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GRAZING PATTERNS AND IMPACTS OF WHITE-TAILED DEER IN A FRAGMENTED FOREST ECOSYSTEM

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ABSTRACT

The conversion of deciduous forests in the upper Midwestern United States to agricultural and residential land uses has changed the relationship between white-tailed deer populations and remaining patches of deciduous forest. This thesis examines the grazing patterns and consequent impacts of white-tailed deer on understory forbs in old-growth Big Woods forest remnants in southeastern Minnesota. Surveys of all understory species at four study sites in 1995, and of a select list of species at 11 study sites in 1996 documented relatively low grazing intensity on spring ephemeral species, high grazing intensity on a few preferred forb species in early and late summer, and a wide range of grazing intensities among sites in all seasons.

To examine deer grazing impacts on the understory plant community, two approaches were used. First, deer impacts on the most intensively grazed early summer forbs, *Trillium* spp., were studied using individual plant exclosure experiments, between site comparisons of grazing intensity and population structure, and transplant experiments. Secondly, impacts on the overall understory herb community were examined using 10 m^2 deer exclosures constructed at high and low deer density study sites.

No effects of deer herbivory were detected at low deer density sites. *Trillium* experiments showed severe impacts of grazing on growth, reproduction, and population structure at sites with high deer density. At the one high deer density site where spring ephemerals were present, a significantly greater increase in *Erythronium* density occurred inside the 10 m^2 exclosures compared to grazed control plots. In late summer, the forb community within exclosures at one high deer study site diverged dramatically from the community in grazed control plots, primarily due to increased abundance and flowering rates of *Laportea canadensis* and *Circaea lutetiana* inside exclosures, and increased abundance and flowering rates of unpalatable *Eupatorium virginana* and *Hackelia virginiana* outside exclosures. However, significant deer effects were not observed at a second high deer density site where *Laportea canadensis is* abundant. Results from the exclosure experiments and the pattern of among-site variation in grazing intensity indicates that impacts on the late-summer understory community will be most severe when local deer densities are high and palatable forb species are rare.

Forest surveys showed that grazing intensity varies widely among Big Woods remnants in southeastern Minnesota. The predictability of grazing intensity based on winter deer density, landscape composition surrounding forest fragments, and characteristics of forb populations within a stand was examined using the 1996 surveys of 11 study sites. Regression analyses showed that alfalfa availability is an important determinant of grazing intensity in early summer, and the availability of row crops, alfalfa, and fields is an important determinant in late summer. In early summer, the effects of landscape composition also depended on winter deer density (high vs. low) and the flowering rate of palatable forbs within the forest stand (high vs. low). In late summer, among-site variation in grazing explained by landscape composition could be equally well explained by winter deer density and forb abundance within the stand. Results indicate that agricultural practices surrounding and the current abundance of forb populations within parks designed to protect fragmented forest communities should be important considerations in addition to deer density when managing local deer populations.

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INTRODUCTION

This thesis consists of five chapters, each containing results and discussion which stand alone but reference one other. All studies were conducted in the same region of southeastern Minnesota, but the specific sites used in each study vary, and hence are redescribed in each chapter. The first chapter presents the results of surveys conducted to identify understory plants grazed by white-tailed deer and to examine the variation in grazing patterns between areas which differ in deer density. The second chapter examines deer grazing impacts on a highly preferred group of understory forbs, Trillium spp., using experiments with both natural and transplanted populations. Chapter 3 presents results from an exclosure experiment examining deer impacts on the overall understory forb community, in particular focusing on species that dominate the late-summer community. A theoretical framework for understanding the results from Chapter 3 is then presented in Chapter 4. Finally, to aid in the management of deer impacts on protected Big Woods forests, the ability to predict deer grazing intensity within a forest based on winter deer density, landscape composition, and characteristics of the understory community is examined in Chapter 5.

GRAZING PATTERNS OF WHITE-TAILED DEER *Odocoileus virginianus* AND PLANT COMMUNITY CONSERVATION IN A FRAGMENTED FOREST ECOSYSTEM

Abstract: The selectivity and intensity of herbivory by white-tailed deer during spring and summer was examined in four old-growth remnants of the highly fragmented maple-basswood forest ecosystem in southeastern Minnesota, USA. Herbivory intensity during the spring, early summer, and late summer was significantly greater at sites with higher local deer densities, and herbivory in the ground layer was focused on herbaceous species. Although the overall grazing intensity was relatively low in spring and summer, deer exerted high grazing rates on a few forb species due to their selective foraging pattern. High use of species from the Liliaceae family was observed during spring and early summer. Crazing in late summer shifted to a new set of species approaching anthesis. Certain preferred forb species such as *Trillium* spp. which were rare at high deer density sites still experienced high grazing intensities. Foraging patterns were generally not correlated with the spatial distribution of herbaceous species within a stand, except at high deer densities where the pattern of grazing was related to the distribution of a preferred forb species. The potential for high local densities of deer in predominantly agricultural regions such as southeastern Minnesota combined with the documented selective foraging patterns indicates that white-tailed deer populations must be an important consideration in both the conservation and restoration of forest community remnants in midwestem and eastern North America.

