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WHITE-TAILED DEER BROWSING ON SIX SHRUB SPECIES OF TALLGRASS PRAIRIE

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ABSTRACT—White-tailed deer (*Odocoileus virginianus*) populations have in the past, and continue today, to increase in the Great Plains and North America. However, their impact on native plant species and endangered ecosystems such as the tallgrass prairie is poorly documented. To better understand the consequences of increasing deer numbers for native shrubs in grasslands, we assessed the extent of their summer browsing activity on six shrub species (wild plum, rough-leaved dogwood, smooth sumac, fragrant sumac, and coralberry) along transects that spanned riparian margins to upland tallgrass prairie. The proportion of terminal shoots browsed was quantified along established white-tail deer trails and in parallel transects off trails in watersheds that varied in fire history at the Konza Prairie Biological Station (Kansas). Proximity to deer trails was a strong determinant of deer browsing activity. Along trails, 20% of the twigs surveyed (N = 60,032) were browsed, whereas off trails less than 1% of twigs (N = 14,785) were browsed. Coralberry and

rough-leaved dogwood comprised 80% of the shrub cover along trails, whereas wild plum, prickly ash, smooth sumac, and fragrant sumac had less cover, in that order. However, browsing was greatest on wild plum and rough-leaved dogwood (between 40% and 50% of available twigs), and the proportion of twigs browsed out of the total twigs used was highest for rough-leaved dogwood. Based on preference ratios (use/ abundance), white-tail deer are likely to have the greatest impact on the less common wild plum and smooth sumac as well as rough-leaved dogwood. Interestingly, white-tail deer avoided the most common shrub, coralberry, at this time of year. Our results suggest that even in summer, when deer tend also to forage on herbaceous species in grasslands, deer browsing may have significant local impacts on woody species of tallgrass prairies in the Great Plains. Concurrent increases in woody plant cover and abundance in grasslands throughout the Great Plains suggest that deer browsing is not yet intense enough to prevent shrub expansion into tallgrass prairie.

KEY WORDS: browsing, Kansas, Konza Prairie, shrubs, tallgrass prairie, white-tailed deer

Introduction

Frequent fire, climatic extremes, and the activities of large mammalian herbivores all played key roles in the origin and maintenance of the tallgrass prairies of the Great Plains (Axelrod 1985; Knapp et al. 1998). Historically, bison (*Bos bison*) were the dominant and most numerous large mammalian grazer in Great Plains grasslands, and their near extinction has been well documented (Berger and Cunningham 1994; see also Louda, editor *Great Plains Research* 11:1 [Spring 2001]). Today, in grasslands where bison have been reintroduced, research has confirmed their keystone role in the prairie (Knapp et al. 1999).

Less is known about the historical numbers and effects of another large herbivore, the white-tailed deer (*Odocoileus virginianus*). This ungulate also was nearly extirpated from many tallgrass prairie regions, such as Kansas, by the early 1900s (Bee et al. 1981; Finck et al. 1986). Today, whitetailed deer are common throughout the Great Plains, and their numbers have increased to the point that there are concerns about an overabundance of this herbivore here and in other regions of the United States (Healy et al. 1997).

Unlike bison, which feed predominantly on grasses and spend most of their time in grass-dominated habitats (Hartnett et al. 1997; Knapp et al. 1999), white-tailed deer are browsers on a large number of woody species (Gee et al. 1991; Kie and Bowyer 1999). Thus, foraging by these herbivores could have an impact on a wide variety of habitats. Although numerous studies have documented white-tailed deer foraging behavior, diet, and habitat use (e.g., Radwan and Crouch 1974; Anderson and Loucks 1979; Arnold and Drawe 1979; Alverson et al. 1988; Strole 1988; Hobbs 1996), relatively few generalizations can be made across habitats (Russell et al. 2001). Indeed, much of our knowledge of this species is based on studies conducted in forested areas. Information on foraging by deer resident in tallgrass prairies is rare (Gee et al. 1991; Russell et al. 2001), despite the common observation that white-tailed deer occur in upland grassland habitats (Finck et al. 1986).

