

Factors affecting white-tailed deer-browsing rates on early growth stages of soybean crops

GREGORY M. COLLIGAN, Department of Entomology and Wildlife Ecology, University of Delaware, Newark, DE 19716, USA

JACOB L. BOWMAN, Department of Entomology and Wildlife Ecology, University of Delaware, Newark, DE 19716, USA jlbowman@udel.edu

JOSEPH E. ROGERSON, Department of Entomology and Wildlife Ecology, University of Delaware, Newark, DE 19716, USA

BRUCE L. VASILAS, Department of Plant and Soils Sciences, University of Delaware, Newark, DE 19716, USA

Abstract: White-tailed deer (*Odocoileus virginianus*) damage to soybean crops is a concern for soybean producers. Although researchers have documented decreases in the intensity of deer-browse on soybean plants as the growing season progresses, an understanding of the mechanisms driving the decrease in deer-browse is necessary for reduction and mitigation of deer damage to soybean crops. We tested 4 hypotheses to determine why deer-browse rates decrease 3 weeks after plant emergence: (1) plant phenology affects plant palatability; (2) diet change occurs; (3) deer damage induces a plant response making soybean leaves less palatable; and (4) deer consume fewer leaves but the same amount of leaf biomass as the season progresses. We recorded deer-browse in double- and single-crop soybean fields in Little Creek, Delaware, during the 2005 to 2006 growing seasons. To test if plant phenology affected deer-browse, we conducted a forage analysis of soybean leaves at different growth stages. Although forage quality components were variable across the growing season, white-tailed deer dietary requirements were met or exceeded in all cases. We compared deer diet composition using microhistological analyses across the early soybean growing season. The proportion of soybeans in the diet increased from 13 to 37% from late May to early July. We tested for an induced plant response by comparing the browse rates of plots that were protected from deer-browsing until 4 weeks after plant emergence to plots that received no protection. Although we documented greater browse rates in the protected plots once protection was removed, we also documented that protected plots had taller plants, suggesting that deer may have been attracted to the taller plants. The amount of soybean leaf biomass that deer were consuming across the growing season increased from the early to late growth stages of soybeans. Based on our results, we believe that the increasing biomass of soybean leaves is the most plausible explanation for the decrease in browsing rate that we observed as soybeans matured.

Key words: crop damage, *Glycine max*, human–wildlife conflicts, *Odocoileus virginianus*, soybean, white-tailed deer

WHITE-TAILED DEER (*Odocoileus virginianus*) diet in agricultural landscapes is typically dominated by agronomic crops (Nixon et al. 1991). The heterogeneous row crop landscape and variable planting and harvesting chronology of agricultural landscapes provide deer with a plethora of highly palatable food sources year-round. Availability and use of agricultural crops have caused deer abundance to exceed the cultural carrying capacity in rural landscapes (Conover 1994, Conover 1997). Most agricultural producers reported that deer caused significant economic damage to crops (Conover 1994), and Conover (1997) conservatively estimated that deer were responsible for \$100 million in damage to agricultural productivity annually in the United States.

Soybeans (*Glycine max*) are a preferred food

item by deer; in some parts of the southeastern United States, agricultural producers have stopped planting soybeans because deer damage is severe and unavoidable (Wallace et al. 1996). Most deer-browsing on soybean plants occurs during the plants' early growth stages (DeCalesta and Schwendeman 1978, Garrison and Lewis 1987, Rogerson 2005). Although browse intensity decreases as the growing season progresses (Lyon and Scanlon 1987, Rogerson 2005), the reason for this decrease is unknown. Rogerson (2005) proposed 4 hypotheses for why deer-browse on soybeans declined 3 weeks after plant emergence: (1) soybean plants may become less palatable in the reproductive growth stages; (2) deer may switch to alternate food sources as the growing season progresses; (3) deer-browse on soybean

plants may induce plant responses making soybean leaves less palatable; and (4) deer may continue to consume the same amount of leaf biomass, but an increase in the biomass of individual leaves causes deer to remove fewer leaves. Determining the validity of these hypotheses may provide further insight for new management techniques needed to reduce deer damage to soybean crops.

Soybeans may become less palatable to deer as plants mature from vegetative to reproductive stages. Lyon and Scanlon (1987) observed more deer in soybean fields during vegetative growth stages compared to reproductive growth stages. As soybean plants matured toward the reproductive growth stages, Lyon (1984) documented that soybeans occurred in deer diets with decreasing frequency, which suggested that deer ate fewer soybean leaves later in the growing season. Conversely, Nixon et al. (1991) documented that deer fed on soybean crops for the entire growing season.

The availability of different food sources, primarily other row crops, may influence deer-browsing rates on soybean plants. Certain row crops are more attractive to deer at particular times during the growing season than others. Deer preferred to eat wheat (Hartman 1972) and corn (Nixon et al. 1991, VerCauteren and Hygnstrom 1993) when those crops are at particular growth stages. Nixon et al. (1991) documented the importance of wheat for deer in agricultural landscapes in early spring. Corn also becomes a preferred food item during the silking-tasseling growth stages (Nixon et al. 1991, VerCauteren and Hygnstrom 1993). The availability of these crops at those preferred growth stages may influence deer-browsing on soybeans.

Defoliation of soybean plants by deer may elicit a chemical response, thereby decreasing the palatability of the remaining leaves. Previous research indicated that chemical changes occurred within soybean plants in response to insect herbivory (Klubertanz et al. 1996, Peterson and Higley 1996). Kogan and Fisher (1991) found that some chemical changes induced by insect defoliation defended the plant against subsequent defoliation. However, the mode of feeding for insects and deer is different; deer tend to eat whole leaves, whereas insects feed by chewing portions of leaves or sucking

on the phloem. Research investigating soybean plant reaction to leaf clipping, as it relates to vegetative growth and plant chemical reaction, is nonexistent.

