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An Assessment of Prairie Management Practices for Maintaining Habitat Quality for the Endangered Poweshiek Skipperling Butterfly in Canada

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Abstract.—The Poweshiek skipperling (*Oarisma poweshiek*) was once a common prairie butterfly in central North America, but is now critically endangered in Canada and the United States. The Poweshiek skipperling is confined to the largest remaining tall grass prairie in Canada, which is currently managed using grazing and fire to maintain prairie habitat and prevent forest and shrub encroachment. To support re-introduction, restocking, and recovery of this critically endangered species, it is necessary to understand the habitat conditions preferred by skipperlings. By surveying prairie sites with Poweshiek skipperling across age and treatment categories (1–2 y since burn, 4–6 y since burn, >15 y since burn, and grazing), we identified commonly-used nectar plants and recorded physical variables known to influence plant diversity. We measured soil variables, including macronutrients, compaction, pH, texture, and moisture content, and used multivariate statistics to test for significant differences in site characteristics and plant community across treatments. For each site, we captured plant diversity, abundance, and cover, as well as total plant biomass. We found the oldest burn sites had the fewest skipperlings. Intermediate burn sites and lightly grazed sites contained the most skipperlings. In 95% of nectaring observations, adult skipperlings were feeding on Black-eyed Susan (*Rudbeckia hirta*), upland white aster (*Solidago ptarmicoides*), and Self-heal (*Prunella vulgaris*). Characteristics in the physical components of sites and plant communities did not significantly differ across treatment types for most variables with the exception of the oldest burns, which showed significantly higher levels of soil compaction, live biomass, bare ground, less flowering species during the flight period, less flowering stems, and increased presence of nonnative and invasive species. Poweshiek skipperling is at high risk of imminent extirpation, and we recommend that the management regimes be adjusted to plan for a consistent supply of habitat conditions and plant species composition exemplified by our intermediate burn sites. We suggest fire return intervals of 4–6 y using patch burns in combination with grazing, permitted at times that minimize the impact on immature stages of Poweshiek skipperling. This management is needed to provide suitable habitat conditions to maintain the current population and allow for successful restocking and recovery.

Introduction

Almost all of the tall grass prairie in North America has been lost due to human disturbance (Samson and Knopf, 1994; COSEWIC, 2003; Samson *et al.*, 2004; Koper *et al.*, 2010) and less than 1% remains in Canada (Vankosky *et al.*, 2017). Undisturbed and unploughed fragments of prairie now mostly exist in preserves, parks, and areas with soil too poor for agriculture (Swengel and Swengel, 1999; Westwood *et al.,* 2020). This substantial loss of habitat has resulted in population declines of many prairie-obligate species. Proper

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management of the remaining habitat is critical to ensure populations of these species survive into the future.

A frequent source of uncertainty in making management decisions is how best to emulate natural prairie disturbance regimes (Wagle and Gowda, 2018). Natural disturbances have historically played an important role in the prairie landscape with wildfire, drought, and grazing by large ungulates and other animals helping to maintain prairies before the advent of intensive farming (Middleton, 2013). The alteration of these disturbance regimes by humans over the last 150 y has negatively impacted prairie habitat quality. For example, extirpation of bison, wildfire suppression, and encroaching woodlands have reduced the extent of remaining tall grass prairie (Hulbert, 1988; Collins and Wallace, 1990; Coppedge *et al.*, 1998; Dornbush, 2004; Grant *et al.*, 2004; Hamilton, 2005; Towne and Kemp, 2008). In addition, the absence of fire, herbivory, native species interactions, and the resulting accumulation of litter in poorly managed or unmanaged grasslands often leads to replacement of important native grasses by shrubs, trees, or exotic weeds, or a decrease in overall germination of plants (Collins and Wallace, 1990; Trager *et al.*, 2004; Maret and Wilson, 2005). Community diversity can also be adversely affected when grasses are left unmanaged or overgrazed as populations of some grasses increase at the expense of others (Delaney *et al.*, 2016). Therefore, appropriate emulation of fire and grazing in management plans is essential in order to maintain prairie habitat integrity.

One example of a prairie-obligate species that has undergone a substantial decline in population over the last century is the Poweshiek skipperling, *Oarisma poweshiek*, (Parker, 1870). Poweshiek skipperling is listed as endangered in Canada and the United States (COSEWIC, 2014; Department of the Interior-FWS, 2015; Canada Gazette, 2019). It was historically common in tall grass prairies in Manitoba, Canada, and in the upper U.S. Midwest from North and South Dakota to Michigan and south to Iowa (McCabe and Post, 1977; Catling and Lafontaine, 1986; Schlicht, 1997; Swengel and Swengel, 1999; Smith *et al.*, 2016b; Belitz *et al.*, 2018; Westwood *et al*,. 2020). Only two small populations now remain, in Manitoba and Michigan (Belitz *et al.*, 2018; Grantham *et al.*, 2020; Westwood *et al.*, 2020).

There is limited life history and habitat information for the Canadian population of Poweshiek skipperling (Catling and Lafontaine, 1986; Klassen *et al.*, 1989), which has resulted in key data gaps for methods needed to improve protection and conservation efforts for this species. Most of the published studies on life history and conservation have occurred in the southern portion of the range (McAlpine, 1973; Scott, 1986; Dana, 1991; Borkin, 1995; Belitz *et al.*, 2019). In Canada, the Poweshiek skipperling was first reported in 1985 (Catling and Lafontaine, 1986), although the species was anecdotally noted as abundant in the early 1980s where it occurred in scattered prairie tall grass remnants in south eastern Manitoba (Klassen *et al.*, 1989, R. Westwood, unpubl. data).

Poweshiek skipperling appears to be able to colonize a range of natural tall grass prairie habits. It is an obligate inhabitant of wet to mesic tall grass prairies in Canada (Catling and Lafontaine, 1986; COSEWIC, 2003; Westwood *et al.*, 2020). In Michigan, Poweshiek skipperling prefers alkaline-fen habitats (Belitz *et al.*, 2019), and in North and South Dakota, Minnesota, and Iowa, it was found in drier, mesic prairies intermixed with stream margins, moist prairie stretches or moist meadows (McCabe and Post, 1977; Opler and Krizek, 1984; Swengel and Swengel, 1999). The wet-mesic tall grass prairies where Poweshiek skipperling occurs in Manitoba vary in size, occurring as open grasslands bordered by bluffs of Bur oak (*Quercus macrocarpa* Michx.) and Trembling aspen (*Populus tremuloides* Michx.) (Catling and Lafontaine, 1986; Westwood *et al.*, 2020).

Prairie-specialist butterflies, such as the Poweshiek skipperling, typically remain within their particular habitat remnants for their entire lifecycle with very low dispersal in comparison to many other butterfly species found in Canada (Burke *et al.*, 2011), making them highly sensitive to disturbance (Swengel, 1998; Swengel and Swengel, 1999; Ries *et al.*, 2001; Ries and Debinski, 2001). In the United States, Poweshiek skipperling has demonstrated a negative response to fire, (*e.g.*, poorly timed during the season causing removal of nectar sources, too frequent or too large), often being absent up to 5 y after a burn in areas where recolonization is possible (Swengel, 1996; COSEWIC, 2003; Swengel *et al.*, 2011; Swengel and Swengel, 2014). Poweshiek skipperling, like many prairie-obligate species, relies on regular disturbance to maintain its habitat in an optimal state, but it is also sensitive to disturbance. Given that Poweshiek skipperling is now confined to small remnant prairie sites, this paradox makes management logistically challenging. After significant disturbance, there is also a risk that isolated populations in fragmented prairie landscapes may be easily extirpated and it is unlikely that they will be repopulated (Selby, 2005).

The cryptic nature of the immature stages of Poweshiek skipperling has made incorporating biological and ecological characteristics of species life history into prairie management planning particularly challenging. Poweshiek skipperling is univoltine (COSEWIC, 2003; Selby, 2005) and females lay eggs singly on leaves of host plants or plants adjacent to host plants (COSEWIC, 2003; Shepard, 2005; Dupont-Morozoff, 2013). Adults are normally active for 2 to 3 wk from late June to mid-July, with peak numbers of adults present during the second week of July in Canada (Klassen *et al.*, 1989; COSEWIC, 2003; Dupont-Morozoff, 2013; Dearborn and Westwood, 2014). Adults lay eggs in mid-July, larvae are present throughout the summer (Henault 2021), larvae diapause over winter and pupate the following June (COSEWIC 2003).

Disturbance can impact various aspects of insect life history, and, in the case of the Poweshiek skipperling, the availability of adult nectar sources and host plants to support larval development are critical (COSEWIC, 2014). In the United States, Holzman (1972) suggested larval host plants may include Slender spike rush (*Eleocharis tenuis* (Willd.) Schult.), Elliptic spike rush, *Eleocharis elliptica* Kunth, and possibly other sedges. In Michigan, Pointon (2015) reported the larval host plants may include Prairie dropseed, *Sporobolus heterolepis* A. Gray and Mat muhly, *Muhlenbergia richardsonis* (Trin.) Rydb. Observations in Minnesota and Wisconsin indicate that prairie grasses, especially Prairie dropseed, and Little bluestem, *Schizachyrium scoparium* Nash., are likely important larval hosts (Borkin, 1995; Borkin, 1996; Dana, 1999 unpubl.) and that Big bluestem, (*Andropogon gerardii* Vitman) and Side-oats grama (*Bouteloua curtipendula* (Michx.) Torr) may also be used as alternate feeding sources. The identities of the important adult nectar sources and larval host plants were unknown in Canada during the period of this study. In 2018 larval feeding on four grass species (Prairie dropseed, Mat muhly, Little bluestem and Big bluestem) in the wild was documented in Canada (Henault 2021). Poweshiek skipperling has since been reared to adulthood in both the Minnesota Zoo and Assiniboine Park Zoo butterfly conservation programs, primarily on Prairie dropseed (Runquist and Nordmeyer, 2019; Burns *et al.*, 2020).

