Deer Impact on Vegetation in Natural Areas in Southeastern Nebraska

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ABSTRACT: We studied the effect of browsing by white-tailed deer (*Odocoileus virginianus* Zimmerman) on vegetation at three sites with high densities of deer and six sites with low densities of deer along the Missouri and Platte Rivers in southeastern Nebraska in 1995-1996. Vegetation volume from 0-1 m high was similar between sites with high and low deer densities (P > 0.05). From 1-2 m high, vegetation volume was less at sites with more deer in both years (P < 0.05). Densities for eight of 11 small woody plant categories (< 3 cm dbh) were less common at sites with high densities of deer (P < 0.05). Overall densities of small trees (3-15 cm dbh) were similar between sites with high and low densities of deer. However, small hackberry trees (*Celtis occidentalis* L.) were more common (P = 0.03), while all other small trees were less common (P = 0.038), at sites with more deer. Frequencies of ground cover plants were not randomly distributed (χ² = 588.2, P < 0.001, df = 12). Shrubs were less common and grasses more common than expected at sites with more deer. Forests at sites with high densities of deer are in the process of succeeding to a state dominated by hackberry in the overstory with reduced woody vegetation and increased grasses in the understory due to intensive browsing by deer.

Index terms: browse, *Odocoileus virginianus*, understory, vegetation, white-tailed deer

INTRODUCTION

Abundant populations of deer in North America have received increasing attention in recent decades (McShea et al. 1997; Warren 1997; Côté et al. 2004). Effects of overabundant deer populations have included altered plant communities (Augustine and Frelich 1998; Russell et al. 2001; Horsley et al. 2003), deer-automobile collisions (Bashore et al. 1985; Hubbard et al. 2000; Etter et al. 2002), and disease transmission (Nettles 1997; Krumm et al. 2005). The ecological effects of browsing and grazing by deer have also been investigated in Europe (Pollard and Cooke 1994; Putman and Moore 1998), South America (Relva and Veblen 1998), and New Zealand (Wardle et al. 2001).

Densities of white-tailed deer (*Odocoileus virginianus* Zimmerman) in eastern North America previous to European settlement were estimated at 2-4 deer/km² (McCabe and McCabe 1984; Alverson et al. 1988). Post-settlement densities of deer were estimated at 1-6 deer/km² in the Midwest agricultural region (Gladefelter 1984). The effects of overabundant deer populations were seen at deer densities approaching 20 deer/km² in Massachusetts (Healy 1997) and Pennsylvania (Bowles and Campbell 1993). Deer densities in national parks in the eastern United States have been >50 deer/km² for >20 yr. (Porter and Underwood 1999) with densities in some national parks in the eastern U.S. exceeding 60 deer/km² (Porter et al. 1994). Densities ranged from 15-25 deer/km² in the Missouri River valley of Nebraska and Iowa (VerCauteren and Hygnstrom 1998). The goal of most wildlife agencies in the Midwest has been to maintain overwinter densities from 10-15 deer/km² (Menzel 1984). In Missouri, deer density goals varied from as high as 15 deer/km², where
viewing deer was desired, to 8 deer/km², where ecosystem integrity was important (Hansen and Beringer 1997).

Browsing by deer can alter the structure of forest vegetation, species composition, and forest regeneration. Density of understory vegetation and recruitment of hemlock-hardwood seedlings decreased after 20 years of heavy browsing by deer in northwestern Pennsylvania (Hough 1965). Significant differences in the density of understory vegetation and species composition existed between areas inside and outside of a fence that excluded deer for 30 years in north-central Minnesota (Ross et al. 1970). Recruitment of tree seedlings outside the enclosure was almost nonexistent. Griggs et al. (2006) found in Great Smoky Mountains National Park that both richness of sapling species and density of woody stems were greater where deer were excluded. Enclosures with high densities of deer had reduced understory density, lowered height of surviving seedlings, and produced fewer tree seedlings than enclosures with low densities of deer (Tilghman 1989). In addition, plant species composition shifted with a decrease in species browsed by deer and an increase in species not browsed by deer. Foraging by deer negatively affected 98 species of rare herbaceous plants in Illinois (Miller et al. 1992). Extensive browsing by deer can increase cover by grass and ferns and decrease herbaceous cover (Waller and Alverson 1997; Carson et al. 2005). Densities of deer as low as 4 deer/km² have prevented regeneration of some woody and herbaceous species (Alverson et al. 1988). Griggs et al. (2006) suggested that extensive deer browsing may have long-term impacts on browse-intolerant plant species.

