Deer Browsing Effect on Prairie Forbs

White-tailed deer (*Odocoileus virginianus* Zimmermann) browsing effects on quality of tallgrass prairie community forbs

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Abstract

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We examined the effect of white-tailed deer *(Odocoileus virginianus* Zimmermann) browsing on community quality of tallgrass prairie forbs at a site in northeastern Illinois over a period of ten years (1992-2001). Deer densities in the study area varied from 32-50 km^{-2} (83-130 deer mi^{-2}) between 1992 and 1997 and declined to 7-9 km^{-2} (18-23 mi^{-2}) following initiation of hunting. In a plot protected from deer browsing, abundances of browse-sensitive species increased and unpreferred and browse-tolerant species decreased. Community quality of forbs measured with a new index, Weighted Mean Fidelity, decreased on the unprotected plot until deer density was reduced. Several commonly used indices of floristic quality, mean *C* and floristic quality index, were unable to detect changes in community quality because the compliment of species on our site did not change over time. However, changes occurred in the relative abundances of species with different coefficients of conservatism, which was detected by Weighted Mean Fidelity. In contrast, on the protected plot community quality initially declined, followed

by an increase, suggesting a lag time for recovery from browsing. Previous studies on our study site demonstrated that diversity of prairie forbs was maximized at an intermediate level of deer browsing, supporting the intermediate disturbance hypothesis, which posits that diversity is maximized at intermediate levels of disturbance. However, we found that community quality of forbs declined as duration of intense deer browsing (disturbance) increased, and was highest after eight years of protection from browsing, suggesting a potential trade-off between maximizing diversity and maintaining quality of forb communities that land managers should consider.

Key Words: *Odocoileus virginianus*, tallgrass prairie, forbs, floristic quality, disturbance, community quality, browsing effects

Introduction

Worldwide expansion of grasslands and savannahs since the Miocene was associated with the adaptive radiation of large mammals that were adapted to grazing (Stebbins 1981; Anderson 1982, 1990; Axelrod 1985; McNaughton 1993; Oesterheld et al. 1999). Adaptive responses of prairie grasses to herbivores that reflect a coevolutionary relationship between grazers and grasses includes the presence of silica in epidermal cells of grasses, perennating organs below ground level, and aboveground production in excess of that which can decompose in a single year (Stebbins 1981; Anderson 1982, 1990). In North American tallgrass prairies, Bison (*Bos bison* L.) is considered to be a keystone species by affecting plant species composition and abundances, diversity, nutrient cycling and primary production (Knapp et al. 1999). Bison favor growth of subordinate species, including C3 forbs, by preferentially grazing dominant grasses (Fahnestock and Knapp 1993; Steuter et al. 1995; Damhoureyeh and Hartnett 1997; Knapp et al. 1999). Forbs contribute the greatest amount of species richness to the prairie (Howe 1994; Knapp et al. 1999) and this differential grazing pattern increases plant species diversity (Collins et al. 1998; Knapp et al. 1999). Bison grazing also favor structural heterogeneity in grasslands and this enhances bird diversity

(Knopf 1996). White-tailed deer (*Odocoileus virginianus* Zimmermann), unlike bison, consume little if any of the dominant C4 grasses and preferentially browse prairie forbs, consuming nearly 19% of the standing crop of forb stems (Anderson et al. 2001). This selective browsing pattern of deer influences species abundances, diversity patterns, and apparently competitiveness among forbs (Anderson et al. 2001; Anderson et al. 2005).

Previous studies on our study site (Anderson et al. 2005) indicate that under conditions of high browsing intensity browse tolerant and unpreferred forb species were competitively favored, while under conditions of low browsing intensity, preferred forb species are favored if they are superior competitors. Thus, a trade-off exists between the ability of a species to compete and to tolerate disturbance (Collins et al. 1995). This results in low diversity at high and low levels of disturbance and higher diversity at intermediate levels of disturbance, because of the coexistence of competitive and disturbance tolerant species under these conditions, a pattern seen among prairie forbs (Anderson et al. 2005). Community quality is an attribute that incorporates species composition and the proportional abundance of species of varied fidelity to native prairie remnants.