At the Konza Prairie Biological Station, a 3487 ha tallgrass prairie site in northeastern Kansas, nocturnal spotlight censuses suggested that as many as 400 white-tailed deer may be present in midsummer (van der Hoek unpublished data 1998). This is about twice the number of bison at the site (Knapp et al. 1999). Although these deer are observed throughout the Konza Prairie, they establish conspicuous trails through the broad ravines that lead from the lowland gallery forests to the upland grasslands. These trails are typically lined with shrubs that contributed to the dramatic increase in woody species observed in recent decades in grasslands (Abrams 1986; Steinauer and Bragg 1987; Briggs and Gibson 1992, Briggs et al. in press). The concurrent increase in the abundance of woody species and white-tailed deer has likely led to increased interactions among shrubs and this herbivore, potentially altering plant community composition and affecting ecosystem processes. Since deer are selective in their diet (Berteaux et al. 1998), white-tailed deer could affect the rate of spread of various shrub species by selecting or avoiding particular shrub species.

The objectives of our research were to (1) quantify the extent of whitetail deer browsing on six common shrub species of tallgrass prairie; (2) compare the intensity of browsing along deer trails, where presumably white-tail deer are most common, to that nearby but away from the trails; and (3) assess the extent of browsing in watersheds managed with different fire regimes. White-tail deer vary their feeding habits seasonally, and they have been reported to select forbs more frequently than woody species in the summer in grasslands (Gee et al. 1991; Ortega et al. 1997). However, the potential negative effects of their browsing on woody plants is likely the greatest in late spring and summer. At this time, carbon reserves in shrubs have been committed to the production of leaves, and overall potential carbon gain in shrubs is greatest during this period (Knapp 1986). Thus, we focused on summer in our analysis of potential deer impacts on shrubs. We predicted that white-tailed deer prefer some shrub species over others; that white-tail deer trails would serve as high-impact feeding sites; and that in watersheds that were burned frequently, where shrub cover is lowest, the impact of white-tail deer browsing would also be lowest.

Methods

Research was conducted at the Konza Prairie Biological Station, an unplowed, native tallgrass prairie located in the Flint Hills of northeastern Kansas (39°05'N, 96°35'W). Greater than 90% of the site is comprised of tallgrass prairie with gallery forests confined to areas along streams. Less than 100 ha of Konza Prairie Biological Station is under cultivation for crop production. The prairie is dominated by warm-season perennial grasses, primarily Andropogon gerardii (big bluestem), Sorghastrum nutans (Indian grass), and Schizachyrum scoparius (little bluestem). Shrubby habitats, dominated by Symphoricarpos orbiculatus (coralberry) and Cornus drummondii (rough-leaved dogwood), occur along limestone outcrops. Shrubs are more common in unburned than frequently burned prairie. The two largest streams on the site support mature gallery forests dominated by Quercus macrocarpa (bur oak), Quercus muehlenbergii (chinkapin oak), Celtis occidentalis (hackberry), and Ulmus americana (American elm).

As part of the National Science Foundation's Long-Term Ecological Research Program, Konza Prairie is divided into a series of replicated experimental watersheds (average size = 60 ha) that have burned at different frequencies since 1971. Overlaid on this fire regime since 1987 are watersheds that are ungrazed or grazed year-round by bison (Knapp et al. 1998). Six watersheds with well-established deer trails were selected for our study. These watersheds with deer trails included two that have been burned annually for more than 10 years, two burned at four-year intervals, and two watersheds protected from fire (unburned). Although half of these watersheds had bison, evidence of bison grazing activity was minimal along the white-tail deer trails (personal observation). Bison prefer flat upland grassdominated habitats (Nellis and Briggs 1997). Thus, watersheds were assessed only with respect to fire frequency. These watersheds were located several km from the nearest agriculture sites, and all were adjacent to the well-developed gallery forest (Abrams 1986) that follows Kings Creek, a major drainage stream on Konza Prairie; (Knapp et al. 1998).