A wide range of nectar sources utilized by Poweshiek skipperling have been reported in the U.S., including Rough false sunflower (*Heliopsis scabra* Dunal), Purple coneflower (*Echinacea angustifolia* DC), Tickseed (*Coreopsis palmate* Nutt), Black-eyed Susan (*Rudbeckia hirta* L.), and Pale-spike lobelia (*Lobelia spicata* Lam.) (Swengel and Swengel, 1999). On drier prairie habitats, Purple coneflower is most commonly visited (Swengel and Swengel, 1999), whereas on wetter prairie habitats favorite nectar plants include Black-eyed Susan and Pale-spike lobelia (Selby, 2005). In Canada, Catling and Lafontaine (1986) reported that Poweshiek skipperling visited the flowers of *L. spicata.* Quantifying the extent to which various disturbance regimes impact the abundance of these plant species is necessary in order to determine how best to manage remaining Poweshiek skipperling habitat.

Although habitat loss has had significant impacts on the decline of the Poweshiek skipperling, incomplete knowledge of important components of life history and habitat requirements may have contributed to further decline due to incompatible prairie management activities (Schlicht and Orwig, 1992; Reed, 1997; Swengel *et al.*, 2011; Swengel and Swengel, 2014). There is a need to determine how best to use fire and grazing to maintain a productive prairie ecosystem and still support Poweshiek skipperling, which relies on particular habitat conditions for long-term survival. Identifying optimal habitat requirements can allow managers to tailor prairie management activities to maintain a landscape that can support this species, and may also assist with the modification or creation of new habitats for reintroduction purposes. The primary focus of our study was to determine which disturbance approach or combination would be best suited to support continued survival of Poweshiek skipperling in Manitoba. Due to the scarcity of Powesheik skipperling, we used adult survey data to inform our interpretation of results with respect to the relative merits of different regimes. Our objectives were to: (1) determine how disturbance may negatively or positively change physical and edaphic site characteristics that may influence skipperling presence, and (2) measure the effects of disturbance on the presence of potential larval host plants and floral nectar resources used by skipperlings. Based on our results, we also provide recommendations for managers working in our study region.

METHODS

SITE SELECTION

The study was located in the 4500 ha Manitoba Tall Grass Prairie Preserve (MTGPP) in southeastern Manitoba (49°09′N, 96°40′W), Canada (Joyce and Morgan, 1989; Westwood *et al.*, 2020). The MTGPP is approximately 237.6 m above sea level (Environment Canada, 2010) with shallow, rocky, highly calcareous soils which are unsuitable for most agricultural uses (Catling and Lafontaine, 1986; Westwood and Borkowsky, 2004). Drainage in the MTGPP is poor with soil composed of lacustrine parent material, sandy loam to clay loam upper horizons and a thin organic surface layer (Canada Soil Inventory, 1989; Westwood and Borkowsky, 2004). The annual precipitation is approximately 562.6 mm, with 78% (440.7 mm) as rainfall (Environment Canada, 2010). The climate is boreal continental with mean temperatures of −17.1 C and 19.8 C for January and July, respectively (Environment Canada, 2010), with an average annual temperature of 3.4 C.

During the 1980's and early 1990's, the remaining Poweshiek skipperling populations in Manitoba and the U.S. remained relatively stable until approximately 2000 when an east to west range wide decline occurred (COSEWIC 2014; Belitz et al. 2018; Belitz et al. 2020). This decline was noticed in Manitoba by the mid 2007 (Dupont Morozoff 2013), leaving a limited number of sites to carry out this research. The Manitoba population appeared robust in 1980s and 1990s (Klassen et al. 1989; R. Westwood unpubl. data) until at least 2002 when Webster (2003) carried out the first systematic survey for Poweshiek skipperling in the MTGPP using a timed survey method. In May 2008, we selected some of the sites Webster (2003) found positive for Poweshiek skippering in addition to positive sites from more recent surveys (Morden, 2006; Bates, 2007; R. Westwood, unpubl.data). We selected 11 of 12

TABLE 1.—Summary of history, area and size of study sites found in the Manitoba Tall Grass Prairie Preserve 2008–2009

Treatment type & sites	Treatment descriptor	Year last burned (S = spring and F = fall)	Year last grazed	Years since last burn or graze	Approx. area occupied by Poweshiek skipperling (ha)	Grazing intensity A.U.M./ha[1]	Number of adult Poweshiek skipperlings observed (2008 & 2009)
Burn 1993							
Burn 1993A	Old 1	Pre-1995	Pre-1995	15	7.31	NA	5 & 0
Burn 1993B	Old 2	Pre-1995	Pre-1995	15	3.93	NA	6 & 0
Burn 2002–2004							
Burn 2002A	Intermediate 1	2002	Pre-1995	6	44.2	NA	90 & 52
Burn 2002B	Intermediate 2	2002	NA	6	41.7	NA	1 & 0
Burn 2004	Intermediate 3	2004	Pre-1995	4	13.2	NA	77 & 2
Burn 2006–2008							
Burn 2006A	Recent 1	2006F	Pre-1995	2	13.2	NA	76 & 6
Burn 2006B	Recent 2	2006F	Pre-1995	2	39.2	NA	4 & 0
Burn 2008	Recent 3	2008S	Pre-1995	0.3	46.3	NA	3 & 1
Grazed	Grazed						
Graze 2006	Grazed 1	2005F	2007	1	31.2	0.39	8 & 15
Graze 2008A	Grazed 2	2007F	2008	0	22.9	1.8	51 & 3
Graze 2008B	Grazed 3	2002F	2008	0	21.9	0.27	1 & 0

[1] A.U.M./ha = Animal Unit Months per hectare

remaining known sites in MTGPP with skipperlings present, which limited the number of replicates available for our treatment categories. We categorized the study sites by fire return interval as recent burns (1 to 2 y), intermediate burns (4 to 6 y) and old burns (>15 y) in a manner similar to McCullough *et al.* (2019). The burn sites were grouped into three age categories: two sites burned in 1993 (old burns), three sites burned between 2002 and 2004 (intermediate burns), and three sites burned between 2006–2008 (recent burns). There were also three sites last grazed by livestock between 2006 and 2008 (grazed sites). Table 1 provides a summary of the descriptors used for each site used in this paper with location of sites shown in Figure 1. Each site was located within one quarter section of land (65.7 ha), and the approximate area within each quarter section utilized by Poweshiek skipperling was calculated using aerial photographs (Table 1). All sites contained variable amounts of upland prairie interspersed with woodland and marshland (Semmler and Westwood 2013). Most sites were surrounded in forest and/or extensive wetlands with few travel corridors evident for Poweshiek skipperling adults to easily disperse (Dupont-Morozoff 2013). Sites were interspersed within the MTGPP with the average straight-line distance between sites being 5.17 km (range 0.43–12.15 km).

The Nature Conservancy of Canada uses grazing and prescribed spring fires as part of the disturbance regime in the MTGPP, although occasional unplanned human-caused fall wildfires also occur in prairie. The three grazed sites had experienced partial burns from fall wildfires in the past (Table 1). Studies have shown that timely burning and moderate grazing within the same sites can increase plant diversity and heterogeneity and are more reflective of the natural condition of tall grass prairies prior to European colonization (Fuhlendorf and Engle 2004, Fulhendorf *et al.* 2008, Moranz *et al.* 2014), although this management

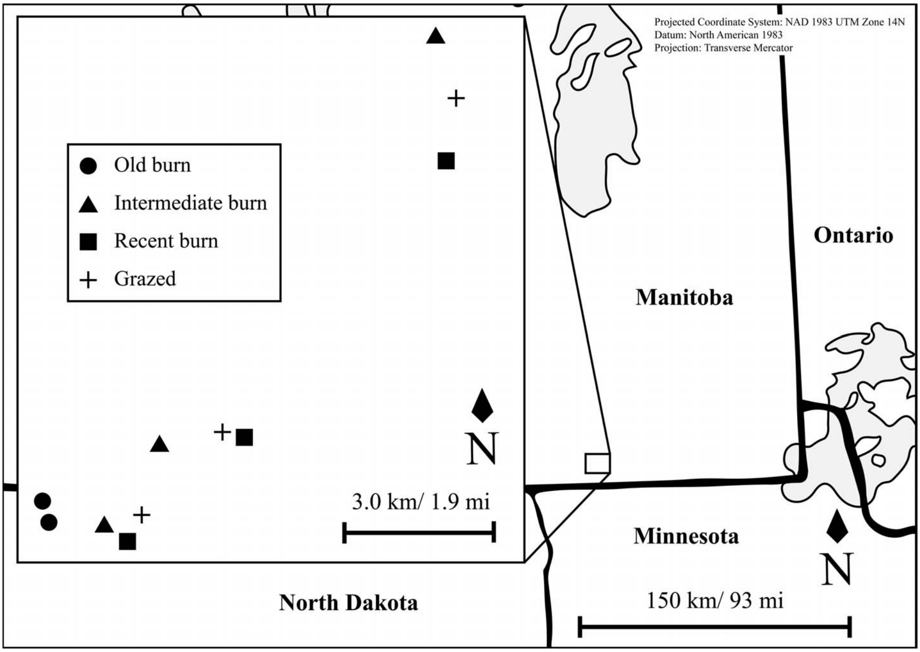

FIG. 1.—Study region with inset of research sites (labelled as symbols) in the Manitoba Tall Grass Prairie Preserve.

approach did not occur in all of the sites before and during the time of our study due to dry conditions preventing use of planned spring burns.