In this paper, we examine changes in forb community quality resulting from varied intensities and length of time since exposure to deer browsing. We measure forb community quality with a new index, Weighted Mean Fidelity, which increases with an increase in the abundance of prairie forbs with high fidelity to relatively undisturbed remnant prairies. In contrast, mean *C* and the Floristic Quality Index consider species' presence or absence but are insensitive to changes in species abundance (Swink and Wilhelm 1994; Taft et al. 1997; Francis et al. 2000; Rooney and Rogers 2002; Matthews 2003). We predict that deer browsing will reduce forb community quality at high frequency of browsing by creating disturbances favoring species adapted to disturbance and negatively affect the prairie forbs with high fidelity to relatively undisturbed remnant prairies.

Methods

Study site

The study site is located in the 218 ha (538 acres) Heidecke Lake Fish and Wildlife Area (HLFWA), which is adjacent to the west side of the 1,027 ha (2,537 acres) Goose Lake Prairie State Park (GLPSP), about 70 km (42 miles) southwest of Chicago in northeastern Illinois, Grundy County. The study site and sampling methods are the same as those of Anderson et al. (2001, 2005) and are summarized below. In May 1992, a 33 m x 48 m (99 ft x 158 ft) study area was selected in the HDFWA because of its high diversity of prairie forbs. The one hundred species of forbs noted in this area allowed us to determine the selective patterns of deer browsing when a large number of forb species were available. Northern prairie dropseed [*Sporobolus heterolepis* (Gray) Gray], a species associated with high quality remnant tallgrass prairies (Swink and Wilhelm 1994), is the dominant grass species on the site (Anderson et al. 2001) The site received spring burns in 1992, 1997, and 2000 but not during the rest of the study. The study area was divided equally into two plots and three parallel transect lines extending the full length of each plot were established. From the transect beginning, points were located at 1 m (3.3 ft) and then at 2 m (6.6 ft) intervals for a distance of 46 m (152 ft). The center of a 25 cm x 25 cm (10 in x 10 in) quadrat was located at a randomly determined distance to the left or right of the transect at each point, resulting in 24 points per transect and 72 quadrats per plot. Browsed and unbrowsed forb stems were counted by species in quadrats. Sampling occurred in seven years: late June (2000) or July in 1992, 1993, 1994, 1997, 1999, and 2001.

One-half of the study area was fenced to exclude deer but not small mammals in December 1992. Areas fenced were selected to maximize similarity between fenced and unfenced areas. Percent similarity (Gauch 1982) between protected and unprotected plots based on forb stem counts was 81.5% for the June 1992 sample, a high similarity value. Two random samples of the same site result in similarity values of about 82-85% (Bray and Curtis 1957; Beals 1960). The size of the deer herd was substantially reduced on HLFWA and adjacent GLPSP by controlled hunting beginning in the fall of 1997.

Winter deer counts from helicopter on HLFWA and GLPSP were combined because deer move freely between the two areas. Deer densities following controlled hunting were 7-9 km^{-2} (18-23 mi^{-2}) in 1998 and 1999 compared to 32-50 deer km^{-2} (83-130 mi^{-2}) before hunting (1992-1996). Deer densities after initiation of hunting are similar to estimates of pre-European settlement densities (3-8 deer km^{-2}, 8-20 deer mi^{-2}) in most favorable habitats (Horsley, Stout, and deCalesta et al. 2003) and those for historic conditions in the Midwest (4 to 19 deer km^{-2}, 10-49 deer mi^{-2}) (Dahlberg and Guettinger 1956; McCabe and McCabe 1984). Prior to 1997, densities are somewhat lower than 20th Century estimates of deer densities (>60 deer km^{-2}, >157 deer mi^{-2}) in areas with mixed forest and agricultural lands (Horsley, Stout, and deCalesta et al. 2003), but they are higher than the 27 deer km^{-2} (70 deer mi^{-2}) reported by Nixon et al. (1991) for areas in the farming belt of east central Illinois. We assessed recovery from the excessive deer browsing on unprotected plots by monitoring our plots prior to deer management under conditions of high deer densities and under reduced deer densities after initiation of a hunting program.