Data on shrub abundance, cover, and white-tail deer browsing were collected in midsummer (July 1998), following a three-month period of

foraging by white-tail deer after leaf flush in the spring. The trail that appeared most heavily utilized by white-tailed deer was selected from among the two or three available in each watershed. In each watershed, we established two transects: one along the white-tailed deer trail and one parallel to it at a minimum of 7 m away from the trail. We distributed a total of 48 circular quadrats (10 m²) along these transects using a stratified random sampling procedure stratified by topography. Thus, along each transect, 16 sampling plots, 8 on the white-tail deer trail and 8 off the trail, were established in the lower, middle, and upper third of each trail. We established plot centers by randomly selecting an initial distance from the beginning of a transect and then using the nearest shrub as the center of the first plot. Subsequent plots were equally spaced along the transects. Distance between plots depended on the size of the watershed and the density of shrub species along the transect (typically 15 m between plots in large watersheds; 7 m in small ones). Plots on the parallel off-trail transect were established perpendicular to the on-trail plots, also using shrubs to center the plots. Within each circular plot we recorded the number of stems (abundance) and canopy cover of the six most common shrub species. Species assessed were coralberry, rough-leaved dogwood, wild plum (Prunus americana), smooth sumac (Rhus glabra), fragrant sumac (Rhus aromatica), and prickly ash (Zanthoxylum americanum). Shrub canopy cover was estimated as the proportion of the plot covered by each species.

Within each plot, we counted the number of twigs available for browsing and the number browsed by white-tail deer on one individual of each of the six shrub species (if present) located nearest the center of the plot. Twigs available for browsing were defined as terminal growth from the present season 1 cm in length. Nearly all browsing by deer occurred within the zone of the upper 25% of the shrub canopy (maximum height of 1.75 m; personal observation). Each twig was scored as either browsed or unbrowsed.

Several species-specific measures were calculated to evaluate the availability and selection among shrub species by white-tail deer (Wetzel et al. 1975; Strole and Anderson 1992). The first measure was the relative abundance of each species, defined as the ratio of the number of twigs of each shrub species per plot divided by the total number of available twigs of all species in the plot (x 100). The second measure was the species-specific proportion of available twigs browsed, defined as the ratio of the number of twigs of a shrub species browsed per plot divided by the total number of twigs of that species in the plot (x 100). The third measure was relative use of a species, defined as the ratio of the number of twigs of that shrub species browsed per plot divided by the total number of all twigs browsed per plot (x 100). Finally, a preference ratio was calculated as the ratio of relative use to relative abundance.

Effects of species, fire regime, watershed, topographic position, trail proximity, and their interactions on the percentage of cover and relative abundance of the shrub species were statistically analyzed using general linear models (SAS Institute, Inc. 1997). Replicate watersheds were nested within the three burning treatments (1, 2, and 20 yrs between fires). Relative topographic position was incorporated in our sampling to reduce bias related to quadrat locations but, because this factor was continuous and absolute topographic position varied among watersheds, we analyzed data from entire transects without respect to relative topographic location. Proportional values were arcsine transformed prior to analysis. Variables that quantified white-tail deer browsing were analyzed using nonparametric tests (Kruskal-Wallis analysis; SAS Institute, Inc. 1997) to alleviate statistical complications associated with nonindependence of twigs browsed on individual shrubs.

Results

Shrub cover and the browse pattern of white-tailed deer were not consistently related to either fire frequency or watershed (Tables 1 and 2). However, plant species and the existence of trails had strong effects on shrub cover and browse pattern. Thus, in addition to assessing total shrub cover, shrub abundance, and browsing activity, we also analyzed each species separately to compare on- and off-trail values of deer browsing.

Shrub cover was almost four-fold higher along trails than off, and four of the six plant species were more common along deer trails (Fig. 1). Coralberry and rough-leaved dogwood were the two most common species along trails, comprising over 80% of the shrub cover, whereas only coralberry was encountered frequently in the plots off the trails (Fig. 1). For Konza Prairie Biological Station as a whole, large-scale surveys of shrub cover show that smooth sumac has the greatest cover, with rough-leaved dogwood and coralberry the next most abundant species (Briggs unpublished data). This latter ranking reflects the widespread distribution of smooth sumac from lowland to upland topographic positions at Konza Prairie Biological Station.