Fontenelle Forest is a large natural area that lies in the Missouri River Valley, bounded to the east by the Missouri River and extensive agricultural fields in Iowa, to the north by Omaha, Nebraska, and to the west and south by Bellevue, Nebraska (Figure 1). Deer were scarce in the area in the 1960s, but increased rapidly in the following decades due to abundant food resources, no hunting, and an absence of predators. In the 1990s, densities of deer in the area ranged from 14-45 deer/km² (Hygnstrom and VerCauteren 1999). Diamond (1992) observed no seedlings of linden (*Tilia americana* L.), oak (*Quercus* spp.), or hickory (*Carya* spp.), although mature linden, oak, and hickory were common throughout the forest. The only young trees seen were pioneer species, including hackberry (*Celtis occidentalis* L.) and hop hornbeam (*Ostrya virginiana* Mill.). Exotic deer-tolerant species such as barberry (*Berberis thunbergii* DC.), tree-of-heaven (*Ailanthus altissima* Desf.), and snakeroot (*Sanicula* sp.) were seen, whereas native understory shrubs and forbs were not. Gubanyi (2001) attributed reduced understory vegetation, increased grass cover, and altered tree composition at Fontenelle Forest to intense deer browsing, which was consistent with Diamond’s (1992) suggestion that changes in vegetation composition were the result of years of intense browsing by a large deer herd.

Although Diamond’s observations were suggestive, no quantitative studies of the effects of deer on natural areas in the Great Plains have been published. We compared three natural areas with a history of high densities of deer to six natural areas that had comparatively low densities of deer to assess the relationship between density of deer and vegetation structure and plant species composition. We predicted that areas with a known history of high densities of deer would have less vegetation volume, fewer shrubs and tree saplings (<3 cm

![Figure 1. Location of natural areas along the Missouri and Platte Rivers in eastern Nebraska used to study effects of deer browsing on vegetation, including Hormel Park (1), Two Rivers State Recreation Area (2), Schramm State Park (3), DeSoto National Wildlife Refuge (4), Neale Woods Nature Preserve (5), Dodge Park (6), Fontenelle Forest Upland (7), Fontenelle Forest Floodplain (8), and Gifford Point Wildlife Management Area (9). Map created using data base at School of Natural Resources, University of Nebraska-Lincoln, Lincoln, NE 68583-0961.](image-url)
dbh), fewer small trees (3-15 cm dbh), and differences in species composition.

**METHODS**

**Study Area**

We established plots at nine natural areas along the Missouri and Platte Rivers in southeastern Nebraska (Figure 1; Table 1). Three sites (one upland, two floodplain) had been impacted by intensive browsing by deer since the 1980s. Results from radio-telemetry studies indicated that deer herds at these sites were distinct from each other (Hygnstrom and VerCauteren 1999). Six sites (two upland, four floodplain) had not been impacted by extensive deer browsing.

