Effects of White-Tailed Deer on Populations of an Understory Forb in Fragmented Deciduous Forests

DAVID J. AUGUSTINE*‡ AND LEE E. FRELICH†

*Department of Fisheries and Wildlife, University of Minnesota, 1980 Folwell Ave., St. Paul, MN 55108, U.S.A.
†Department of Forest Resources, University of Minnesota, St. Paul, MN 55108, U.S.A.,
email freli001@maroon.tc.umn.edu

Abstract: *The effects of grazing by white-tailed deer* (Odocoileus virginianus) *on populations of* Trillium *spp. were examined in remnant, old-growth patches of the highly fragmented Big Woods forest ecosystem in southeastern Minnesota. We conducted three separate studies involving an exclosure experiment, transplant experiments, and comparisons of* Trillium *populations among study sites. The highest grazing intensity was observed where deer occurred at high overwinter concentrations (~25–35/km²); significantly lower grazing intensities occurred at low overwinter density (~5–10/km²). Deer focused their grazing on large, reproductive plants; at sites with high deer density,* Trillium *population structure was skewed toward small plants, and deer consistently caused over 50% reduction in reproduction during the growing season. Protection of individual plants from deer for two growing seasons resulted in dramatically increased flowering rates and significantly greater leaf area compared to control plants. No significant impact of current-year herbivory on reproduction in the following year was detected. Nevertheless, flowering rates at one site with high overwinter deer densities for at least the past 5 years suggest that the cumulative effects of grazing over several years can reduce reproduction in subsequent years. Transplant experiments with* Trillium grandiflorum *also showed that deer had significant effects on growth and reproduction where deer occur at high density. Our results suggest that changes in landscape structure and local deer abundance have altered plant-deer relationships such that grazing can lead to the local extirpation of sensitive forbs such as* Trillium *spp. As a result, active, long-term management of deer at low densities appears necessary for the conservation and restoration of fragmented forest communities in eastern North America.*

Efectos del Venado Cola Blanca en Poblaciones de *Trillium* spp. en Bosques Decidous Fragmentados

Resumen: *Los efectos de ramoneo por venado cola blanca* (Odocoileus virginianus) *en poblaciones de* Trillium *spp. fueron examinadas en parches remanentes de bosque maduro del ecosistema altamente fragmentado del bosque Big Woods en el sureste de Minnesota. Realizamos tres estudios separados que involucraron un experimento en un encierro, experimentos de transplante y comparaciones de poblaciones de* Trillium *entre sitios de estudio. La intensidad del ramoneo más alta se observó donde los venados se concentraron para pasar el invierno (~25–35/km²), mientras que intesidades menores de ramoneo ocurrieron a bajas densidades durante el invierno (~5–10/km²). Los venados enfocaron su consumo en plantas reproductivas grandes; en sitios con alta densidad de venados la estructura poblacional de* Trillium *estuvo sesgada a plantas pequeñas y los venados consistentemente ocasionaron una reducción mayor al 50% en la reproducción durante la temporada de crecimiento. La protección de plantas individuales de la depredación de los venados por dos temporadas de crecimiento resultó en un dramático incremento en la tasa de florecimiento y una cobertura de hojas significativamente mayor comparando con plantas control. No se detectó un impacto significativo de la herbivoría del año en curso en la reproducción del año siguiente. Sin embargo, las tasas de florecimiento en un sitio con alta densidad de venados durante el invierno por al menos cinco años consecutivos sugiere que el efecto acumulativo del ramoneo a lo largo de varios años puede reducir la reproducción*

en años subsecuentes. Experimentos de transplantes con Trillium grandiflorum *mostraron también que los venados tienen un efecto significativo en el crecimiento y reproducción en sitios donde los venados ocurren el altas densidades. Nuestros resultados sugieren que los cambios en la estructura del paisaje y la abundancia local de venados han alterado las relaciones planta-venados a un punto en el que el ramoneo podría conducir a la extirpación local de especies sensitivas como lo son* Trillium *spp. Como resultado, aparenta ser necesario el manejo activo a largo plazo de venados a bajas densidades para la conservación y restauración de comunidades de bosques fragmentados en el este de Norteamérica.*

Introduction

Human-induced changes in the abundance of mammalian herbivores, through changes in hunting practices, predation pressure, and exotic introductions, can critically alter the structure and dynamics of ecosystems worldwide (Howard 1966; Harper 1969; Spatz & Mueller-Dombois 1973; Leuthold 1996; McShea & Rappole 1997). One documented consequence of increased white-tailed deer densities in eastern North America is the deleterious effect on populations of sensitive tree species and the resulting potential for local species extirpations (Anderson & Loucks 1979; Frelich & Lorimer 1985; Allison 1990). Although extensive research has examined winter browsing effects on forest communities (Graham 1952; Beals et al. 1960; Tilghman 1989; Strole & Anderson 1992; Anderson & Katz 1993), considerably less attention has been paid to growing-season deer herbivory and its potential effects on understory herbaceous plant communities (Miller et al. 1992; Anderson 1994; Balgooyen & Waller 1995; Rooney 1997). As managers continue to face difficult decisions concerning the management of deer populations, often with limited available information, a better understanding is needed of the effects deer exert on native plant communities.

