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Effect of Browsing by Deer on the Growth and Reproductive Success of Lactuca canadensis (Asteraceae)

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ABSTRACT.—We studied the effect of deer-browsing on reproductive success of the forb *Lactuca canadensis* (Asteraceae) in an old field at Cedar Creek Natural History Area, Minn. Height and vertical growth between 2 sample dates were significantly reduced as a result of browsing by deer. The number of flower heads per plant was over seven times greater on unbrowsed vs. browsed plants. Fruits from browsed and unbrowsed plants showed a bimodal weight distribution. Unbrowsed plants had a greater proportion of large fruits, with the result that average fruit weight was greater for unbrowsed plants than for browsed plants. Our data indicate that *Lactuca canadensis* is not able to compensate for damage resulting from browsing by deer.

INTRODUCTION

In most cases herbivory is detrimental to a plant because of the loss of tissues and nutrients (Belsky, 1986; Allison, 1990). For example, Canada yew (*Taxus canadensis*) showed reduced reproductive effort after browsing, and slow recovery after being protected from deer (Allison, 1990). In some cases, however, it has been shown that herbivory can be beneficial to the plant. For example, plants of the thistle *Jurinea mollis* that were attacked by lepidopteran larvae had more flowering stems and produced more seeds than plants that were not attacked (Inouye, 1982). Smooth sumac (*Rhus glabra*), a clonal perennial shrub, increased growth and likelihood to produce fruits 1 yr after it was browsed by deer (Strauss, 1991). Low to moderate grazing intensities increased overall aboveground productivity in several grass species in the Serengeti (McNaughton, 1979). The biennial forb, scarlet gilia (*Ipomopsis aggregata*), showed a 2.4-fold increase in reproductive fitness when 95% or more of its aboveground biomass was naturally or experimentally browsed (Paige and Whitham, 1987). In all of these cases plants overcompensated in response to browsing with increased growth and reproductive output. In this study we examined the effect of browsing by white-tailed deer (*Odocoileus virginianus*) on the monocarpic perennial forb, *Lactuca canadensis*. Using a local population of plants growing inside and outside an experimental deer exclosure, we compared growth and reproductive output of plants that were exposed to or protected from browsing by deer.

METHODS

This study was conducted at the Cedar Creek Natural History Area, located approximately 50 km N of Minneapolis, Minn. Cedar Creek is located on glacial outwash deposited at the end of the Wisconsin glaciation, hence soils are very sandy (Grigal *et al.*, 1974). Cedar

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Creek includes many old fields that were abandoned from agriculture during the past 75 yr. Soils in these fields tend to be low in nitrogen and in organic matter (Inouye *et al.*, 1987), and plant communities in Cedar Creek old fields are typically dominated by herbaceous vegetation for long periods after abandonment from agriculture (Inouye *et al.*, 1994).

Deer are abundant at Cedar Creek. Many move into the area in the autumn from surrounding agricultural areas and most trees at forest-field margins are browsed during the winter or spring (Inouye *et al.*, 1994). In the spring some deer leave the area, but a large number remain throughout the summer, during which time soft-stemmed forbs can be an important part of the diet for white-tailed deer (Korschgen *et al.*, 1980; Weckerly and Kennedy, 1992).

Data for this study were collected in Cedar Creek field #28, last cultivated in 1988, located just N of Beckman Lake. In 1990, replicated gopher exclosures (12 × 12 m), gopher + deer exclosures (12 × 15 m), and reference plots (12 × 12 m) were established in this field. Plots were placed along the S and E sides of the field, 10 m from the forest-field margin, with 8–10 m between adjacent plots. Exclosures were fenced below ground with welded wire that extended 1.2 m down from the soil surface and, at that depth, 0.6 m horizontally away from the plot. Galvanized hardware cloth (0.64 cm mesh) was attached to the welded wire at ground level and extended 45.7 cm above the ground. Aluminum flashing 15.2 cm wide was attached to the top of the hardware cloth. Gopher + deer exclosures were fenced aboveground with 1.8-m tall poultry netting.

