

## **White-tailed deer (*Odocoileus virginianus*) and fire effects on flowering diversity of tallgrass prairie forbs**

Author(s): Roger C. Anderson and M. Rebecca Anderson Erica A. Corbett

Source: The Journal of the Torrey Botanical Society, 144(3):243-253.

Published By: Torrey Botanical Society

<https://doi.org/10.3159/TORREY-D-15-00024.1>

URL: <http://www.bioone.org/doi/full/10.3159/TORREY-D-15-00024.1>

---

BioOne ([www.bioone.org](http://www.bioone.org)) is a nonprofit, online aggregation of core research in the biological, ecological, and environmental sciences. BioOne provides a sustainable online platform for over 170 journals and books published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Web site, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at [www.bioone.org/page/terms\\_of\\_use](http://www.bioone.org/page/terms_of_use).

Usage of BioOne content is strictly limited to personal, educational, and non-commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

## White-tailed deer (*Odocoileus virginianus*) and fire effects on flowering diversity of tallgrass prairie forbs<sup>1</sup>

Roger C. Anderson<sup>2</sup> and M. Rebecca Anderson

School of Biological Sciences, Illinois State University, Normal, IL 61790

Erica A. Corbett

Department of Biology, Southeastern Oklahoma State University, Durant, OK 74701

**Abstract.** We studied the effect of white-tailed deer (*Odocoileus virginianus* Zimmermann) browsing and fire on diversity and number of prairie-forb flowering stems in a remnant tallgrass prairie in northern Illinois. Our study included two plots protected from deer browsing since 1992 and two unprotected plots. All plots were burned twice in late April of 1990 and 1991. Deer densities of 32–50 km<sup>-2</sup> (1992–96) declined to 7–9 km<sup>-2</sup> in 1998 and 1999 after controlled hunting. Similarity between protected and unprotected plots was initially 82%, declined to 49% during the period of high deer density, and increased to 68% in 2001 with managed hunting. Flowering stems for all forbs were tallied in 1998–2001. Diversity (Shannon index [*H'*] and effective number of stems [HO]) of flowering stems was higher on protected than on unprotected plots for all study years. Differences in composition and diversity between protected and unprotected plots were associated with interactions between fire and protection from deer browsing as measured by total number of flowering stems, which was significantly higher on protected than on unprotected plots in nonburn years (3.4–3.5-fold) but not in burn years (1.0–1.2-fold). The two leading species on protected plots (ashy sunflower [*Helianthus mollis* Lam.] and Culver's root [*Veronicastrum virginicum* (L.) Farw.]) tended to have fewer flowering stems in burn years and always had them in protected plots (54-fold and 70-fold higher in protected plots for the two species, respectively). For the second leading species on unprotected sites (wild quinine [*Parthenium integrifolium* L.]), the number of flowering stems was significantly higher in burn years (27-fold); however, there was no significant difference in the number of stems between protected and unprotected plots. These results show strong interactions between fire and deer-browsing disturbances in communities recovering from deer overabundance.

Key words: deer, diversity, fire, prairie forbs

Historically, the dominant mammalian grazer on North American tallgrass prairies was bison (*Bison bison* L.). However, today, bison herds sufficiently large to function as they did historically are limited to a few large prairie reserves, mostly in the western portion of the North American tallgrass prairies. Of the 36,057,523 ha of historic prairie that occurred in the US upper Midwest (Illinois, Indiana, Iowa, Minnesota, Missouri, and Wisconsin), only 73,270 ha (0.2%) of high-quality remnant prairie remains (Robertson *et al.* 1997). Because of agriculture, urbanization, and invasion by woody species after fire suppression, most

remnant tallgrass prairies consist of small, isolated fragments. The dominant ruminant mammalian herbivore in those prairie remnants is the white-tailed deer (*Odocoileus virginianus* Zimmermann) (Anderson 2006).

In tallgrass prairies, grasses are the dominant plants, contribute most of the total biomass (Knapp *et al.* 1999), and support most of the herbivore biomass. Although forbs support a smaller amount of the biomass used by herbivores than do grasses, forbs have the greatest species richness in tallgrass prairies (Howe 1994, Hartnett and Fay 1998), and enhance the diversity of herbivores, granivores, and pollinators in prairies (Reed 1994, Damhour-eyeh and Hartnett 1997, Howe and Brown 1999). Prairie forbs and C4 grasses respond differently to deer browsing, bison grazing, and fire. During the spring and summer, white-tailed deer selectively browse prairie forbs and consume 3.5–18.9% of available forb stems, but they consume little, if any, C4 grasses (Anderson *et al.* 2001, 2005). For browsers, such as white-tailed deer, their small rumen, and the rapid rate of materials moving through it, results in deer selectively consuming forbs with cells high in soluble fractions of

<sup>1</sup> The Illinois Department of Natural Resources (IDNR), through the Pittman-Robertson Program of the U.S. Department of Interior, provided funds for this research. We thank Jonathan Bauer, Gail Corbett, Danny Gustafson, Timothy Kelley, Janeen Laatsch, Jennifer Nelson, Marsha Rickey, Karl J. Roberts, and Michelle Simone for assistance with data collection.

<sup>2</sup> Author for correspondence: rcander@ilstu.edu  
doi: 10.3159/TORREY-D-15-00024.1

©Copyright 2017 by The Torrey Botanical Society

Received for publication May 22, 2015, and in revised form October 25, 2016; first published July 13, 2017.

carbohydrates (Fulbright and Ortega 2006, Garibaldi *et al.* 2007) and cell walls rich in rapidly fermentable components, such as pectin (Hummel *et al.* 2006). In contrast, grazers with large rumens use grass as a primary energy source, which requires a long period of rumen retention for microbial breakdown of hemicellulose and cellulose in cell walls to volatile fatty acids (Fulbright and Ortega 2006, Clauss *et al.* 2008, Duncan and Poppi 2008). Bison are grazers (Damuth and Janis 2011) and can increase diversity and abundance of prairie forbs because they consume mostly grasses and, thereby, reduce competitiveness of grasses against forbs (Collins *et al.* 1998, Knapp *et al.* 1999). They are considered a “keystone” species that affects diversity of prairie forbs, insects, and other species (Collins *et al.* 1998, Knapp *et al.* 1999, Joern 2005).