Alverson et al. (1988, 1994) suggested that human-induced changes in the distribution of plant communities can alter plant-herbivore relationships and can potentially cause significant herbivore impacts within the new landscape. In Minnesota, dramatic changes in the structure of forest landscapes have changed the distribution and abundance of white-tailed deer (Berner & Simon 1993). In southeastern Minnesota, some 8000 km^2 of contiguous mesic deciduous forest in the presettlement landscape dominated by elms (*Ulmus americana* and *Ulmus rubra*), sugar maple (*Acer saccharum*), and American basswood (*Tilia americana*) (Daubenmire 1936; Grimm 1984) have been almost entirely converted to agricultural and suburban land uses. Today, the only remaining fragments of this forest type, commonly termed Big Woods forest, are on the order of 8–32 ha (Jakes 1980; Vasilevsky & Hackett 1980), and conservation plans focus on protecting existing old-growth fragments, restoring forest corridors between fragments,

and restoring characteristic species. Deer were extirpated or extremely rare in this region of the state from the late 1800s through the 1920s, and counties in southeastern Minnesota were still closed to hunting in most years during the 1950s and 1960s to promote population recovery (Berner & Simon 1993). Over the past three decades, deer populations in southeastern Minnesota have increased steadily (Berner & Simon 1993; Dexter 1996).

Recent surveys conducted in four old-growth Big Woods remnants in southeastern Minnesota documented selective deer foraging patterns on understory forbs (Augustine 1997). Species in the genus *Trillium* were consistently grazed to a greater degree than most forb species at different levels of *Trillium* abundance and deer density. Although studies have suggested that deer can eliminate selected herbaceous species from forest patches (e.g., Alverson et al. 1988; Anderson 1994), this has not been experimentally addressed. Our objectives were therefore to examine (1) the effect of deer herbivory on the size structure of *Trillium* populations at various local deer densities, (2) the effect of deer herbivory on the reproductive potential of *Trillium* populations, and (3) the potential influence of deer on restoration of *Trillium* to the forest community.

Methods

Study Area

Studies were conducted at three old-growth Big Woods remnants located in Rice County (44°15'N, 93°20'W) and Hennepin County (45°N, 93°30'W) in southeastern Minnesota. The sites are dominated by sugar maple, American basswood, and elms (>80% of relative dominance by basal area); they exhibit an all-aged distribution of tree sizes and contain large (50–100 cm diameter at breast height [dbh]) individuals of the three dominant tree species (Augustine 1997). Ironwood (*Ostrya viginana*) is an important subcanopy species. Sites contain loamy soils developed from glacial moraines or silty soils developed from loess-covered glacial till (Grimm 1984). The three forests were selected to include two sites with

relatively high local deer densities and one site with a comparatively low local deer density based on 1993–1994 aerial counts.

Species Descriptions

Trillium cernuum and *Trillium flexipes* are long-lived, nonclonal forbs found in the understory of mesic deciduous forests in eastern North America (Gleason & Cronquist 1991). In Minnesota, specimens have been collected throughout the Big Woods region (Ownbey & Morley 1991). In many remaining Big Woods forests in Minnesota, including all three study sites, *T. cernuum and T. flexipes* occur sympatrically, and individuals with hybrid characteristics are commonly observed (Rogers 1981; D.J.A., personal observations). As a result, we considered these species as a single *T. flexipes–T. cernuum* complex.

Trillium grandiflorum is a long-lived, nonclonal forb distributed throughout rich, broad-leaved deciduous forests in eastern North America (Gleason & Cronquist 1991). *Trillium grandiflorum* has been collected from deciduous forests throughout central Minnesota and from stands south, east, and west of the Rice County sites included in this study (Ownbey & Morley 1991). A 1972 survey of a mature Big Woods forest fragment approximately 5 km north of one of the Rice County sites included in this study also documented the presence of *T. grandiflorum* (N. Falkum, personal communication). *Trillium grandiflorum* does not occur naturally in any of the study sites at this time.

Individual *Trillium* plants consist of a single stem (rarely two) supporting a whorl of three leaves in the larger size classes and a single leaf in juvenile plants. *Trillium grandiflorum* seeds germinate in the spring and produce adventitious roots (no leaves) in the first growing season, a cotyledon leaf in the second growing season, and a single leaf in the third growing season (Hanzawa & Kalisz 1993). In Minnesota all three *Trillium* species reach anthesis in late May through early June, and flowering plants begin to develop fruits in June. Both *T. grandiflorum* and *T. flexipes* exhibit a similar population size structure with comparatively high mortality rates of seeds and juvenile size classes and low mortality for larger size classes (Kawano et al. 1986; Ohara & Utech 1988).

Study Design

Three separate studies were used to examine the effects of deer on *Trillium* populations. First, we examined deer grazing intensity and the effect of grazing on population size structure at the two high-deer-density sites (H1 and H2) and the one low-deer-density site (L1). Second, we used small deer exclosures placed around individual *Trillium* plants, each paired with an unexclosed control plant, to measure the magnitude of the effects of deer on growth and reproduction at a site with high deer density. Finally, we examined potential deer influences on plant community restoration efforts by establishing transplanted populations of *Trillium grandiflorum* at one site with high deer density and one with low deer density. This species was chosen because *T. grandiflorum* is palatable to deer (Anderson 1994; Balgooyen & Waller 1995), is absent from many extant Big Woods forests, and is known to have occurred throughout the Big Woods region in Minnesota. The two sites where *T. grandiflorum* was transplanted are located toward the southern edge of the species' range and hence may represent stressful growing conditions where herbivore effects could be especially severe. Randomly chosen *Trillium* transplants were individually protected from deer at each site, creating a 2 × 2 factorial experiment with high and low grazing pressure and protected and unprotected plants.