Lactuca canadensis L. (Asteraceae) is a tall branched plant that produces many small flowers. *Lactuca canadensis* occurs throughout most of northeastern and N central U.S. and parts of Canada typically in thickets, at the edges of woods or in clearings (Fernald, 1950). It is a highly variable plant, particularly in terms of leaf shape, but all the individuals in this population had deeply lobed leaves and were morphologically similar within each treatment. *Lactuca canadensis* produces a large amount of sticky, milky sap. Sap from species of *Lactuca* has been shown to contain various compounds that may serve to deter herbivory (Lebeda, 1986). For example, sap from *Lactuca canadensis* has been found to contain the guaianolides lactucin and lactucopikrin (Gonzalez, 1977). Studies of lettuce (*Lactuca sativa* L.) have shown that latex in this cultivated species can effectively trap both aphids and whiteflies (Dussourd, 1995); thus it can serve as an effective mechanical deterrent for some herbivores.

At Cedar Creek *Lactuca canadensis* is present in fields of various ages but is rather rare. *Lactuca canadensis* or *Lactuca* spp. occurred in 15 of 22 old fields surveyed in 1983 (Inouye *et al.*, 1987) and in six of those same fields when they were resurveyed in 1989, but the proportion of cover it occupied was never greater than 0.0018 with an average of 0.0004. *Lactuca canadensis* can be an annual or a monocarpic perennial (Fernald, 1950). The population of plants focused on in this study included small non-flowering rosettes as well as flowering plants, suggesting that these were not annuals.

The population of *Lactuca canadensis* plants used in this study was within a 10 × 12 m area bisected by one side of a gopher + deer exclosure. All plants were tagged and measured in June and August (199?). Data collected in June included maximum height, rosette diameter, number of places where the plant had been browsed, and distance to the closest conspecific (nearest neighbor distance). Data taken in August included maximum height, number of places where the plant had been browsed, and an estimate of the number of flowering heads per plant. The number of flowering heads was estimated by counting the number of 'flowering branches' that grew off the main stem. A 'flowering branch' was defined as any branch that had at least one flower head growing directly off it. In cases where a browsed plant had multiple stems, branches were counted on each stem. To estimate the number of flowering heads per plant, the number of mature flowering heads on a flowering branch was counted for a sample of branches on a subset of plants both inside and outside the exclosure. For unbrowsed plants, flowering heads were counted on the lowest branch and on every 10th branch moving up the main stem; sampling was stratified in this way because the number of flowering heads per branch decreased with height on the main stem. When possible, this same method was used for browsed plants. When there was no vertical stratification of branches, flowering heads were counted on randomly chosen branches. Total number of flowering heads per plant was estimated by multiplying the average number of flowering heads per branch times the number of flowering branches.

Height growth was calculated as the difference in height between the two census dates.

Fruits were collected from approximately half the plants inside and outside the exclosure. Flowering heads containing only fruits that were pale brown and nearly transparent were deemed immature and were excluded from the sample, as were flowering heads that showed evidence of parasitism by hymenopteran larvae. Of the fruits that were collected from each plant, 40 were chosen at random and weighed individually on an electronic microbalance.

One-way analysis of variance was used to compare plant height, height growth, nearest neighbor distance, number of flowering branches, number of flowers per branch, and total flowers per plant for plants inside and outside the exclosure. The effect of the number of places where plants had been browsed on plant height and number of flowers was analyzed with a simple regression. These analyses were all performed using StatView II for the Macintosh.

Fruit weights for plants inside and outside the exclosure were compared two ways. First, one-way Analysis of Variance (ANOVA) was used to compare average fruit weight (one value per plant) for plants inside and outside the exclosure. A more powerful test would have been to use a nested ANOVA in which fruits were nested by plant; however, transformation of individual fruit weights did not correct for heterogeneous variances. Heteroscedasticity was not a problem for the ANOVA of average fruit weight. As a second means of comparing fruit weight for browsed and unbrowsed plants, the distribution of individual fruit weights inside and outside the exclosure was compared using a Kolmogorov-Smirnov two-sample test. These analyses were performed with Systat 5.03 for DOS.