A reduction in browse rates could result from leaves increasing in size across the growing season. Deer tend to browse soybean leaves from the top of the plant, and the upper-most leaves are generally thicker than leaves at lower nodes, which results in greater individual leaf weights (Lugg and Sinclair 1980). Additionally, both leaf expansion rates and leaf area of an individual soybean leaf increase across vegetative growth stages (Leadley and Reynolds 1989). New soybean leaves are thicker and larger and grow faster than older leaves, so deer need to consume fewer leaves to become satiated as the growing season progresses.

Investigation into mechanisms driving the decrease in browse activity is important because determining the mechanism may allow the formulation of new strategies for reducing deer damage to soybean. Our objectives were to determine if a decrease in browse rates was caused by: (1) soybean plants becoming less palatable as the plants matured from vegetative to reproductive stages; (2) a shift in deer diets; (3) deer-browsing inducing a soybean plant response making the leaves less palatable; or (4) changes in individual leaf biomass.

Study site

The study site was located on the Delmarva Peninsula on the coastal plain of Delaware, 10 km south of Little Creek, Delaware, on Route 9 (Figure 1). The farm was owned and operated by Dr. Chester and Sally Dickerson and was representative of farms found on the Delmarva Peninsula (Rogerson 2005). Agricultural fields comprised 80% of the farm, with the remaining 20% being forested. Fields used for crop production ranged from 8 to 20 ha. The soils on the study site relevant to crop production were Woodstown loam (Aquic Hapludults), Sassafras sandy loam (Typic Hapludults), Mattapex silt loam (Typic Hapludults), and Falsington loam (Typic Endoaquults). The row crops produced on our study area were soybeans, corn (*Zea mays*), and wheat (*Triticum aestivum*). Single-crop soybeans were planted on June 1, 2005, and May 10, 2006, and harvested on November 3, 2005, and October 16, 2006, respectively.



Figure 1. Soybean field in study site.

Double crop soybeans were planted after the wheat harvest on July 15, 2005, and July 11, 2006, and harvested in the fall on December 7, 2005, and November 10, 2006, respectively. Deer density on the study area was 21 deer/km² (Bowman 2006). Sweetgum (*Liquidambar styraciflua*), sycamore (*Platanus occidentalis*), red maple (*Acer rubrum*), white oak (*Quercus alba*), pin oak (*Quercus palustris*) and American holly (*Ilex opaca*) dominated the forested portions of the study site (Rogerson 2005). The average maximum and minimum temperature during the growing season (May through October) were 26.6° C and 15.6° C, respectively, and precipitation averaged 10.5 cm (National Climatic Data Center 2004).

Methods

We conducted our research in 1 double-crop (i.e., soybeans planted after winter wheat was harvest in early July and harvested in the fall) and 1 single-crop (i.e., planted in spring and harvested in the fall) soybean field annually. Based on observations by the agricultural producer and Rogerson (2005), we selected fields that had historically high deer use. We selected fields bordered by only 1 forest edge, which was typical of farm fields on the Delmarva Peninsula. In each selected field, we systematically placed 4.6-m² circular plots at the midpoint of 6 distance intervals (0–10, 11–20, 21–30, 31–40, 41–50, and 51–60 m) from the forest-field edge in each field (Figure 2). A centralized 1-m² plot for sampling was placed

within the larger plot. We spaced plots in the same distance class 2 m apart from plot edge to edge. We systematically assigned a treatment to each plot: (1) protected before plant emergence until 4 weeks after emergence; (2) never protected; or (3) protected before plant emergence and for the entire growing season. We protected the plots that were assigned a protection treatment using 1.22-m-high welded wire fences. Fences were large enough to provide a 0.5-m buffer around the centralized 1-m² plots. The buffer prevented deer browsing next to fences or differences in sunlight

exposure from affecting the centralized 1-m² plots. Plots protected for the entire growing season were used for the continuation of Rogerson's (2005) yield study and were not used for this study. In 2005, we had 5 replicates of each treatment within each distance interval for a sample size of 60 in each field (i.e., 90 including plots used for the continuation of the yield study). Due to the amount of browse observed in 2005, we doubled the number of replicates within each treatment in 2006 for a sample size of 120 in each field (i.e., 180 including plots used for the continuation of the yield study).

Browse rates

We estimated browse rates of soybean leaves across the growing season by calculating the proportion of leaves browsed within each plot. Soybean leaves are compound leaves, comprised of 3 leaflets. We considered a leaf to be browsed when the entire leaf (i.e., all 3 leaflets) was eaten, which was always the case. To determine the proportion of leaves browsed within each plot, we divided the number of leaves eaten by the total number of leaves available in each plot. We counted the number of leaves browsed every 7 to 10 days in a centralized 1 m² plot (within each 4.6-m² plot) starting 1 week after plant emergence and ending approximately at the reproductive growth stage 6 (R6; Ritchie et al. 1997), when plant leaves begin to senesce (i.e., approximately 8 to 10 weeks after the plant's emergence). Additionally, we measured the average height of plants in each plot, each week.



Figure 2. A diagram of the arrangement of the plots used to measure deer-browsing on soybeans in Little Creek, Delaware, 2055–2006.