Methods of data analysis

Changes in community quality in protected and unprotected plots over time were assessed using: (1) mean Coefficient of Conservatism (mean *C*), (2) Weighted Coefficient of Conservatism (WCC), (3) the Floristic Quality Index (FQI), (4) Weighted Floristic Quality Index (WFQI) (Swink and Wilhelm 1994; Taft et al. 1997; Francis et al. 2000; Rooney and Rogers 2002; Matthews 2003) and (5) a new index, Weighted Mean Fidelity (WMF). We used the Coefficients of Conservatism (*C* value) for native species, which range from zero to ten, that were developed by Swink and Wilhelm (1994) as our measure of fidelity. The subjective coefficients reflect species' tolerance to habitat degradation and fidelity to native remnant habitats (Swink and Wilhelm 1994; Taft et al. 1997; Francis et al. 2000; Rooney and Rogers

2002; Matthews 2003). Species tolerant of disturbance and occurring in a variety of habitats have lower

C values than species occurring in relatively undisturbed native remnant habitats with high habitat

fidelity. Only species for which *C* values could be determined were used in the study. This requirement

excluded plants that could be identified only to the genus level but belonged to a genus that had several

species each with a different *C* value (e.g., *Gentianopsis* Ma). This meant that even if a plant occurred in

a single quadrat, which would allow an investigator to indicate that the plant represented a single

species, it was excluded.

The WCC was calculated by multiplying the *C* value by the stem counts for each species and

summing these values for each sample, and the WFQI was derived by multiplying WCC by the square

root of the number of species. To calculate WMF, the *C* value for each native species of forb was

weighted by stem counts of that species in the sample. These values were summed across species and

divided by the total number of stems of all species in the sample. Both mean *C* and the WMF vary from

zero, only species of the lowest fidelity to remnant prairies present, to ten, only species of high fidelity to

native remnant prairies present.

(1) **Mean Coefficient of Conservatism (mean *C*)** =
 N
($\sum$ Coefficients of Conservatism of native species)/number of native species (N)
i=1

(2) **Weighted Coefficient of Conservatism (WCC) =**

 N
$\sum$ Coefficient of Conservatism x stem count
i=1

(3) **Floristic Quality Index (FQI)** = mean *C* * √N

(4) **Weighted Floristic Quality Index (WFQI)** = WCC * √N

(5) **Weighted Mean Fidelity (WMF*)* =**

 N
($\sum$ Coefficient of Conservatism x stem count)/Total stems of all species
i=1

Taft et al. (1997) developed species *C* values for Illinois but we used the species coefficients developed by Swink and Wilhelm (1994) specifically for the Chicago region of Illinois, in which our study site occurs, as recommended by Rooney and Rogers (2002).

Literature cited follows Mohlenbrock (2002).

Results

Across protected and unprotected plots and dates, mean *C* ranged from 5.0 to 6.1 and FQI ranged from 29.3 to 36.0. However, of the various indices used in this study, only the WMF had significant differences between protected and unprotected plots averaged over sampling dates. Species richness averaged across years was higher for the protected plot than the unprotected plot (mean $\pm$ SE, 39.14 $\pm$8.29 and 34.39 $\pm$ 1.06, respectively) but these differences were not significant (Table 1). The only index correlated with species richness was WCC, but this correlation was negative (Table 2).

There were no interpretable patterns for Mean *C* or FQI between protected or unprotected plots over time (Figure 1A & 1B, respectively). Nevertheless, the WFQI and the WMF showed separation of protected and unprotected plots over time with the WMF showing separation between the two plots sooner than WFQI (Figure 1C and 1D). Both indices showed an initial decline during the first three years of the study (1992, 1993, and 1994) for protected and unprotected plots. Weighted Coefficient of Conservatism is not shown in Figure 1, but it was significantly and strongly correlated with WFQI (r = 0.991, P< 0.0001), Table 2.

