R E S E A R C H   A R T I C L E

●

White-tailed Deer (*Odocoileus virginianus* Zimmermann) Browsing Effects on Tallgrass Prairie Forbs: Diversity and Species Abundances

Roger C. Anderson[1,4]
Debra Nelson[2]
M. Rebecca Anderson[1]
Marcia A. Rickey[3]

[1]Behavior, Ecology, Evolution and Systematics Section
4120 Department of Biological Sciences
Illinois State University
Normal, Illinois 61790-4120

[2]Illinois Department of Natural Resources
8916 Wilmot Road
Spring Grove, Il 60081

[3]Archbold Biological Station
P.O. Box 2057
Lake Placid, Florida 33862

●

[4] Corresponding author:
rcander@ilstu.edut

ABSTRACT: We examined the effect of white-tailed deer (*Odocoileus virginianus* Zimmermann) browsing on diversity (Shannon Index) and abundance 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 deer km^{-2} between 1992 and 1997 and declined to 7-9 deer km^{-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. These changes initially enhanced diversity, but later, diversity declined as dominance of browse-sensitive species increased and evenness declined. On an unprotected plot, diversity declined from 1992 through 1997 as evenness decreased, resulting from declines in abundances of browse-sensitive species and increased abundances of unpreferred and browse-tolerant species. However, diversity increased on the unprotected plot after 1997 as deer density was reduced and abundances of preferred browse-sensitive species increased. We conclude that diversity of prairie forbs will be maximized at some intermediate level of deer browsing. Our results support the intermediate disturbance hypothesis, which posits that diversity is maximized at intermediate levels of disturbance.

Index terms: disturbance, diversity, evenness, forbs, intermediate disturbance hypothesis, *Odocoileus virginianus*, Shannon Index, tallgrass prairie, white-tailed deer

INTRODUCTION

North American grasslands evolved under conditions of grazing from large ungulates and are adapted to grazing (Stebbins 1981; Anderson, 1982, 1990; Axelrod 1985). Coevolution of large mammalian grazers and grasses is widely accepted and 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, are thought to be adaptive responses of prairie grasses to herbivores (Stebbins 1981; Anderson 1982, 1990). Bison (*Bos bison* L.) is a keystone species in tallgrass prairies and affects plant species composition and abundances, diversity, nutrient cycling, and primary production (Knapp et al. 1999). Bison preferentially graze dominant grasses (Steuter et al. 1995, Knapp et al. 1999) and by so doing favor growth of subordinate species, including C3 forbs (Fahnestock and Knapp 1993, Damhoureyeh and Hartnett 1997, Knapp et al. 1999). Because forbs contribute the greatest amount of species richness to the prairie (Howe 1994, Knapp et al. 1999), this differential grazing pattern increases plant species diversity (Collins et al. 1998, Knapp et al. 1999).

In contrast to bison, white-tailed deer (*Odocoileus virginianus* Zimmermann) preferentially browse prairie forbs, consuming as much as 18.9% of the standing crop of forb stems (Anderson et al. 2001). However, deer browse little if any on dominant C4 grasses. Deer selectively browse forbs, and this browsing pattern could influence species composition and diversity patterns among forbs (Anderson et al. 2001). The balance between browsing frequency and competitiveness could affect forb species relative abundances. Browse tolerant and unpreferred species could be favored under conditions of high browsing intensity, while under conditions of low browsing intensity, preferred species could be favored if they are superior competitors.

The intermediate disturbance hypothesis (Connell 1978) proposes that disturbances have the potential to either enhance or diminish diversity depending on disturbance frequency and intensity and that diversity is maximized at intermediate levels of disturbance. However, Collins et al. (1995) note that implicit in the intermediate disturbance hypothesis is that a trade-off exists between the ability of a species to compete and to tolerate disturbance. Under conditions of frequent disturbance, superior competitors decline because they are intolerant of disturbance. However, disturbance-tolerant species are reduced in occurrence with infrequent disturbance conditions, because they are unable to compete with the dominant species. Species richness is expected to be the highest at intermediate frequencies of disturbance when conditions are suitable for competitive species and those tolerant of disturbance. The results of studies that examined concordance between the intermediate disturbance hypothesis and

of disturbance frequency are inconsistent in their conclusions (Collins et al. 1995, Stallins 2002, Ikeda 2003, Potts 2003). Application of intermediate disturbance hypothesis to deer browsing effects on diversity of prairie forbs would posit that forb diversity would be reduced at high and low frequency of browsing; and at an intermediate browsing frequency, forb diversity would be maximized.