The effect of white-tailed deer browsing on the diversity of prairie forbs generally follows the intermediate disturbance hypothesis (Connell 1978). Connell (1978) proposed the disturbances can either enhance or diminish diversity depending on disturbance frequency and intensity and that maximization of diversity occurs at intermediate levels of disturbance. However, other studies reported that changes in diversity in grasslands involving fire and grazing showed patterns varying between disturbance and diversity (Collins *et al.* 1995). Diversity consists of two components: (a) species richness (S), that is, the number of species, and (b) evenness (J), the distribution of abundance among the species (Pielou 1975, Magurran 1988, Stirling and Wilsey 2001). Evenness increases as abundance becomes more equitably distributed among the species. Deer browsing can increase or decrease diversity of prairie forbs depending on browsing intensity (Anderson *et al.* 2005), largely because of changes in evenness. In the absence of browsing, forb diversity can decline because of increased abundance of conservative prairie forbs, which have strong fidelity to high-quality remnant sites with little disturbance, and a decrease in abundance of browse-tolerant species of forbs (Swink and Wilhelm 1994, Taft *et al.* 1997). These conservative species are generally preferred deer-browse species, and at low browsing pressure, they apparently are competitively superior to disturbance-tolerant species and increase in abundance. However, at high-intensity deer browsing, forb diversity also declines because species that are less preferred as browse and disturbance-tolerant

species increase, and conservative, preferred-browse species decline. Highest diversity occurs at intermediate levels of browsing intensity, which results in conservative and browse-tolerant species maintaining moderate levels of abundance (Anderson *et al.* 2005, 2006).

Fire generally increases flowering and production of C4 prairie grasses on burned sites compared with unburned sites (Curtis and Partch 1950, Hulbert 1986, Collins *et al.* 1998, Hartnett and Fay 1998), but timing of the burn can affect those results (Knapp 1985). In the eastern portion of the tallgrass prairie, periodic fires are needed to maintain species richness (Leach and Givnish 1996), and forb diversity is enhanced by frequent fires, which reduces encroachment of competing woody species (Bowles and Jones 2013). However, less is known about response of individual forb species to prairie fires than is known about C4 grasses (Hartnett 1991). Fire effects on the flowering of forb species are mixed and are dependent on the frequency of burning (Hartnett 1991), when the species initiates growth and flowers during the growing season, and when the burn occurs (Lovell *et al.* 1983; Rosburg 2001). Dormant-season and early spring (March to early April) burns generally increase the flowering of forbs (Lovell *et al.* 1983; Gibson and Hulbert 1987); however, late-spring burns (Mid-May) can reduce or eliminate flowering of cool season, early flowering species (Lovell *et al.* 1983, Howe 1999, Rosburg 2001).

We determined short-term effects (1998–2001) of two spring burns, presence or absence of deer browsing, and the interaction between the two, on the production of prairie forb flowering stems (stems with flower buds, flowers, or fruits) for all species combined and separately for four focal species (1998–2001). The focal species were the two forb species producing the most flowering stems in plots protected or unprotected from deer browsing. The focal species were *Helianthus mollis* Lam. and *Veronicastrum virginicum* (L.) Farw. in protected plots, and *Silphium integrifolium* Michx. and *Parthenium integrifolium* L. in unprotected plots. Only the generic names will be used for the four-focal species hereafter. We predicted that the numbers and diversity of forb flowering stems would increase with burning and decrease with deer browsing after 1998.

Nomenclature for plants follows the USDA NRCs PLANTS Database (USDA.NRCs 2016).

**Materials and Methods.** **STUDY SITE.** Our study site was a species-rich remnant prairie in the Illinois Department of Natural Resources' 218-ha Heidecke Lake Fish and Wildlife Area (HLFWA) in northeastern Illinois, Grundy County, about 70 km southwest of Chicago, IL. The HLFWA is adjacent to the west side of the 1,027-ha Goose Lake Prairie State Park (GLPSP). The study site and plot design for this study were the same as those of Anderson *et al.* (2001) and are summarized below. In May 1992, a 33 m × 48 m area in the HLFWA was selected for study because of its high diversity of prairie forbs (100 species). The study site was the only area within the HLFWA/GLPSP that had forb species richness and abundance sufficiently high to determine patterns of deer browsing preferences for species of forbs.

**EXPERIMENTAL DESIGN.** The study area was divided into four equal-sized plots (16.5 m × 24 m) and was sampled for browsed and unbrowsed stems of forbs by species beginning in the summer of 1992. Three parallel transect lines extending the full length of each plot (24 m) were established at 4, 8, and 12 m along the shorter (16.5 m) side of the plot. Along each transect line, the initial sampling point was located at 1 m and subsequent points were located at 2-m intervals for a distance of 23 m from the transect beginning. At each of the 12 points per transect, the center of a 25 cm × 25 cm quadrat was located at a randomly determined distance on the left or right side of the transect. Counts were made of browsed and unbrowsed forb stems by species in the quadrats, in late June (2000) or in July 1992, 1993, 1994, 1997, 1999, and 2001. The site was burned in the springs of 1999 and 2001 between April 15 and April 30.

In December 1992, one half of the study area was fenced to exclude deer but not small mammals. We chose two plots to be fenced or not fenced to maximize similarity between deer protected plots and unprotected plots. For the June 1992 sample, before establishment of the enclosure, the percentage of similarity (Gauch 1983) between protected and unprotected plots, based on forb stem counts, was 82%, which is a high similarity value. Two random samples of the same site resulted in similarity values of about 82–85% (Bray and Curtis 1957, Beals 1960).

**MANIPULATING SIZE OF THE DEER HERD.** Beginning in fall of 1997, the deer herd was substantially reduced on HLFWA and the adjacent GLPSP by

controlled hunting. Winter deer densities before 1997 were 32–50 deer km<sup>-2</sup> (1992–96) but declined to 7–9 km<sup>-2</sup> in 1998 and 1999 after controlled hunting. The pre-1997 estimates were greater than the 27 deer km<sup>-2</sup> reported for areas in the farming belt of east-central Illinois, which were 36% forested and experienced moderate hunting pressure (Nixon *et al.* 1991). After 1997, deer densities were similar to estimates of pre-European settlement densities in most favorable habitats (3.1–7.7 deer km<sup>-2</sup>) (Horsley *et al.* 2003) and those of historic conditions in the Midwest (4–19 deer km<sup>-2</sup>) (Dahlberg and Guettinger 1956, McCabe and McCabe 1984). Our study plots were monitored before deer management under conditions of high deer densities (1992–97) and under reduced deer densities after initiation of the hunting program (1998–2001), permitting us to assess recovery from excessive deer browsing on unprotected plots.