Three types of forest/woodland communities occur in floodplains in eastern Nebraska (Steinauer and Rolfsmeier 2000). Cottonwood-dogwood floodplain woodland, characterized by an overstory of mature cottonwood (*Populus deltoides* Bartr. ex Marsh) and a shrub understory dominated by rough-leaved dogwood (*Cornus drummondii* C.A. Mey.), was observed at DeSoto National Wildlife Refuge (DeSoto) and Dodge Park (Dodge). Other tree species found at these sites included green ash (*Fraxinus pennsylvanica* Marsh.), box elder (*Acer negundo* L.), and hackberry. Virginia creeper (*Parthenocissus quinquefolia* L.), poison ivy (*Toxicodendron radicans* L.), and scouring rush (*Equisetum hyemale* L.) were common in the understory. Eastern floodplain woodland was observed at Two Rivers State Recreation Area (Two Rivers), DeSoto, Fontenelle Forest, and Gifford Point Wildlife Management Area (Gifford Point). These sites had a cottonwood overstory and dogwood shrub zone but also had a sparse subcanopy of mixed hardwood species including silver maple (*Acer saccharinum* L.), box elder, green ash, honey locust (*Gleditsia triacanthos* L.), mulberry (*Morus spp.* L.), and American elm (*Ulmus americana* L.). The shrub zone included Virginia creeper and poison ivy but lacked the scouring rush found in the cottonwood-dogwood floodplain woodland. Coralberry (*Symphoricarpos orbiculatus* Moench.) and gooseberry (*Ribes missouriensis* Nutt.) were also common in the understory. Eastern floodplain forest, which forms when subcanopy species of the eastern floodplain woodland community replaces the cottonwood canopy, was found at Hormel Park (Hormel) and Fontenelle Forest. These sites had a similar species composition to the eastern floodplain woodland, but had a more closed canopy and greater density of subcanopy species. Oak and linden were also present in the canopy.

All upland sites in the study area (Table 1) were typical southeastern upland forest in Nebraska (Steinauer and Rolfsmeier 2000). Canopy species at these sites included bitternut hickory (*Carya cordiformis* Wang.), hackberry, ash (*Fraxinus spp.* Marsh.), black walnut (*Juglans nigra* L.), oak species, and linden. Redbud (*Cercis canadensis* L.), red mulberry (*Morus rubra* L.), hop hornbeam, and red elm (*Ulmus rubra* Michx.) were observed in the subcanopy, and rough-leaved dogwood, coralberry, poison ivy, and Virginia creeper inhabited the understory.

**Vegetation Plots**

We established one or two 400-m x 50-m plots at each natural area (Table 1). Plots were placed along preexisting transects established to conduct breeding bird point counts (Gubanyi 2001). Plots were aligned such that the transect ran longitudinally through the center of each plot. In all, we established 13 plots at nine natural areas.

<table>
<thead>
<tr>
<th>Site</th>
<th>River</th>
<th>Elevation</th>
<th>Deer Density</th>
<th>Site Area</th>
<th>Forest Area</th>
<th>Vegetation Plots</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fontenelle</td>
<td>Missouri</td>
<td>floodplain</td>
<td>high</td>
<td>293</td>
<td>781</td>
<td>2</td>
</tr>
<tr>
<td>Fontenelle</td>
<td>Missouri</td>
<td>upland</td>
<td>high</td>
<td>233</td>
<td>206</td>
<td>2</td>
</tr>
<tr>
<td>Gifford Point</td>
<td>Missouri</td>
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<td>high</td>
<td>527</td>
<td>781</td>
<td>1</td>
</tr>
<tr>
<td>DeSoto</td>
<td>Missouri</td>
<td>floodplain</td>
<td>low</td>
<td>3166</td>
<td>115</td>
<td>1</td>
</tr>
<tr>
<td>Dodge</td>
<td>Missouri</td>
<td>floodplain</td>
<td>low</td>
<td>180</td>
<td>205</td>
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<tr>
<td>Hormel</td>
<td>Platte</td>
<td>floodplain</td>
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<td>68</td>
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<td>1</td>
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<tr>
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<td>upland</td>
<td>low</td>
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<td>124</td>
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<td>Platte</td>
<td>upland</td>
<td>low</td>
<td>134</td>
<td>45</td>
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<tr>
<td>Two Rivers</td>
<td>Platte</td>
<td>floodplain</td>
<td>low</td>
<td>394</td>
<td>65</td>
<td>1</td>
</tr>
</tbody>
</table>

*All sites categorized as high deer density had ≥ 2.4 pellet groups per 10-m² plot (n = 100), whereas all sites categorized as low deer density had ≤ 1.2 pellet groups.*

*Site area = total area managed by ownership that included plot(s).*

*Forest area = area of undivided forest patch containing plot(s).*
Deer Pellet-Group Counts

We conducted pellet-group counts at each natural area to generate data for the development of an index to the density of deer in the study area (Neff 1968). We randomly located 50 10-m² circular plots perpendicular to the transect running through each plot. We established each circular plot by placing a pole in the center and plotting the circumference with a 1.78-m cord attached to the pole. Two people searched each plot and recorded the number of pellet groups observed. We counted pellet groups at all nine natural areas from 22 February to 23 March 1995 and from 23 March to 13 April 1996.