Plant phenology

We monitored forage quality to test the hypothesis that the browse-rate decrease was caused by soybean plants becoming less palatable as the plants matured from vegetative to reproductive stages. We compared the forage quality of soybean leaves by growth stage (i.e., vegetative growth stages 1, 3, and 5, and reproductive growth stages 2, 3, and 5) across the growing season in double-crop and single-crop fields. We randomly selected 5 plants 0 to 25 m from the field edge and clipped leaves from the uppermost portion of the plants, mimicking deer-browse. For each replicate, we clipped enough leaves to fill a 1-L bag. Immediately upon clipping, we placed samples in a cooler and kept them cool to maintain sample integrity. We sent the samples to Cumberland Valley Analytical Services, Hagerstown, Maryland, for standard forage quality analyses. We used crude protein (CP), calcium (Ca), phosphorous (P), sodium (Na), and digestibility, in the form of acid detergent fiber (ADF) and neutral detergent fiber (NDF) to evaluate the forage quality of soybean leaves for different plant growth stages (Campbell et al. 2002). Acid detergent fiber is a measure of the amount of cellulose and lignin and is used to calculate energy content. Neutral detergent fiber measures the total fiber of forage and can be used to determine intake rates. We used a

1-way ANOVA for each field type to investigate differences in forage quality of soybean leaves across the growing season. If we detected differences, we used a Fisher's Protected Least Significant Difference as a means separation test.

Diet change

We monitored deer diets using microhistological analysis to test the hypothesis that the browse rate decrease was caused by a diet shift. We collected deer fecal samples weekly from May 17 until July 1, covering the time period from before single-crop soybeans were planted to just before the emergence of double-crop soybeans. We stopped sampling before double-crop soybean emergence to prevent any influence on diet that double-crop soybeans may have had. Each week we collected and froze 8 to 12 pellets from 10 to 12 different piles of fresh scat. We collected pellets from the woodlot adjacent to the single-crop soybean field. This woodlot was equidistant from our full-season soybean field, 1 field planted in corn, and 1 field planted in wheat. We combined 1-week samples (all pellets collected for a given week) into 2-week intervals to attain appropriate sample sizes (Holechek and Vavra 1981). We sent samples to the Washington State University Wildlife Habitat Nutrition Laboratory, Pullman, Washington, which conducted a food-habitat diet composition analysis for each composite

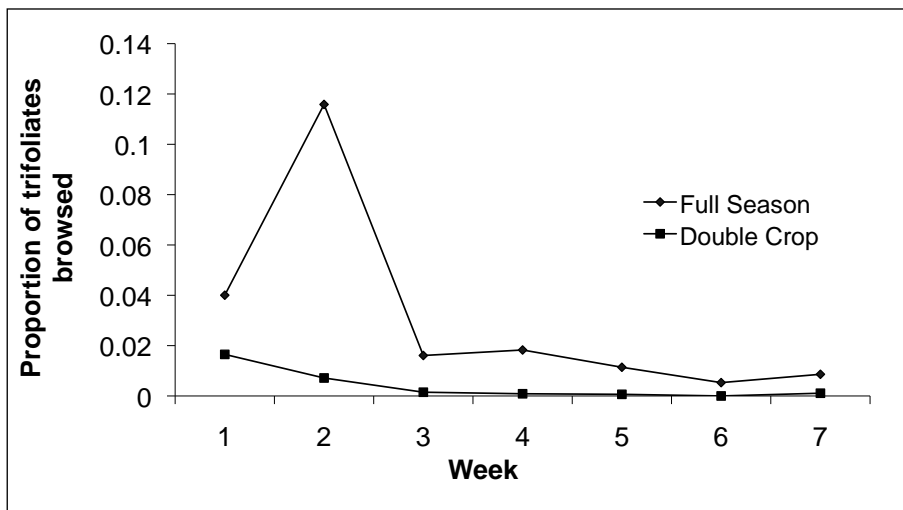


Figure 3. Mean proportion of soybean leaves browsed by week in Little Creek, Delaware, 2005–2006.

sample. Samples were analyzed by forage class (crops, grass, forbs, and shrubs) and major forage plants (>5% occurrence in the sample). For each sample, 8 slides were made and viewed 25 times, for a total of 200 views per sample (Holechek and Vavra 1981). From these views, the percentage of each forage class and the specific plants in the diet were estimated.

Induced plant response

We protected plots from browsing until 4 weeks after plant emergence to test the hypothesis that any decrease in browse rate was caused by deer-browsing inducing a soybean plant response making the leaves less palatable. Although this approach would not allow us to determine the mechanism of reduction in palatability, it did allow us to determine if this mechanism occurred. If deer-browse did elicit a response by the plant that decreased plant palatability in the weeks following fence removal (i.e., weeks 5 to 7), we expected to see more browse in the plots that were protected for 4 weeks compared to the unprotected plots. For this analysis, we had 2 treatments: unprotected plots that were browsed during weeks 1 to 4 and plots protected from browse until week 4. During weeks 5 to 7, we compared the proportion of leaves browsed per plot for the 2 treatments using 1-way ANOVAs for each week, field type, and year. Based on Rogerson (2005), we suspected that protected plants might be taller than unprotected plants. If

protected plants were taller, their height may have influenced deer browsing. Therefore, if we detected a difference in browse rates between the treatments, we compared the plant heights of the 2 treatments during weeks 4 to 7 using 1-way ANOVAs for each week, field type, and year.