**DETERMINING EFFECT OF DEER BROWSING ON FORB FLOWERING.** Data on the number of browsed and unbrowsed stems and flowering and fruiting of forbs were collected in the 25-cm × 25-cm quadrats, but those quadrats were too small to adequately measure reproductive success. However, we were unaware of that shortcoming until after 1997, when there was a sufficient number of samples to make that assessment. Consequently, the influence of deer browsing on reproductive success of forbs was determined using belt transects beginning in 1998 and continuing annually for 4 yr until 2001. The number of flowering stems (stems with any reproductive structure: flower buds, flowers, or fruits) of prairie forbs occurring within a meter on either side of three transect lines established per plot (two unprotected and two protected plots) were counted by species. Transects extended the shorter length of the plots (16.5 m). However, the first and last meters of the transect were not sampled because they were disturbed when personnel entered and exited the plots, resulting in transects that were each 14.5 m long and 2 m wide. Those data were obtained in late July 1998 (July 19–24), 1999 (July 23 and 30), 2000 (July 21), and 2001 (July 27).

**CHARACTERISTICS OF THE FOUR FOCAL SPECIES.** Previously, *Helianthus* and *Veronicastrum* were shown to respond negatively to deer browsing, *Silphium* responded positively, and *Parthenium* did not show a significant positive or negative

response to deer browsing (Anderson *et al.* 2005). The range in flowering dates and heights for the four species—*Helianthus*, *Veronicastrum*, *Silphium*, and *Parthenium*, respectively—were July 26–September 15, June 21–August 24, July 20–August 14, June 14–September 16 (Swink and Wilhelm 1994) and 0.5–1.0, 0.8–2.0, 0.5–1.5, and 0.5–1.0 m (Gleason 1963). None of the focal species were early spring bloomers.

**DATA ANALYSIS. CHANGES IN VEGETATIVE STEM COUNTS IN RESPONSE TO DEER BROWSING.** For the four focal species, the total number of stems (browsed and unbrowsed stems combined) sampled in 25-cm × 25-cm quadrats in 1992 and 2001 were tested for significant differences between protected and unprotected plots using the chi-square test. For 1992 samples, all four plots were unprotected until December after summer sampling. However, for this analysis, *protected* and *unprotected* refer to samples taken in the two plots that were eventually protected or unprotected in December 1992.

**FLOWERING STEMS.** Flowering stems for the three transects in each plot were summed by species, resulting in two sample replicates for protected and unprotected plots. Those data were log square-root transformed to improve normality of residuals. Normality was tested with box plots, normal probability plots, residuals plotted over predicted values, and Shapiro-Wilk tests. All transformed data met the assumptions of ANOVA. Flowering stem data for all species combined and the two leading species in the protected plots, *Helianthus* and *Veronicastrum*, and in unprotected plots, *Silphium* and *Parthenium*, were analyzed separately with repeated-measures ANOVA. Statistical significance was accepted at  $P \leq 0.050$ , and marginal significance were results at  $P = 0.051$ – $0.06$ .

For each year, Tukey's honestly significant difference (HSD) test, which corrects for type I experimental errors, was used to test for significant differences between protected and unprotected plots for each focal species separately (SAS Institute INC. 2002–2014).

**DIVERSITY OF FLOWERING STEMS (ALL SPECIES COMBINED).** The Shannon diversity index  $H' = -\sum[(p_i)(\ln p_i)]$ , where  $p_i$  is a species proportion abundance of flowering stems (Magurran 1988), was calculated for protected and unprotected plots. For that analysis, we combined the two replicates

for each treatment. The Shannon diversity index ( $H'$ ) was used to compare diversity of protected and unprotected plots for each year, which were tested for significant differences using modified  $t$  tests (Magurran 1988). The Shannon values were also converted to  $HO$  (effective number of species) ( $\exp[H']$ ), which is the number of species in a sample, if all had equal abundances, required to produce the observed value of diversity ( $HO$ ). We used  $\exp(H')$  because comparing Shannon index values across treatments can inaccurately estimate differences in diversity among treatments (Hill 1973, Jost 2006, Flores and Clay 2010). Species richness ( $S$ ) was obtained and evenness ( $JO = H' / \ln S$ ) (Pielou 1975), which expresses how evenly abundance (individual flowering stems) is distributed among the species, was also calculated.

Differences between protected and unprotected plots across the 4 yr were tested for significance for the three metrics ( $HO$ ,  $S$ , and  $JO$ ) with chi-square tests. Linear regression and Pearson correlation across all years and protection ( $N = 8$ ) were used to test for relationships among  $H'$ ,  $S$ ,  $JO$ , and  $HO$ .

**Results. STEM DENSITIES IN PROTECTED AND UNPROTECTED PLOTS.** The number of browsed and unbrowsed stems combined, tallied in the 25-cm × 25-cm quadrats for the four focal species (*Helianthus*, *Veronicastrum*, *Silphium*, and *Parthenium*), showed varied patterns of change from the first sampling period (1992), before deer exclosures were established, to the last sample in 2001, after a reduction of the deer herd in 1997 (Table 1). *Helianthus* had a large, significant increase in stems in protected plots, 19-fold between 1992 and 2001, and a small (4–17), but significant, increase in stems in unprotected plots between 1992 and 2001. In protected plots, *Veronicastrum* had a 3.5-fold increase in stems but nearly the same number of stems between the two samples in unprotected plots. *Parthenium* stems nearly doubled on protected plots between the two samples, but there was a nonsignificant decrease in stems on unprotected plots. *Silphium* stems increased significantly between 1992 and 2001 (193–301) on unprotected plots, but, unlike the three other focal species, stem counts on protected plots declined significantly (53%) between 1992 and 2001 (Table 1).

**FLOWERING STEM TRANSECT COUNTS.** For the 4 yr of the study, the total number of flowering stems tallied were greater in the protected than the

Table 1. Changes in number of vegetative stems (browsed and unbrowsed combined) tallied in 72, 25-cm  $\times$  25-cm quadrats before exclosures were established in 1992 and in the last sample of the plots taken in 2001, 9 yr after the exclosures were established. For 1992 samples, all plots were unprotected until December after sampling occurred. *Protected* and *unprotected* refers to samples that were taken in plots that were protected or unprotected after 1992.