RESULTS

The population of *Lactuca canadensis* in field 28 was very localized. Only a few flowering plants, one in an adjacent gopher exclosure and two others in a nearby gopher + deer exclosure, were observed in the rest of the field. The 10 × 12 m area bisected by the gopher + deer fence contained 77 plants, 38 inside the exclosure (24 in flower) and 39 outside the exclosure (25 in flower). Most plants were within 3 m of the fence, with a few individuals up to 6 m from the fence. Average nearest neighbor distance was similar inside and outside the exclosure (Table 1), as was the survival rate of plants between sampling dates (100% both inside and outside the exclosure).

Plants in flower that were not browsed produced a single stem (3–4 cm in diam) with deeply lobed leaves on the lower half and flowering branches on the upper half (Fig. 1). Browsing occurred primarily in the spring and early summer and by the 1st sampling date in June the main stem of all the plants outside the exclosure had been browsed to less than 10 cm above the ground. On these plants multiple branches at the base of the main stem elongated and produced additional flowering branches (Fig. 1). In addition to flowers, these branches typically produced a few unlobed leaves not found on flowering branches of unbrowsed plants.

TABLE 1.—Averages are for all flowering *Lactuca canadensis* plants within a 10 × 12 m area bisected by the fence of an exclosure, except for nearest neighbor distance (NND) which includes rosettes as well as flowering individuals. There were 38 *L. canadensis* inside the exclosure with 24 of them flowering, and 39 outside the exclosure with 25 of them in flower. Average fruit weights are for all individual seeds. F and P values are results of one-way ANOVAs (df = 1, 11)

		Inside	Outside	ANOVA
Nearest neighbor distance (cm)	Ave	61.8	54.1	F = 0.26
	SD	81.1	47.7	P = 0.61
	Range	4–415	4–200	
June height (cm)	Ave	39.0	8.3	F = 95.64
	SD	15.0	4.3	P < 0.001
	Range	14–61	1–21	
August height (cm)	Ave	136.9	63.8	F = 135.59
	SD	28.3	13.4	P < 0.001
	Range	75–174	30–87	
Number of flowering branches	Ave	53.8	25.1	F = 10.36
	SD	40.1	19.4	P = 0.002
	Range	19–223	5–76	
Flowering heads per branch	Ave	33.7	11.5	F = 21.54
	SD	36.4	9.7	P < 0.001
	Range	3–178	2–57	
Flowering heads per plant	Ave	1725	231	F = 16.88
	SD	1702	144	P < 0.001
	Range	171–5904	48–630	
Average fruit weight (mg × 10^{-2})	Ave	0.469	0.403	F = 3.73
	SD	0.132	0.142	P = 0.079
	Range	0.124–0.705	0.123–0.696	

Plant height was significantly greater inside the exclosure on both sampling dates (Table 1); height growth between the sample dates also was greater for plants inside the exclosure. Plants in the exclosure had significantly more flowering branches, more flowering heads per branch and more flowering heads per plant (Table 1).

There was no significant relationship between plant height or number of flowers per plant and the number of points at which a plant was browsed.

Based on the one-way ANOVA, average fruit weight for browsed plants was marginally significantly less than that for unbrowsed plants (Table 1). Fruits from both browsed and unbrowsed plants had bimodal weight distributions (Fig. 2). Although the range of seed weights was similar for browsed and unbrowsed plants, lower seed weights were more common for browsed plants (69% of seeds weighed less than 0.45 mg) than for unbrowsed plants (45% of seeds weighed less than 0.45 mg). Results of the Kolmogorov-Smirnov test indicated that the distribution of fruit weights was significantly different for fruits collected inside and outside the exclosure (maximum difference = 0.258, $P < 0.001$).