The grazing intensity is managed in the MTGPP and measured in animal unit months (AUMs). One AUM is the amount of forage required by an animal for 1 mo per ha. An animal unit is defined as a mature (453.59 kg) cow or the equivalent and is based on an average consumption rate of 11.79 kg of forage dry matter per day (Ruyle and Ogden, 1993). One AUM may also include both a cow and suckling calf (Smith *et al.*, 2016a). The grazing intensity varied between sites (Table 1). Grazed 1 and 2 sites were grazed for a shorter period during the summer, whereas Grazed 3 site was grazed for longer periods during the summer, although the actual grazing dates were unavailable.

Within areas of previously-observed Poweshiek skipperling adult activity in each site, we established two 40 × 40 m plots (except in the old burn sites, in which dominance of wooded and marshland areas only allowed for the placement of one plot). Plots were placed at least 150 m apart and at least 20 m from wooded areas or discontinuities, such as roads and open marsh. For grazed sites, research plots were placed in areas that had not been subject to wildfire within the last several years to best of our knowledge.

In each plot, five equally-spaced 40 m transects were established running parallel in a north-south direction for skipperling and plant surveys and collection of physical data. Transects were placed in parallel, as clumps of trees or marsh prevented placing single longer transects in several sites. The following physical variables that may be sensitive to disturbance type and can influence plant growth and form were measured in plots between June and September in 2008 or 2009: plant biomass, soil pH, soil moisture, soil compaction, soil nutrients and soil structure. Pogue *et al.* (2018) investigated the presence of many of the soil nutrients examined in this study (including soil calcium concentration) and soil pH in Powesheik skipperling habitats in Michigan, in which several of the potential larval host plants prefer to grow in alkaline, calcareous soils. Livestock grazing has been widely reported to change soil compaction and soil bulk density levels (*see* Royer *et al.*, 2008), which can influence soil water content and potentially impact microclimate conditions at the soil surface where larvae of Dakota skipper (*Hesperia dacotae* (Skinner)) may reside. Magoba *et al.* (2015) found the level of soil compaction is negatively correlated with arthropod species richness near the soil surface, which is where Poweshiek skipperling immature stages reside for almost the entire lifecycle.

SAMPLING METHODS

Soil pH and percent soil moisture content were measured using a Kelway Soil Meter (Kelway Instruments Co., Inc. P.O. Box 54, Wyckoff, NJ 07481 U.S.A.). Soil moisture (%) and pH were measured at approximately 8 cm below the soil surface. Nine measurements were made per plot by taking three randomly placed readings each on transects one, three, and five. Soil compaction was measured at depths of 10 and 20 cm using a Field Scout SC 900 Soil Compaction Meter (Spectrum Technologies Inc, 12360 South Industrial Dr. East - Plainfield, Illinois 60585). Three measurements were made at random locations along transects one to five for a total of 15 measurements per plot.

A soil sample to a depth of approximately 12 cm was taken from one random location along transects one, three, and five in each plot. The samples from each of the two plots (total of six) were mixed and three samples removed to represent each site. The samples representing each site were analyzed for an aggregate of organic constituents including organic matter, soil pH, calcium, magnesium, sodium and physical and aggregate properties of sand, silt and clay textures.

Plant biomass samples (including above ground stems, leaves, and flowers) were collected from each plot in fall 2008 to determine the relative differences in live plant biomass between sites. In each plot two 0.5 m^2 grids were randomly placed along each of the five transects. All of the above ground biomass was removed within the grids by cutting plants off at ground level and placing material in paper bags. Samples may have contained dead plant material (litter) decomposing from the previous year. Samples were returned to the laboratory and dried and weighed to the nearest gram.

Flowering plant surveys were conducted during the midpoint of flight period in both 2008 and 2009. The number of stems of all flowering forbs and shrubs were counted and identified along each of the five transects in each plot up to 1 m on either side of the transect. Nonflowering plant species were not recorded during the flowering plant survey.

The percent cover of all graminoids, forbs and bare ground was recorded in each plot in August 2008 following Schultz and Dlugosch (1999) and Benson *et al.* (2007) except in the Grazed 3 site due to presence of livestock. Two 1 m-square grids were randomly placed along each of the five transects in each plot to measure cover of plant species and bare ground. Bare ground was defined as areas devoid of standing forbs and graminoids, but may have contained decomposing plant litter. Plants that could not be clearly identifiable to species in the field or laboratory were grouped at a higher taxonomic level (*e.g.*, "*Carex* L. spp." or "*Poaceae* Barnhart spp"). *Deschampsia cespitosa* (L.) P. Beauv. and *S. heterolepis* were grouped together due to difficulty of identification of immature plants. All species were identified in the field or samples were collected and verified in the laboratory and/or with an experienced botanist. Species identification was based on Looman and Best (1981), Johnson

TABLE 2.—Summary of significant physical and plant characteristics in the Manitoba Tall Grass Prairie Preserve (mean ± SE) based on treatment type

	Treatment type				
Soil characteristics	Old burns	Intermediate burns	Recent burns	Grazed	
Soil compaction (kpa) depth = 10 cm	241.1 ± 17.3a[1]	310.0 ± 16.5a	216.0 ± 19.4a	356.1 ± 24.3b	F = 7.79, P < 0.001
Soil compaction (kpa) depth = 20 cm	608.7 ± 90.7b	433.0 ± 20.8a	360.2 ± 38.8a	528.1 ± 35.6b	F = 3.34, P = 0.020
pH	6.68 ± 0.04b	6.67 ± 0.04b	6.54 ± 0.03a	6.72 ± 0.03b	F = 3.67, P = 0.013
Percent soil organic matter	47.1 ± 0.8b	16.9 ± 1.3a	15.8 ± 1.1a	13.8.8 ± 3.7a	F = 22.02, P = 0.001
Soil calcium (mg/kg)	9160.0 ± 60.0b	6586.7 ± 69.8a	6470.3 ± 283.1a	5140.0 ± 767.1a	F = 11.26, P = 0.005
Percent forb cover (m2)	14.0 ± 1.9a	18.3 ± 1.3ab	24.3 ± 2.0b	21.9 ± 1.9b	F = 3.91, P = 0.010
Percent bare ground (m2)	42.9 ± 2.7b	21.9 ± 1.8a	23.3 ± 3.9a	21.6 ± 1.9a	F = 6.41, P < 0.001
Percent graminoid cover (m2)	43.5 ± 2.5a	59.4 ± 2.2b	54.3 ± 2.1b	56.3 ± 2.1b	F = 5.53, P = 0.001
Biomass (g/0.5m^2)	343.2 ± 23.1c	252.8 ± 13.8b	190.6 ± 9.6a	219.8 ± 10.9ab	F = 15.36, P < 0.001

[1] Means in rows followed by different letters are significantly different

et al. (1995), and Vance (1999) and authorities and names updated using Tropicos.org (Missouri Botanical Garden, 2020; s*ee* Table 3 for a taxonomic list of flowering plants and graminoids found in surveys).

The checklist method of surveying to confirm the presence and relative abundance of Poweshiek skipperling adults (Royer *et al.*, 1998) was used in 2008 and 2009 within each study site (including transects) using a predetermined path. The area surveyed was the same in each site in both 2008 and 2009 and was also similar to areas surveyed between 2005 and 2007. In 2008, surveying time was variable between sites (primarily due to weather conditions and time available for surveys), and, for both years, individual skipperlings could have been observed and recorded more than once. In 2009 the survey was standardized to the number of person hours of observation for each site to allow for standardized comparisons of skipperling abundance between sites.

STATISTICAL ANALYSIS

The number of skipperling observations per site during the study are reported by year (Table 1); however, as standardized timed surveys were only available for the second year of the study the 2008 survey observations are not directly comparable to the 2009 skipperling surveys. Analysis of Variance (ANOVA) was used to compare the soil and plant variables among the different disturbance types. The measurements for soil variables (compaction,

TABLE 3.—Summary of the presence/absence of flowering forb/shrub species in 2008 and 2009 and graminoid species in 2008 identified in study sites of the Manitoba Tall Grass Prairie Preserve. Common = species with ≥0.5% of total stems and common graminoids = species with ≥5% total cover for all sites