Species	1992		2001		Chi-square tests (d.f. = 1)			
	Protected	Unprotected	Protected	Unprotected	Protected		Unprotected	
					Value	P	Value	P
<i>Helianthus</i>	10	4	192	17	163.9	< 0.0001	7.2	0.0072
<i>Veronicastrum</i>	64	48	229	45	92.9	< 0.0001	0.1	0.7757
<i>Silphium</i>	178	193	112	301	15.0	0.0011	23.6	< 0.0001
<i>Parthenium</i>	67	64	117	53	13.6	0.0002	1.0	0.3091

unprotected plots and were 28,199 and 17,289, respectively. On unprotected plots, three species had more than 1,000 stems tallied: *Silphium* (9,062), *Parthenium* (3,262), and *Solidago juncea* Aiton (2,043). The two leading species for flowering stem counts on the protected plots were *Helianthus* (5,637) and *Veronicastrum* (3,908). Five other species had 1,000 or more stems tallied on the protected plots: *Parthenium* (3,839), *Silphium* (3,251), *Tradescantia ohiensis* Raf. (2,248), *S. juncea* (1,832), and *Rudbeckia subtomentosa* Pursh (1,342). The first and second leading species on unprotected plots had 52.4% and 20.0% of the total flowering stems, respectively, whereas on protected plots the two leading species had 19.9% and 7.2%, respectively.

**EFFECT OF DEER BROWSING AND FIRE ON FLOWER STEM PRODUCTION.** *All Species Combined.* Results of repeated-measures ANOVA showed significant effects for protection, ( $F_{1,2} = 21.09$ ,  $P = 0.0433$ ), time ( $F_{3,6} = 55.08$ ,  $P < 0.001$ ), and time  $\times$  protection interaction ( $F_{3,6} = 26.03$ ,  $P < 0.001$ ). Plots protected from deer browsing had significantly more flowering stems than unprotected plots in nonburn years 1998 and 2000, a 3.5-fold and 3.3-fold increase for the 2 yr, respectively. However, in burn years (1999 and 2001), there were no significant differences in the number of flowering stems in protected and unprotected plots (Fig. 1).

*Focal Species.* *Helianthus* flowering was significantly affected by protection ( $F_{1,2} = 40.52$ ,  $P = 0.0238$ ), time ( $F_{3,6} = 31.34$ ,  $P = 0.0005$ ), and the interaction between time and protection ( $F_{3,6} = 22.89$ ,  $P = 0.0011$ ). For each year, protected plots had significantly more flowering stems than unprotected plots had. Total flowering stems were 54-fold higher on protected plots. (Fig. 2A, B).

Generally, *Helianthus* had more flowering stems in nonburn than burn years.

Flowering of *Veronicastrum* was significantly affected by protection ( $F_{1,2} = 231.11$ ,  $P = 0.0043$ ), time ( $F_{3,6} = 4.97$ ,  $P = 0.0457$ ), and the interaction between time and protection was marginally significant ( $F_{3,6} = 4.72$ ,  $P = 0.0507$ ). There were significant differences in the number of flowering stems between protected and unprotected plots for all years, with protected plots having a 70-fold higher total number of flowering stems than unprotected plots (Fig. 2D, E). *Veronicastrum* flowering stems were not encountered in transects sampled in unprotected plots in 1998 and averaged three or fewer flowering stems in the other study years. In protected plots, there were more flowering stems in nonburn years than there were in burn

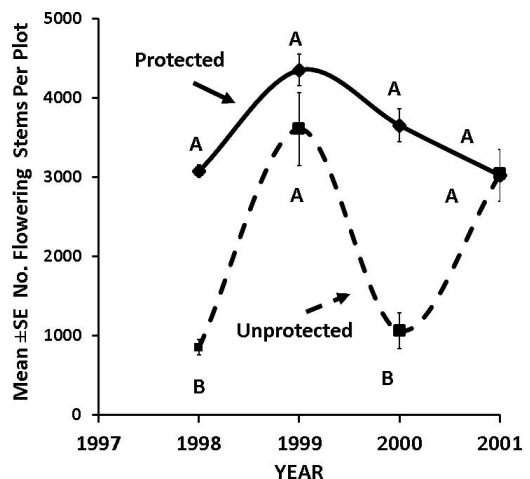


FIG. 1. Total number of flowering stems on protected (solid line) and unprotected plots (dashed line) during the 4 yr of the study. Burn years were 1999 and 2001. Within-a-year means with different letters are significantly different.