In this paper, we consider changes in forb species abundance and diversity resulting from varied intensities and length of time since exposure to deer browsing. We predict that deer browsing will: (1) cause a shift in species composition favoring unpreferred forb species over preferred species and (2) affect diversity of forbs so that an intermediate frequency of browsing will maximize diversity.

METHODS

Study Site

The study site is located in the Illinois Department of Natural Resources's 218 ha Heidecke Lake Fish and Wildlife Area (HLFWA) in northeastern Illinois, Grundy County, about 70 km southwest of Chicago. The HLFWA is adjacent to the west side of the 1027 ha Goose Lake Prairie State Park (GLPSP). The study site and sampling methods are the same as those of Anderson et al. (2001) and are summarized below. In May 1992, a 33-m x 48-m study area in the HDFWA was selected for study because of its high diversity of prairie forbs. The 100 species of forbs noted in this area provided us with the opportunity to determine the selective patterns of deer browsing when a large number of forb species were available. The dominant grass species on the site is northern prairie dropseed [*Sporobolus heterolepis* (Gray) Gray] (Anderson et al. 2001), a species associated with high quality remnant tallgrass prairies (Swink and Wilhelm 1994). The experimental area encompassed nearly all the remnant. The site was burned in the springs of 1992, 1997, and 2000 but not during the rest of the study. The study area was divided into two equal sized plots. Three parallel transect lines extending the full length of

each plot were established. Along each transect line, points were located at 1 m and then at 2 m intervals for a distance of 46 m from the transect beginning. At each of the 24 points per transect, the center of a 25-cm x 25-cm quadrat was located at a randomly determined distance to the left or right of the transect. Counts were made of browsed and unbrowsed forb stems by species in quadrats. Sampling occurred in late June (2000) or July in 1992, 1993, 1994, 1997, 1999, and 2001.

In December 1992, one-half of the study area was fenced to exclude deer but not small mammals. For the June 2000 sample, before the establishment of the exclosure, percent similarity (Gauch 1983) between protected and unprotected plots based on forb stem counts was 81.5%. This is 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). Beginning in the fall of 1997, the size of the deer herd was substantially reduced on HLFWA and adjacent GLPSP by controlled hunting. Deer counts on HLFWA and GLPSP are combined because deer move freely between the two areas. Winter deer densities based on counts from helicopters declined from 32-50 deer km^{-2} before hunting (1992-1996) to 7-9 km^{-2} in 1998 and 1999 following controlled hunting. Deer densities after 1997 were similar to estimates of pre-European settlement densities in most favorable habitats (3.1 to 7.7 deer km^{-2}) given by Horsley et al. (2003) and those for historic conditions in the Midwest (4 to 19 deer km^{-2}) (Dahlberg and Guettinger 1956, McCabe and McCabe 1984). Before 1997, the densities were somewhat lower than the estimates of deer densities (>60 deer km^{-2}) in areas with mixed forest and agricultural lands in the later part of the 20th Century (Horlsey et al. 2003). However, the pre-1997 estimates were higher than the 27 deer km^{-2} reported by Nixon et al. (1991) for areas in the farming belt of east central Illinois that were 36% forested and experienced moderate hunting pressure. Monitoring of our plots occurred prior to deer management under conditions of high deer densities and under reduced deer densities after initiation of a hunting program. The reduced deer density permitted us to assess

recovery from the excessive deer browsing on unprotected plots.