DISCUSSION

Browsing by deer affected *Lactuca canadensis* by reducing plant height, causing a change in the morphology of the plant, and, based on the number of flowering heads per plant, causing over a 7-fold reduction in reproductive output (Table 1, flowering heads per plant). Although we did not directly measure it, changes in plant height and the morphology of leaves on flowering stems suggest that there may have been significant reductions in pho-

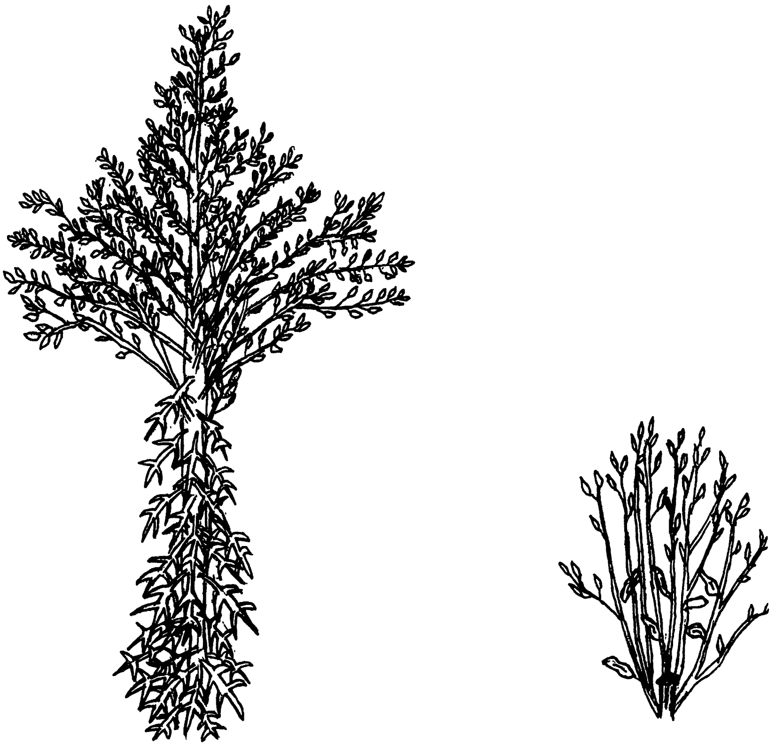

FIG. 1.—Typical morphologies of unbrowsed (left) and browsed (right) plants. Removal of the main stem results in production of smaller flowering branches originating from the remains of the main stem. The flowering branches of the browsed plant have a few small, unlobed leaves in contrast to the large, deeply lobed leaves that grow on the lower half of the plant in unbrowsed individuals

tosynthetic surface area as a result of browsing. It does not appear that browsing benefits *L. canadensis* in any way, unlike some other plants which have been shown to overcompensate for the effect of browsing and have improved reproductive outputs.

We did not determine if the number of fruits per flowering head was different for browsed and unbrowsed plants, and such differences could influence our estimates of relative reproductive output. However, even if the number of fruits per flowering head was smaller for unbrowsed plants, it is unlikely that such a difference would compensate for the more than seven-fold decrease in the number of flowering heads on browsed plants.

The effect of browsing can be attributed to deer because a single plant growing in a gopher exclosure adjacent to the study population was also browsed, indicating that gophers and other small mammals were not responsible for the damage to the plants. Some other forbs (*e.g., Hieracium longipilum, Verbascum thapsus*) are also browsed by deer at Cedar Creek, but they are more common and the proportion of browsed plants is typically much lower than that observed for *Lactuca canadensis* in this study.