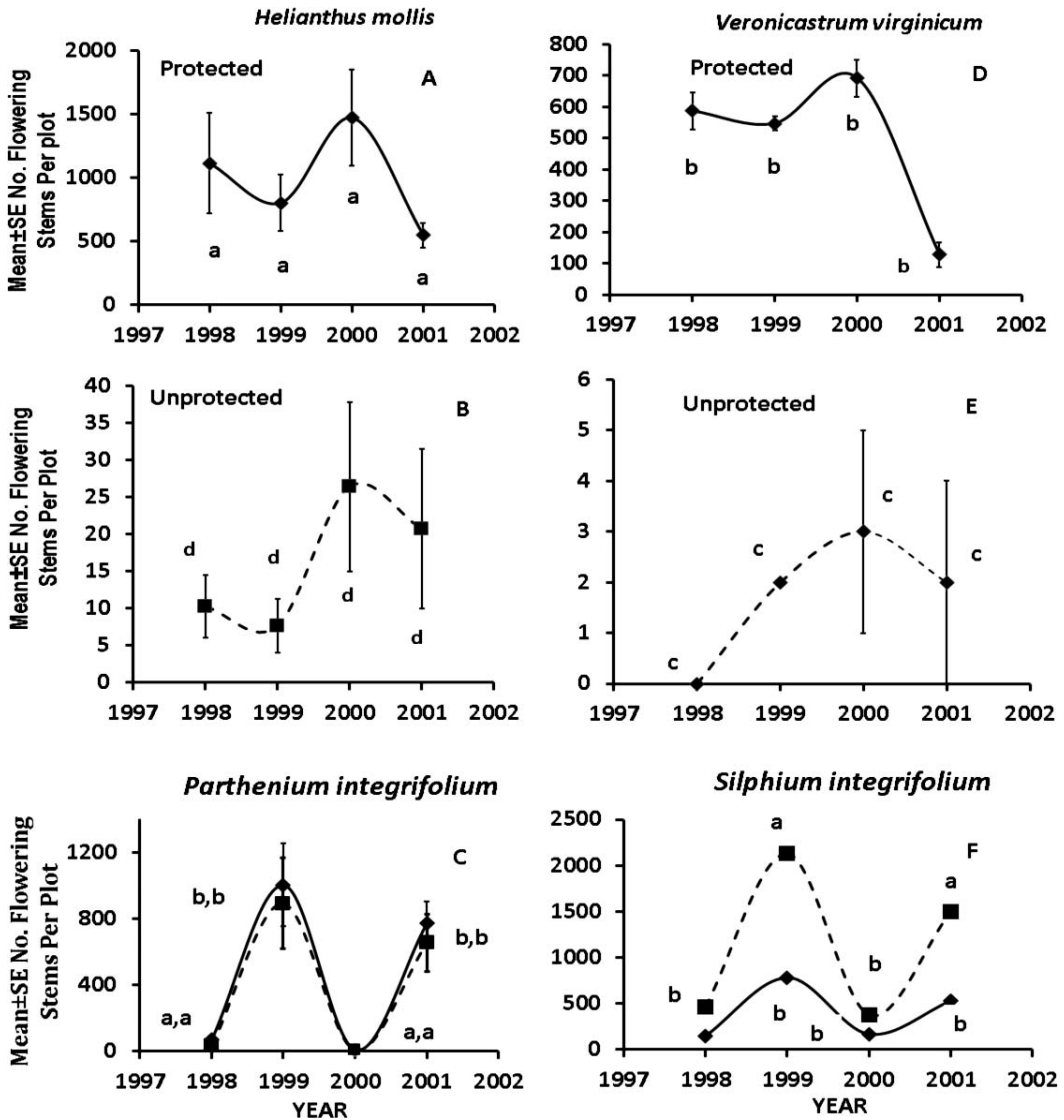


FIG. 2. Number of flowering stems for the focal species (*Helianthus*, *Veronicastrum*, *Parthenium* and *Silphium*) on protected and unprotected plot. Solid lines indicate protected plots, and dashed lines are unprotected plots. Means with different lowercase letters within a year are significantly different. On protected plots, *Helianthus* (A and B) and *Veronicastrum* (D and E) had significantly more flowering stems than unprotected plots within a year. Note that the scales for the protected and unprotected plots are different for *Helianthus* and *Veronicastrum*. For *P. integrifolium* (C), there were no significant differences between protected and unprotected plots. However, in burn years (1999 and 2001), there were significantly more flowering stems than in nonburn years. Protected and unprotected plots were significantly different within burn years (1999 and 2001) but not in nonburn years (1998 and 2000) for *Silphium* (Fig. 2F).

years, with a sharp 5.4-fold decline in flowering stems between 2000 (nonburn year) and 2001 (burn year).

There were significant effects on flowering stems of *Parthenium* from time ( $F_{3, 6} = 531.00$ ,  $P < 0.0001$ ) but not protection ( $F_{1, 2} = 0.57$ ,  $P =$

0.5304) or the interaction between time and protection ( $F_{3, 6} = 3.53$ ,  $P = 0.0883$ ). There were no significant differences between protected and unprotected plots for any of the 4 yr; however, flowering of *Parthenium* was 27-fold higher in burn than in nonburn years (Fig. 2C).

Table 2. Shannon diversity index ( $H'$ ) testing for differences between protected and unprotected plots for each of the 4 yr of the study separately. Burn years (1999 and 2001) are marked with an asterisk.

Year	Protection	$H'$	$t$	d.f.	$P$
1998	Protected	2.21	13.67	2,474	< 0.001
	Unprotected	1.70			
1999*	Protected	2.24	48.33	14,425	< 0.001
	Unprotected	1.28			
2000	Protected	1.92	5.58	3,507.087	< 0.001
	Unprotected	1.77			
2001*	Protected	2.26	24.08	11,709	< 0.001
	Unprotected	1.70			

The flowering of *Silphium* was significantly affected by protection ( $F_{1,2} = 23.37$ ,  $P = 0.0404$ ) and time ( $F_{3,6} = 40.40$ ,  $P = 0.0179$ ); however, the interaction between time and protection ( $F_{3,6} = 0.30$ ,  $P = 0.6560$ ) was not significant. Unprotected plots had more total flowering stems than protected plots had for all 4 yr of the study (a 4.3-fold increase); however, those differences were significant only in the burn years (a 5.3-fold increase) (Fig. 2F).

DIVERSITY ( $H'$  AND  $HO$ ), EVENNESS ( $JO$ ), AND SPECIES RICHNESS ( $S$ ). For our data set, there was a highly significant correlation between  $H'$  and  $HO$  ( $F_{1,6} = 266.36$ ,  $P < 0.0011$ , adjusted  $R^2 = 0.974$ ). However, for testing for differences between protected and unprotected plots within each year, we chose to use  $H'$  rather than  $HO$  because the degrees of freedom are substantially larger for  $H'$  than for  $HO$  when differences between protected and unprotected plots are compared (Table 2).

There is only 1° of freedom for  $HO$  chi-square tests because there were only two cells for this analysis. The Shannon index ( $H'$ ) indicated that protected plots had significantly greater diversity than unprotected plots for all 4 yr of the study (Table 2). However, with a large number of degrees of freedom,  $t$  tests can indicate significance between samples with small differences.

On protected plots,  $HO$  and  $S$  were always higher than on nonprotected plots for all years. However, for  $JO$  the results were the same, except for the nonburn year 2000, when evenness was essentially the same on protected and unprotected plots (Table 3). Chi-square tests indicated that there were only significant differences between protected and unprotected plots for  $JO$  in 1999, a burn year. Not unexpectedly, we found a nonsignificant relationship between  $S$  and  $HO$  (adjusted  $R^2 = 0.1336$ ,  $F_{1,6} = 2.08$ ,  $P = 0.1994$ ) and  $S$  and  $H'$  (adjusted  $R^2 = 0.0845$ ,  $F_{1,6} = 1.65$ ,  $P = 0.24680$ ). However,  $JO$  counted for 74.6% of the variance in

Table 3. Testing for differences between protected and unprotected plots by year for effective number of species, evenness, and species richness of flowering stems in burn and nonburn years. Burn years (1999 and 2001) are marked with an asterisk. All chi-square tests were d.f. = 1.