Deer Density Estimation

Three methods were used to estimate seasonal deer densities at each study site. First, winter density was measured by deer pellet-group counts. Pellet groups were counted within a 4-m radius of 46–50 fixed sampling points at each site immediately following snowmelt (14–20 March in 1995 and 1–12 April in 1996). Because leaf-fall in October creates a relatively uniform layer of litter, late-winter pellet-group counts represent accumulation only for the late fall and winter months, providing an index of overwinter deer presence within the stand. Counts were converted to relative estimates of deer per square kilometer based on a 150-day deposition period assuming 13 pellet groups produced per deer per day (Eberhardt & van Etten 1956). Density differences between sites were compared by means of likelihood ratio tests for log-linear models (Agresti 1996).

We used aerial counts to obtain a second estimate of winter deer density at each study site as a check on pellet count estimates (White 1992; Jordan et al. 1993). Aerial counts were conducted in January 1996, and the area flown at each site included the mature Big Woods stand and a surrounding mosaic of second-growth forest, wetlands, and shrubland. Winter deer density from aerial counts was expressed as the number of deer counted, uncorrected for observer bias, divided by the total area of permanent winter cover, defined as forests, wooded wetlands, and shrubland, within the area flown (Augustine 1997). An analysis of aerial count versus pellet count estimates at six Big Woods forests in southeastern Minnesota showed that both methods provide consistent results for deciduous forests, except in severe winters where alternative winter habitat is locally available (Augustine 1997).

Deer density during spring and summer was measured at each site with three automated cameras attached to infrared deer monitors (Non-typical Engineering, Green Bay, Wisconsin, U.S.A.), which were moved to new, randomly located positions every 7 days (Augustine 1997). Because we had only six monitors, L1 and H2 were sampled in 1995, and H1 was sampled in 1996. Data obtained from camera monitors were analyzed in terms of the number of deer photographed per week.

Grazing Intensity and *Trillium* Size Structure

We sampled naturally occurring *Trillium cernuum* and *T. flexipes* at L1, H1, and H2 using fixed, uniformly spaced 50-m transects. A 2-m transect width was sampled at L1 where *Trillium* was abundant, and a 4-m width was used at H1 and H2. Transects were first sampled during 5–9 May 1995, when plants were emerging from the ground and each *Trillium* stem was marked with a numbered aluminum tag. At this time, the reproductive status (flowering or nonflowering) of each plant was recorded. Because *Trillium* was extremely rare at H2, few plants were observed along transects. We therefore conducted extensive understory searches at this site and marked all plants found between 14 April and 15 May 1995.

Marked plants were re-surveyed during 19–22 June (after *Trillium* anthesis) to record reproductive status, whether each plant was grazed by deer, any other herbivore damage, stem height, and the length and width of one randomly selected leaf for plants that were not completely defoliated. Deer grazing always resulted in 100% defoliation and was recognized by the rough cut of the stem, typically at a height of 15–30 cm. Plants were rechecked for deer grazing in August 1995.

In 1996 marked plants at each site were surveyed during 5–8 May and 17–20 June to record the same measurements as in 1995. In addition, because relatively little deer grazing occurs before early May, the length of the emerging leaf bundle of each plant was recorded in the May survey to obtain a pre-grazing distribution of plant sizes for each population. Plants were rechecked for deer grazing in late June and late July 1996.

Trillium individuals sampled at each site may not be independent with respect to growth if they are located close to one another. For data analyses any time two marked plants were located within 20 cm of one another, we deleted one randomly selected plant in the pair from the sample; all reported sample sizes and analyses are based on this subset of plants.

For *Trillium* species, Kawano et al. (1986) found that leaf area is a good measure of biomass and hence the growth stage of an individual. We estimated leaf area in the field as plant leaf area = leaf length × leaf width × 0.5 × number of leaves. We measured true leaf area for a sample of 30 *T. grandiflorum* and 30 *T. cernuum–T.*

flexipes using an Agvision Monochrome System for Leaf Analysis to establish whether this method provides a reliable estimate of individual leaf area.

Trillium Exclosure Experiment and *T. grandiflorum* Transplant Experiments

To examine the effects of deer on individual growth and reproduction in a naturally occurring *Trillium* population, site H1 was searched during 9–10 May 1995 to find and mark 50 *Trillium* with leaf length of at least 4 cm. Plants were paired (25 pairs) based on size, reproductive status, and location, and one plant in each pair was protected with an individual welded-wire deer exclosure. Plants were monitored for reproduction, deer grazing, other herbivore damage, stem height, and the length and width of one randomly selected leaf on 9–10 May 1995, 27 June 1995, 7 May 1996, and 19 June 1996; they were checked for deer grazing on 17 August 1995 and 26 July 1996.