Forbs and shrubs		Old burns	Intermed. burns	Recent burns	Grazed	Common species
Achillea millefolium L. (Common yarrow)	Ach mil	-	X	X	X	-
Agoseris glauca (Pursh) Raf. (False dandelion)	Ago gla	-	-	X	X	-
Anemone canadensis L. (Canada anemone)	Ane can	-	X	X	X	X
Anemone cylindrica A. Gray (Long-fruited anemone)	Ane cyl	-	X	-	-	-
Apocynum cannabium L. (Hemp dogbane)	Apo can	-	X	X	-	-
Asclepias incarnata L. (Swamp milkweed)	Asc inc	X	-	-	X	-
Asclepias ovalifolia Decne. (Dwarf milkweed)	Asc ova	X	X	X	X	-
Campanula aparinoides Pursh (Marsh bellflower)	Cam apa	X	-	-	-	X
Campanula rotundifolia L. (Harebell)	Cam rot	-	X	X	X	X
Castilleja coccinae (L.) Spreng. (Scarlet paintbrush)	Cas coc	-	X	X	X	-
Cirsium arvense (L.) Scop. (Canada thistle)	Cir arv	X	-	X	-	-
Cirsium Mill. spp. (Thistle)	Cir sp	X	-	-	-	-
Cicuta L. spp. (Water-hemlock)	Cic sp	X	X	X	X	-
Crepis tectorum L. (Narrow-leaved hawk's-beard)	Cre tec	X	X	X	X	X
Dalea candida Willd. (White prairie-clover)	Dal can	-	-	X	-	-
Dalea purpurea Vent. (Purple prairie-clover)	Dal pur	-	X	X	X	X
Erigeron philadelphicus L. (Philadelphia fleabane)	Eri phi	-	X	-	-	-
Euthamia graminifolia (L.) Nutt. (Flat-topped goldenrod)	Eut gra	X	-	X	X	X
Galium boreale L. (Northern bedstraw)	Gal bor	-	X	X	X	X
Glycyrrhiza lepidota Pursh (Wild licorice)	Gly lep	-	X	X	X	-
Helianthus angustifolius L. (Narrow-leaf sunflower)	Hel ang	X	-	X	X	-
Heliopsis scabra Dunal (Rough false sunflower)	Hel sca	-	X	-	X	-
Hieracium umbellatum L. (Umbellate hawkweed)	Hie umb	-	X	X	X	X
Hypericum perforatum L. (St. John's-wort)	Hyp per	X	-	-	-	-
Hypoxis hirsuta (L.) Coville (Star-grass)	Hyp hir	-	X	X	X	X
Krigia Schreb. sp. (Dwarf-dandelion)	Kri sp	X	X	X	X	-
Lathyrus palustris L. (Marsh vetchling)	Lat pal	X	X	X	X	-
Lathyrus L. sp. (Wild pea)	Lat sp	-	X	X	-	-
Liatris ligulistylis (A. Nelson) K. Schum. (Meadow blazingstar)	Lia lig	-	X	X	X	-
Lilium philadelphicum L. (Wood lily)	Lil phi	-	X	X	X	-
Linum virginianum L. (Yellow flax)	Lin rig	-	X	X	X	X
Lithospermum canescens (Michx.) Lehm. (Hoary puccoon)	Lit can	-	X	X	-	-
Lobelia kalmii L. (Brook lobelia)	Lob kal	X	X	X	X	X
Melilotus albus Medik. (White sweet-clover)	Mel alb	-	X	X	X	-
Mentha canadensis L. (Field mint)	Men can	X	-	-	-	X
Monarda fistulosa L. (Wild bergamot)	Mon fis	-	-	X	X	-
Oenothera biennis L. (Yellow evening-primrose)	Oen bie	X	X	-	X	-
Packera paupercula (Michx.) Á. Löve & D. Löve (Balsam groundsel)	Pac pau	-	-	-	X	-
Parnassia palustris L. (Northern grass-of-parnassus)	Par pal	-	X	X	X	X
Pedicularis canadensis L. (Forest lousewort)	Ped can	-	-	X	X	-
Platanthera praeclara Sheviak & M.L. Bowles (Western prairie fringed orchid)	Pla pra	-	-	X	-	-
Polygala senega L. (Seneca snakeroot)	Pol sen	-	X	X	X	X

TABLE 3.—Continued

Forbs and shrubs		Old burns	Intermed. burns	Recent burns	Grazed	Common species
Potentilla anserina L. (Silverweed)	Pot ans	X	X	X	X	X
Potentilla fruticosa L. (Shrubby cinquefoil)	Pot fru	X	X	X	X	-
Prunella vulgaris L. (Self-heal)	Pru vul	-	X	X	X	X
Rudbeckia hirta L. (Black-eyed susan)	Rud hir	X	X	X	X	X
Packera cana (Hook.) W.A. Weber & Á. Löve (Silvery groundsel)	Pac can	-	X	X	X	-
Sisyrinchium montanum Greene (Blue-eyed grass)	Sys mon	-	X	X	X	-
Solidago canadensis L. (Canada goldenrod)	Sol can	-	X	X	X	X
Solidago ptarmicoides (Torr. & A. Gray) B. Boivin (Upland white aster)	Sol pta	-	X	X	X	X
Solidago rigida L. (Rigid goldenrod)	Sol rid	-	-	X	X	X
Spiraea alba Du Roi (Narrow-leaved meadowsweet)	Spi alb	X	-	-	X	-
Stachys palustris L. (Marsh hedge-nettle)	Sta pal	X	-	-	-	X
Thalictrum dasycarpum Fisch. & Avé-Lall. (Tall meadow rue)	Tha das	-	X	X	X	X
Thalictrum venulosum Trel. (Veiny meadow rue)	Tha ven	-	-	X	X	-
Triantha glutinosa (Michx.) Baker (Sticky asphodel)	Tri glu	-	X	-	X	-
Trifolium pratense L. (Red clover)	Tri pra	-	-	X	X	-
Vicia americana Muhl. ex Willd. (Americana vetch)	Vic ame	-	X	X	-	-
Zigadenus elegans Pursh (Smooth camas)	Zig ele	-	X	X	X	X
Zizia aptera (A. Gray) Fernald (Heart-leaved alexanders)	Ziz apt	-	X	X	X	X
Graminoids						
Andropogon gerardi Vitman (Big bluestem)	And ger	-	X	X	X	X
Bromus ciliatus L. (Fringed brome)	Bro cil	-	X	X	-	-
Calamagrostis canadensis (Michx.) P. Beauv. (Canada reedgrass)	Cal can	X	X	X	X	X
Carex L. spp. (Sedge)	Car spp	X	X	X	X	X
Deschampsia cespitosa (L.) P. Beauv. (Tufted hairgrass)/ *Sporobolus heterolepsis* (A. Gray) A. Gray (Prairie dropseed)	Des cae/ Spo het	X	X	X	X	X
Calamagrostis neglecta (Ehrh.) Gaertn. (Narrow reed grass)	Cal neg	-	X	X	X	-
Elymus trachycaulus (Link) Gould (Slender wheat grass)	Ely tra	-	X	X	X	-
Hierochloe odorata (L.) P. Beauv. (Sweet grass)	Hie odo	-	X	X	-	-
Juncus L. spp. (Rush)	Jun spp	X	X	X	X	X
Muhlenbergia richardsonis (Trin.) Rydb. (Mat muhly)	Mul ric	X	X	X	X	X
Phalaris arundinacea L. (Reed canary grass)	Pha aru	X	-	-	-	-
Schizachyrium scoparium (Michx.) Nash (Little bluestem)	Sch sco	-	X	X	X	-
Sporobolus michauxianus (Hitchc.) P.M. Peterson & Saarela (Prairie cord grass)	Spo mic	X	X	X	X	X
Phleum pratense L. (Timothy)	Phl pra	-	X	X	-	-
Poa compressa L. (Canada blue grass)	Poa com	-	X	X	-	-
Poa palustris L. (Fowl bluegrass)	Poa pal	-	X	X	X	-
Poa pratensis L. (Kentucky blue grass)	Poa pra	-	-	-	X	-
Sorghastrum nutans (L.) Nash (Indiangrass)	Sor nut	-	X	X	X	X

pH, moisture content, nutrients, structure), live biomass, percent cover of forbs, graminoids and bare ground and the number of flowering stems for each transect were included in the analysis. Prior to analysis, data for each variable were tested for departure from the normal distribution using the Kolmogorov-Smirnov test and examining the distribution of residual variance. Where necessary, the data were transformed to meet the assumptions of ANOVA. Sites were considered independent of one another with all comparisons made at the site level (data for plots within sites averaged), with sites treated as replicates. Sites were blocked into four treatments as described above (old burns, intermediate burns recent burns, and grazed sites). When differences between the treatments were determined to be significant by ANOVA, Fisher's protected least significant difference procedure was used to separate means (Saville, 1990). ANOVA was also used to compare the number of stems of blooming forbs and shrubs and number of blooming forb and shrub species between treatments during the flight period in both years. Survey results for the flight period in both years of the study were averaged for the analysis. ANOVA was conducted using the R programming language, version 3.6.0 (R Development Core Team, 2019).

Indicator Species Analysis (Dufrệne and Legendre, 1997) was used to investigate the presence of characteristic indicator plant species in each treatment type for the graminoid and flowering plant surveys, using PC-ORD Version 6 (McCune and Grace, 2002; McCune and Mefford, 2011). Indicator plant species identified here can be used in the future to assess the potential of new sites for reintroduction and to provide prairie managers in other parts of the range guidance in evaluating habitat diversity. Survey results for the flight period in both years of the study were averaged for the analysis. Additionally, a multi-response permutation procedure (MRPP) (McCune and Grace, 2002; McCune and Mefford, 2011) was conducted to test for species compositional differences between treatments for both the flowering species stems and percent cover of graminoid species.

Responses of the flowering and graminoid species to the environmental variables were investigated using nonmetric multidimensional scaling in PC-Ord Version 6 (McCune and Grace, 2002; McCune and Mefford, 2011). We used a 2-dimensional ordination plot to visualize variation in plant composition among the four treatment types. Abundance values consisted of stem densities for flowering species (stems per meter) and percent cover estimates for graminoid species. The number of stems in each plot per site for nectar plants was totaled for both years and then averaged for the multivariate analysis. Data sets were standardized by the relative proportion to the total to highlight the relative contribution of a response to the highest value in a sample (Peck, 2010). A Sorensen (Bray- Curtis) distance measure was employed using a random starting configuration with a Monte Carlo test consisting of 250 runs for observed and randomized data. For all analyses an alpha value < 0.05 was considered significant.