Vegetation Volume

We established an index of vegetation volume at each natural area using a 4-m pole (2 cm diameter) divided into 1-dm units (Mills et al. 1991). The pole, when placed vertically in the vegetation, defined a series of 40 connected cylinders, each with a height and radius of 1 dm. If vegetation was observed within a 1-dm cylinder, it was considered a “hit.” The number of “hits” was recorded for each 1-m layer above the ground. The total number of “hits” for the 4-m pole was the total vegetation volume. Each 1-m layer ranged from 0 to 10 “hits” per sampling point and the total vegetation volume ranged from 0 to 40 “hits” per sampling point. We recorded vegetation volume at 50 points placed at random distances perpendicular to each of the transects. We collected data on vegetation volume data at all nine natural areas from 30 May to 20 June 1995 and 20 May to 23 May 1996.

Small Woody Plant Density

We estimated the density of small woody plants (any plant < 3 cm dbh) at each natural area by randomly placing 30 10-m² circular plots along each transect and identifying and counting all small woody plants rooted within each plot. Plants were categorized into 11 groups for analysis: dogwood, coralberry, gooseberry, poison ivy, hackberry, elm, ash, other tree species, total tree species, total shrub species (i.e., species always < 3 cm dbh), and total small woody plants. We collected data on small woody plants at all nine natural areas from 27 June to 2 August 1995.

Tree Coverage

We collected data on tree coverage following procedures outlined in James and Shugart (1970) and Noon (1981). We randomized the placement of 10 0.04-ha circular plots along each transect and identified and counted all trees (> 3 cm dbh) within each plot. Each tree was put into one of nine size categories based on diameter at breast height (dbh) (Noon 1981). We calculated the basal area (A = π r²) for each tree found within each plot based on the mid-value of the dbh for the size class of the tree. We obtained a dominance value for each tree species by summing the basal areas of each species found in a plot. The density of each tree species was expressed as the number of trees/0.04-ha. The frequency of each tree species was calculated by the number of 0.04-ha plots in which a species was found divided by the total number of 0.04-ha plots at that site. We converted density, dominance values, and frequency values into relative values and summed them to create importance values for tree species at each site. We scaled tree importance values to percent-ages and tabulated these for comparisons of tree importance values across the study sites. We collected data on tree coverage at eight natural areas from 27 June to 2 August 1995. Tree coverage at the Dodge site was collected from 4 August to 10 August 1993, and data were not recollected in the later study period.

Ground Cover

At each natural area, we estimated the frequency of ground cover types using the procedures outlined in James and Shugart (1970) and Noon (1981), and randomized the placement of 50 78.5-m² circular plots along each transect. Two perpendicular lines bisected each plot, passing through the center. We recorded the ground cover type observed through a viewer with cross hairs at 1-m intervals along each line. We collected 20 samples of ground cover type for each plot and 1000 records for each site. Ground cover types included grass/sedge, forb, litter, bare ground, shrub, scouring rush, moss, fern, and slash. Bare ground, scouring rush, moss, and fern were grouped for analysis because of low occurrence. We collected ground cover data at all nine natural areas from 4 May to 11 May 1995.

Data Analysis

Data were not normally distributed and sample sizes were considered small. Therefore, we used Wilcoxon signed rank tests to compare data from 1995 and 1996. We used Mann-Whitney U tests to compare vegetation data from natural areas with high and low densities of deer. We used Chi-square to analyze frequencies of five ground cover categories across four natural areas categories (high deer density, upland; high deer density, floodplain; low deer density, upland; and low deer density, floodplain). We used α = 0.10 as a rejection criteria to guard against Type II errors of falsely accepting null hypotheses of no difference between sites with high and low densities of deer. All statistical analyses were conducted using Statview (SAS 1999).

