provided research experience for eight undergraduate students during the process of this grant. This included one undergraduate student who led the seed predation data collection and won supplemental funding from a Prairie Biotics Research grant to support that effort. The experiment was part of an upper level ecology course field trip where students were taken to the site to learn about the experiment, why it is important, and to sample prairie communities in a nearby restored prairie. In addition, we gave short lectures on the purpose and objectives of the experiment to the volunteer prescribed fire crew each time that prescribed fires occurred.

Conclusions, Implications for Management, and Future Research:

These results have important implications for the application of fire in prairie management under changing climate conditions. First, managing using either burning or mowing maintained plant diversity over time, regardless of winter conditions. Second, while mowing and fall burning and similar effects on plant community responses in the absence of snow manipulations, mowing resulted in greater sensitivity of plant emergence, flower production, and seed production to winter conditions compared to fall burns, potentially because mowing lacks the growth-stimulating effect of fire. This may lead to larger long-term community impacts if mowing is substituted for burning as winter conditions continue to change. Third, flower production affects potential reproduction and pollinator resources and it was sensitive to winter conditions when burns happened. However, burning also increased flower production overall. Fourth, seed predation is a large force that governs seed establishment, so seed additions should be paired with litter removal to minimize the loss of seeds.

Ultimately, greatest diversity is likely to be promoted by varying the season in which prescribed burns occur. While we measured plant responses to changes in fire timing and winter conditions, there are other factors to investigate in future research such as soil nutrient levels and microbial communities. Frequent fire has been shown to reduce available Nitrogen (Ojima et al., 1994) while colder soils can have the opposite effect (Groffman et al., 2001b). The interaction between the two might modify the long-term effect of frequent fire on prairie vegetation.

We achieved our objectives of examining how disturbance timing, snow depth, and their interaction affect plant and community responses. Our study demonstrates how disturbance is not only critical for maintaining community diversity, but also sets the stage for plant responses to climate change. Both disturbance-mediated litter cover over winter and snow depth affected minimum soil temperatures and spring soil thaw dates, with cascading effects on plant performance and community composition. In our experiment, fire presence and timing changed the magnitude, and sometimes the direction, of the effects of winter temperature treatments. Accounting for disturbance regime legacies may provide the key to understanding and predicting how species and communities will respond to changing climates.

Literature Cited:

Ambroise, V., Legay, S., Guerriero, G., Hausman, J.F., Cuypers, A., Sergeant, K., 2020. The Roots of Plant Frost Hardiness and Tolerance. Plant Cell Physiol. 61, 3–20. https://doi.org/10.1093/pcp/pcz196

Anderson, R., 1990. The historic role of fire in the North American grassland, in: Fire in North American Tallgrass Prairies. pp. 8–18.

Archibald, S., Lehmann, C.E.R., Gómez-Dans, J.L., Bradstock, R.A., 2013. Defining pyromes and global syndromes of fire regimes. Proc. Natl. Acad. Sci. U. S. A. 110, 6442–6447. https://doi.org/10.1073/pnas.1211466110

Augspurger, C.K., 2013. Reconstructing patterns of temperature, phenology, and frost damage over 124 years: Spring damage risk is increasing. Ecology 94, 41–50. https://doi.org/10.1890/12-0200.1

Bowles, M.L., Jones, M.D., 2013. Repeated burning of eastern tallgrass prairie increases richness and diversity, stabilizing late successional vegetation. Ecol. Appl. 23, 464–478. https://doi.org/10.1890/12-0808.1

Brye, A.K.R., Norman, J.M., Gower, S.T., 2002. The Fate of Nutrients Following Three- and Six-year Burn Intervals in a Tallgrass Prairie Restoration in Wisconsin The Fate of Nutrients Following Three- and Six-year Burn Intervals in a Tallgrass Prairie Restoration in Wisconsin 148, 28–42.

Chamberlain, C.J., Cook, B.I., García de Cortázar-Atauri, I., Wolkovich, E.M., 2019. Rethinking false spring risk. Glob. Chang. Biol. 25, 2209–2220. https://doi.org/10.1111/gcb.14642

Dalgleish, H.J., Hartnett, D.C., 2008. The effects of fire frequency and grazing on tallgrass prairie productivity and plant composition are mediated through bud bank demography, in: Herbaceous Plant Ecology.