We transplanted 120 *T. grandiflorum* rhizomes to site L1 and 120 rhizomes to site H2 in August 1994. Individuals were planted along transects at a minimum spacing of 3 m to ensure that each represented an independent observation. At both sites, 40 transplants were randomly selected and each plant was protected with a separate, welded-wire deer exclosure. Plants were monitored for reproductive status, deer grazing, other herbivore damage, stem height, and the length and width of one randomly selected leaf on 11–12 May 1995, 17–18 June 1995, 11–12 May 1996, and 17–18 June 1996; they were rechecked for deer grazing on 26–27 August 1995 and 25–26 July 1996.

Results

Deer Densities

Winter density based on pellet-group counts was significantly lower at L1 than at the high deer sites in both seasons of both years (Fig. 1; likelihood ratio tests, $\Delta G^2 > 12.25$, df = 1, $p < 0.001$, for all comparisons). Pellet-group counts in 1995 showed winter concentrations of 24–31 deer/km^2 at H1 and H2 compared to 4 deer/km^2 at L1 (Fig. 1). Aerial counts showed an overwinter concentration of 25–36 deer/km^2 of permanent cover at H1 and H2 and 11 deer/km^2 at L1 (Fig. 1). The pellet count estimate at H1 was significantly lower in 1996 than 1995 (Fig. 1), but aerial counts conducted in both years at this site showed a constant density (23.4 and 25.3 deer/km^2). The change in pellet density was likely due to increased use of two conifer patches and a large south-facing slope adjacent to site H1 during the more severe winter conditions in 1996. Overall, combined estimates of winter deer density show higher local overwinter

concentrations at H1 and H2 than at L1 during the study period.

Winter aerial counts have been conducted intermittently over the past 8 years at H2 and L1 and every winter for the past 5 years at H1 (J. Moriarty and J. Vorland, personal communication). High deer densities have been present at H1 for at least the past 5 years, whereas the current density at H2 is the result of a rapid increase between 1989 and 1993. Density at L1 has been low over the past 8 years.

The automated cameras provided a sensitive index of growing-season deer density, which was approximately three times higher at H2 than at L1 in 1995 ($\Delta G^2 = 14.6$, df = 1, $p < 0.001$) and four times higher in 1996 at H1 than the 1995 index for L1 ($\Delta G^2 = 31.3$, df = 1, $p < 0.0001$; Fig. 1).

Grazing Intensity and *Trillium* Size Structure

We examined grazing intensity and population size structure for a sample of 143, 28, and 76 marked plants in 1995 and 164, 47, and 90 marked plants in 1996 at L1, H1, and H2, respectively. Most grazing on *Trillium* occurred between early May and the second sampling period in late June, except at H2 in 1995 (Table 1). Grazing intensity was significantly different among sites in both
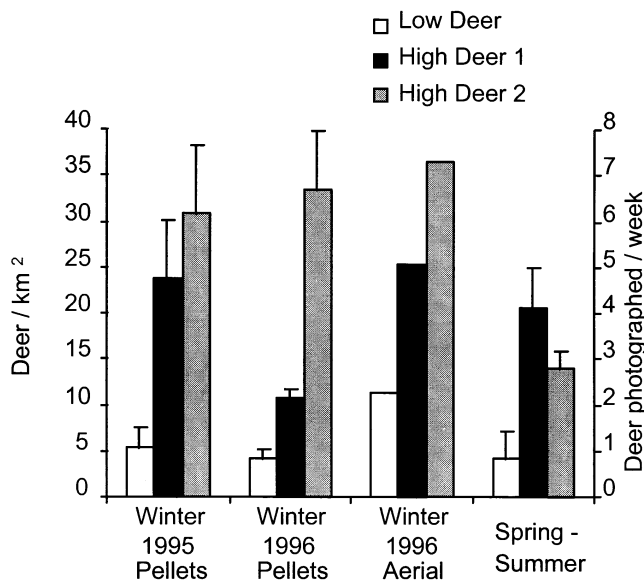

Figure 1. Seasonal deer densities at three study sites, estimated with three methodologies. Winter density was measured by (1) pellet-group counts converted to an estimate of deer/km² ±1 SE, assuming 13 pellet-groups per deer per day and (2) aerial counts. Relative deer density estimates for spring-summer are expressed as the number of deer photographed per week ±1 SE and were measured at H1 and L1 in 1995 and H2 in 1996.

years (Table 1; $\chi^2 = 32.15$ and 27.04, df = 2, $p < 0.0001$). The highest grazing intensity occurred at H2 in both years and was two to five times higher than overall grazing intensities at both L1 and H1. No differences in overall grazing intensity were detected between L1 and H1 in 1995 or 1996 (Table 1; $\chi^2 = 0.29$, $p = 0.59$; $\chi^2 = 0.6$, $p = 0.80$). In addition to deer grazing, some plants were defoliated by lepidopteran larvae that sever the base of the stem. At L1, H1, and H2 respectively, lepidopterans damaged 0.0, 0.0, and 6.6% of plants in 1995 and 0.0, 0.6, and 4.4% of plants in 1996.