Data Analysis

Total stem count data obtained for forbs in protected and unprotected plots were analyzed using Detrended Correspondence Analysis (DCA) ordination (McCune and Mefford 1997) with forb counts for protected and unprotected plots each year constituting a sample, resulting in 14 samples for the seven years in which sampling occurred. This ordination method is an effective multivariate procedure to summarize directional changes in species composition and abundance among samples over time (Anderson et al. 2000, Gibson et al. 2000). For each sample, forb species richness was determined and diversity, using the Shannon diversity index (H') and evenness (J) were calculated. Differences in Shannon indices between protected and unprotected plots for each year were compared using t-tests (Magurran 1988). A Bonferroni correction was used to correct for multiple comparisons (alpha = 0.05/7 = 0.017). We tested for differences in mean species richness between protected and unprotected plots averaged across years using a t-test for samples with equal variances.

RESULTS

When sample scores for the first two axes resulting from the Detrended Correspondence Analysis were examined in two dimensions, protected and unprotected plots were close to one another in 1992 (Figure 1). Over time, samples from protected and unprotected plots separated along the first axis. Samples from the protected plot had increasingly smaller axis one scores as the length of time the plot was protected increased. Samples from the unprotected plot had progressively larger axis one scores until after initiation of deer control measures in 1997. These trends indicate that differences in forb species composition and/or abundance between the two plot types increased over time. After initiation of deer control measures, however, unprotected plot samples began to trend back towards the positions they
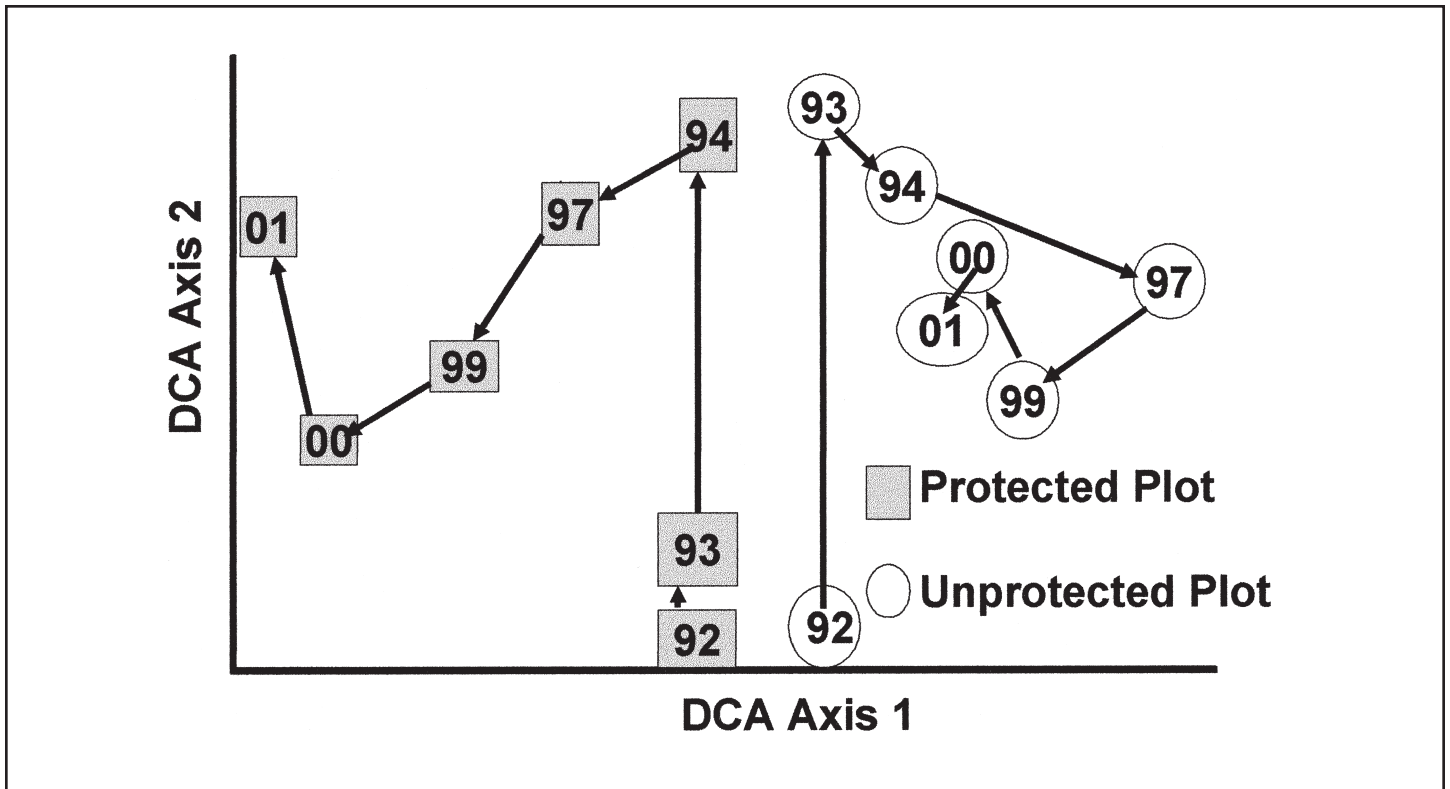
Figure 1. DCA ordination of protected and unprotected plots using samples of forb stem counts made in seven years. Numbers within the symbols indicate the year in which the sample was obtained. Axis 1 represents a gradient of decreasing time from protection from deer browsing.