The comparison of shrub cover on and off trails (Fig. 1) suggests that white-tailed deer create trails in tallgrass prairie where shrub cover is high. Of the six most common shrub species located along these trails, a clear

TABLE 1

AND ABUNDANCE OF TWIGS							
Shrub cover							
Treatment and interactions	df	F	Р				
Burn	2	0.92	0.40				
Watershed	3	1.98	0.14				
Trail	1	206.0	< 0.0001				
Species	5	161.8	< 0.0001				
Burn, Trail	2	1.77	0.17				
Burn, Species	10	3.28	0.003				
Trail, Species	5	37.07	< 0.0001				
Trail, Watershed	3	1.86	0.14				
Species, Watershed	15	2.86	0.002				
Burn, Species, Trail	10	1.36	0.19				
Burn, Trail, Species, Watershed	15	2.71	0.004				

TREATMENT EFFECTS ON SHRUB COVER AND ABUNDANCE OF TWIGS

Relative abundance of twigs

Treatment and interactions	df	F	Р	
Burn	2	1.78	0.17	
Watershed	3	3.95	0.008	
Trail	1	31.30	< 0.0001	
Species	5	212.64	< 0.0001	
Burn, Trail	2	1.81	0.16	
Burn, Species	10	2.79	0.002	
Trail, Species	5	14.60	< 0.0001	
Trail, Watershed	3	3.36	0.02	
Species, Watershed	15	2.10	0.008	
Burn, Species, Trail	10	2.91	0.0013	
Burn, Trail, Species, Watershed	15	1.16	0.30	

Note: Burn = three fire regimes (at 1, 4, 20 yr fire intervals). Watershed = two replicate watersheds within each fire regime.

Trail = plots sampled on vs. off white-tailed deer trails in riparian fringe.

Species = six shrub species samples.

df = degree of freedom

 $\tilde{F} = F$ -test

P = Probability

Only species and trail effects were consistently significant at p < 0.05; thus, each species also was analyzed separately to contrast trail effects (see Fig. 1).

TABLE 2

NONPARAMETRIC ANALYSIS OF THE PROPORTION OF AVAILABLE TWIGS BROWSED AND THE RELATIVE USE OF TWIGS BY WHITE-TAILED DEER

Proportion of available twigs browsed						
Effect	<i>df</i>	Chi-square	P			
Burn	2	0.3	0.32			
Watershed	5	1.6	0.90			
Trail	1	< 0.0001				
Species	5	58.6	< 0.0001			
	Relative use	;				
Effect	df	Chi-square	Р			
Burn	2	0.6	0.73			
Watershed	5	1.8	0.88			
Trail	1	3.6	0.06			
Species	5	48.1	< 0.0001			

Note: Nonparametric analysis conducted using the Kruskal-Wallis test.

Figure 1 (opposite page). Cover (**A**) and the relative abundance (**B**) of twigs available for browsing for the six common shrub species found in tallgrass prairie at the Konza Prairie Biological Station, northeastern Kansas. Data were combined from transects that spanned lowland to upland topographic positions in six watersheds. Two transects were established in each watershed, one along a well-defined white-tailed deer trail (on trail) and one at least 7 m away and parallel to the trail (off trail). Also shown is the total cover for all six species combined (top inset). Species abbreviations are: Syor = Symphoricarpos orbiculatus (coralberry); Codr = Cornus drummondii (rough-leaved dogwood); Pram = Prunus americana (wild plum); Zaam = Zanthoxylum americanum (prickly ash); Rhar = Rhus aromatica (fragrant sumac); Rhgl = Rhus glabra (smooth sumac). Error bars indicate 1 SE of the mean. Asterisks denote significant statistically differences in cover or relative abundance between on and off trail transects (P<0.05).