Leaf biomass

We monitored the amount of biomass removed by browsing to test the hypothesis that the browse-rate decrease was caused by changes in individual leaf biomass. To estimate the amount of available soybean leaf biomass each week, we clipped 1 completely unrolled leaf at the highest node from 30 random plants within each distance class, mimicking deer-browse. We dried the clippings at 43° C for 2 weeks. We estimated consumed biomass for each week by multiplying the number of leaves browsed in the unprotected plots by the average dry leaf weight within each distance class. We investigated differences in weekly browse rates using a repeated-measures ANOVA blocking on distance class for each field type and year. If we detected differences, we used an LSD as a means separation test. We conducted all analyses with SAS (version 9.1, Cary, N.C.) at an alpha level of 0.05.

Results

Browse rates

Browse rates decreased from week 1 to 7 (Figure 3). Single-crop fields had a more

Table 1. Summary of nutritional values for soybean leaves for different growth stages in double-crop fields in Little Creek, Delaware. Minimum requirements of these nutritional values are provided to meet nutritional needs for comparison. Acid detergent fiber (ADF) and neutral detergent fiber (NDF) are measures of digestibility without published minimum requirements.

	Minimum requirements	V1 ¹	V3	V5	R2	R3	R5
		\bar{x} (SE)	\bar{x} (SE)	\bar{x} (SE)	\bar{x} (SE)	\bar{x} (SE)	\bar{x} (SE)
Crude protein (%): growth and maintenance	5.8–9.9 ²	26.66 (1.01)	32.22 (2.27)	34.90 (0.34)	35.77 (0.22)	37.09 (0.55)	37.82 (0.74)
Calcium (%): development	0.40 ³	1.17 (0.03)	1.31 (0.02)	1.05 (0.01)	1.15 (0.05)	1.09 (0.03)	1.10 (0.02)
Phosphorous (%): spring	0.16 ⁴	0.53 (0.02)	0.50 (0.10)	0.45 (0.01)	0.49 (0.01)	0.44 (0.01)	0.46 (0.01)
Sodium (%): maintenance and antlers	0.01 ⁵	0.02 (0.01)	0.01 (0.01)	0.01 (0.01)	0.02 (0.01)	0.03 (0.01)	0.03 (0.02)
ADF (%)		23.98 (0.49)	23.74 (3.08)	19.51 (0.06)	18.63 (0.63)	19.72 (0.32)	19.05 (0.31)
NDF (%)		29.18 (0.28)	30.24 (2.86)	23.65 (0.32)	23.58 (0.40)	25.17 (0.98)	25.43 (0.30)

¹ V represents vegetative stage and R represents reproductive stage

² From Asleson et al. 1996

³ From Ullrey et al. 1973

⁴ From Grasman and Hellgren 1993

⁵ From Hellgren and Pitts 1997

Table 2. Summary of nutritional values for soybean leaves for different growth stages in single-crop fields in Little Creek, Delaware. Minimum requirements of these nutritional values from the literature are provided for comparison. Acid detergent fiber (ADF) and neutral detergent fiber (NDF) are measures of digestibility without published minimum requirements.

	Minimum requirements	V2 ¹	V3	V5	R2	R3
		\bar{x} (SE)	\bar{x} (SE)	\bar{x} (SE)	\bar{x} (SE)	\bar{x} (SE)
Crude protein (%): growth and maintenance	5.8-9.9 ²	29.63 (0.57)	32.62 (0.37)	26.34 (0.49)	29.10 (0.99)	39.45 (0.52)
Calcium (%) development	0.40 ³	0.90 (0.02)	0.97 (0.03)	0.81 (0.02)	0.84 (0.01)	0.91 (0.01)
Phosphorous (%): spring	0.16 ⁴	0.35 (0.01)	0.43 (0.01)	0.38 (0.01)	0.38 (0.01)	0.44 (0.01)
Sodium (%): maintenance and antlers	0.01 ⁵	0.02 (0.01)	0.02 (0.01)	0.01 (0.01)	0.01 (0.01)	0.02 (0.01)
ADF (%)		20.06 (0.38)	20.07 (0.35)	22.64 (0.51)	23.39 (0.19)	20.72 (0.32)
NDF (%)		25.10 (0.30)	25.97 (0.58)	28.18 (0.56)	27.16 (1.07)	25.56 (0.67)

¹ V represents vegetative stage and R represents reproductive stage

² From Asleson et al. 1996

³ From Ullrey et al. 1973

⁴ From Grasman and Hellgren 1993

⁵ From Hellgren and Pitts 1997

pronounced decrease than double-crop fields (Figure 3).

Plant phenology

Among the growth stages, there were differences in crude protein (double crop, $F_{5,24} = 14.19$, $P < 0.001$; single crop, $F_{4,25} = 83.34$, $P < 0.001$), percentage calcium (double crop, $F_{5,24} = 10.64$, $P < 0.001$; single crop, $F_{4,25} = 10.76$, $P < 0.001$), and percentage phosphorous (double crop, $F_{5,24} = 6.84$, $P < 0.001$; single crop, $F_{4,25} = 26.30$, $P < 0.001$) for the double- and single-crop fields (Tables 1 and 2). Sodium did not differ by growth stages for double- or single-crop fields (double crop, $F_{5,24} = 1.11$, $P = 0.379$; single crop, $F_{4,25} = 0.31$, $P = 0.868$; Tables 1 and 2). Crude protein, Ca, P, and Na values met or exceeded the minimum requirement for deer across all growth stages in both double-crop and single-crop fields (Tables 1 and 2). Acid detergent fiber differed by growth stage in double-crop ($F_{5,24} = 3.40$, $P = 0.018$) and single-crop fields ($F_{4,25} = 15.30$, $P < 0.001$; Tables 1 and 2). Neutral detergent fiber also differed by growth stages in the single-crop ($F_{4,25} = 2.77$, $P = 0.049$) and the double-crop fields ($F_{5,24} = 5.05$, $P = 0.003$; Tables 1 and 2).