The occurrence of a bimodal seed weight distribution is not surprising; it occurs in many weedy and some nonweedy annuals (Flint and Palmblad, 1978; Philipupillai and Ungar, 1984; Obeso, 1993). It has been suggested that the occurrence of two different-sized seeds, which typically vary in their germination behavior and/or dispersal ability, can extend the

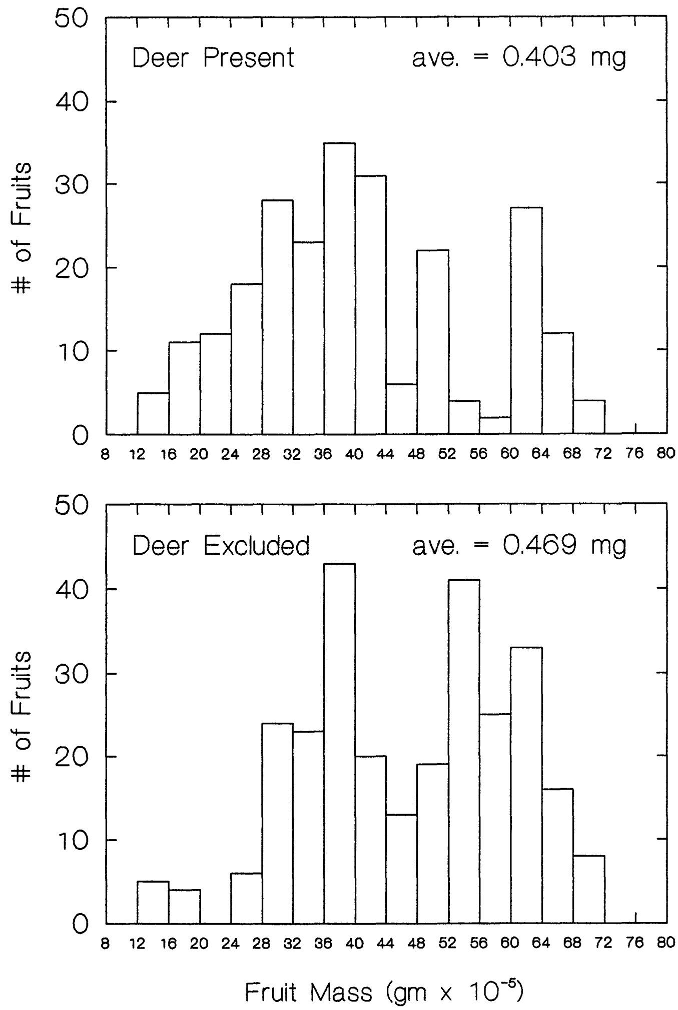

FIG. 2.—The distribution of fruit weights of individual fruits from plants outside (top) and intside (bottom) of a deer exclosure. The two distributions are significantly different (Kolmogorov-Smirnov test, $P < 0.001$)

germination range of the offspring on a spatial or temporal scale (Philipupillai and Ungar, 1984). In most species with dimorphic seeds, larger seeds will germinate faster whereas the smaller seeds remain in the seed bank and germinate throughout a longer period of the growing season. This is advantageous because it allows the population to be replaced by germination of the smaller seeds if some event such as drought, cold or flood destroys the early seedlings. In addition, there may be selective pressure toward a wider range of seed sizes in plants where seed dispersal is strongly associated with seed mass, as is typically the case in wind-dispersed species, thereby creating a larger seed shadow (Byrne and Mazer, 1990). Other authors have suggested that dimorphic seeds are advantageous in unpredictable or heterogenous environments because each seed type may be better adapted to different conditions (Philipupillai and Ungar, 1984; Janzen, 1977).

Browsed plants produced fewer heavier seeds. This may simply be the result of a reduction in photosynthetic surface area on browsed plants; however, it could be advantageous in two ways. First, by producing lighter seeds a plant may be able to increase the number of seeds it produces. This may, of course, result in a decrease in the probability of establishment of any individual seed. Second, in a wind-dispersed plant such as *Lactuca canadensis,* lighter seeds are more likely to disperse farther than heavier seeds (Matlack, 1987; Byrne and Mazer, 1990; Obeso, 1993). Since browsed plants were shorter than unbrowsed plants, dispersal distances for seeds of the same weight are likely to be shorter for browsed plants than for unbrowsed plants. Browsed plants could partially compensate for this by producing lighter seeds that have a wider dispersal range.

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