occupied on axis 1 earlier in the study and towards the protected plot samples (Figure 1), suggesting recovery of the vegetation from deer browsing.

Thus, based on the position of the 14 samples on axis 1, the first axis of the DCA ordination axis expressed a gradient of decreasing time of protection from deer browsing. Samples with the lowest axis one scores resulted when the fenced plot had experienced the longest period of protection, and samples with highest axis one scores resulted after the unprotected plot experienced the longest period of exposure to intense deer browsing. The second and third axes of the ordination did not yield interpretable patterns, and apparently represent unexplained variation unrelated to browsing protection.

To examine individual species' responses to this gradient of increasing interval of time since first protected from deer browsing, stem counts (browsed plus unbrowsed) for species were plotted against DCA sample scores on the first axis of the ordination.

Pearson correlations were used to determine the significance and direction of species' responses to the gradient. Species with positive correlations had their highest stem counts in samples with high axis one scores and responded favorably to increasing periods of intensive deer browsing. In contrast, species with negative correlations had increasing stem counts in plots as a function of the length of time plots were protected from deer browsing. Nineteen species that had at least 10 stem counts greater than zero in the fourteen samples were examined in this analysis. Five of 19 species had significant positive correlations and eight had significant negative correlations with plot DCA axis one scores (Table 1, Figure 2).

Changes in the Shannon Index were more strongly related to variation in evenness (r^2 = 0.61, P<0.01) than to changes in species richness (r^2 = 0.20, P>0.05). Species richness was initially higher for the sample taken on the plot that eventually became protected than for the sample from the unprotected plot (39 vs. 34 species in 1992,

on protected and unprotected plots, respectively) (Table 2). This pattern of species richness was consistent for most years of the study, except for 1994 when more species were sampled on the unprotected plot than the protected plot. Averaged across sample years, there were significantly (P=0.040, t= 2.30, df = 12) fewer species sampled on the unprotected plot than the protected plot (mean $\pm$ SE, = 43.3 $\pm$ 2.4 and 36.9 $\pm$1.4, for samples from protected and unprotected plots, respectively).

In the first year of the study (1992), diversity as measured by the Shannon Index was not significantly different between unprotected plots and protected plots. However, in subsequent years, diversity was higher for samples taken from protected plots than samples from unprotected plots until 1999 and 2000, when there was no significant difference between protected and unprotected plots. In 2001, the unprotected plot had significantly greater diversity than the protected plot (Table 2).

Evenness tended to decline on the unpro-

Species	Pearson Correlation Coefficients
Monarda fistulosa	0.736
Heuchera richardsonii	0.706
Solidago canadensis	0.678
Silphium integrifolium	0.634
Amorpha canescens	0.572
Tradescantia ohiensis	-0.871
Veronicastrum virginicum	-0.847
Comandra umbellata	-0.826
Helianthus mollis	-0.768
Stachys palustris	-0.700
Aster azureus	-0.700
Rosa carolina	-0.654
Rudbeckia subtomentosa	-0.552

tected plot over time until 2001, whereas evenness increased on the protected plot between 1992 and 1994 and then declined (Table 2). The decline in evenness on the protected plot after 1994 was largely due to several species responding positively to the absence of deer browsing pressure and producing large increases in number of stems between 1997 and 2001. These species included *Comandra umbellata* (L.) Nutt. (110 to 310 stems) and *Veronicastrum virginicum* (L.) Farn. (114 to 229 stems). *Helianthus mollis* Lam. demonstrated a modest increase in stems in the protected plot between 1997 and 2000 (164 to 194 stems) but a more dramatic increase across the entire period of our study (1992 to 2001) in this plot (10 to 194 stems).