Diet change

In the first sampling period, deer diets were comprised primarily of shrubs and forbs (Table 3). Oak (*Quercus* spp.), dwarf sumac (*Rhus copallina*), and blackberry (*Rubus* spp.) were important shrub food sources. Beggarticks (*Bidens polylepis*), spotted touch-me-not (*Impatiens campensis*), small white morning glory (*Ipomoea lacunose*), smartweed (*Polygonum* spp.), common greenbrier (*Smilax rotundifolia*), and white clover (*Trifolium repens*) were important forb food sources. After the first sampling period, shrubs and forbs comprised <13% of the deer diet and row crops consisted of $\geq 77\%$ of the diet (Table 3). Wheat and soybean crops were the most common food items in deer diets during sampling periods 2 to 4 and the proportion of the diet comprising soybeans increased over the sampling periods (Table 3).

Induced plant response

For double fields in 2005 and 2005, browse rates during weeks 5 through 7 did not differ

Table 3. Diet composition by forage class for white-tailed deer in Little Creek, Delaware.

Forage class	5/17–5/24	5/30–6/13	6/14–6/29	6/30–7/1
Crops	11.6	76.7	81.5	88.9
Wheat	7.3	59.9	47.7	47.8
Corn	3.3	4.1	5.9	4.2
Soybeans	0.0	12.7	27.9	36.9
Grasses	12.3	8.6	4.2	2.8
Forbs	24.6	5.5	6.5	4.8
Shrubs	50.3	7.5	7.2	3.3

between plots protected for 4 weeks and unprotected plots (Table 4). In the 2005 single-crop field, browse rates during weeks 5 through 7 also did not differ between plots protected for 4 weeks and unprotected plots (Table 4). In the 2006 single-crop field, browse rates were greater in week 5 for plots protected for 4 weeks compared to unprotected plots, whereas browse rates were similar between treatments in weeks 6 through 7 (Table 4).

Plant height was greater in protected plots compared to unprotected plots ($F_{1,76} = 13.11$, $P < 0.001$). The difference in plant height between the treatments decreased in weeks 5 ($F_{1,76} = 12.71$, $P < 0.001$) and 6 ($F_{1,76} = 8.45$, $P = 0.005$) until, by week 7, plant height did not differ between the treatments ($F_{1,76} = 2.77$, $P = 0.100$).

Leaf biomass

The amount of biomass removed by deer in the double-crop field did not differ by week in 2005 ($F_{6,162} = 0.78$, $P = 0.583$) or 2006 ($F_{6,354} = 0.92$, $P = 0.482$), but did differ by week in the single-crop field in 2005 ($F_{6,174} = 2.44$, $P = 0.027$) and 2006 ($F_{6,354} = 5.87$, $P < 0.001$; Figure 4). In 2005, biomass consumed during week 7 was more than triple that of any other week (Figure 4). In 2006, week 5 had more than double the amount of consumed biomass than any other week (Figure 4).

Discussion

Browse rates

Our results were similar to those of other authors who observed decreasing browse rates across the growing season (DeCalesta and Schwendeman 1978, Garrison and Lewis 1987, Rogerson 2005). The periods of greatest deer-browse that we documented were shorter than

Table 4. Average proportion of leaves browsed for plots were protected from deer herbivory for weeks 1–4 and plots that were unprotected weeks for 1–4 in Little Creek, Delaware.

Crop	Year	Week	Unprotected		Protected		<i>df</i>	<i>F</i> -value	<i>P</i>
			\bar{x}	SE	\bar{x}	SE			
Double	2005	5	0.000	0.0000	0.000	0.0000			NA ¹
		6	0.000	0.0000	0.000	0.0000			NA
		7	0.000	0.0000	0.000	0.0002	F _{1,33}	0.16	0.690
	2006	5	0.000	0.0000	0.000	0.0000	F _{1,75}	0.24	0.629
		6	0.000	0.0000	0.000	0.0000			NA
		7	0.001	0.0005	0.000	0.0000	F _{1,75}	3.38	0.070
	Single	2005	5	0.000	0.0000	0.002	0.0016	F _{1,34}	0.40
6			0.000	0.0000	0.005	0.0043	F _{1,34}	0.25	0.618
7			0.025	0.0254	0.005	0.0049	F _{1,34}	1.78	0.191
2006		5	0.014	0.0048	0.052	0.0112	F _{1,94}	6.77	0.011
		6	0.014	0.0046	0.020	0.0058	F _{1,94}	0.46	0.498
		7	0.002	0.0015	0.002	0.0015	F _{1,94}	0.03	0.862

¹NA = no analysis for weeks when no browse was observed for either treatment.

those described by Garrison and Lewis (1987) and Rogerson (2005). We observed the greatest browse rates (proportion of leaves browsed) during the first 2 weeks after plant emergence. Garrison and Lewis (1987) found that browse intensity was greatest in the first 4 weeks after plant emergence, whereas Rogerson (2005) found that browse intensity was greatest in the first 3 weeks after plant emergence.

Plant phenology

Decreasing leaf browse rates may be the result of leaves becoming less palatable as soybean plants mature (Rogerson 2005 and Lyon and Scanlon 1987). Although we found significant variation in forage quality components (i.e., Ca, CP, Na, and P) for different growth stages, the nutrient requirements for white-tailed deer were met or exceeded in all cases (Ullrey et al. 1973, Grasman and Hellgren 1993, Asleson et al. 1996, and Hellgren and Pitts 1997). Therefore, it is unlikely that variation in these nutrients caused a decrease in palatability.