RESULTS

Deer Pellet-Group Counts and Density Index

Counts of pellet groups ranged from a mean high of 6.1 pellet groups/10 m² in Fontenelle Forest floodplain in 1995 to a low of 0.1 pellet groups/10 m² at Hormel in 1996 (Figure 2). Pellet group counts did not differ between years (Wilcoxon signed-rank, P = 0.575, n = 9). The mean number of pellet groups for 1995 and 1996 combined was greater at three sites with a known history of high densities of deer (U = 0, P = 0.020, Figure 2).

Vegetation Volume

Total vegetation volume and vegetation volume from 0-1 m high were greater in 1995 than 1996 (Wilcoxon signed-rank, P = 0.050, n = 9 and P = 0.008, n = 9, re-
respectively). Vegetation volume from 0-1 m high did not differ between sites with high and low densities of deer in 1995 and 1996 (\(U = 8, P = 0.796\), and \(U = 4, P = 0.197\), respectively, Figure 3). Vegetation volume from 1-2 m high was less at sites with high densities of deer in 1995 and 1996 (\(U = 1, P = 0.039\), and \(U = 1, P = 0.039\), respectively). Vegetation volume from 2-3 m high did not differ between sites with high and low densities of deer in 1995 but was less at sites with high densities of deer in 1996 (\(U = 3, P = 0.121\), and \(U = 2, P = 0.071\), respectively). Vegetation volume from 3-4 m high did not differ between sites with high and low densities of deer in 1995 and 1996 (\(U = 8, P = 0.796\), and \(U = 5.5, P = 0.366\), respectively).

**Small Woody Plant Density**

We counted 5930 small woody plants in 140 10-m\(^2\) circular plots at eight natural areas. Total woody plant mean density per site ranged from 1.2 to 52.4 plants/10-m\(^2\) plot. Densities in eight of 11 small woody plant categories (including total woody plants, total sapling trees, and total shrub species) were less at sites with high densities of deer (\(P < 0.05\), Figure 4). Elm and ash saplings and dogwood and coralberry were less abundant at sites with high densities of deer. Only gooseberry, poison ivy, and hackberry saplings did not differ between sites with high and low densities of deer (\(P > 0.10\), Figure 4).

**Tree Coverage**

We counted 9187 trees in 122 0.04-ha circular plots at nine natural areas. Hackberry, elm, mulberry, ash, and rough-leaved dogwood were found at all nine sites. Cottonwood and sycamore (Platanus occidentalis L.) were found only at floodplain sites, and hop hornbeam was found only at upland sites. Importance values in areas of high densities of deer were higher for hackberry (\(U = 0, P = 0.020\) but lower for dogwood (\(U = 2, P = 0.071\)). Densities of small, medium, and large trees did not differ between sites with high and low densities of deer (Table 2). The density of small hackberry was greater, however, in sites with high densities of deer, whereas small tree density (minus hackberry) was less (Table 2). At sites with high densities of deer, total density of hackberry was greater and density of dogwood was lower (Table 2).
Ground Cover

Litter, forbs, and grasses were the most common ground covers at all natural areas. Frequencies of ground cover were not randomly distributed ($\chi^2 = 588.2, P < 0.001, df = 12$). Grass was observed more frequently than expected at floodplain sites with high densities of deer and made the greatest contribution to the $\chi^2$ test statistic ($\chi^2 = 237.7$). Shrubs were observed less than expected at sites with high densities of deer, and made significant contributions to the $\chi^2$ test statistic ($\chi^2 = 57.5$ for floodplain sites and 36.7 for the upland site with a high density of deer).

**DISCUSSION**

Pellet group counts indicated that the highest densities of deer in the nine natural areas occurred in the flood plains of Fontenelle Forest and Gifford Point and the uplands of Fontenelle Forest. These results are corroborated by helicopter counts of the same areas in 1995 and 1996 in which densities of deer exceeded 27 deer/km$^2$ (S. Hygnstrom, University of Nebraska-Lincoln, unpubl. data). At that time, these densities were the highest in Nebraska (K. Menzel, Nebraska Game and Parks Commission, pers. comm.).