We examined two measures of *Trillium* population structure: the distribution of plant sizes within a population and the proportion of flowering plants in a population. Leaf length and width measurements provided a highly significant predictor of true leaf area ($r^2 = 0.99$, $F = 8512$, $p < 0.0001$). In addition, the size class of the emerging leaf bundle (in 0.5 cm increments) measured in early May was a significant predictor of the leaf area of ungrazed plants in June after anthesis (weighted regression, $r^2 = 0.96$, $F = 239$, $p < 0.0001$). Measurements of leaf bundle length in early May were used to construct a pre-grazing plant-size distribution (≤1% were grazed before May sampling), and leaf area estimates from late June were used to construct a post-grazing size distribution for each of the three populations.

No significant differences were detected among the size-class distributions of the three populations in early May (one-tailed K-S statistics ≤0.06, $p \geq 0.8$ for all comparisons; Fig. 2). By late June (postanthesis and postgrazing), significant differences in the size distributions of the three populations were observed (Fig. 2). At H1 the population consisted predominantly of individuals with leaf area under 80 cm², which differed significantly from L1 (K-S statistic = 0.28, $p = 0.05$). The distribution at H2 was shifted toward an increased frequency of smaller plants in the population but was not statistically different from that of the other sites (K-S statistics <0.21, $p > 0.26$). Although no early May measurements were made in 1995, the distribution of plant sizes in late June 1995 at each site was similar to that observed in June 1996.

In early May, prior to the majority of deer grazing, the proportion of the plants flowering in each population provides another measure of the population's structure prior to the within-season effects of grazing. In early May of 1995 and 1996, the flowering rate at H1 (4% and 15%) was significantly lower than that at both L1 (27% and 34%) and H2 (32% and 38%) ($\chi^2 \geq 7.0$, $p \leq 0.008$ for all comparisons). No difference was detected in the May flowering rate between H2 and L1 in either year ($\chi^2 \leq 0.6$, $p \geq 0.40$).

Flowering individuals experienced a higher rate of grazing than the overall *Trillium* population (flowering and nonflowering plants) at all three study sites (Table 1). Grazing intensity on reproductive plants was significantly greater at H2 than L1 in both years (Table 1; $\chi^2 =$

Table 1.   *Trillium* density and deer grazing intensity at three study sites in southeastern Minnesota.

Site*	Trillium *stems/* 10 m² ± SE	Grazed (%) Overall growing season	Grazed (%) Emergence-anthesis	Grazed (%) Post-anthesis	Reproductive plants grazed (%)
1995					
Low deer density (L1)	1.5 ± 0.4	10.5	10.5	0.0	23.7
High deer density 1 (H1)	0.07 ± 0.05	7.1	7.1	0.0	—
High deer density 2 (H2)	0.02 ± 0.01	42.1	18.4	23.7	58.3
1996					
Low deer density (L1)	2.0 ± 0.5	16.5	14.6	1.8	35.7
High deer density 1 (H1)	0.07 ± 0.05	19.1	12.8	6.4	76.9
High deer density 2 (H2)	0.01 ± 0.06	45.6	40.0	5.6	64.7

*Sites H1 and H2 had 3–4 times higher winter and growing-season densities than L1, based on aerial counts, pellet counts, and infrared camera monitors (Fig. 1).

7.57 and 7.14, $p < 0.007$). The sample of reproductive plants was extremely small at H1 due to their rarity; 4 of 8 marked reproductive plants were grazed in 1995 and 10 of 13 plants were grazed in 1996. The 1996 grazing rate was significantly higher than the proportion of reproductive plants grazed at L1 (Table 1; $\chi^2 = 6.42$, $p = 0.01$).

To examine the effects of grazing in 1995 on *Trillium* reproduction in 1996, we compared plants that flowered and were grazed by deer in 1995 to plants that flowered and were ungrazed in 1995 for data pooled across all study sites. In early May 1996, flowering rates were not significantly different between the grazed and ungrazed sample (80%, $n = 25$ versus 90%, $n = 44$ respectively, $\chi^2 = 1.67$, $p = 0.20$). Given the sample sizes, the chance of detecting a 0.35 difference in flowering rates at alpha $= 0.1$ was 90%.

Effects of pollinator limitation on these populations appeared to be minimal because 87–100% of ungrazed flowering plants were developing fruits by the late June sampling dates at all sites.

Response of a *Trillium* Population to Protection from Herbivory

The exclosure experiment at H1 revealed a dramatic response of *Trillium* to release from herbivory after only two growing seasons. At the beginning of the experiment in May 1995, plant size was similar for exclosed ($\overline{x} = 43.86$ cm²) versus unexclosed ($\overline{x} = 45.49$ cm²) plants (paired t test, $t = 0.54$, $p = 0.3$), and 28% of the plants in both experimental groups were flowering. In 1996, after 1 year of protection from deer herbivory, the leaf area of unprotected plants in early May was significantly lower than the leaf area of paired, protected plants (26.8 cm² versus 37.1 cm², $t = 2.72$, $p = 0.007$). After two growing seasons, the flowering rates of protected versus unprotected plants diverged dramatically, such that by June 1996 the flowering rate of protected plants was 19 times greater than the rate for unprotected plants (Fig. 3; $\chi^2 = 27.0$, $p < 0.0001$).