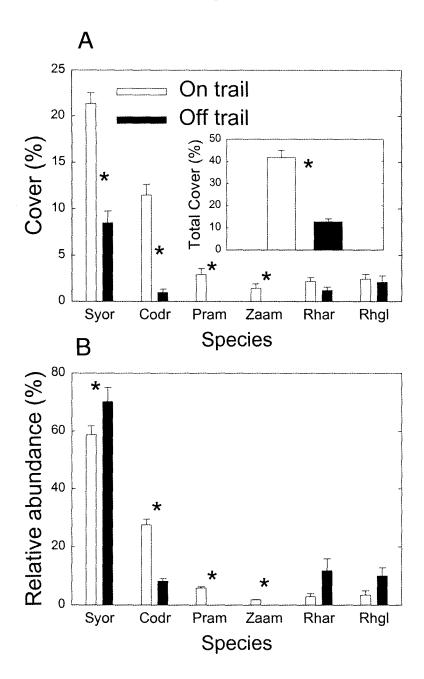


Figure 1.

hierarchy of cover occurred. Coralberry and rough-leaved dogwood were the most abundant, while the other four shrub species each contributed <5%to the total cover. Interestingly, the proportion of available twigs browsed along these trails (Fig. 2) was not related to absolute shrub cover or to the relative abundance of the twigs available (Fig. 1). The proportion of available twigs browsed was greatest for wild plum and rough-leaved dogwood (between 40% and 50%). However, the relative use was clearly highest for rough-leaved dogwood (Fig. 2 and Table 3), reflecting its high abundance (Fig. 1).

The preference ratios suggest that the three shrub species most likely impacted by white-tailed deer browsing were wild plum, smooth sumac, and rough-leaved dogwood. All three of these shrubs had a preference ratio between 2 and 4, showing that the number of twigs browsed was severalfold greater than expected based on the relative abundance of twigs (Fig. 2). Both rough-leaved dogwood and wild plum had over 40% of their twigs browsed. Cover and proportion of available twigs of smooth sumac browsed by deer were lowest of these three shrubs, and this species was distributed equally on and off trails (Fig. 1). In contrast, coralberry, which was very common on and off trails, appeared to be avoided by deer at this time of year; its preference ratio was <0.1 (Fig. 2 and Table 3).

Discussion

The lack of a detectable effect of fire frequency on shrub cover along the white-tail deer trails was surprising, given the well-documented relationship between high fire frequency and reductions in woody plant abundance in tallgrass prairie (Briggs and Gibson 1992). However, our sampling was restricted to protected ravines where white-tail deer trails were most common. Even in ravines in frequently burned watersheds, shrub cover can be substantial (Briggs et al. in press).

Figure 2 (opposite page). A: Proportion of available twigs browsed (black) and the relative use of twigs (white) for six common shrub species found along ravines in tallgrass prairie at the Konza Prairie Biological Station, northeastern Kansas. Data were combined from transects along white-tailed deer trails that spanned lowland to upland topographic positions in six watersheds. **B**: The preference ratio (relative use/ relative availability) for the six shrub species. Species abbreviations (as in Fig. 1) are: Syor = coralberry, Codr = rough-leaved dogwood, Pram = wild plum, Zaam = prickly ash, Rhar = fragrant sumac, and Rhgl = smooth sumac. Error bars indicate 1 SE of the mean.

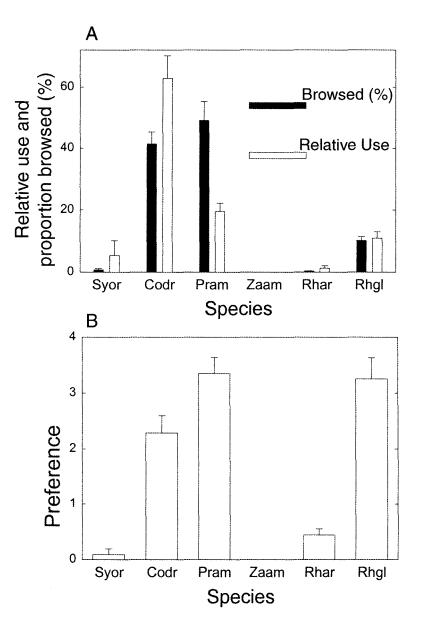


Figure 2.