RESULTS

In 2008 and 2009, 320 and 79 Poweshiek skipperlings were observed, respectively (Table 1). The intermediate burn sites contained the largest number of skipperling observations amongst all treatment types in both years (Table 1). The old burn sites had few skipperlings in 2008 with no skipperlings in the 2009 season. Overall the old and recent burned sites and the grazed sites contained less than 42% of the total skipperlings observed during the study. Poweshiek skipperling was most commonly observed nectar feeding on Black-eyed Susan, *R. hirta*, (60% of the observations), Upland white aster, *Solidago ptarmicoides* (Torr. and A. Gray) B. Boivin (30%) and Self-heal, *Prunella vulgaris* L. (5%).

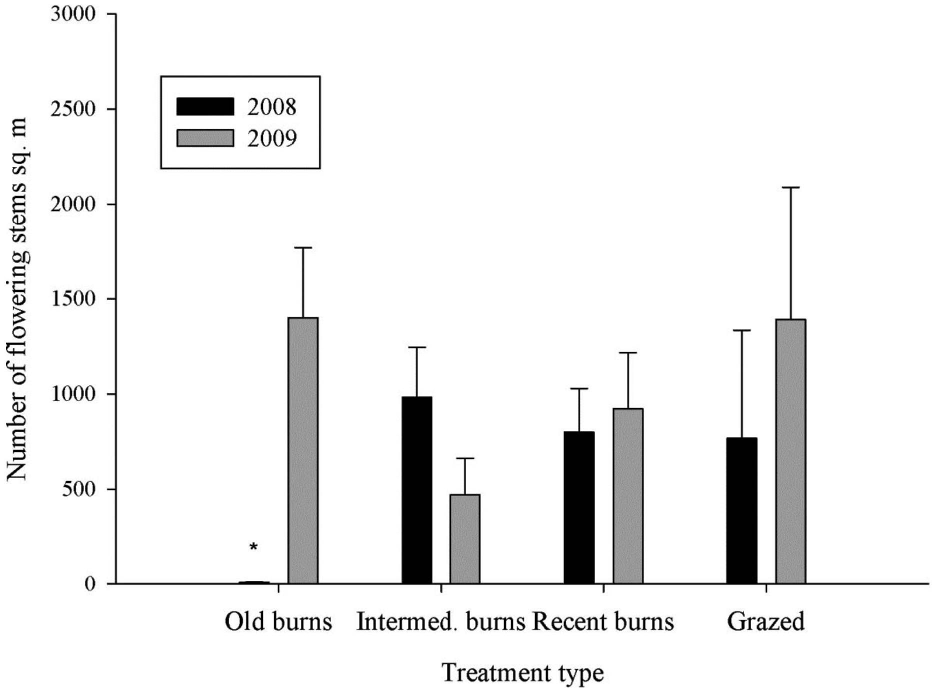

FIG. 2.—Number of flowering forb/shrub species found in 2008 and 2009 by treatment type (mean ± SE) in the Manitoba Tall Grass Prairie Preserve. * denotes significant difference between treatment by year.

Most soil characteristics varied by treatment type, although soil moisture and texture did not. Soil compaction at a depth of 10 cm in the grazed sites was significantly greater than compaction in the other treatments (Table 2). Soil compaction at a depth of 20 cm in the grazed and old burn sites was significantly greater than the intermediate and recent burn sites (Table 2). The recent burn sites were less acidic than the other three treatment types (Table 2). Organic matter and available calcium were significantly higher in the old burned sites compared to the other treatment types (Table 2). There was no significant difference in soil moisture levels between treatment types or differences in levels of available magnesium or sodium. Soil texture (percent sand/silt/clay) was similar in all sites.

Vegetation characteristics also varied notably among the treatments. Live biomass was greatest in the old burn sites and lowest in the recent burn sites (Table 2). The old burns contained the lowest percent graminoid cover and the greatest amount of bare ground, whereas there was no difference in graminoid cover or the percent of bare ground between the other treatments (Table 2). The old and the intermediate burns had less forb cover in comparison to the recent burns and the grazed sites (Table 2).

During the flight period in 2008, the old burns had significantly fewer flowering species ($F = 6.76$, $P = 0.018$) (Fig. 2) and fewer flowering stems than the other treatments ($F = 14.07$, $P = 0.002$) (Fig. 3). The number of flowering species (Fig. 2) and stem counts remained similar within the intermediate and recent burn and grazed sites in 2008 and 2009 (Fig. 3). In the old burn treatment, the number of flowering stems in 2009 was considerably higher

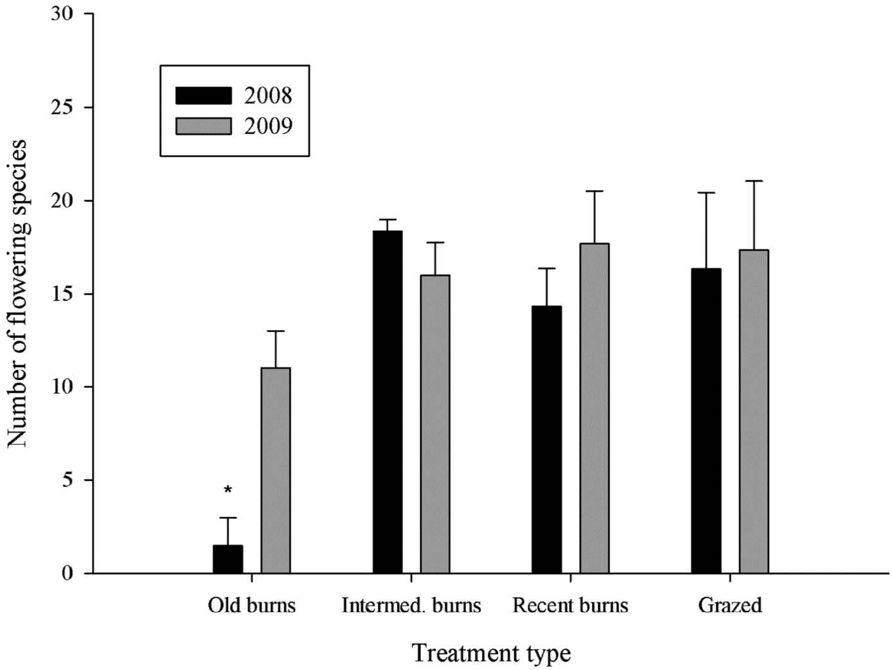

FIG. 3.—Number of nectar forb/shrub stems found in the Manitoba Tall Grass Prairie Preserve in 2008 and 2009 by treatment type (mean ± SE). * denotes significant difference

than in 2008 (Fig. 3), although 55% of the flowering stems in 2009 were Marsh Bellflower (*Campanula aparinoides* Pursh.).

A summary of all plant species recorded in the study and their association by site type appears in Table 3. Forb and shrub species with more than 0.5% of the total stems counted in all plots are identified as "common species" in Table 3. The number of stems of *R. hirta, S. ptarmicoides* and *P. vulgaris* (the species with 95% of Poweshiek skipperling nectar feeding observations) were compared between the treatments. In 2008, these three species were absent in the old burns. There was no significant difference in the number of stems between these species in the intermediate and recent burns and the grazed sites. In 2009, *S. ptarmicoides* and *P. vulgaris* were again absent from the old burns while a few *R. hirta* stems were recorded. Similarly, there was no significant difference in the number of stems for all three species between the other burn and graze treatments in 2009.

The percent cover of graminoids, including potential larval host plants documented in the literature, was estimated for each site. Graminoid species with more than 5.0% of the total cover are identified as "common species" in Table 3. *Andropogon gerardii* was most plentiful in the intermediate and recent burn sites (Table 4). *Muhlenbergia richardsonis* was most abundant in the old burn sites and least abundant in the grazed sites (Table 4). *Sorghastrum nutans* (a nonhost species) was more common in the intermediate burn sites and *Schizachyrium scoparium* was more abundant in the grazed plots and the recent burned sites. *Phalaris arundinacea* (an invasive nonhost species) was abundant in the old burns but absent in the other treatments. There was no significant difference in the percent cover of the remaining graminoid species between the four treatments.