All of the weighted indices had moderate to strong Pearson correlations with each other that ranged from 0.630 to 0.991; however, after application of the conservative Bonferroni correction to the alpha value (Sokal and Rohlf 1995) only the correlation between WCC and WFQI was significant as previously noted. The non-weighted indices (mean *C* and FQI) had weak non-significant correlations with the weighted indices that ranged from -0.362 to +0.220 and had a moderately weak non-significant correlation with each other (r = 0.558) (Table 2).

Five species responded positively to deer browsing by increasing their stem counts *Monarda fistulosa* L (wild bergamot)*, Heuchera richardsonii* R. Br*. (Richardson's alumroot)*, Solidago canadensis* L. (Canada goldenrod)*, Silphium integrifolium* Michx. (wholeleaf rosinweed)*,* and *Amorpha canescens* Pursh (leadplant)*.* Eight species responded negatively to browsing*: Tradescantia ohiensis* Raf. (bluejacket)*, Veronicastrum virginicum* (L.) Farw*.* (Culver's root), *Comandra umbellata* (L.) Nutt. (bastard toadflax), *Helianthus mollis* Lam. (Ashy sunflower), *Stachys palustris* L. (marsh hedgenettle)*, Symphyotrichum oolentangiense* (Riddell) G.L. Nesom var*. oolentangiense.* (sky-blue aster), *Rosa carolina* L (Carolina rose)*,* and *Rudbeckia subtomentosa* Pursh. (sweet coneflower) (Anderson et al. 2001; 2005)*.* The five species that increased in stem counts as the duration of intense browsing increased on the unprotected site had a mean *C* of 5.4 $\pm$ 1.4, whereas the seven species that decreased in stem counts in response to browsing had a mean *C* of 6.5 $\pm$ 0.8. Changes in abundances would have no affect on mean *C* or FQI but they influence the weighted measures of quality.

To demonstrate changes in species abundance on protected and unprotected plots, stem counts of three species (*C. umbellata, H. mollis,* and *V. virginicum)* that had substantial increases in stem counts on protected plots but declined on the unprotected plot until after deer hunting was initiated were compared with two species (*S. integrifolium* Michx. and *S. canadensis* L.) that increased in stem counts on the unprotected plots. Comparisons were made at the beginning and end of the study (1992 and 2001) and the summer before deer hunting was initiated (1997) (Table 3).

Between 1992 and 2001, stem counts increased for *C. umbellata* (125 to 310 stems), *V. virginicum* (64 to 229 stems) and *H. mollis* (10 to 192 stems) on protected plots and decreased on unprotected plots until after 1997 when deer density was reduced (Table 3). These three species have *C* values of seven, seven and nine, respectively. In contrast, S. *integrifolium* and *S. canadensis* increased in the unprotected plot throughout the study period. *Silphium integrifolium* stem counts increased from 193 to 301 between 1992 and 2001 and *S. canadensis* stems increased more than seven fold from 16 to

123 on the unprotected plot. These two species have *C* values of five and one, respectively. Stem counts of *S. integrifolium* decreased on the protected plots, whereas *S. canadensis* increased stem counts between 1992 and 1997 but then declined by 2001. These changes in stem counts would markedly decrease the values of the weighted indices on the unprotected sites until 1997 and increase them on the protected sites throughout the study period.

Discussion

Mean *C* and FQI

Swink and Wilhelm (1994) indicate that areas with a mean *C* greater than 4.5 or with a FQI greater than 35 have "at least marginal natural area quality" and sites with a mean *C* greater than 4.5 or higher and FQI of 45 or greater have "natural area potential." Our study site meets the criterion based on mean *C*, which ranged from 5.0 to 6.1, but the site falls short of meeting the criteria for "marginal or potential" natural area with FQI ranging from 29.3 to 36.0. However, our plots were species rich, compared to areas of comparable size on GLPSP, which includes a 622 ha dedicated State of Illinois Nature Preserve. The reason for the FQI indicating a lower quality site than the mean *C* is that our study plots are relatively small (16 m x 48 m, 16 ft x 158 ft) and FQI is strongly influenced by sample size, because the number of species increases as the sample area increases. As the number of species increases, the FQI can become larger (Francis et al. 2000; Rooney and Rogers 2002; Matthews 2003) even if mean *C* remains the same. Consequently, FQI, WFQI, and WCC have no upper limit, whereas, mean *C* and WMF have an upper limit of 10.