Silphium integrifolium Michx. and *Solidago canadensis* L. increased in the unprotected plot throughout the study period. *Silphium* stem counts increased from 193 to 301 between 1992 and 2001, and *Solidago* stems increased more than seven fold from 16 to 123 on the unprotected plot during the same time. The increased dominance of these two species contributed to the decline in evenness on the unprotected plot that continued until deer hunting began on GLPSP in 1997, and the deer density was reduced to less than 25% of that before 1997. The increase in diversity on the unprotected plot appeared to be due to moderate increases in stem counts for

several species between 1997 and 2002, including *Comandra* (30 to 67), *Veronicastrum* (20 to 40), *Eryngium yuccifolium* Michx. (1 to 14), and *Helianthus mollis* (10 to 17), which increased evenness on the unprotected site.

DISCUSSION

Our results demonstrate the way in which selective deer browsing influences species abundances and diversity 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* Pursh., 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 likely responded to the decline in abundance of preferred species. Similarly, Anderson and Briske (1995) reported that selective herbivory of a late-seral dominant grass (*Schizachyrium scoparium* (Michx.) Nash) was the primary mechanism contributing to its replacement by less competitive mid-seral species [*Bothricola saccharoides* (Sw.) Rydb. and *Stipa leucotricha (Nassella leucotricha* (Trin. & Rupr.) Pohl)] that increase with grazing intensity. Associated with the increased dominance of
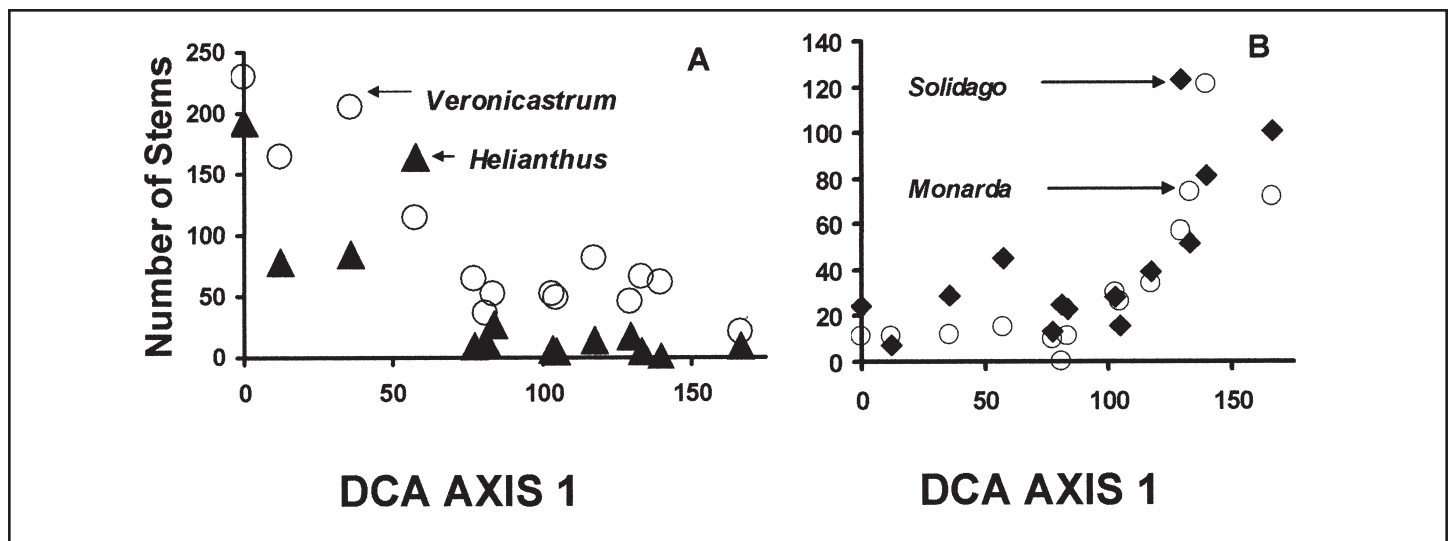

Figure 2. Stem counts plotted over sample plots ordered using Detrended Correspondence Analysis of forb stem count data. Panel A shows plots for two species with negative correlation between stem counts and Axis 1 scores and Panel B shows the same plot for two species with positive correlations.