TABLE 4.—Percent cover comparison of significant grass species in the Manitoba Tall Grass Prairie Preserve, including graminoid larval food hosts for Poweshiek skipperling per m^2 (mean ± SE)

	Treatment type				
	Old burns	Intermediate burns	Recent burns	Grazed	
*Andropogon gerardii**	0.0 ± 0.0a[1]	19.6 ± 1.7c	15.2 ±1.6.4bc	11.6 ± 1.9b	F = 11.37, P < 0.001
*Deschampsia cespitosa/ Sporobolus heterolepis**	2.3 ± 0.8a	2.6 ± 0.6a	6.4 ±1.1c	1.5 ± 0.5a	F = 8.08, P = 0.010
*Muhlenbergia richardsonis**	10.6 ± 2.9c	8.1 ± 1.1bc	5.6 ±0.8ab	5.1 ± 0.8a	F = 3.50, P = 0.016
Sorghastrum nutans	0.0 ± 0.0a	12.8 ± 2.6b	3.7 ±1.0a	1.1 ± 0.4a	F = 11.80, P = 0.010
*Schizachyrium scoparium**	0.0 ± 0.0a	0.0 ± 0.0a	0.2 ± 0.1a	1.5 ± 0.6b	F = 1.79, P < 0.040
Phalaris arundinacea	10.2 ± 4.7b	0.0 ± 0.0a	0.0 ± 0.0a	0.0 ± 0.0a	F = 13.00, P< 0.001

[1] Means in rows followed by different letters are significantly different
* Larval host plants (Henault 2021)

Indicator Species Analysis (ISA) for flowering plant stem counts identified *Sisyrinchium montanum* Greene and *Packera paupercula* (Michx.) Á. Löve and D. Löve as significant indicator species for the intermediate burn sites (Table 5, Fig. 4). *Cirsium* Mill. spp. was an indicator species for the recent burn sites. Indicator species for the old burn sites included *C.aparinoides*, *Mentha canadensis* L., *Stachys palustris* L., *Cirsium arvense* (L.) Scop. and *Asclepias incarata* L. (Table 5). There were no indicator species for the grazed sites. The ISA analysis for graminoids identified *Phalaris arundinacea* as a significant indicator species for the old burns and *Sorghastrum nutans* as a significant indicator for the intermediate burn sites (Table 5, Fig. 5). There were no other species identified as treatment indicators in the analysis.

The MRPP tests confirmed habitat partitioning and identified significant differences between treatments for flowering forbs and shrubs (A = 0.344, P = 0.008) (Table 6). The average distances within groups were: 0.151 for old burns, 0.232 for intermediate burns,

TABLE 5.—Indicator species analysis of significant flowering forb and graminoid species found in study sites in the Manitoba Tall Grass Prairie Preserve during the 2008/2009 field seasons. Treatments 1 = Old burns, 2 = Intermediate burns and 3 = Recent burns. Indicator value (IV), mean, standard deviation (SD), and P-value (P)

Indicator species	Treatment	IV	Mean	SD	P
Flowering plants					
Campanula aparinoides	1	100.0	36.3	17.5	0.018
Mentha canadensis	1	100.0	31.2	19.5	0.019
Stachys palustris	1	100.0	39.2	16.4	0.019
Circium arvense	1	98.4	47.4	18.6	0.019
Packera paupercula	2	94.1	36.4	17.6	0.015
Sisyrinchium montanum	2	93.9	44.9	18.6	0.008
Cirsium spp.	3	83.0	51.1	16.3	0.036
Asclepias incarnata	1	87.1	37.1	19.3	0.055
Graminoids					
Phalaris arundinacea	1	100.0	37.8	20.0	0.047
Sorghastrum nutans	2	71.7	45.5	16.9	0.024

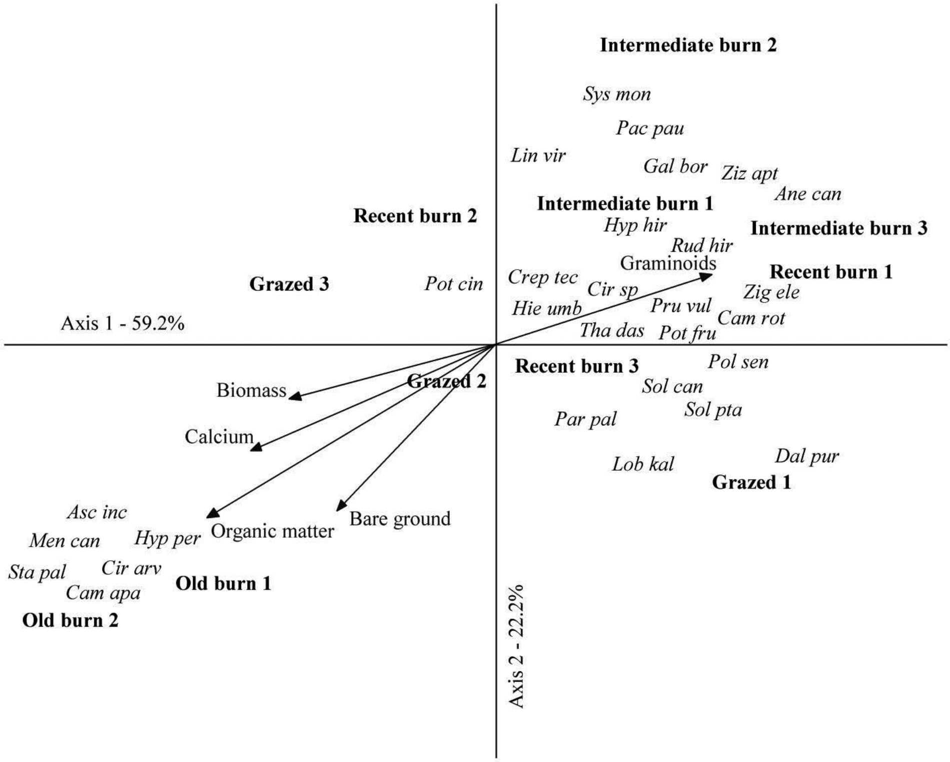

FIG. 4.—Nonmetric multidimensional scaling biplot results for variation in flowering plant species by site in the Manitoba Tall Grass Prairie Preserve (final stress = 8.06, P = 0.004). Only flowering plants with ≥0.5% of stems found in all sites are shown. Refer to Table 3 for abbreviations for nectar plant species.

0.419 for recent burns and 0.449 for grazed sites. The old burn treatment was significantly different than all other treatments, and the intermediate burns were significantly different than the grazed sites (Table 6). For graminoids, the MRPP identified significant differences in graminoid composition between the old burns and the other treatments (A = 0.185, P = 0.038). The average distances within groups were: 0.663 for old burns, 0.269 for intermediate burns, 0.475 for recent burns and 0.282 for grazed sites. There was no significant difference between the distances of the other burn and graze treatments in the graminoid analysis.

The flowering species association with treatment type was examined in a significant ordination (resulting in two dimensions; Axis 1 = 59.2 %, Axis 2 = 22.1 %; minimum stress = 8.06, P = 0.004) (Fig. 4). Approximately 81% of the total variation in the data matrix was explained by this ordination. The old burn sites were well separated from the other treatments toward the negative end of the first axes. Person correlation vectors for *A. incarnate* ($r^2 = 0.706$), *C. aparinoides* ($r^2 = 0.432$), *Hypericum perforatum* L. ($r^2 = 0.535$), *M. candensis* ($r^2 = 0.809$), *C. arvense* ($r^2 = 0.482$) and *S. palustris* ($r^2 = 0.619$) were associated with old burn sites. The three primary nectar plants for Poweshiek skipperling in the MTGPP (*R. hirta*, *S. ptarmacoides* and *P. vulgaris*) were situated midway between the six intermediate and

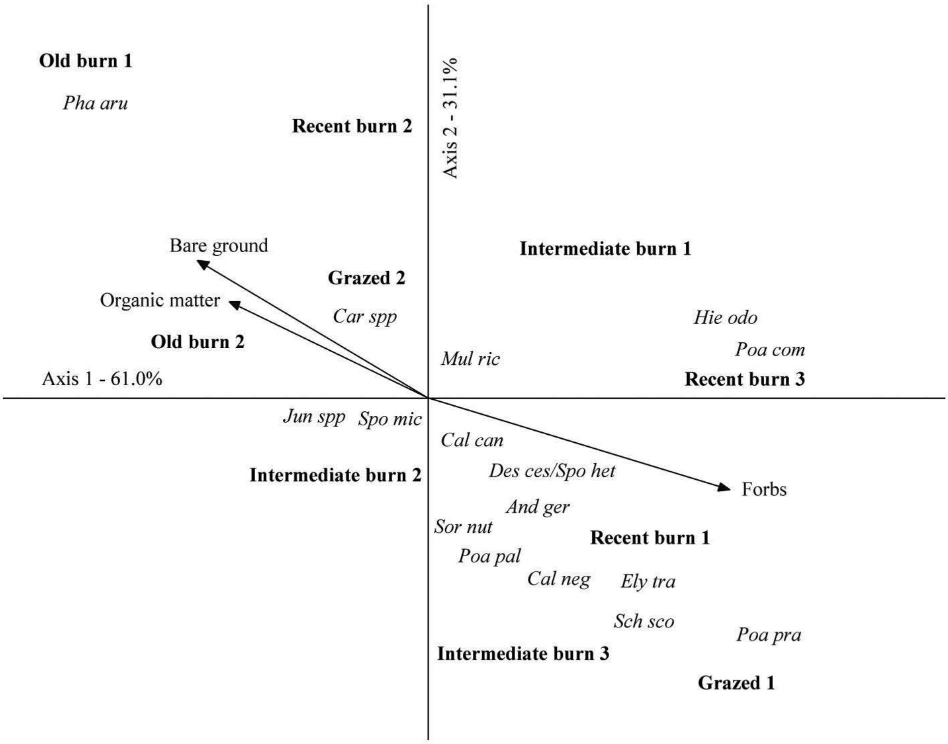

FIG. 5.—Nonmetric multidimensional scaling biplot results for variation in graminoid species by site in the Manitoba Tall Grass Prairie Preserve (final stress = 5.91, P = 0.020). Refer to Table 3 for abbreviations for graminoid species.

recent burn sites. Grazed sites were located between the intermediate and recent burns and the old burns (Fig. 4). The Pearson correlation vectors for organic matter ($r^2 = 0.853$), bare ground ($r^2 = 0.350$), soil calcium concentration ($r^2 = 0.587$) and biomass ($r^2 = 0.539$) trended to the old burns while the vector for graminoids ($r^2 = 0.517$) trended to the remaining burned sites.