Year	Protected	Unprotected	Chi-square	$P$ -value
Diversity (effective number of species)				
1998	9.11	5.47	0.908	0.340
1999*	9.39	3.59	2.591	0.107
2000	6.82	5.87	0.071	0.789
2001*	9.58	5.47	1.122	0.289
Evenness				
1998	0.656	0.553	0.931	0.334
1999*	0.625	0.374	6.306	0.012
2000	0.530	0.540	0.0093	0.923
2001*	0.614	0.491	2.245	0.133
Species richness				
1998	29	22	0.960	0.326
1999*	36	31	0.373	0.541
2000	38	26	2.245	0.113
2001*	40	32	0.888	0.556



*HO* (adjusted  $R^2 = 0.7469$ ,  $F_{1, 6} = 49.71$ ,  $P = 0.0004$ ) and 91% of the variance in  $H'$  ( $R^2 = 0.9100$ ,  $F_{1, 6} = 71.76$ ,  $P = 0.0001$ ). These results indicate that, for our sample, diversity ( $H'$  and *HO*) were more affected by *JO* than by *S*.

**Discussion.** FOCAL SPECIES. Initially, we predicted that the numbers and diversity of forb flowering stems would be increased by burning and decreased by deer browsing after 1998. Our result showed that fire and deer browsing had significant effects and interactions on the number of flowering stems; however, the effects of those two factors varied depending upon the species being considered. *Helianthus* and *Veronicastrum* flowering stem production was negatively affected by deer browsing and generally by burning. *Silphium* had more flowering stems in unprotected plots than in protected plots, especially in burn years. Flowering of *Parthenium* was stimulated by burning in protected and unprotected plots, and there was no year in which there was a significant difference in flowering stems between protected and unprotected plots for that species. The decrease of total flowering stems (all species combined) in nonburn years, and the large increase of total flowering stems in the burn years, were due to *Silphium* and *Parthenium*.

Burning stimulated flower production in *Parthenium* and *Silphium* but for different reasons. In contrast to *Parthenium*, there were more *Silphium* flowering stems on unprotected plots than there were on protected plots for all years because there were nearly three times as many total vegetative stems (browsed and unbrowsed) in 2001 on unprotected plots ( $n = 301$ ) than there were on protected plots ( $n = 112$ ). However, the increase in *Silphium* flowering stems in burn years on protected and unprotected plots was due to a reduction in the damage to flowering heads caused by the fire-sensitive prairie weevil, *Haplorhynchites aeneus* Boehman.

Adults of the prairie endemic weevil *H. aeneus* consume pollen of several *Silphium* species, (*S. integrifolium*, *Silphium terebinthinaceum* Jacq., and *Silphium laciniatum* L.). Female weevils partially clip peduncles of flower heads, so they remain on the plant. Eggs are laid into flowering heads, and emerging larvae feed on *Silphium* ovules (Kluger *et al.* 2011). Consequentially, *H. aeneus* can significantly affect the reproduction of its hosts; however, the perennial nature of *Silphium*

prevents their local extinction. Loss of *Silphium* flowering heads, however, could have a negative effect on pollinators relying on *Silphium* as a food source (Kluger *et al.* 2011).

Thus, deer browsing resulted in an increased abundance of *Silphium* on unprotected plots, and burning eliminated or reduced the weevil's negative impact on the flowering of *Silphium*, resulting in no significant difference in the number of flowering stems of *Silphium* on protected and unprotected plots in nonburn years (1998 and 2000), but significantly fewer flowering stems on protected plots than on unprotected plots in burn years (1999 and 2001).

COMMUNITY RESPONSE. Community effects of fire are different in communities strongly affected by deer browsing and those with higher diversity as a result of protection from deer browsing. Flowering stem diversity ( $H'$  and *HO*) was higher on protected than it was on unprotected plots for all study years, which was largely due to evenness (*JO*). The difference in evenness is illustrated by the number of species required to produce about 50% of the total stems counted in protected and unprotected plots. The leading species (*S. integrifolium*) on unprotected plots accounted for more than one half (52.3%) of all flowering stems, contributing to the low evenness, especially on unprotected plots in burn years (1999 and 2001). In contrast, on protected plots, the seven leading species contributed only 48.5% of the total flowering stems; thus, flowering stem were more equitably distributed among species in protected plots than they were in unprotected plots. Selective deer browsing had an important role in the reduced evenness and diversity on unprotected plots. Four of the seven leading species on protected plots were negatively affected by deer browsing (*Helianthus*, *T. ohiensis*, *Veronicastrum*, and *R. subtomentosa*) (Anderson *et al.* 2005).

Our study demonstrates that prairies can recover from intensive browsing after a reduction in deer abundance. Overall, intensive deer browsing reduced flowering of most prairie forbs and appears to stimulate flowering of a few species, which resulted in a loss of diversity of flowering stems because of declines in evenness and species richness. To maximize biological diversity in small, isolated prairie remnants, deer densities need to be maintained at moderately low levels (Anderson *et al.* 2005, 2006). Before

establishment of deer exclosures in 1992, the area that was eventually fenced and the unprotected area were highly similar in forb species composition and abundance (82% similarity) and did not differ significantly in species diversity and richness (Anderson *et al.* 2005). However, in 1997, before deer density was reduced using managed hunting, similarity between protected and unprotected plots declined to 49%, and then increased to 68% in 2001 after 4 yr (1997–2000) of managed hunting.

Within most of the species' range in eastern North America, there is an overabundance of white-tailed deer (Risenhoover *et al.* 1997, Rooney and Waller 2003, Cote 2004). Decisions land managers make about deer management are often influenced by hunters who prefer that deer densities be maintained at high levels to increase hunter success (Alverson *et al.* 1988, Nugent and Fraser 1993, deCalesta and Stout 1997, Woolf and Roseberry 1998, Miller and Graefe 2001, Cote 2004, Putman and Staines 2004). It is important for land managers to know whether reduction in the size of deer herds will have positive effects on prairies, and at what level of deer densities, the recovery of prairie quality has been shown to occur. Our results in this article and those of others (Anderson *et al.* 2005, 2006) indicate that reducing deer abundances can increase quality and diversity of prairies and provide a benchmark for deer densities (7–9 km<sup>-2</sup>) that should maintain high-quality prairies.