Previous studies found that the diet of white-tailed deer in grasslands varies significantly across seasons, with browsing of woody plants at a minimum in summer (Gee et al. 1991). In fact, on our transects away from the white-tailed deer trails, we found little evidence that white-tail deer were feeding on any of the six shrub species during the early summer (only 14 out of 14,785 twigs examined were browsed). Moreover, the proportion of available twigs browsed off trails was at most 1.4% for any species and averaged <0.2% for all species combined (Table 2). However, browsing on shrubs along deer trails was substantial, even in the early summer; almost 20% of all twigs were browsed (11,724 of 60,032) and some species experienced 40% - 50% of their twigs browsed. Such browsing in late springearly summer could reduce shrub productivity. The resources needed for growth are available primarily at this time of year (Knapp et al. 1998), and browsing leads to loss of young, rapidly photosynthesizing leaves. Thus, localized effects of deer browsing could be significant at this time of year.

Although coralberry was the most common shrub along trails, this shrub showed little evidence of being browsed (Fig. 2). Also, the rare species fragrant sumac and prickly ash were minimally used as browse (Table 3). Instead, one of the less abundant species, wild plum, was the shrub most likely affected by white-tailed deer browsing. The proportion of available twigs browsed in wild plum approached 50% (Fig. 2 and Table 3), and the relative use of this species by white-tail deer was more than three times its relative abundance. In addition, both the abundant rough-leaved dogwood and the less common smooth sumac were also browsed more frequently than expected given their availability (Fig. 2). These results are consistent with those from elsewhere. For example, both wild plum and rough-leaved dogwood species were preferred browse plants in central Illinois forests (Strole and Anderson 1992).

Our results suggest that white-tail deer browsing of woody species in grasslands could be important even in the summer. However, these effects were localized, in this case along established white-tail deer trails. As noted in other studies, shrub species use by white-tail deer do not reflect just the abundance of the forage species available (Strole and Anderson 1992). By showing preferences among the shrubs available, white-tail deer browsing in early summer may have its greatest impact on some of the less common shrubs. Species that are avoided in summer, however, may become more preferred species at other times of year (Gee et al. 1991), and selection of fruits by white-tail deer in the fall or winter also may have a significant effect on shrub population dynamics.

TABLE 3

AERIAL COVER, RELATIVE ABUNDANCE OF TWIGS, AND THE PROPORTION OF TWIGS BROWSED FOR THE SIX SHRUB SPECIES IN TALLGRASS PRAIRIE AT KONZA PRAIRIE IN NORTHEASTERN KANSAS

Species	Cover		Abundance			Proportion browsed			
	On	Off	Р	On	Off	Р	On	Off	Р
Buckbrush	21.3 (1.2)	8.5 (1.3)	<0.001	58.7 (2.7)	70.1 (4.5)	0.007	0.8 (0.4)	0.09 (0.1)	0.003
Dogwood	11.5 (1.2)	1.0 (0.4)	< 0.001	27.5 (2.6)	8.2 (2.70)	0.03	41.5 (3.9)	0	< 0.001
Plum	2.9 (0.7)	0.0 (0.0)	< 0.001	5.8 (1.4)	0.0 (0.0)	0.008	49.2 (6.2)	-	
Prickly ash	1.4 (0.5)	0.0 (0.0)	0.005	1.8 (0.7)	0.0 (0.0)	0.27	0.0 (0.0)	-	
Aromatic sumac	2.2 (0.4)	1.2 (0.4)	0.08	2.8 (0.7)	11.8 (2.98)	0.02	0.3 (0.1)	0	< 0.001
Smooth sumac	2.4 (0.6)	2.1 (0.7)	0.72	3.4 (0.9)	9.9 (2.8)	0.09	10.2 (1.2)	1.39 (0.9)	< 0.001

Note: Mean values (with standard error given in parentheses) are for shrubs located either on or off (adjacent to) established white-tailed deer trails.

Clearly, herbivores such as white-tail deer can influence the success of woody plants in a species-specific fashion (Huntly 1991; Russell et al. 2001). Thus, as white-tail deer and woody plant populations increase in tallgrass prairie, this plant-herbivore interaction will become increasingly important in influencing plant community composition in the Great Plains.

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