Daubenmire, R., 1959. Canopy coverege method of vegetation analysis. Northwest Sci. 33.

Gilman, S.E., Urban, M.C., Tewksbury, J., Gilchrist, G.W., Holt, R.D., 2010. A framework for community interactions under climate change. Trends Ecol. Evol. 25, 325–331. https://doi.org/10.1016/j.tree.2010.03.002

Groffman, P.M., Driscoll, C.T., Fahey, T.J., Hardy, J.P., Fitzhugh, R.D., Tierney, G.L., 2001a. Colder soils in a warmer world: A snow manipulation study in a northern hardwood forest ecosystem. Biogeochemistry 56, 135–150. https://doi.org/10.1023/A:1013039830323

Groffman, P.M., Driscoll, C.T., Fahey, T.J., Hardy, J.P., Fitzhugh, R.D., Tierney, G.L., 2001b. Effects of mild winter freezing on soil nitrogen and carbon dynamics in a northern hardwood forest. Biogeochemistry 56, 191–213. https://doi.org/10.1023/A:1013024603959

Guiden, P.W., Connolly, B.M., Orrock, J.L., 2018. Extreme cold consistently reduces seedling growth but has species-specific effects on browse tolerance in summer. Am. J. Bot. 105, 2075–2080. https://doi.org/10.1002/ajb2.1203

Henderson, Richard, A., 1990. Ten-year response of a Wisconsin prairie remnant to seasonal timing of fire. Proc. Twelfth North Am. Prairie Conf.

Howe, H., 1994. Response of early and late flowering plant to fire season in experimental prairies. Ecol. Appl. 4 SRC-G, 121–133.

IPCC, 2014. Climate Change 2014: Synthesis Report. Contributions fo Working Groups I, II, and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change.

Johnstone, J.F., Allen, C.D., Franklin, J.F., Frelich, L.E., Harvey, B.J., Higuera, P.E., Mack, M.C., Meentemeyer, R.K., Metz, M.R., Perry, G.L.W., Schoennagel, T., Turner, M.G.,

2016. Changing disturbance regimes, ecological memory, and forest resilience. Front. Ecol. Environ. 14, 369–378. https://doi.org/10.1002/fee.1311

Khvorostyanov, D. V., Krinner, G., Ciais, P., Heimann, M., Zimov, S.A., 2008. Vulnerability of permafrost carbon to global warming. Part I: Model description and role of heat generated by organic matter decomposition. Tellus, Ser. B Chem. Phys. Meteorol. 60 B, 250–264. https://doi.org/10.1111/j.1600-0889.2007.00333.x

Kindscher, K., Wells, P. V., 1995. Prairie plant guilds: a multivariate analysis of prairie species based on ecological and morphological traits. Vegetatio 117, 29–50. https://doi.org/10.1007/BF00033257

Knapp, A.K., Seastedt, T.R., 1986. Limits Detritus Accumulation of Tallgrass Prairie Productivity The effects of its plant litter on ecosystem function make the. Bioscience 36, 662–668.

Kreyling, J., 2010. Winter climate change: a critical factor for temperate vegetation performance. Ecology 91, 1939–1948. https://doi.org/10.1890/07-1861.1

Kreyling, J., Grant, K., Hammerl, V., Ar, M.A.S., Malyshev, A. V, Peñuelas, J., Pritsch, K., Sardans, J., Schloter, M., Schuerings, J., Jentsch, A., Beierkuhnlein, C., 2019. Winter warming is ecologically more relevant than summer warming in a cool-temperate grassland 1–9. https://doi.org/10.1038/s41598-019-51221-w

Kuznetsova, A., Brockhoff, P.B., Christensen, R.H.B., 2017. lmerTest Package: tests in linear mixed effects models. J. Stat. Softw. 82, 1–26. https://doi.org/10.18637/jss.v082.i13

Ladwig, L.M., Chandler, J.L., Guiden, P.W., Henn, J.J., 2019. Extreme winter warm event causes exceptionally early bud break for many woody species. Ecosphere 10. https://doi.org/10.1002/ecs2.2542

Ladwig, L.M., Damschen, E.I., Martin-Blangy, S., Alstad, A.O., 2018. Grasslands maintained with frequent fire promote cold-tolerant species. J. Veg. Sci. 29, 541–549. https://doi.org/10.1111/jvs.12635