Table 2. Diversity and species richness of the protected and unprotected plots during the period of study based on forb stem counts in quadrats. With a Bonferron correction significance was accepted at a corrected alpha of 0.017, ** = P<0.01, *** =P<0.001.

Date	Protected	Unprotected
1992		
Species Richness	39	34
Shannon Index (H')	2.56	2.71
Evenness (J)	0.698	0.768
1993		
Species Richness	48	37
Shannon Index (H')	2.98***	2.671
Evenness (J)	0.77	0.739
1994		
Species Richness	31	33
Shannon Index (H')	2.74***	2.47
Evenness (J)	0.797	0.706
1997		
Species Richness	48	37
Shannon Index (H')	2.88***	2.48
Evenness (J)	0.743	0.686
1999		
Species Richness	49	44
Shannon Index (H')	2.75	2.64
Evenness (J)	0.706	0.697
2000		
Species Richness	43	35
Shannon Index (H')	2.38	2.40
Evenness (J)	0.632	0.675
2001		
Species Richness	45	38
Shannon Index (H')	2.6	2.78**
Evenness (J)	0.683	0.758

higher than on the unprotected plot from 1993 through 1997, due in part to increased evenness on the protected plot and decreased evenness on the unprotected plot. In the first two years that data were collected following initiation of deer control measures, 1999 and 2000, there were no significant differences in diversity between protected and unprotected plots. However, in 2001 the unprotected plot had significantly higher diversity than the protected plot. Changes in diversity between 1997 and 2001 reflect two trends: (1) increased dominance of browse sensitive species on the protected plot that lowered evenness, and (2) recovery of browse sensitive species on the unprotected plot after 1997, when deer densities were reduced by the hunting program leading to increased diversity on the unprotected plot. Thus, diversity was negatively impacted by high levels of browsing and by extended complete protection. These results support the intermediate level disturbance hypothesis.

On our study site, deer browsing may interact with competitive relationships among species to affect diversity. Evenness, which ultimately declined over time in the protected plot, was strongly influenced by a dramatic increase in *Helianthus mollis.* This species, and several other members of the genus *Helianthus,* are known to be allelopathic (Curtis and Cottam 1950, Wilson and Rice 1968, Anderson et al. 1978). While *H. mollis* was heavily browsed outside the protection of the exclosure, it consistently increased in the protected plot contributing to the reduction in evenness. Release from deer browsing pressure and production of allelopathic chemical (s) that negatively affect competitors may have contributed to increased abundance of *H. mollis* over time in the protected plot.

Although the species sampled differed slightly among sampling dates and plots, there were no detectible changes in species present on the site over time. Differences were largely due to chance occurrence of some of the less abundant species in some samples but not others.

unpreferred and browse tolerant species on unprotected plots, there was a decline in diversity because of decreased evenness among the prairie forbs. Once deer density was reduced on the unprotected plot, diversity increased in a period of four years (1997 to 2001). This is a relatively short period of recovery following release from browsing pressure, which may take decades in forest communities (Anderson and Katz 1993). However, Townsend and Meyer (2002) reported rapid recovery of the forest shrub *Hamamelis virginiana* L. (witch hazel) when it was released from deer browsing.