Within a growing season, plants can be defoliated by deer, mechanical damage to the stem, and lepidopteran larvae. During both growing seasons, the proportion of plants that were not defoliated by the late June sample was significantly higher for protected than for unprotected plants (Fig. 3; 1995: $\chi^2 = 7.71$, $p = 0.006$; 1996: $\chi^2 = 22$, $p < 0.0001$). These differences reflect the fact that deer grazed 36% and 44% of the unprotected sample in 1995 and 1996, respectively. For protected and unprotected plants combined, 12% and 8% experienced lepidopteran damage in 1995 and 1996, respectively, with no significant difference between treatments ($p \geq 0.8$).

Trillium grandiflorum Transplant Experiments

In early May 1995, 58 unprotected and 19 protected transplants emerged at L1, and 56 unprotected and 18 protected transplants emerged at H2 following high overwinter mortality at both sites. At this time mean plant leaf area was similar inside and outside exclosures at both sites ($t \leq 1.20$, $p \geq 0.24$). In 1995, deer grazing intensity on unprotected plants was significantly greater at H2 than at L1 (Table 2; $\chi^2 = 14.9$, $p < 0.0001$). No grazing on transplants was observed after late June. The overall proportion of transplants damaged by lepidopteran larvae was also significantly greater at H2 (31.1% versus 7.9%, $\chi^2 = 12.92$, df $= 1$, $p = 0.0003$). At H2, however, the proportion of transplants retaining leaves through anthesis was significantly greater for protected plants (available to lepidopteran larvae only) than for unprotected plants (available to deer and lepidopteran larvae) ($\chi^2 = 7.4$, df $= 1$, $p = 0.007$). No significant difference was detected between protected and unprotected plants at L1 ($\chi^2 = 0.09$, df $= 1$, $p = 0.76$).

Following 1 year of protection from deer herbivory, mean leaf area in early May 1996 at H1 was significantly greater for protected than unprotected plants ($t_2 = 2.49$, $p = 0.027$). Grazing intensity decreased from 1995 to 1996 at H2 and increased at L1, such that in 1996 there

was no significant difference in the proportion of unprotected *Trillium* grazed ($\chi^2 = 0.99$, $p = 1.0$). In 1996 at H1, 35% of the unprotected plants disappeared due to unknown causes, whereas only 15% disappeared at L1, possibly resulting in a greater underestimate of deer grazing intensity at high deer density. All observed deer grazing occurred before late June. In 1996 the proportion of plants damaged by lepidopteran larvae was low at both sites (1.8% and 5.6%, respectively). Survival rates past anthesis in 1996 were higher inside exclosures than outside at both low (Table 2; $\chi^2 = 4.94$, $p = 0.03$) and high deer density ($\chi^2 = 2.86$, $p = 0.09$).

Flowering rates of transplants were similar inside and outside exclosures at the beginning of the experiment in early May 1995 at both low deer density (94% versus 84%, $\chi^2 = 1.34$, $p = 0.25$) and high deer density (78% versus 80%, $\chi^2 = 0.04$, $p = 0.84$). No significant difference was detected between the proportion of transplants flowering in the post-anthesis sample (late June) for protected versus unprotected plants at L1 in 1995 (Table 2; $\chi^2 = 0.00$, df = 1, $p = 0.97$) or in 1996 (52.9% versus 38.2%, $\chi^2 = 1.16$, $p = 0.28$). At H2 a significantly greater proportion of transplants was flowering at anthesis inside than outside exclosures in 1995 ($\chi^2 = 4.32$, df = 1, $p = 0.04$) and 1996 ($\chi^2 = 5.1$, df = 1, $p = 0.02$).

Discussion

Deer Impacts on Natural *Trillium* Populations

The effects of herbivory on a plant population depend on the degree to which plants are defoliated and the effect of defoliation on individual reproduction and growth. Deer effects on individual *Trillium* are especially severe because one bite causes 100% defoliation and loss of the flower or fruit from reproductive plants, no regrowth occurs within that growing season, and *Trillium* do not reproduce clonally. At two forests where hunting has been prohibited for more than 5 years and deer densities are high, deer consistently removed more than 50% of reproductive individuals from the population each year, caused reductions in plant size, and altered the distribution of plant size-classes in the population. In contrast, at a site where deer are hunted on an annual basis, deer density was three to four times lower, and grazing had
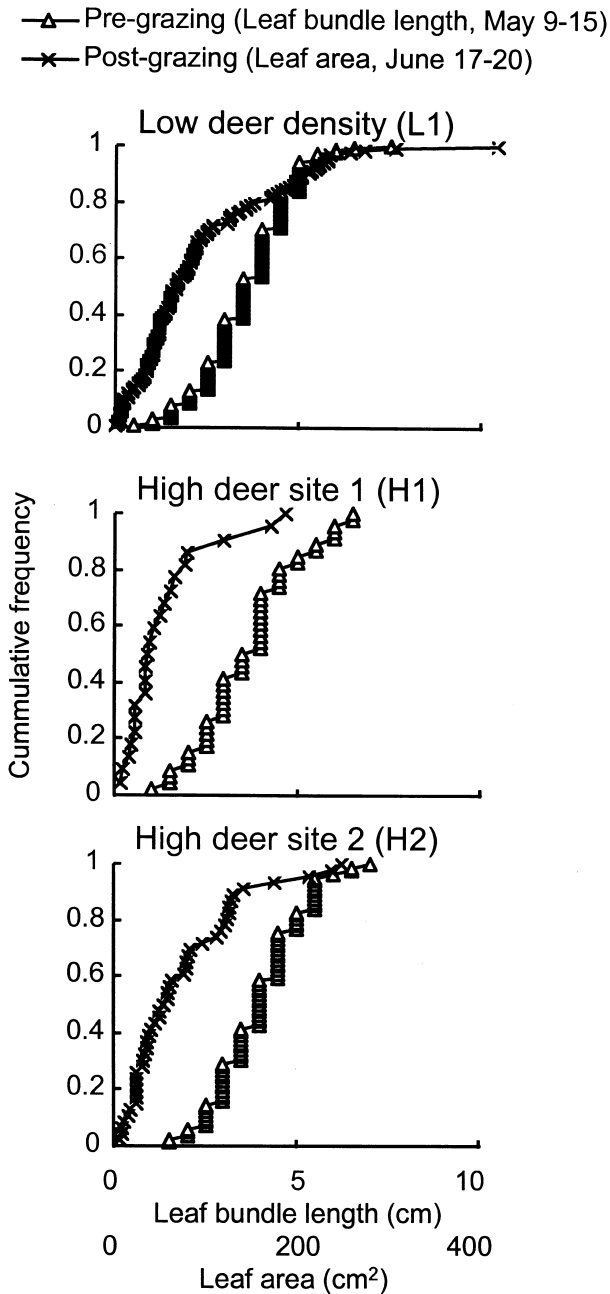