Ladwig, L.M., Ratajczak, Z.R., Ocheltree, T.W., Hafich, K.A., Churchill, A.C., Frey, S.J.K., Fuss, C.B., Kazanski, C.E., Muñoz, J.D., Petrie, M.D., Reinmann, A.B., Smith, J.G., 2016. Beyond arctic and alpine: The influence of winter climate on temperate ecosystems. Ecology 97, 372–382. https://doi.org/10.1890/15-0153.1

Lubbe, F.C., Henry, H.A.L., 2019. Plant rhizome positioning in the soil and under litter: Trade-offs of frost avoidance versus growth. Perspect. Plant Ecol. Evol. Syst. 41, 125500. https://doi.org/10.1016/j.ppees.2019.125500

Malyshev, A. V., Henry, H.A.L., 2012. Frost damage and winter nitrogen uptake by the grass Poa pratensis L.: Consequences for vegetative versus reproductive growth. Plant Ecol. 213, 1739–1747. https://doi.org/10.1007/s11258-012-0127-0

Maret, M.P., Wilson, M. V., 2000. Fire and seedling population dynamics in western Oregon prairies. J. Veg. Sci. 11, 307–314. https://doi.org/10.2307/3236811

McCain, K.N.S., Baer, S.G., Blair, J.M., Wilson, G.W.T., 2010. Dominant Grasses Suppress Local Diversity in Restored Tallgrass Prairie. Restor. Ecol. 18, 40–49. https://doi.org/10.1111/j.1526-100X.2010.00669.x

Muffler, L., Beierkuhnlein, C., Aas, G., Jentsch, A., Schweiger, A.H., Zohner, C., Kreyling, J., Hickler, T., 2016. Distribution ranges and spring phenology explain late frost sensitivity in 170 woody plants from the Northern Hemisphere. Glob. Ecol. Biogeogr. 25, 1061–1071. https://doi.org/10.1111/geb.12466

Ojima,', D.S., Schimel, D.S., Parton3, ? W J, 0wensby4, C.E., 1994. Long-and short-term effects

of fire on nitrogen cycling in tallgrass prairie, Biogeochemistry.

Ojima, D., Schimel, D., Parton, W., Owensby, C., 1994. Long- and short-term effects of fire on nitrogen cycling in tallgrass prairie. Biogeochemistry 24, 67–84.

Old, S.M., 1969. Microclimate , Fire , and Plant Production in an Illinois Prairie. Ecol. Monogr. 39, 355–384.

Orrock, J., Danielson, B., Brinkerhoff, R., 2004. Rodent foragin is affected by indirect, but not by direct, cues of predation risk. Behav. Ecol. 15, 433–437.

Pardee, G.L., Jensen, I.O., Inouye, D.W., Irwin, R.E., 2019. The individual and combined effects of snowmelt timing and frost exposure on the reproductive success of montane forbs. J. Ecol. 107, 1970–1981. https://doi.org/10.1111/1365-2745.13152

Parmesan, C., 2006. Ecological and Evolutionary Responses to Recent Climate Change. Annu. Rev. Ecol. Evol. Syst. 37, 637–669. https://doi.org/10.1146/annurev.ecolsys.37.091305.110100

Pauli, J.N., Zuckerberg, B., Whiteman, J.P., Porter, W., 2013. The subnivium: A deteriorating seasonal refugium. Front. Ecol. Environ. 11, 260–267. https://doi.org/10.1890/120222

Pavlovic, N.B., Leicht-Young, S.A., Grundel, R., 2011. Short-term effects of burn season on flowering phenology of savanna plants. Plant Ecol. 212, 611–625. https://doi.org/10.1007/s11258-010-9851-5

Peterson, D.W., Reich, P.B., Wrage, K.J., David, W., Peter, B., Keith, J., 2007. Plant functional group responses to fire frequency and tree canopy cover gradients in oak savannas and woodlands Plant functional group responses to fire frequency and tree canopy cover gradients in oak savannas and woodlands 18, 3–12.