#### Literature Cited

- ALVERSON, W., W. D. WALLER, AND D. M. SOLHEIM. 1988. Forest too deer: edge effects in northern Wisconsin. *Conserv. Biol.* 2: 348–358.
- ANDERSON, R. C. 2006. Evolution and origin of the central grassland of North America: climate, fire, and mammalian grazers. *J. Torrey Bot. Soc.* 133: 626–647.
- ANDERSON, R. C., E. A. CORBETT, M. R. ANDERSON, G. A. CORBETT, AND T. M. KELLEY. 2001. High white-tailed deer density has negative impact on tallgrass prairie forbs. *J. Torrey Bot. Soc.* 128: 381–392.
- ANDERSON, R. C., D. NELSON, M. R. ANDERSON, AND M. A. RICKEY. 2005. White-tailed deer browsing effects on tallgrass prairie forbs: diversity and species abundances. *Nat. Areas J.* 25: 19–25.
- ANDERSON, R. C., D. NELSON, M. R. ANDERSON, AND M. RICKEY. 2006. White-tailed deer (*Odocoileus virginianus* Zimmermann) browsing effects on quality of tallgrass prairie community forbs, pp. 63–68. *In* D. Egan and J. Harrington [eds.], *Proceedings of the 19th North American Prairie Conference*. University of Wisconsin-Madison, Madison, WI.
- BEALS, E. 1960. Forest bird communities in the Apostle Island of Wisconsin. *Wilson Bull.* 72:156–181.
- BRAY, J. R. AND J. T. CURTIS. 1957. An ordination of the upland forest communities of southern Wisconsin. *Ecol. Monogr.* 27: 325–349.
- BOWLES, M. L. AND M. D. JONES. 2013. Repeated burning of eastern tallgrass prairie increases richness and diversity, stabilizing late successional vegetation. *Ecol. Appl.* 23: 464–478.
- CLAUSS, M., T. KAISER, AND J. HUMMEL. 2008. The morphophysiological adaptations of browsing and grazing animals, pp. 47–88. *In* I. J. Gordon and H. H. T. Prins [eds.], *The Ecology of Browsing and Grazing*. Springer-Verlag, Heidelberg, Germany.
- COLLINS, S. L., S. M. GLENN, AND D. J. GIBSON. 1995. Experimental analysis of intermediate disturbance and initial floristic composition: decoupling cause and effect. *Ecology* 76: 486–492.
- COLLINS, S., A. KNAPP, J. BRIGGS, AND E. STEINAUER. 1998. Modulation of diversity by grazing and mowing in native tallgrass prairie. *Science* 280: 745–747.
- CONNELL, J. H. 1978. Diversity in tropical rainforest and coral reefs. *Science* 199: 1302–1320.
- COTE S. D., T. P. ROONEY, J. TREMBLAY, C. DUSSAULT, AND D. M. WALLER. 2004. Ecological impacts of deer overabundance. *Annu. Rev. Ecol. Evol. Syst.* 35: 113–147.
- CURTIS, J. T. AND M. L. PARTCH. 1950. Some factors affecting flower production in *Andropogon gerardii*. *Ecology* 31: 488–489.
- DAHLBERG, B. AND R. GUETTINGER. 1956. The white-tailed deer in Wisconsin. Game Management Division, Wisconsin Conservation Department Technical Bulletin 14, Alma, WI.
- DAMHOUREYEH, S. A. AND D. C. HARTNET. 1997. Effects of bison and cattle on growth, reproduction, and abundances of five tallgrass prairie forbs. *Am. J. Bot.* 84: 1719–1728.
- DAMUTH, J. AND C. M. JANIS. 2011. On the relationship between hypsodonty and feeding ecology in ungulate mammals and its utility in palaeoecology. *Biol. Rev.* 86: 733–758.
- DECALESTA, D. S. AND S. L. STOUT. 1997. Relative deer density and sustainability: a conceptual framework for integrating deer management with ecosystem management. *Wildl. Soc. Bull.* 25: 252–258.
- DUNCAN, A. J. AND D. P. POPPI. 2008. Nutritional ecology of grazing and browsing ruminants, pp. 89–148. *In* I. J. Gordon and H. H. T. Prins [eds.], *The Ecology of Browsing and Grazing*. Springer-Verlag, Heidelberg, Germany.
- FLORY, S. L. AND K. CLAY. 2010. Non-native grass invasion alters native plant composition in experimental communities. *Biol. Invasions* 12: 1285–1294.
- FULBRIGHT, T. E. AND J. A. ORTEGA. 2006. White-tailed deer habitat: ecology and management of rangelands (perspectives on south Texas). Texas A&M University, Kingsville, TX.
- GARBALDI, L. A., M. SEMMARTIN, AND E. J. CHANETAN. 2007. Grazing induced changes in plant composition affect litter quality and nutrient cycling in flooding Pampa grasslands. *Oecologia* 151: 650–662.