Diversity was not significantly different between the protected and unprotected plots in 1992. However, diversity increased on the protected plot after 1992 and was

CONCLUSIONS

Because of the limitations of our sampling design with a protected and an unprotected plot at a single site, the results from our study require further testing, and the conclusions are limited to our study site. Nevertheless, from a management perspective, our long-term monitoring results suggest that some deer browsing may be beneficial to tallgrass prairie forb diversity. Disturbances, such as those made by deer, prairie dogs (*Cynomys ludovicianus* Ord) (Fahnestock and Delting 2002), pocket gophers (*Geomys bursarisus* Shaw) (Huntley and Inouye 1988, Stueter et al. 1995), and bison (Knapp et al. 1999), alter competitive interactions among prairie species in ways that can encourage diversity. Disturbances created by burrowing animals can enhance diversity by increasing abundance of fugitive prairie species, although non-indigenous annuals also colonize these disturbance sites (Platt 1975). Nevertheless, maintenance of the full complement of prairie forbs should be the goal of most prairie management. For large ungulates and burrowing animals to provide the historic perturbations that enhanced prairie diversity, our preserves must be large enough to permit these processes to occur, and care must be given to maintain herbivore populations at levels that will sustain prairie diversity.

ACKNOWLEDGMENTS

Roger C. Anderson is Distinguished Professor of Plant Ecology at Illinois State University. His research focuses on restoration and community ecology, including effects of deer herbivory on vegetation, historic vegetation, the ecology of invasive plants, and fire effects on vegetation. He has served as a member of the Illinois Nature Preserves Commission and is a member of the Editorial Board for Restoration Ecology.

M. Rebecca Anderson is currently working in the area of conservation biology, and holds a M.S. degree in Botany from the University of Wisconsin-Madison. She is a doctoral candidate in the Department of Biological Sciences studying the conservation genetics of American ginseng. Membership on the land trust ParkLands Foundation Board of Directors involves her in local conservation and restoration of natural communities.

Debra Nelson is a District Natural Heritage Biologist for the Illinois Department of Resources. Her work involves natural areas management and endangered species monitoring and protection in Northeast Illinois. Current special projects include wetland restoration at Volo Bog State Natural Area and restoration of habitat for Eastern Prairie Fringed Orchid and Karner Blue Butterfly at Illinois Beach State Park. She is also working with state and local highway commissioners to contain the roadside spread of leafy spurge.

Marcia Rickey is a Research Assistant at Archbold Biological Station, Plant Ecology Lab. Her research focuses on community sampling, data management, and statistical analyses of community data, including data on the effects of fire and mechanical surrogates on Florida scrub and sandhill.

LITERATURE CITED

Anderson, R.C. 1982. An evolutionary model summarizing the roles of fire, climate and grazing animals in the origin and maintenance of grasslands: an end paper. Pp. 297-308 *in* J. Estes, R. Tyrl, and J. Brunken, eds., Grasses and Grasslands: Systematics and Ecology. University of Oklahoma Press, Norman.

Anderson, R.C. 1990. The historic role of fire in North American grassland. Pp. 8-18 *in* S.L. Collins and L.L. Wallace, eds., Fire in North American Tallgrass Prairies. University of Oklahoma Press, Norman.

Anderson, R.C., A.J. Katz, and M.R. Anderson. 1978. Allelopathy as a factor in the success of *Helianthus mollis* Lam. Journal of Chemical Ecology 4:9-15.

Anderson, R.C., and A.J. Katz. 1993. Recovery of browse-sensitive tree species following release from white-tailed deer *Odocoileus virginianus* Zimmerman browsing pressure. Biological Conservation 63:203-208.

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. The Journal of the Torrey Botanical Society 128:381-392.

Anderson, R.C., J.E. Schwegman, and M.R. Anderson. 2000. Micro-scale restoration: a 25-year history of a southern Illinois barren. Restoration Ecology 8:296-306.

Anderson, V.J., and D.D. Briske. 1995. Herbivore-induced species replacement in grasslands: is it driven by herbivory tolerance or avoidance? Ecological Applications 5:1014-1024.

Axelrod, D.I. 1985. Rise of the grassland biome, central North America. Botanical Review 51:163-202.

Beals, E. 1960. Forest bird communities in the Apostle Islands of Wisconsin. Wilson Bulletin 72:156-181.

Bray, J.R., and J.T. Curtis. 1957. An ordination of the upland forest communities of southern Wisconsin. Ecological Monographs 27:325-349.

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.

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.

Connell, J.H. 1978. Diversity in tropical rainforests and coral reefs. Science 199:1302-1310.