Sites with high densities of deer had less vegetation volume than sites with low densities. Vegetation between 1-2 m high was predominately woody vegetation, and differences in this height zone can be attributed to a greater intensity of browsing by deer at sites with high densities of deer. Browse utilization surveys conducted at Fontenelle Forest and Gifford Point in 1995 also indicated a high level of browsing (> 60% of available twigs browsed; Hygnstrom and VerCauteren

Table 2. Density of trees between sites with high and low densities of deer in nine natural areas in southeastern Nebraska, during spring, 1995 and 1996.

<table>
<thead>
<tr>
<th>Tree Category</th>
<th>High Mean (SE)</th>
<th>Low Mean (SE)</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total hackberry trees</td>
<td>35.1 (11.92)</td>
<td>9.6 (5.40)</td>
<td>0.039</td>
</tr>
<tr>
<td>Small hackberry</td>
<td>20.8 (5.44)</td>
<td>7.2 (4.80)</td>
<td>0.039</td>
</tr>
<tr>
<td>Dogwood</td>
<td>1.9 (1.11)</td>
<td>20.2 (12.26)</td>
<td>0.039</td>
</tr>
<tr>
<td>Small trees (minus hackberry)</td>
<td>17.1 (7.55)</td>
<td>48.6 (15.44)</td>
<td>0.038</td>
</tr>
<tr>
<td>Total small trees</td>
<td>37.8 (11.68)</td>
<td>55.8 (14.56)</td>
<td>0.197</td>
</tr>
<tr>
<td>Total medium trees</td>
<td>16.8 (0.09)</td>
<td>16.0 (2.24)</td>
<td>0.999</td>
</tr>
<tr>
<td>Total large trees</td>
<td>1.7 (0.23)</td>
<td>1.8 (0.72)</td>
<td>0.897</td>
</tr>
<tr>
<td>Total trees</td>
<td>73.4 (19.50)</td>
<td>81.3 (14.46)</td>
<td>0.796</td>
</tr>
</tbody>
</table>

$^a$All sites categorized as high deer density had $\geq 2.4$ pellet groups per 10-m$^2$ plot ($n = 100$), whereas all sites categorized as low deer density had $\leq 1.2$ pellet groups.

$^b$Small tree: 3-15 cm dbh; medium tree: 15-53 cm dbh; large tree: > 53 cm dbh.
1999). Vegetation between 0-1 m high was a mix of grasses, forbs, and woody plants. Small woody plants were less common at sites with high densities of deer whereas grasses and forbs were more common at these sites. Increased grass abundance in relation to increased deer abundance has also been observed in Minnesota (Ritchie et al. 1998), Pennsylvania (Horsley et al. 2003), and on Anticosti Island (Tremblay et al. 2006). Grasses and forbs not browsed by deer apparently replaced vegetation browsed by deer in this zone, resulting in no difference in vegetation volume.

Only woody vegetation was observed from 2-3 m and 3-4 m high. If intense browsing by deer was a recent phenomenon, then its effect should not be observed in the vegetation height zones above the reach of deer (≥ 2 m). However, if intense browsing by deer persisted over several years, reduced woody plant regeneration and the inability of small woody plants (i.e., sapling trees) to grow above the browse line should result in less vegetation in higher height zones. We observed less vegetation from 2-3 m high in areas with high densities of deer in 1996 but not in 1995. Additional data would be needed to determine if long term effects of deer browse had occurred in vegetation above the deer browse line.

Dogwood and coralberry are common understory species in southeastern Nebraska (Steinauer and Rolfsmeier 2000) and, along with elm and ash saplings, are readily browsed by white-tailed deer (Barber 1984). Intensive browsing by deer most likely led to the differences in these species between sites with high and low densities of deer. Only densities of hackberry saplings, gooseberry, and poison ivy were similar among sites with high and low densities of deer. In Illinois, gooseberry was not a favored browse species (Strole and Anderson 1992). Hackberry was not included in a list of 29 woody plant genera considered deer browse in Kentucky (Barber 1984). Strole and Anderson (1992), however, found hackberry was browsed in greater proportions than its availability in Illinois and ranked sixth among nine species browsed by deer. In Fontenelle Forest and Gifford Point, hackberry plants that were 10-15 years old were only 45-60 cm tall and “nearly all woody plants within reach of deer were stunted and deformed by repeated browsing by deer” (Hygnstrom and VerCauteren 1999). Hackberry saplings apparently persisted in Fontenelle Forest and Gifford Point because they were resistant to browsing.