Figure 2. Cumulative frequency distributions of plant sizes in three Trillium *populations experiencing different levels of deer herbivory. The early May distribution is based on the length of emerging leaf bundles (cm), whereas the late-June distribution is based on estimated leaf area (cm²) of ungrazed plants.*
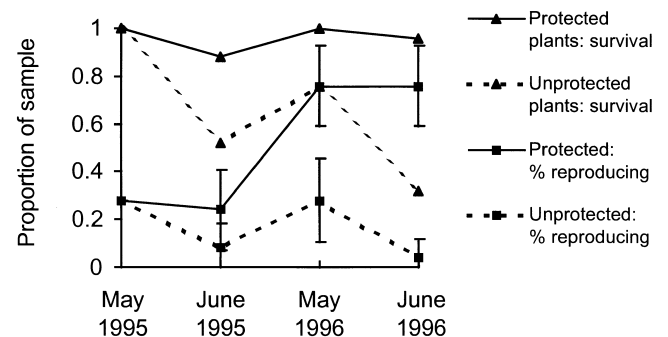

Figure 3. Trends in the flowering rate and survival within a growing season of naturally occurring Trillium *at site H2 for plants protected from deer herbivory versus those of unprotected plants.*

Table 2.   Grazing, growth, survival, and reproduction of *T. grandiflorum* transplants at two study sites in southeastern Minnesota.*

T. grandiflorum *transplant characteristics*	Low deer density site (L1)				High deer density site (H2)			
	unprotected		*protected*		*unprotected*		*protected*	
	1995	*1996*	*1995*	*1996*	*1995*	*1996*	*1995*	*1996*
Grazed (%)	3.4	12.8	—	—	30.4	14.7	—	—
Surviving past anthesis (%)	86.2	61.7	83.3	89.5	17.9	41.2	50.0	65.0
Reproductive post-anthesis (%)	63.9	38.2	64.7	52.9	8.9	14.3	33.3	38.9
Early May leaf area (cm^2)	37.8	43.4	42.4	41.0	43.5	38.6	50.8	65.4

*Site H2 had 3–4 times higher winter and growing-season densities than L1, based on aerial counts, pellet counts, and infrared camera monitors (Fig. 1).

significantly less severe effects on *Trillium* reproduction, growth, and population structure. Although many factors may have led to the current low *Trillium* densities at the sites with high deer density, the documented levels of grazing on flowering plants indicate that high local deer densities are preventing *Trillium* populations from recovering. The exclosure experiment at H1 supported this conclusion and demonstrated that changes in plant size and reproductive rates for unprotected plants can be dramatically reversed when deer herbivory is eliminated for only 2 years (Fig. 3). Observed seed-set rates (≥87%) are higher than reported for *T. flexipes* populations elsewhere (Ohara & Utech 1988), indicating that pollination is not limiting reproduction.

In addition to the within-growing season reduction in *Trillium* reproduction, herbivory can further affect populations if defoliation in one growing season reduces reproduction in subsequent years. The lack of a significant reduction in 1996 flowering rates for grazed compared to ungrazed plants that were reproductive in 1995 indicates that one herbivory event does not have long-term effects on *Trillium* reproduction. Partial defoliation (50%) of *T. grandiflorum* without removal of the flower results in the allocation of resources to sexual reproduction at the expense of future growth and reproduction (Lubbers & Lechowicz 1989). The lack of reduced future reproduction observed in our study may result from the leaf biomass lost to deer being offset by the conservation of energy normally expended on seed production because deer also remove the flower. This result suggests that *Trillium* individuals can be highly resilient to deer grazing over the short term (1–2 years) such that, following a reduction in deer densities, *Trillium* reproductive rates can rapidly return to levels observed at low deer density.