Curtis, J.T., and G. Cottam. 1950. Antibiotic and autotoxic effects in prairie sunflower. Bulletin of the Torrey Botanical Club 77:187-191.

Dahlberg, B., and R. Guettinger. 1956. The white-tailed deer in Wisconsin. Technical Wildlife Bulletin Number 14. Game Management Division, Wisconsin Conservation Department, Madison.

Damhoureyeh, S.A., and D.C. Hartnett. 1997. Effects of bison and cattle on growth, reproduction, and abundances of five tallgrass prairie forbs. American Journal of Botany 84:1719-1728.

Fahnestock, J.T., and J.K. Delting. 2002. Bison-prairie dog-plant interactions in a North American mixed-grass prairie. Oecologia 132:86-95.

Fahnestock, J.T., and A.K. Knapp. 1993. Water relations and growth of tallgrass prairie forbs in response to selective herbivory by bison. International Journal of Plant Science 154:432-440.

Gauch, H.G. 1983. Multivariate Analysis in Community Ecology. Cambridge University Press, New York.

Gibson, D.J., E.D. Adams, J.S. Ely, D.J. Gustafson, D. McEwen, and T.R. Evans. 2000. Eighteen years of herbaceous layer recovery of a recreation area in a mesic forest. The Journal of the Torrey Botanical Society 127:230-239.

Horsley, B., S.L. Stout, and D.S. deCalesta. 2003. White-tailed deer impact on the vegetation dynamics of a northern hardwood forest. Ecological Applications 13:98-118.

Howe, H.E. 1994. Managing species diversity in tallgrass prairie: assumptions and implications. Conservation Biology 8:691-704.

Huntley, N., and R. Inouye. 1988. Pocket gophers in ecosystems: patterns and mechanisms. Bioscience 38:786-793.

Ikeda, H. 2003. Testing the intermediate disturbance hypothesis on species diversity in herbaceous plant communities among a human trampling gradient using a 4-year experiment in an old field. Ecological Research 18:185-197.

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.

Magurran, A.E. 1988. Ecological Diversity and its Measurement. Princeton University Press, Princeton, N.J.

McCabe, R., and T. McCabe. 1984. Of slings and arrows: an historical retrospection, Pp. 19-72. i*n* L. Hall, ed., White-tailed deer: Ecology and Management. Stackpole Books, Harrisburg, Pa.

McCune, B., and M.J. Mefford. 1997. PC-ORD. Multi-variate Analysis of Ecological Data, Version 3.0. MjM Software Design, Gleneden Beach, Ore.

Nixon, C.M., L.P. Hansen, P.A. Brewer, and J.E. Chelsvig. 1991. Ecology of white-tailed deer in an intensively farmed region of Illinois. Supplement to The Journal of Wildlife Management 56: Wildlife Monographs 18:1-77.

Platt, W.J. 1975. The colonization and formation of equilibrium associations on badger disturbance in a tall grass prairie. Ecological Monographs 45:285-305.

Potts, M.W. 2003. Drought in a Bornean everwet rain forest. Journal of Ecology 91:467-474.

Stallins, J.A. 2002. Dune species diversity and function in two barrier island biogeomorphic systems. Plant Ecology 165:183-196.

Stebbins, G.L. 1981. Coevolution of grasses and herbivores. Annals of the Missouri Botanical Garden 68:75-86.

Steuter, A.A., E.M Steinaur, G.L. Hill, and L.L. Tieszen. 1995. Distribution and diet of bison and pocket gophers in a sandhill prairie. Ecological Applications 5:756-766.

Swink, F, and G. Wilhelm. 1994. Plants of the Chicago Region. Indiana Academy of Science.

Townsend, D.S., and A.D. Meyer. 2002. Rapid recovery of witch hazel (*Hamamelis virginiana* L.) by sprouting, following release from white-tailed deer (*Odocoileus virginianus* Zimm.) browsing. Natural Areas Journal 22:290-295.

Wilson, R., and E.L. Rice. 1968. Alleolopathy expressed by *Helianthus annuus* and its role in old-field succession. Bulletin of the Torrey Botanical Club 95:432-448.