The prediction that there would be fewer small trees in natural areas with high densities of deer was supported. Only small hackberry trees were able to survive the intense pressure of browsing at sites with high densities of deer. In Pennsylvania, the density of small trees (2.5-9.0 cm dbh) was independent of deer density (Bowles and Campbell 1993). Bowles and Campbell felt that trees of this size were large enough to survive browsing by deer. Persistent browsing by deer, however, could result in a lack of tree recruitment and fewer small trees. Tree-sized dogwoods observed at the three natural areas with high densities of deer were tall enough for the crown to escape browsing by deer, but shrub-sized dogwoods were virtually absent from these sites (Figure 4). Most of these trees probably reached heights above the browse line before the density of deer increased dramatically.

The prediction that species composition would change in natural areas with high densities of deer also was supported. Over 50 years ago, Garrett (1944) described the forest habitat of Fontenelle Forest as mature forest of elm, cottonwood, ash, box elder, and other trees. Dominant trees in the upland habitat included elm, linden, hickory spp., oak spp., hop hornbeam, Kentucky coffee tree (Gymnocladus dioicus L. (Koch.)), and locust with a dense understory (Staphylea trifolia L.), wahoo (Euonymus atropurpureus Jacq.), and coralberry. Garret made no mention of hackberry in any of the habitats he described in Fontenelle Forest, suggesting hackberry was not as dominant 50 years ago as it is today. Intense browsing by deer appeared to have increased the dominance of hackberry in Fontenelle Forest and Gifford Point and to have increased cover by grasses while reducing that of woody plants in the understory. Although it was not a focus of this study, it is highly likely for species composition was altered as well with a decrease in deer-preferred species and increase in deer-tolerant species.

The ability of deer to alter forest vegetation composition has been well documented. Deer browsing caused eastern hemlock (Tsuga canadensis L. (Carr.)) and witch hobble (Viburnum alnifolium Marshall) to disappear from a Pennsylvania forest understory (Hough 1965). Species composition of canopy and understory vegetation changed in Minnesota because of excessive browsing by deer (Ross et al. 1970). Black cherry (Prunus serotina Ehrh.) replaced several hardwood species in Pennsylvania (Tilghman 1989; Horsley et al. 2003). Stromayer and Warren (1997) noted other examples of forest habitats altered by deer: (1) displacement of hemlock by sugar maple (Acer saccharum Marshall) in the Great Lakes region, (2) altered oak forests in Illinois, (3) reduction of white cedar (Thuja occidentalis L.) from the New Jersey Pine region, and (4) suppression of live oak (Q. virginiana Miller) stands in Georgia.

Deer-browsed forests may take 70 years to return to a former state (Anderson and Katz 1993), and in some instances, plant communities that are heavily disturbed by deer browsing might not be able to recover (Bowles and Campbell 1993; Hygnstrom and VerCauteren 1999; Griggs et al. 2006). Results from studies of deer exclosures, however, have been encouraging. A significant recovery of hemlock occurred after 12 years of protection in exclosures in Wisconsin (Anderson and Katz 1993), and after just one year, an increase in sapling trees and shrub species was observed in four 0.4-ha deer exclosures in eastern Nebraska (Hygnstrom and VerCauteren 1999). In New York, forest vegetation responded favorably to control of deer herds by increased hunting effort (Behrend et al. 1970). Hunting was initiated in 1996 at Fontenelle Forest and Gifford Point to control the density of deer. The presence of woody seedlings and increased health and vigor of plants were observed in the understory after a year of protection from deer browsing in Georgia (Bratton and Kramer 1990) and in Nebraska (Hygnstrom and VerCauteren 1999). However, the lack of regeneration by tree species intolerant
of browsing, the increase in dominance by hackberry, and the introduction of exotic species have created changes in some forests in southeastern Nebraska that may require additional time or intervention by forest and wildlife managers to reverse.

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