Acid detergent fiber (ADF) and NDF are the primary factors for determining forage quality in terms of digestion. High-quality forage, such as alfalfa, has an ADF value of 28% and a NDF value of 38% (Jeranyama and Garcia 2004). The ADF and NDF values for soybean leaves that we observed were lower than those reported by Jeranyama and Garcia (2004) for high-quality cattle forage. Because deer are more efficient digesters than cattle, we believe that the values we observed indicated quality deer forage with respect to digestibility (Robbins 1993). Additionally, ADF and NDF did not exhibit an increasing trend, which would be expected if leaves were becoming less digestible as the growing season progressed (Moen 1985). The double-crop field showed a decrease in ADF and NDF, suggesting that leaves were becoming more palatable as the growing season progressed. Our results suggest that decreasing browse rates during the early growing season are not related to changes in leaf palatability associated with soybean plant phenology,

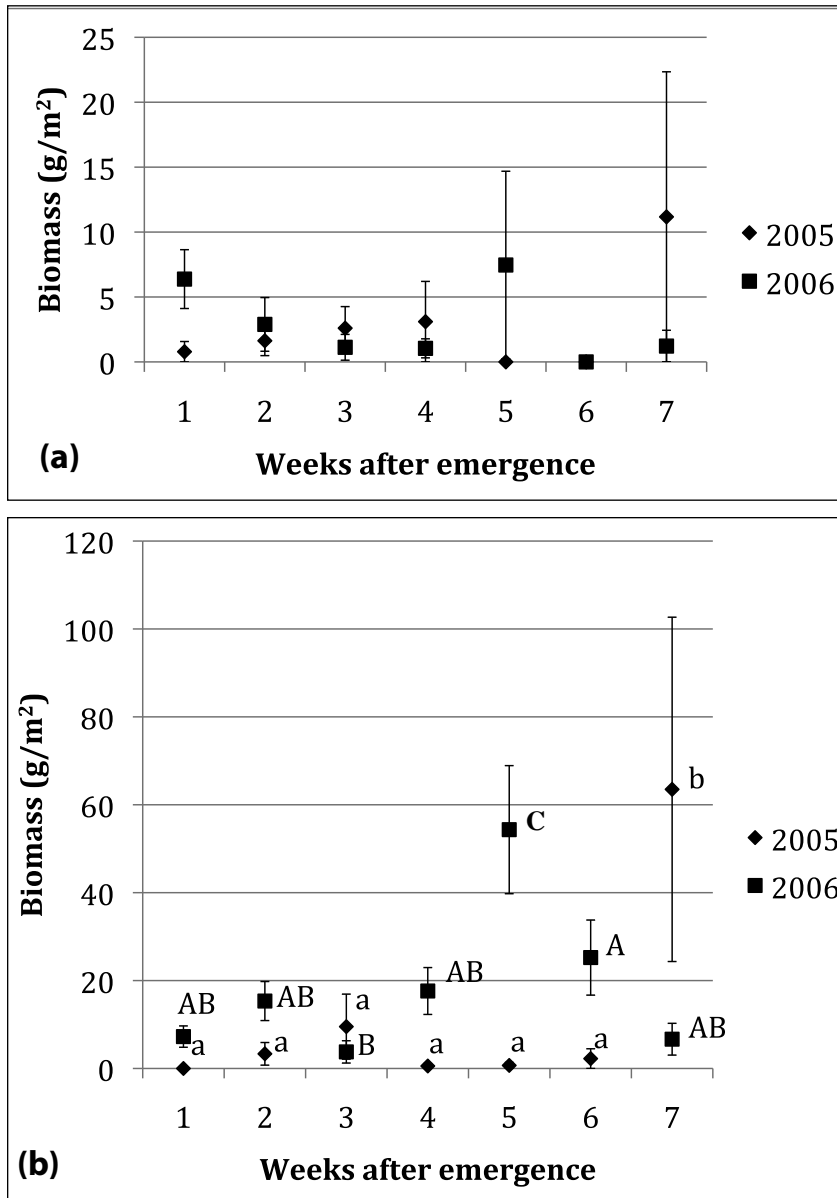


Figure 4. Estimated weekly soybean leaf biomass (g/m²) removed in (a) double- and (b) single-crop soybean fields by week, Little Creek, Delaware, 2005 and 2006.

likely because deer consume new leaves from the uppermost portion of the plant throughout the growing season.

Diet change

The agricultural landscape of the Delmarva Peninsula offers an abundance of highly palatable food items for deer. Rogerson (2005) hypothesized that diet change may have contributed to the decrease in deer browse on soybean plants that he observed 3 weeks after

plant emergence. Like Nixon et al. (1991), we documented deer feeding on all 3 crop types (i.e., corn, soybeans, and winter wheat). From soybean plant emergence, soybean leaves were found in deer diets with increasing frequency as the growing season progressed. Using the same microhistological techniques, Lyon (1984) found that the proportion of deer diets comprised of soybean leaves decreased as the growing season progressed. In contrast to Lyon (1984), our data did not indicate that deer were switching

from soybeans to others crops or native forage during the first 7 weeks after plant emergence. We collected diet samples only during the part of the growing season when double-crop soybean was unavailable to deer to prevent indistinguishable diet components (i.e., double- and single-crop soybeans) from confounding the results. Although conclusions cannot be drawn regarding how diet change may or may not affect deer-browse on double crop soybean crops, the greatest decrease in browse rates was observed for single-crop soybeans. Therefore, our results suggest that a dietary shift away from single-crop soybeans is not the cause of the decrease in browse that we observed.