Nevertheless, the cumulative effects of herbivory over several growing seasons could cause long-term reductions in reproductive success. Comparison of the *Trillium* populations at the two high-deer-density sites showed that, although both populations experience high grazing intensity on large, reproductive plants, H1 contains a significantly lower proportion of flowering plants than H2 in early May before most deer grazing takes place. This likely reflects differences in deer densi-

ties over the past 5–8 years. At H2, high densities have been present only for the past 2–3 years, following a rapid increase in the local deer population between 1989 and 1993. At H1 aerial counts show a consistently high and slightly increasing local deer density from 1992 to 1996. Lower pregrazing flowering rates at this site suggest that cumulative, long-term grazing impacts on reproduction occur when high local deer densities are maintained for at least 5 years.

Although no baseline demographic data are available for *T. cernuum* or *T. flexipes*, the population structure of *T. flexipes* as determined by size-class analysis (Ohara & Utech 1988) is similar to that of *T. grandiflorum* (Kawano et al. 1986). For a *T. grandiflorum* population in Michigan, Hanzawa and Kalisz (1993) found that individuals ranged from 1 to 30 years old and the minimum age of reproductive plants was 17 years. This suggests that, if grazing intensities observed at sites with high deer density continue for more than 15–20 years, deer can drive a population to local extirpation. Conversely, the relatively long generation time of *Trillium* will severely limit the rate at which population densities can recover following a reduction in deer density.

In addition to direct grazing effects on *Trillium*, community-level grazing patterns may affect *Trillium* establishment, growth, and survival. Previous work showed that *Trillium* spp. are grazed to a greater degree than many common forb species (Augustine 1997). At both sites with high deer density, *Trillium* was extremely rare in the understory (Table 1), but it still experienced high grazing intensity. Forb species that are less palatable and more tolerant of grazing occur at comparatively high densities in the forest understory and likely compete for light and establishment sites. Equally important was the observation that high grazing intensities are maintained on reproductive *Trillium* individuals even where they are extremely rare in the overall plant community. Because the preference of deer for *Trillium* has also been documented in Illinois (Anderson 1994) and northern Wisconsin (Balgooyen & Waller 1995), effects observed in this study may occur across a broad geographic region.

This community-level grazing pattern can result in strong negative deer impacts on sensitive species while

the overall groundlayer remains green. Negative impacts may extend to many long-lived understory forbs that, like *Trillium*, can have most leaf area and reproductive structures removed in a bite, that possess no capacity for regrowth after grazing, and that are highly palatable to deer (e.g., *Clintonia*, *Maianthemum*, *Polygonatum*, *Sanguinaria*, *Smilacina*, *Smilax*, and *Uvularia*; Balgooyen & Waller 1995; Augustine 1997; Rooney 1997). This contrasts with the common situation in which deer impacts are recognized and responded to by managers when a "browse line," characterized by the complete absence of vegetation within the groundlayer, begins to develop.

Deer Impacts on Plant Community Restoration

Conservation plans for Big Woods remnants call for the restoration of native species lost during forest fragmentation. In remnants protected from direct human influences, lack of deer management can still impede restoration efforts. The transplant experiments with *Trillium grandiflorum* showed that, as with natural *Trillium* populations, grazing impacts where deer occur at high density include a large reduction in flowering rates and survivorship within the growing season and a decline in plant size across years.

Stem damage by lepidopteran larvae also affected transplant survival, indicating that under reduced deer densities other sources of damage could inhibit transplant success. These experiments show, however, that at high deer density significant additive deer impacts occur even when other important factors affect transplant survival and reproduction (H2, protected versus unprotected plants). Because our objective was to measure deer impacts, we did not assess whether factors such as seed production and subsequent survivorship would be sufficient for successful *T. grandiflorum* establishment. The observed levels of deer grazing, *Trillium* survival and flowering rates, and changes in plant size at the low-deer-density site show that, given suitable conditions for *T. grandiflorum* establishment, deer at low density are not expected to inhibit transplant success. Long-term monitoring is needed to confirm this.

Our combined studies show that deer exert dramatic influences on *Trillium* reproduction and population structure at sites supporting high overwinter deer concentrations (25–35 deer/km^2). Levels of herbivory observed at two sites in southeastern Minnesota suggest that deer can lead to the local extirpation of selected forbs such as *Trillium* in forest fragments and can inhibit efforts to restore populations of palatable species. The most significant effects on population structure were observed where deer occur at high overwinter concentrations for at least 5 years. Significantly lower grazing intensities and higher *Trillium* flowering rates were observed where deer occur at low overwinter density (4–11 deer/km^2) due to annual hunting, but long-term monitoring is needed to determine whether this level of herbivory does not lead to *Trillium* declines. It is important for managers to recognize that, due to growing-season dispersal of deer into the surrounding agricultural landscape, the absolute number of deer responsible for the documented grazing impacts may be substantially less than the winter density, but that sites with high overwinter concentrations still have comparatively high summer deer density and grazing intensity.

Our results suggest that the relationship between deer and forest forb communities in southeastern Minnesota has undergone a rapid change in response to landscape fragmentation and changing deer densities over the past 150 years, such that selective grazing can lead to the local extirpation of sensitive species. As a result, active, long-term management to limit deer densities in parks and preserves through hunting or other effective methods appears necessary for the conservation and restoration of fragmented forest communities in eastern North America.

Acknowledgments

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