Neither mean *C* nor FQI demonstrated significant differences in floristic quality between protected and unprotected sites after a decade of study. While the species sampled and the number of species differed somewhat among sampling dates and plots, there were no detectible changes in species present on the site over time. Except for WCC none of the indices were significantly correlated with species richness. Consequently, neither mean *C* nor FQI were useful applications for detecting changes

on the site due to management. Applied to our data, changes in the value of these indices were largely

due to chance occurrence of less abundant species in some samples but not others. Nevertheless, even

though species composition of the site did not change over time, the relative abundance of forbs

changed in response to deer browsing.

Weighted mean fidelity

Several authors suggested weighting C values with measures of species' abundance because of

the insensitivity of mean C to species abundance (Taft 1997 et al.; Francis et al. 2000; Matthews 2003).

Weighted Mean Fidelity provides differential weighting to species in samples depending upon their

proportional abundances and can detect changes in community quality as a function of the changes in

relative abundance of species with varying C values, whereas mean C does not. However, the weightings

need to be proportional abundances. Otherwise changes in the index reflect those of total abundances

even if the mean C remains the same. For example, a site with two species, one with a C value of 2 and

the other with a C value of 3, and a sample of 50 and100 stems for the two species, respectively, would

have an index value of 400, if absolute values were used as in WCC. If total stem abundance doubled,

the value of the index would double. In contrast, if stem counts were placed on a relative scale the index

would be 2.7 for both samples. Using proportional values places a limit on the amount of weighting for

each sample at 1, so differences between samples result from variation in species relative abundances

and their C values. The index is comparable in approach to the Continuum Index of Curtis and McIntosh

(1951) where each species' adaptation value is weighted by its Importance Value and sum of the

Importance Values for all species in a stand is 300. Because MWF is not sensitive to total stem counts it

should not be affected by increasing sample sizes if species composition and proportional abundance

remain constant. However, this is not the case with WFQI or WCC. Both of these indices increase if stem

counts increase, even if the mean C remains constant. Additionally, WMF is not as sensitive to rare

species as FQI (Swink and Wilhelm 1994), which combines mean C and species richness into a single

index (mean $C*\sqrt{N}$), because WMF weights each species' C value by the proportional abundance of the species in the sample. Consequently, rare species have little influence on the index. This down weighting reduces the importance of low abundance species with C values that are markedly different than the mean C in community samples. This minimal effect of rare species means that the occasional occurrence of a species of low fidelity in a high quality remnant or a species of high fidelity in a degraded habitat has little influence on the WMF. However, if the primary concern of a study was occurrence of rare species with high coefficients of conservatism irrespective of their abundances, then WMF would be less useful for this purpose than some of the other indices, such as mean C.

The most useful application of WMF would involve long-term monitoring of sites to determine effects of environmental disturbances, such as browsing or grazing, input of atmospheric nitrogen, herbicide drift, shrub encroachment, response to management practices including fire or its absence, or restoration efforts. The greater sensitivity of WMF to detect small changes in abundance of species with varying C values than other indices is a positive feature of WMF. Nevertheless, WMF requires quantitative data about species, which is labor intensive, and like any method that assesses floristic quality, expert field identification is a necessity.

Effects on community quality

Our results demonstrate the way in which selective deer browsing influences species abundances, and community quality of forbs in tallgrass prairies. Under conditions of high deer density stem counts of preferred species, such as *Helianthus mollis, Veronicastrum virginicum,* and *Rudbeckia subtomentosa,* declined, whereas there were increases in counts of unpreferred species, such as *Solidago canadensis*, and species that tolerate browsing, such as *Silphium integrifolium* (Anderson et al. 2001). Species that increased in abundance under prolonged deer browsing pressure likely responded to reduced competition resulting from the decline in abundance of preferred species.