TABLE 6.—Multi-response permutation procedure for pairwise comparisons between treatments for flowering forbs and shrub species (mean ± SE) in the Manitoba Tall Grass Prairie Preserve

		Within group homogeneity	
Treatments	Test statistic	A	P
Flowering forbs and shrubs			
Old burns vs intermediate burns	−2.118	0.413	<0.001
Old burns vs recent burns	−2.188	0.439	<0.001
Old burns vs grazed	−2.211	0.439	<0.001
Intermediate burns vs recent burns	0.130	−0.015	0.508
Intermediate burns vs grazed	−1.910	0.142	0.037
Recent burns vs grazed	1.220	−0.095	0.894

The association of treatment type with graminoid species resulted in a significant ordination with 2 dimensions (Axis 1 = 61.0%, Axis 2 = 31.1%; minimum stress = 5.91, P = 0.020) (Fig. 5). Approximately 92.7 % of the total variation in the data matrix was explained by this ordination. Similar to the flowering plant species ordination, most graminoid species tended to clump around the recent and intermediate burns. The old burns sites were separated from the other treatments with *P. arundinacea* growing almost exclusively in these sites (Pearson correlation coefficient $r^2 = 0.603$) (Fig. 5). Organic matter and bare ground were correlated with the old burns (Pearson correlation coefficient r^2 values > 0.400), whereas forbs trended toward several of the recent and intermediate burn sites and one grazed site ($r^2 = 0.404$).

DISCUSSION

In general, we found that the sites that have remained undisturbed for the longest period of time (*i.e.* the old burns) were distinct from more recently grazed and burned sites in terms of both their abiotic and biotic properties, likely because of the buildup of organic matter and the absence of disturbance, altering the plant community composition. These were also the sites with the fewest Poweshiek skipperling individuals, suggesting that time since disturbance might matter more than the type of disturbance in maintaining Poweshiek populations. Hill *et al.* (2018) noted that habitat alteration resulting from fire suppression and over growth of nonnative vegetation can reduce the attractiveness of habitat to specialist butterflies. We found evidence that burning may promote plant growth and environmental conditions more beneficial to Poweshiek skipperling than grazing. We recommend that management regimes should seek to emulate disturbances in such a way as to prevent excess buildup of organic matter, bare ground, and non-native species found in the old burns.

DISTURBANCE AND HABITAT QUALITY

The first objective of our study was to determine how disturbance can positively or negatively change physical and edaphic site characteristics that may influence plants that in turn may influence skipperling habitat quality. Because soil pH affects the biological, chemical and physical properties of soil which in turn influences plant growth and yield (Neina, 2019), ranges outside the optimum could impede growth or health of plant species relied upon by Poweshiek skipperlings. Grazing and burning have had notable effects on soil pH in some prairie studies, such as observing higher pH levels in ungrazed prairies (Walters and Martin, 2003) and burned prairies (Siemann *et al.*, 1997; Picone *et al.*, 2003). We found pH to be significantly lower in the most recently burned sites in comparison to the other burns. We found grazing to have no effect, which parallels the findings of Marrs *et al.* (1989) and Milchunas and Lauenroth (1993). All the pH measurements on our sites were between 6.5 and 6.7, within the optimum range of 5.5–7.0 for many prairie plant species (Islam *et al.*, 1980) and lower than the pH levels of 7.4–7.5 observed by Pogue *et al.* (2018) in prairie fen skipperling habitat in Michigan.

Soil organic matter in the old burns was significantly greater in quantity than in the other treatments. The old burns had remained unmanaged for 15 y prior to our study, which may have allowed for a buildup of litter and subsequent increases in soil organic matter over time. The level of organic matter in the grazed sites was no different than it was in the intermediate and recent burns. Other studies have shown considerable variability in the effects of grazing on soil organic matter, with some indicating organic matter increased after grazing (Walters and Martin, 2003), decreased after intensive grazing over a long time period (Beebe and Hoffman, 1968; Walters and Martin, 2003), or mixed results (Milchunas and Lauenroth, 1993). Schacht *et al.* (1996) reported that organic matter content of the soil in annual burn plots did not affect soil organic matter content, at least on the short term. In our case, it appears that grazing and burning in the recent and intermediate aged burns reduced organic matter in comparison to the old sites. Increased litter accumulation may inhibit the germination and survival of nectar sources or perhaps larval hosts plants, making old burn sites less attractive to Poweshiek skipperling (*see* litter discussion below).

In prairies, annual above ground biomass production generally exceeds decomposition and accumulates on the soil surface as litter (Golley and Golley, 1972). Litter can decrease light penetration and act as a barrier for germinating plants depending on thickness (Maret and Wilson, 2005), and prolonged accumulation of excess litter can cause a decline in prairie productivity (Anderson, 1982; Knapp and Seastedt, 1986). We found old burns to have the highest levels of biomass, with biomass levels in grazed sites similar to those in intermediate and recent burns. Grace *et al.* (2000) also found an accumulation of biomass in sites with more years since disturbance, and our observation of increasing biomass with years since disturbance is likely correlated with increases in soil organic matter.

We did not find differences in soil moisture between sites in our study, but it is important to note that variation in soil moisture at finer scales can be important for Lepidopteran survival. Changes in elevation of only a few centimeters can lead to differences in soil temperature, soil moisture content, and shelter for seedlings (Windhager, 1999) and the ability of metapopulations to survive extreme weather events (Fleishman *et al.*, 2000). These could play a key role in providing appropriate microsite conditions for Poweshiek skipperling and enabling populations to survive adverse events such as flooding, which regularly occurs in the MTGPP.

With regard to soil macronutrients, we observed minimal differences in levels of magnesium and sodium between site treatments, which was consistent with Picone *et al.* (2003) who did not find significant differences between burned and unburned plots in their study. However, they also found no significant differences in calcium levels between treatments, whereas we found significantly higher levels of calcium in old burn sites as compared to other treatments. Calcium can assist plants in absorbing other nutrients, increase resistance to plant diseases, and increase structural support in plant cell walls. In soils, calcium can stabilize organic matter and increase water-holding capacity leading to improved soil structure (Hepler, 2005). Calcium does not negatively impact plant growth unless it is present in large enough amounts to alter the pH of soils, but in our study all sites had optimal pH ranges.

Grazed and old burn sites had significantly higher levels of soil compaction in comparison to the other treatments. Soil compaction primarily increases the bulk density of soils by decreasing soil pore space and reducing water holding capacity (Håkansson and Lipiec, 2000), which can in turn restrict root penetration and availability of moisture for plants. Royer *et al.* (2008) found that soil compaction, presumably a result of long-term cattle grazing, appeared to have an effect on vertical water distribution in soils in Dakota skipper habitat. Larson *et al.* (2020) noted that grazing tends to increase soil bulk density. Grazed sites in our study had the highest levels of soil compaction; however, this compaction did not appear to influence plant species diversity or stem density. Therefore, the levels of soil compaction may not be enough to adversely impact plant growth.

In our study, old burns had significantly less cover of forbs and graminoids and increased areas of bare ground. Although bare ground may be beneficial to the germination of forbs, excess litter cover may inhibit optimal germination. We did not measure the thickness of the litter layer on bare ground, but the amount of bare ground may reduce the amount of habitat available to skipperling larvae. It appears lower amounts of bare ground and more graminoids found in the intermediate and recent burns may provide better habitat for Poweshiek skipperling.

Plant productivity generally increases in grasslands after management (fire or mechanical removal) has removed excess litter resulting from high levels of biomass accumulating on the soil surface (Towne and Owensby, 1984: Abrams *et al.*, 1986: Larson et al., 2020). The amount of litter removal from livestock grazing can vary greatly. The duration, timing and intensity of cattle grazing can impact the presence of certain larval host plants and availability of adult nectar sources as well as soil compaction levels. Grazing intensities of less than 1.5 AUM are considered to be light and may increase plant heterogeneity in pastures (Bloom *et al.*, 2013) as well as stimulate plant production (Abrams *et al.*, 1986). Intensities of greater than 2.5 AUM, if poorly planned, may lead to over grazing (Bloom *et al.*, 2013: Smith et al., 2016a: Delaney *et al.*, 2016). Grazing levels of 4.0 AUM or more can lead to significant levels of bare ground and diminished live vegetative cover and plant homogeneity (Bloom *et al.*, 2013). The grazing intensity in our study varied between the three grazed sites (Table 1); two of the sites received shorter grazing rotations than the third. All sites fell into the low category for grazing pressure (Bloom *et al.*, 2013: Smith *et al.*, 2016a; Delaney *et al.*, 2016).

Timing of grazing may be critical for survival of immature Poweshiek skipperling. There were no data available on the specific months cattle grazed sites in previous years. The only information available is that two sites were grazed intermittently and one site was grazed for a significant part of the summer season. Poweshiek skipperling was present in all three grazing sites during our study, with the number of adult observations similar to that found in the recently burned sites; however, it is possible that grazing in June or July could increase the risk of mortality for immature butterflies or decrease nectar plant availability for adults.