Induced plant response

Rogerson (2005) hypothesized that plants that have been browsed by deer become less palatable following the initial browsing event. Although research indicates chemical changes occurring within soybean plants in response to insect herbivory (Klubertanz et al. 1996, Peterson and Higley 1996), the manner in which insects feed is different from that of deer. Deer tend to eat whole leaves, whereas insects feed by chewing leaves or sucking phloem. We did not observe deer-browse increasing within protected plots once the protection was removed, except for the 2006 single-crop field. Our results suggested that the increase in browsing may have resulted from protected plots being more attractive to deer because of their height. Plots that were protected for 4 weeks were taller than the surrounding plants. We were unsure if the increased height resulted from increased sunlight in smaller plots or from deer-browsing reducing plant height. Anderson (1994) documented that taller white-flowered trillium (*Trillium grandiflorum*) are more attractive to deer than shorter plants of the same species. Because we did not see increased browsing of the protected plots once the protection was removed, we believed that chemical changes in the plant as a result of browsing did not cause the decrease in browsing that we observed as soybeans matured.

Leaf biomass

As the season progresses, deer may have to eat fewer leaves to consume the same amount of biomass. Soybean leaves grow progressively

larger during the first 6 vegetative stages (Leadley and Reynolds 1989), and leaves on the uppermost nodes are thicker and weigh more (Lugg and Sinclair 1980). Although we did not observe significant differences in the amount of biomass consumed across the growing season for double-crop fields, we did observe an increasing trend in biomass usage from single-crop fields. We expected to see similar rates of biomass usage if this hypothesis were true, so the increase in usage was unexpected. Based on our results, we believe that the increasing biomass of leaves is the most plausible explanation for the decrease in browsing that we observed as soybeans matured.

Management implications

When quantifying deer damage to soybean crops, browse rates should be standardized by the amount of biomass removed for a given period. Soybean plants are more susceptible to being killed by deer-browse early in the growing season when the amount of biomass per plant is lowest. In the early part of the growing season, deer remove more biomass per plant than later in the season. Deer damage to soybean crops may look misleadingly severe in the first 3 weeks after plants emerge. Deer-browse on soybeans is continuous across the growing season, but as the growing season progresses browse becomes less apparent to growers and less detrimental to the plants. In areas with moderate deer densities, plants may recover from early season browsing, becoming bushier and may have increased yield as the result of deer-browse (Rogerson 2005). In cases where crop protection is necessary, protection treatments may need to be used only until plants have accumulated enough leaf biomass to sustain browsing. Although mitigation techniques can be effective in the short-term, maintaining healthy, low-density deer populations may be the most cost effective tool in mitigating deer damage on soybean crops.

Acknowledgments

We thank the many technicians that assisted with data collection. We would like to express our sincere gratitude to C. Dickerson and S. Dickerson for allowing us to use their farm for our project and for their more than generous hospitality. We thank E. Tymkiw and D.

Kalb for reviewing drafts of this manuscript. We thank 2 anonymous reviewers and M. R. Conover for providing comments that improved our manuscript. The MacIntire-Stennis Forestry Research Program, University of Delaware, Jack H. Berryman Institute, and Delaware Department of Natural Resources and Environmental Control provided funding for this project.