Ratajczak, Z., Briggs, J.M., Goodin, D.G., Luo, L., Mohler, R.L., Nippert, J.B., Obermeyer, B., 2016. Assessing the potential for transitions from tallgrass prairie to woodlands: Are we operating beyond critical fire thresholds? Rangel. Ecol. Manag. 69, 280–287. https://doi.org/10.1016/j.rama.2016.03.004

RCoreTeam, 2017. R: A language and environment for statistical computing.

Reed, A., Kaufman, G., Kaufman, D., 2004. Influence of fire, topography, and consumer abundance on seed predation in tallgrass prairie. Can. J. Zool. 82, 145901467.

Samson, F., Knopf, F., 1994. Prairie Conservation in North America. Bioscience 44, 418–421. https://doi.org/10.2307/1312365

Schaberg, P.G., D'Amore, D. V., Hennon, P.E., Halman, J.M., Hawley, G.J., 2011. Do limited cold tolerance and shallow depth of roots contribute to yellow-cedar decline? For. Ecol. Manage. 262, 2142–2150. https://doi.org/10.1016/j.foreco.2011.08.004

Seidl, R., Rammer, W., Spies, T.A., 2014. Disturbance legacies increase the resilience of forest ecosystem structure, composition, and functioning. Ecol. Appl. 24, 2063–2077. https://doi.org/10.1890/14-0255.1

Sherry, R.A., Zhou, X., Gu, S., Arnone, J.A., Schimel, D.S., Verburg, P.S., Wallace, L.L., Luo, Y., 2007. Divergence of reproductive phenology under climate warming. Proc. Natl. Acad. Sci. U. S. A. 104, 198–202. https://doi.org/10.1073/pnas.0605642104

Sherwood, J.A., Debinski, D.M., Caragea, P.C., Germino, M.J., 2017. Effects of experimentally reduced snowpack and passive warming on montane meadow plant phenology and floral resources. Ecosphere 8. https://doi.org/10.1002/ecs2.1745

Stuble, K.B., Thomsen, M., Power, M., 2007. Species interactions reverse grassland responses to changing climate. Science (80-.). 315, 640–642. https://doi.org/10.1002/cind.801_2.x

Tedla, B., Dang, Q.L., Inoue, S., 2020. Freeze-thaw events delay spring budburst and leaf

expansion while longer photoperiods have opposite effect under different [CO2] in white birch: Advance it under elevated but delay it under ambient [CO2]. Environ. Exp. Bot. 173, 103982. https://doi.org/10.1016/j.envexpbot.2020.103982

Towne, E.G., Craine, J.M., 2014. Ecological consequences of shifting the timing of burning tallgrass prairie. PLoS One 9. https://doi.org/10.1371/journal.pone.0103423

Veldman, J.W., Buisson, E., Durigan, G., Fernandes, G.W., Le Stradic, S., Mahy, G., Negreiros, D., Overbeck, G.E., Veldman, R.G., Zaloumis, N.P., Putz, F.E., Bond, W.J., 2015. Toward an old-growth concept for grasslands, savannas, and woodlands. Front. Ecol. Environ. 13, 154–162. https://doi.org/10.1890/140270

Wagenius, S., Beck, J., Kiefer, G., 2020. Fire synchronizes flowering and boosts reproduction in a widespread but declining prairie species. Proc. Natl. Acad. Sci. U. S. A. 117, 3000–3005. https://doi.org/10.1073/pnas.1907320117

Wang, G., Baskin, C.C., Baskin, J.M., Yang, X., Liu, G., Ye, X., Zhang, X., Huang, Z., 2018. Effects of climate warming and prolonged snow cover on phenology of the early life history stages of four alpine herbs on the southeastern Tibetan Plateau. Am. J. Bot. 105, 967–976. https://doi.org/10.1002/ajb2.1104

White, P., Jentsch, A., 2001. The Search for Generality in Studies of Disturbance and Ecosystem Dynamics., in: Progress in Botany.