DISTURBANCE AND PLANT DIVERSITY

Our second objective was to measure the effects of disturbance on the presence of floral resources for Poweshiek skipperling adults and the availability of potential larval host plants. We found Poweshiek skipperling nectar feeding on a narrow set of plant species (predominantly *R. hirta* and *S. ptarmicoides*) in this study, whereas Henault (2021) found that females fed on a slightly wider range of species. Therefore, the effects of burn timing and intensity may be important for favoring or reducing the number of specific nectar plants. We did not find a difference in the number of stems of *R. hirta* and *S. ptarmicoides* between most sites in this study, except for their near absence in the old burns. We also found that old burn sites had the lowest percent cover of flowering forb and shrub species and number of species during the flight period, potentially limiting the number of flowering nectar sources for the adult butterflies. The intermediate burns, which had the highest numbers of Poweshiek skipperling, had the lowest percent cover of forbs and shrubs. The intermediate and recent burn sites responsible for most of the skipperling observations were connected more closely in the ordination to the three most common nectar sources for Poweshiek skipperling.

We found Prairie dropseed/Tufted hairgrass (*S. heterolepis/D. cespitosa*), Mat muhly, Little bluestem and Big bluestem) in varying densities in all of the recent burns and grazed sites, although Little bluestem was not found in the intermediate burns in our study, whereas Big bluestem and Little bluestem were absent from the old burns. None of the four grass host plants in MTGPP was identified as an indicator of any particular disturbance type. The old burns also had significantly less graminoid cover, potentially limiting the larval food and adult resources, which are critical for conservation of some Lepidopteran species (Opler and Krizek, 1984). McCullough *et al.* (2019) found that increasing grass cover was positively correlated with the presence of Regal fritillaries (*Speyeria idalia* (Drury)) in a tall grass prairie in Kansas and Moranz *et al.* (2014) reported that nectar sources increased in recent burns, which correlated to increased fritillary abundance. Opler and Krizek (1984) stated that the availability of larval hosts may be critical in the conservation of some lepidopteran species.

In terms of overall plant species richness, past studies show mixed results in finding correlations between plant species richness and butterfly species (*e.g.*, Thomas and Mallorie, 1985; Stefanescu et al., 2004). We found native plant species made up the major plant component in all of the study sites except the old burns and there was little difference in flowering species diversity, overall species diversity, or stem counts between grazed sites and the recent and intermediate burn sites. It appears that in the MTGPP, if sites are left unmanaged for a significant period of time (probably greater than 8 to 10 y), they eventually decrease in vegetative species richness, confirming the findings of Bowles and Jones (2013) that increased fire frequency maintained forb diversity over the long term.

Old burns were closely associated with a unique cluster of plant species by both ordination and Indicator Species Analysis. Several of the species associated with the old burns are often found in wetter areas (Marsh bellflower and Marsh hedge-nettle, (*Stachys palustris* L.; (Looman and Best, 1981), which may be related to parts of the old burns that contained intermit standing water (Table 3). Some of the other plant species associated with the old burns were invaders of disturbed areas (Canada thistle, *Cirsium arvense* (L.) Scop. and Silverweed, *Potentilla anserina* L.). It is possible that increased amounts of bare ground and reduced graminoid and forb cover in old burns could have provided pathways for colonization by invasive and nonnative naturalized species. Although Walters and Martin (2003) observed grazed sites had more invasive and nonnative species than ungrazed sites, we did not observe this pattern.

POWESHIEK SKIPPERLING POPULATION AND HABITAT QUALITY

In 2002, Webster (2003) estimated the skipperling population in the MTGPP to be well over 2000 individuals. The skipperling population appeared to be substantially smaller than estimated by Webster (2003) in the first year of our study (320 observed in 2008), and the relative density of the skipperling population decreased considerably in the second year of the study (79 observed in 2009). Grantham *et al.* (2020) reported on the results of timed systematic surveys used to make population estimates between 2015 and 2018, in which the number of individuals per year was seldom more than 60 in the MTGPP. In our study, there were some physical and plant diversity differences between the treatments (*e.g.*, soil compaction, organic matter, flowering plant and graminoid diversity, *etc.*), but none of these variables could easily explain the drop in the number of skipperlings observed between 2008 and 2009. Although the majority of skipperlings were found in 2008 were located in the intermediate burned sites, in 2009, the relative rate of decline appeared to be similar in all sites. Therefore, although there were some physical and plant related differences between the treatments, the proportional population decline was similar in all sites between years in our study.

It does appear that old burned sites are less supportive of Poweshiek skipperling. This may be related to the absence of known nectar species, increased levels of organic matter and biomass, lower plant species diversity, increased presence of non-native and invasive species, increased patches of bare ground, and/or some combination of all of these factors. It is likely that these sites would need remediation to provide suitable habitat to maintain a population of skipperlings into the future. We note that it is likely that the ongoing decline in abundance of Poweshiek skipperling since 2008 in the MTGPP is not related to habitat quality alone. This is particularly true in that declines have been observed in sites of varying ages and disturbance histories. However, to support the success of restocking and reintroduction efforts, information connecting habitat quality and abundance would likely help to identify the habitat most likely to support successful restocking or colonization of this endangered species.

MANAGING POWESHIEK SKIPPERLING INTO THE FUTURE

The MTGPP actively manages its tall grass prairie using fire and grazing to maintain native prairie and prevent tree and shrub encroachment (Grantham *et al.*, 2021). When fire return intervals exceed ten years the result is often major conversion to shrub and woodland (Ratajczak *et al.*, 2016). It is clear from our study that once sites are left unmanaged for more than a decade, they will likely become unsuitable for skipperlings. Both fire and grazing are useful to manage thatch accumulation to increase plant diversity in prairie remnants (Larson *et al.*, 2020). Although Nature Conservancy management in the MTGPP in the past has included grazing and burning to improve habitat quality for several endangered plants and animals over entire sites, there may be a need to focus disturbance efforts on a finer scale within sites and also experiment with burning and grazing on the same sites over a shorter period of time (Fuhlendorf *et al.* 2004). This could also potentially include mowing, if climate conditions prevent timely used of fire. If long-term conservation of the endangered Poweshiek skipperling is a primary goal in the MTGPP, approaches to habitat management may need to be adjusted to support the success of this species.

Our findings suggest that suitable prairie habitat changes quite quickly in the MTGPP. Based on our observations of finding the most skipperlings in sites 4–6 y since burn, we suggest portions of potentially suitable habitat will require sufficient disturbance every four to six years to remain attractive to the skipperling. However, overly frequent disturbance is most likely detrimental to this species: one to two-year rotational burning or grazing (or poor timing of grazing) cycle could result in population declines or perhaps local extirpation (Swengel, 1996; Swengel and Swengel, 2007). Additionally, disturbance intervals longer than a decade likely reduce the attractiveness and possibly suitability (as suggested by our findings).

Well-timed burning in prairies has been shown to increase plant species richness (Gibson and Hulbert, 1987; Towne and Kemp, 2008; Larsen *et al.*, 2020) and generally does not decrease abundance, richness, and biomass of most arthropod species (Benson *et al.*, 2007). However, burning does seem to impact Lepidopteran species, as Benson *et al.* (2007) found 50% fewer individuals in burned relative to unburned fields a year post-treatment. Over time, abundance may recover post burn, as seen by Leone *et al.* (2019) who found that burned sites had greater Monarch butterfly abundance when compared to grazed sites despite overall plant diversity being similar in the two disturbance types. Focused mid-summer burning could be preferred over spring burning, as this supports higher plant diversity and higher prevalence of *R. hirta* (Howe, 1994). Fire severity has also been identified as an important variable, with high and moderate severity burns stimulating plant regrowth more than low severity burns (Pavlik *et al.*, 2017). As noted previously, burning in patches smaller than the scale of a site should be considered, as this has been found to be beneficial for butterfly habitat, including when light grazing was maintained on the site (McCullough *et al.*, 2019).

Overall, future management approaches could ensure that newly disturbed sites (either burned or grazed) have a nearby source of core habitat to maintain a refuge population as well as to facilitate skipperling movement back into disturbed sites (Swengel, 1996; Swengel and Swengel, 2007). In general, intermediate burn cycles, which minimize the area of core habitat burned at any one time, are recommended (Panzer, 2002; Vogel *et al.*, 2010). If sites are to be grazed, then unselective, heavy grazing that removes larval host plants and nectar sources and severely diminishes the quality and diversity of tallgrass prairie should be avoided (Howe, 1994; Swengel, 2008). We also suggest that if sites are to be grazed or mowed, then it would be best to avoid these activities in June and July to prevent removal of critical nectar sources needed by adults during the flight period.

Importantly, the response of butterfly populations and their habitats to disturbances, such as burning and grazing, is heavily dependent on the timing, location, duration, and intensity of the disturbance (Wagle and Goda, 2019). Our understanding of the effectiveness of these management approaches to protect and sustain existing Poweshiek skipperling populations and other tall grass prairie skippers is still unclear (Royer and Marrone, 1992; Swengel, 1998; Swengel and Swengel, 1999; Environment Canada, 2012). It is critical to determine the physical and biological components essential to provide optimal Poweshiek skipperling habitat to ensure the persistence of locally restricted populations (Swengel and Swengel, 2007). A more controlled and well-replicated approach will be needed to fully understand the impacts of these management actions on Poweshiek skipperlings, their habitat, and their larval host and nectar plants. Further research is required on the impact of management activities on larval survival, especially at different times of the year. In our study, we utilized almost all the known colonized skipperling sites in the TGPP at the time, but more replicate sites would have been advantageous. It will be necessary to determine a 'goldilocks' approach for management, as both abandonment and intensive management of grasslands have been known to be detrimental to endangered Lepidoptera (Schwartz and Fartmann, 2020). To support successful recovery of this species, such experiments will be necessary to support the development of habitat management guidelines that minimize mortality, maximize habitat quality, and provide a range of suitable habitats to support a healthy skipperling metapopulation in the MTGPP.

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