Literature cited

- Anderson, R. C. 1994. Height of white-flowered trillium (*Trillium grandiflorum*) as an index of deer browsing intensity. *Ecological Applications* 4:104–109.
- Asleson, M. A., Hellgren, E. C., Varner, L. W. 1996. Nitrogen requirements for antler growth and maintenance in white-tailed deer. *Journal of Wildlife Management* 60:744–752.
- Bowman, J. L. 2006. An evaluation of deer management in Delaware. Delaware Division of Fish and Wildlife, Dover, Delaware, USA.
- Campbell T. A, W. M. Ford, P. E. Hale, J. M. Wentworth, A. S. Johnson, and K. V. Miller. 2002. Nutritional value of yellow-poplar flowers to deer in the southern Appalachians. *Southeastern Naturalist* 1:425–432.
- Conover, M. R. 1994. Perceptions of grass-roots leaders of the agricultural community about wildlife damage on their farms and ranches. *Wildlife Society Bulletin* 22:94–100.
- Conover, M. R. 1997. Monetary and intangible valuation of deer in the United States. *Wildlife Society Bulletin* 25:298–305.
- DeCalesta, D. S., Schwendeman, D.B. 1978. Characterization of deer damage to soybean plants. *Wildlife Society Bulletin* 6:250–253.
- Garrison, R. L., and J. C. Lewis. 1987. Effects of browsing by white-tailed deer on yields of soybeans. *Wildlife Society Bulletin* 15:555–559.
- Grasman, B. T., and E. C. Hellgren. 1993. Phosphorous nutrition in white-tailed deer: nutrient balance, physiological responses, and antler growth. *Ecology* 74:2279–2296.
- Hartman, D.C. 1972. Behavioral characteristics of the white-tail deer (*Odocoileus virginianus*) in relation to agricultural damage in Columbia County, Pennsylvania. Thesis, Pennsylvania State University, State College, Pennsylvania, USA.
- Hellgren, E. C., and W. J. Pitts. 1997. Sodium economy in white-tailed deer (*Odocoileus virginianus*). *Physiological Zoology* 70:547–555.
- Holechek, J., and M. Vavra. 1981. The effect of slide and frequency observation numbers on the precision of microhistological analysis. *Journal of Range Management* 34: 337–338.
- Jeranyama, P., and A. D. Garcia. 2004. Understanding relative feed value (RFV) and relative forage quality (RFQ). South Dakota State University Cooperative Extension Service. Publication Ex8149. Brookings, South Dakota, USA.
- Klubertanz, T. H., L. P. Pedigo, and R. E. Carlson. 1996. Soybean physiology, regrowth and senescence in response to defoliation. *Agronomy Journal*. 88: 577–582.
- Kogan, M., and D. Fisher. 1991. Inducible defenses in soybean against herbivorous insects. Pages 347–378 in D. W. Tallamy and M. J. Raupp, editors. *Phytochemical induction by herbivores*. Wiley, New York, New York, USA.
- Leadley, P. W., and J. F. Reynolds. 1989. Effect of carbon dioxide enrichment on development of the first six mainstem leaves in soybean. *American Journal of Botany* 76:1551–1555.
- Lugg, D. G., and T. R. Sinclair. 1980. Seasonal changes in morphology and anatomy of field grown soybean leaves. *Crop Science* 20:191–196.
- Lyon, L. A. 1984. Food selection by the white-tailed deer (*Odocoileus virginianus*) in the soybean agroecosystem. *Bulletin of the Ecological Society of America* 65:167.
- Lyon, L. A., and P. F. Scanlon. 1987. Use of soybean fields in eastern Virginia by white-tailed deer. *Proceedings of the Eastern Wildlife Damage Control Conference* 3:108–117.
- Moen, A. N. 1985. Season and twig-length effects on cell composition of red maple. *Journal of Wildlife Management* 49:521–524.
- National Climatic Data Center. 2004. *Climatology of the United States*, No. 20 1971–2000. National Oceanic and Atmospheric Administration, U.S. Department of Commerce, Asheville, North Carolina, USA.
- Nixon, C. M., L. P. Hanson, P. A. Brewer, and J. E. Chelsvig. 1991. Ecology of white-tailed deer in an intensively farmed region of Illinois. *Wildlife Society Monographs* 118.
- Peterson, R. K. D., and L. G. Higley. 1996. Temporal changes in soybean gas exchange fol-

lowing simulated insect defoliation. *Agronomy Journal*. 88:550–554.

Ritchie, S. W., J. J., Hanway, H. E. Thompson, and G. O. Benson. 1997. How a soybean plant develops, Special Report. Cooperative Extension Service, Iowa State University of Science and Technology, Ames, Iowa, USA,

Robbins, C. T. 1993. *Wildlife nutrition and feeding*. Academic Press, San Diego, California, USA.

Rogerson, J. E. 2005. The effect of protection and distance from the forest edge on soybean yield due to white-tailed deer browsing. Thesis, University of Delaware, Newark, Delaware, USA.

Ullrey, D. E., W. G. Youatt, H. E. Johnson, L. D. Fay, B.L. Schoepke, W.T. Magee, and K. K. Keahey. 1973. Calcium requirements of weaned white-tailed deer fawns. *Journal of Wildlife Management* 37:187–194.

VerCauteren, K. C., and S. E. Hygnstrom. 1993. White-tailed deer home range characteristics and impacts relative to field corn damage. *Proceedings of the Great Plains Wildlife Damage Control Workshop* 11:218–219.

Wallace, S. U., J. H. Palmer, J. M. Barnes, L. C. Francoeur, and G. K. Yarrow. 1996. Strategies for reducing deer damage to soybeans. *Clemson University Cooperative Extension Publication IL 59*. Clemson, South Carolina, USA.

GREGORY M. COLLIGAN is currently a wildlife technician at Denali National Park in Alaska. He also works with the U.S. Forest Service, Pacific Southwest Research Station in California and Oregon researching Pacific fisher ecology. He received his M.S. degree in wildlife ecology from the University of Delaware in 2007 and B.S. degree in environmental biology from Unity College (Maine) in 2003.



JACOB L. BOWMAN is an associate professor of wildlife ecology at the University of Delaware. He



received his B.S. degree in forestry and wildlife with a minor in biology from Virginia Tech in 1992, his M.S. degree in wildlife ecology (with a minor in statistics) from Mississippi State University (MSU) in 1996, and his Ph.D. degree in forest resources

with an emphasis in wildlife ecology from MSU in 1999. Additionally, he has worked for the National Park Service at Shenandoah National Park. His research interests include human–wildlife interactions, GIS applications in wildlife ecology, population dynamics, and carnivore and large mammal ecology and management.

JOSEPH E. ROGERSON completed his B.S. degree in wildlife and fisheries resources at West Virginia University in 2003 and his M.S. degree in wildlife ecology at the University of Delaware in 2005. Currently, he works for the Delaware Division of Fish and Wildlife as the state's game mammal biologist. He is a certified wildlife biologist and past president of the Maryland-Delaware Chapter of The Wildlife Society. He enjoys spending time with his wife and daughter and hunting nearly anything that has an open season.



He enjoys spending time with his wife and daughter and hunting nearly anything that has an open season.

BRUCE L. VASILAS (photo unavailable) received his B.S. and M.S. degrees in soil biochemistry from the University of Maryland and his Ph.D. degree in soil microbiology for the University of Minnesota. He is professor of agronomy and soil management at the University of Delaware. His research interests are environmental assessment of anthropogenic disturbance to wetlands, water quality in natural wetlands, hydric soil identification and use in characterizing wetland hydroperiods, and wetland delineation.