- GAUCH, H. G. 1983. Multivariate analysis in community ecology. Cambridge University Press, New York, NY.
- GIBSON D. J. AND L. C. HULBERT. 1987. Effects of fire, topography, and year-to-year climatic variation on species composition in tallgrass prairie. *Vegetatio* 72: 175–185.
- GLEASON, H. A. 1963. Illustrated Flora of the Northeastern United States and Adjacent Canada. Volume 3. Hafner Publishing Company, Inc., New York, NY.
- HARTNETT, D. 1991. Effects of fire in tallgrass prairie on growth and reproduction of prairie coneflower (*Ratibida columnifera*: Asteraceae). *Am. J. Bot.* 78: 429–435.
- HARTNETT, D. AND P. A. FAY. 1998. Plant populations; patterns and processes, pp. 81–100. *In* A. K. Knapp, J. M. Briggs, D. C. Hartnett, and S. Collins [eds.], *Grassland Dynamics: Long-Term Ecological Research in Tallgrass Prairie*. Oxford University Press, NY.
- HILL, M. O. 1973. Diversity and evenness: a unifying notation and its consequence. *Ecology* 54: 427–432.
- HORSLEY, S. B., S. L. STOUT, AND D. S. DECALESTA 2003. White-tailed deer impact on the vegetation dynamics of a northern hardwood forest. *Ecol. Appl.* 13: 1398–118.
- HOWE, H. F. 1994. Managing species diversity in tallgrass prairie: assumptions and implications. *Conserv. Bio.* 8: 691–704.
- HOWE, H. F. 1999. Response of *Zizia aurea* to seasonal mowing and fire in a restored prairie. *Am. Midl. Nat.* 141: 373–380.
- HOWE, H. F. AND J. S. BROWN. 1999. Effect of birds and rodents on synthetic tallgrass communities. *Ecology* 80: 1776–1781.
- HULBERT, L. C. 1986. Fire effects on tallgrass prairie, pp. 139–142. *In* G. K. Clambey and R. H. Pemble [eds.], *Proceedings of the Ninth North American Prairie Conference*. Tri-College University for Environmental Studies, North Dakota State University, Fargo, ND.
- HUMMEL, J., K.-H. SUDEKUM, W. J. STREICH, AND M. CLAUSS. 2006. Forage fermentation patterns and their implications for herbivore ingesta retention times. *Funct. Ecol.* 20: 989–1002.
- JOERN, A. 2005. Disturbance by fire frequency and bison grazing modulate grasshopper assemblages in tallgrass prairie. *Ecology* 86: 861–873.
- JOST, L. 2006. Diversity and entropy. *Oikos* 113: 363–375.
- KLUGER, E. C., S. H. BERBLOCHER, J. F. TOOKER, AND L. M. HANKS. 2011. Consequences of habitat fragmentation for the prairie endemic weevil *Haplorhynchites aeneus*. *Environ. Entomol.* 40:1388–1396. doi: <http://dx.doi.org/10.1603/EN11054>.
- KNAPP, A. K. 1985. Effect of fire and drought on the ecophysiology of *Andropogon gerardii* and *Panicum virgatum* in a tallgrass prairie. *Ecology* 66: 1309–1320.
- KNAPP, A., J. BLAIR, J. BRIGGS, S. COLLINS, D. HARTNETT, L. JOHNSON, AND E. TOWNE. 1999. The keystone role of bison in North American tallgrass prairie. *Bioscience* 49: 39–50.
- LEACH, M. K. AND T. J. GIVNISH. 1996. Ecological determinants of species loss in remnant prairies. *Science* 273: 1555–1558.
- LOVELL, D. L., R. A. HENDERSON, AND E. L. HOWELL. 1983. The response of forb species to seasonal timing of prescribed burns in remnant Wisconsin prairies, pp. 11–15. *In* R. Brewer [ed.], *Proceedings of the Eight North American Prairie Conference*. Department of Biology, Western Michigan University, Kalamazoo, MI.
- MAGURRAN, A. E. 1988. *Ecological Diversity and Its Measurement*. Princeton University Press, Princeton, NJ.
- MCCABE, T. R. AND R. E. MCCABE. 1984. Of slings and arrows: an historical retrospection, pp. 19–72. *In* H. Hall [ed.], *White-Tailed Deer: Ecology and Management*. Stackpole Books, Harrisburg, PA.
- MILLER, G. A. AND A. R. GRAEFE. 2001. Effect of harvest success on hunter attitudes towards white-tailed deer management in Pennsylvania. *Hum. Dimens. Wildl.* 6: 189–203.
- NIXON, C., L. P. HANSEN, P. A. BREWER, AND J. E. CHELSVIG. 1991. Ecology of white-tailed deer in an intensively farmed region of Illinois. *Wildl. Monogr.* 118: 1–77.
- NUGENT, G. AND K. W. FRASER. 1993. Pests or valued resources? conflicts in management of deer. *N. Z. J. Zool.* 20: 361–366.
- PIELOU, F. C. 1975. *Ecological Diversity*. Wiley, New York, NY.
- PUTMAN, R. J. AND B. W. STAINES. 2004. Supplementary winter feeding of wild red deer *Cervus elaphus* in Europe and North America: justification, feeding practice and effectiveness. *Mammal Rev.* 34: 285–306.
- REED, C. 1994. Species richness of insects on prairie flowers in southeastern Minnesota, pp. 103–115. *In* D. C. Hartnett [ed.], *Proceedings of the 14th North American Prairie Conference*, Kansas State University, Manhattan, KS.
- RISENHOOVER, K. L., W. Y. UNDERWOOD, AND J. L. COOKE. 1997. A spatially explicit modeling environment for deer management strategies, pp. 366–379. *In* W. J. McShea, H. B. Underwood, and J. H. Rappole [eds.], *The Science of Overabundance: Deer Ecology and Population Management*. Smithsonian Institution Press, Washington, DC.
- ROBERTSON, K. R., R. C. ANDERSON, AND M. SCHWARTZ. 1997. The tallgrass prairie mosaic, pp. 55–87. *In* M. Schwartz [ed.], *Conservation in Highly Fragmented Landscapes*. Chapman and Hall, New York, NY.
- ROONEY, T. P. AND D. M. WALLER. 2003. Direct and indirect effects of white-tailed deer in forest ecosystems. *For. Ecol. Manag.* 181: 165–176.
- ROSBURG, T. R. 2001. Effects of late spring fires on the survival, growth, and production of prairie forbs, pp. 48–58. *In* N. P. Berstein and J. L. Strander [eds.], *Proceedings of the 17th North American Prairie Conference*. North Iowa Area Community College, Mason City, IA.
- SAS INSTITUTE INC. 2002–2014. Base SAS 9.4. SAS Institute Inc., Cary, NC, USA.

- STIRLING, G. AND D. WILSEY. 2001. Empirical relationships between species richness, evenness, and proportional diversity. *Am. Nat.* 158: 286–299.
- SWINK, F. A. AND G. S. WILHELM. 1994. *Plants of the Chicago Region*, 4th ed. Indiana Academy of Science, Indianapolis, IN.
- TAFT, J. B., G. S. WILHELM, D. M. LADD, L. A. MASTERS. 1997. Floristic quality assessment for vegetation in Illinois, a method for assessing vegetation integrity. *Erigenia* 15: 3–95.
- [USDA, NRCS] US DEPARTMENT OF AGRICULTURE, NATURAL RESOURCES CONSERVATION SERVICE. 2016. The PLANTS Database. Retrieved August 28, 2016 from National Plant Data Team, <<http://plants.usda.gov>>.
- WOOLF, A. AND J. L. ROSEBERRY. 1998. Deer management: our profession's symbol of success or failure. *Wildl. Soc. Bull.* 26: 515–521.