Deer browsing also shifted the community on our study site towards an increase in dominance

of forbs that have lower fidelity to remnant prairie communities than those that dominate the prairie under conditions of low or no browsing pressure. Community quality of prairie forbs decreased on the unprotected plot until deer density was reduced in 1997. In contrast, on the protected plot WMF initially declined, but then it tended to increase, suggesting a lag time for recovery from browsing.

Our previous work (Anderson et al. 2005) demonstrated that diversity (H') of prairie forbs decreases at high and low levels of deer browsing intensity and is maximized at intermediate browsing intensity, supporting the intermediate disturbance hypothesis of Connell (1978). However, based on the WMF any increase in deer browsing intensity decreases floristic quality by increasing the abundance of browse tolerant and unbrowsed species, which tend to have lower coefficients of conservatism, than browse sensitive species. This means that land managers concerned with maintaining tallgrass prairies of high diversity should consider balancing floristic quality with diversity. In small remnants and restorations, deer will likely seek out preferred browse species, which are likely to be species with high C values, and could extirpate these species from the site. On large prairies with moderate to low deer browsing pressure, browsing might be beneficial to prairie by maintaining species with lower floristic quality that nonetheless are part of the tallgrass prairie flora.

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Table 1 Comparison (mean ± SE) of various floristic quality measures for protected and unprotected plots. Differences between means for protected and unprotected plots were tested for statistical significance using t-tests.

	Protected	Unprotected	P>t[1]
Number of Species	39.14 ± 8.29	34.39 ± 1.06	0.35
Mean Coefficient of Conservatism	5.25 ± 0.09	5.60 ± 0.15	0.07
Floristic Quality Index	32.34 ± 0.60	32.74 ± 1.00	0.73
Weighted Coefficient of Conservatism	5746.28 ± 919.59	3849.71 ± 302.54	0.08
Weighted Floristic Quality Index	908.27 ± 136.76	655.33 ± 45.81	0.12
Weighted Mean Fidelity	6.09 ± 0.08	5.4 ± 0.12	P<0.001

[1] The alpha for acceptance of statistical significance with a Bonferroni correction is (0.05/6 = 0.0083).

Table 2. Pearson Correlation Matrix for Various Measures of Floristic Quality. Upper value of a pair is the correlation coefficient and the lower value is the probability level.

Quality Index	FQI	WCC	WTFQI	WMF	NOSPP
MEAN *C*	0.558	-0.362	-0.285	-0.237	-0.570
	0.037	0.202	0.322	0.413	0.033
FQI		0.212	0.220	0.121	0.315
		0.4653	0.449	0.678	0.271
WCC			**0.991**	0.644	**0.720**
			P<0.0001	0.012	**0.003**
WFQI				0.630	0.634
				0.015	0.014
WMF[1]					0.447
					0.084

Abbreviations for measures of floristic quality are MEAN *C* (Mean Coefficient of Conservatism), FQI (Floristic Quality Index), WCC (Weighted Coefficient of Conservatism), WFQI (Weighted Floristic Quality Index), WMF (Weighted Mean Fidelity), and (NOSPP) Number of Species. The alpha for acceptance of statistical significance with a Bonferroni correction is (0.05/15 = 0.003). Correlations in bold type are statistically significant.

Table 3. Changes in stem counts for three species that decreased in abundance in response to prolonged deer browsing and two species that increased under those conditions.

	Protected Plot				Unprotected Plot		
Year	1992	1997	2001		1992	1997	2001
Decreasers							
Comandra umbellata	125	100	310		110	30	67
Helianthus mollis	10	164	192		4	10	17
Veronicastrum virginicum	64	114	229		48	20	45
Increasers							
Silphium integrifolium	178	167	112		193	293	301
Solidago canadensis	13	45	24		16	101	123

Figure Caption

Figure 1. Changes in various quality indices during the study on protected and unprotected plots.