Williams, C.M., Henry, H.A.L., Sinclair, B.J., 2015. Cold truths: How winter drives responses of terrestrial organisms to climate change. Biol. Rev. 90, 214–235. https://doi.org/10.1111/brv.12105

Wipf, S., 2010. Phenology, growth, and fecundity of eight subarctic tundra species in response to snowmelt manipulations. Plant Ecol. 207, 53–66. https://doi.org/10.1007/s11258-009-9653-9

Appendix A:

Contact Information for Key Project Personnel

Dr. Jonathan J. Henn (Ph.D., University of Wisconsin-Madison 2020)
Email: henn.jonathan@gmail.com
Phone Number: 763-772-4813
Address: 14420 Carlson Pkwy, Plymouth, MN 55447

Dr. Ellen I. Damschen (Professor, University of Wisconsin-Madison)
Email: damschen@wisc.edu
Phone Number: 608-262-2636
Address: 451, Birge Hall, 430 Lincoln Drive, Madison, WI 53706

Appendix B:

Research and outreach products

Graduate Thesis:
Henn. J. J. 2020. Plant community and environmental change: building links through functional traits. Dissertation

Conference Abstracts:
Henn, J. J., L. M. Ladwig, E. I. Damschen. 2019. Winter climate change, snow depth, and prescribed fire affect prairie plant persistence and growth. Ecological Society of America, Louisville, TN (oral presentation).

Henn, J. J., L. M. Ladwig, E. I. Damschen. 2019. Winter climate change, snow depth, and prescribed fire affect prairie plant persistence and growth. New Phytologist Next Generation Scientists Symposium, Dublin, Ireland (oral presentation).

Henn, J. J., L. M. Ladwig, E. I. Damschen. 2019. Winter climate change, snow depth, and prescribed fire affect prairie plant persistence and growth. International Association for Landscape Ecology World Congress. Milan, Italy (oral presentation).

Henn, J. J., L. M. Ladwig, E. I. Damschen. 2019. Winter climate change, snow depth, and prescribed fire affect prairie plant persistence and growth. Midwest Ecology and Evolution Conference. Terre Haute, IN (oral presentation).

Posters:
Henn, J. J., L. M. Ladwig, E. I. Damschen. 2020. Prairie plant growth and phenology are influenced by season of fire and winter snow conditions. Ecological Society of America, (poster presentation).

Anderegg, G.*, E. I. Damschen, J. J. Henn. 2019. Seed predation in restored tallgrass prairies changes throughout the year and is affected by litter cover. Ecological Society of America, Louisville, TN (poster presentation).

Anderegg, G.*, E. I. Damschen, J. J. Henn. 2019. Seed predation in restored tallgrass prairies changes throughout the year and is affected by litter cover. Midwest Ecology and Evolution Conference, Terre Haute, IN (poster presentation).

Henn, J. J., L. M. Ladwig, E. I. Damschen. 2018. Winter climate, fire and species characteristics affect prairie plant response to climate change. Graduate Climate Conference. Seattle, WA (poster presentation).

Publications:
Anderegg, G., J. J. Henn, J. L. Orrock, E. I. Damschen. *In preparation.* Litter removal in restored prairies reduces seed predation during times when seed predation would otherwise be high. *Restoration Ecology.*

Henn, J. J., E. I. Damschen. *In preparation.* Interactive effects of management timing and winter climate change on prairie plant community composition and floral abundance. *Ecological Applications.*

Henn, J. J., E. I. Damschen. *In preparation.* Tallgrass prairie plant growth, phenology, and fecundity under varying fire timing and winter conditions. *American Journal of Botany.*

Henn, J. J., E. I. Damschen. *In preparation.* Plant growth and tolerance functional traits determine species responses to winter climate change. *Functional Ecology.*

Henn, J. J., L. M. Ladwig, E. I. Damschen. *In preparation.* Disturbance type and timing affect growth and investment tradeoffs in grassland plants. *Rangeland Ecology and Management.*

Ladwig, L. M., J. J. Henn, S. M. Kinsler*, T. L. Liebsch*, E. I. Damschen. *In preparation.* The timing of cold hardiness in prairie plants. *Functional Ecology.*

Field Demonstration Summary:
Field demonstration for 15 UW-Madison summer ecology students. Students spent a day walking through the prairie, learning about this experiment, and sampling prairie plant community composition.

Outreach Materials:
Research Briefs to be distributed by the Tallgrass prairie and oak savanna fire consortium. These will be prepared upon acceptance of publications.

Planned report of results for the Prairie Enthusiasts annual meeting in 2021.

Appendix C:

Project metadata

See final project page in JFSP database for project metadata. Data will be archived in the Forest Service Research Data Archive upon publication of results in peer reviewed journals.