INTRODUCTION

As human activities continue to fragment natural communities and ecosystems worldwide, it becomes imperative that we understand the biotic processes affecting the r structure and diversity of natural community remnants. Research examining a wide range of natural plant communities has demonstrated that mammalian herbivores may significantly influence plant species diversity and biotic processes (Alverson *et al*. 1988, McNaughton *et al.* 1988, McInnes *et al.* 1992*,* Frank & McNaughton 1993). However, the impacts of mammalian herbivores on natural communities following changes in landscape structure have not been fully explored. In Minnesota, extensive habitat alterations following European settlement changed the distribution of native ungulate herbivores (Berner & Simon 1993), and resulted in locally elevated white-tailed deer densities in certain southern farmland and urban/residential areas of the state. One documented consequence of increased deer densities in other regions is the deleterious effect on populations of sensitive native plants, with the potential for species extirpations in small forest patches (Beak *et al.* 1960, Anderson & Loucks 1979*,* Alverson *et al.* 1988, Anderson & Katz 1993, Anderson 1994).

In the eastern United States, research has emphasized the impacts of winter browsing by deer on woody plants (e.g. Graham 1952, Beals *et al. 1960,* Frelich & Lorimer 1985, Alverson *et al*. 1988, Tilghman 1989*),* and recent work hag examined deer impacts on other components of forest ecosystems including small mammals and migratory songbirds (McShea & Rappole 1992, deCalesta 1994). Far less attention has been focused on the influence of spring and summer deer herbivory on herbaceous plant communities (Bratton 1979, Anderson 1994, Balgooyen & Waller 1995). Impacts of grazing can occur through the overall removal of plant tissues and, more importantly, through the effects of selective foraging which can change competitive relationships among different species in the plant community (e.g. Ritchie & Tdman 1995, Furbish & Albano 1994, Swank & Oechel 1991, Crawley 1983). A survey of preserve managers in the United States and qualitative plant community observations suggested that spring and summer grazing by deer may be altering the composition of understory herbaceous plant communities (Alverson *et al.* 1988, Miller *et al*. 1992, Cottam & Curtis 1956).

Prior to European settlement of Minnesota, deciduous forests were distributed in a strip from the northwestern to the southeastern corner of the state, bordering prairies to the west and south and mixed deciduous-coniferous forests to the northeast (Marschner 1974). Daubenmire (1936) termed a central, contiguous 7,750 km^2 portion of this forest the "Big Woods" and considered it to be a relatively homogeneous climax forest dominated by sugar maple *Acer saccharum* and basswood *Tilia americana* Analyses of the *1847-56* United States public land survey showed that the characteristic tree taxa of these forests are elm *Ulmus* spp., sugar maple, basswood, ironwood *Ostrya virginiana,* bitternut hickory *Carya cordiformis*, butternut *Juglans cinerea,* and ash *Fraxinus spp.* (Grimm 1984). Today this forest type has been almost entirely converted to urban or agricultural use, with only scattered stands, primarily on the order of 8 - 32 ha, remaining on private and public lands (Jakes 1980, Vasilevsky & Hackett 1980).

The current species composition of such stands has likely been affected by interactions between a wide range of factors including historical land-use practices (logging and livestock grazing), land-use practices in the surrounding landscape, local species' distributions at the time of fragmentation, stochastic events, and elevated deer densities. Because the deer population is one factor which can be controlled, understanding the ongoing interaction between local deer populations and the composition of remaining Big Woods fragments is of direct importance for the conservation and restoration of this forest type.

The degree of foraging selectivity and the proportion of a given species grazed can be affected by both local deer density and the relative abundance of different species within the plant community. I quantitatively monitored the understory plant community at four of the highest quality Big Woods remnants in Minnesota in order to

1) Measure the overall intensity of deer herbivory within Big Woods remnants during the spring and summer, and relate this to local deer density and forage availability,

2) Document the degree of foraging selectivity among herbaceous species and relate this to deer density and the relative availability of forage species within the understory community, and

3) Interpret the implications of these foraging patterns for the conservation of native plant communities within fragmented forest remnants.

STUDY AREA

The study was conducted at four sites covered by a closed, homogeneous canopy containing overstory trees >50cm dbh. The canopy layer was dominated by sugar maple, elm (*Ulrnus americana* and *U. rubra),* and basswood (combined relative basal area >0.80) with oaks not dominant (relative basal area <0.20). Green ash *Fraxinus pennsylvanica,* black ash *F. nigra,* hackberry *Celds occidentalis,* bitternut hickory, northern red oak *Quercus rubra,* white oak *Quercus alba,* box elder *Acer negundo,* black cherry *Prunus serotina,* butternut, and black walnut *Juglans nigra,* are less abundant elements of the canopy. Ironwood is an important subcanopy species (Appendix A). The region experiences a continental, cold-temperate humid climate with warm summers and cold winters. Annual average temperatures was 6.7-7.0°C in the Hennepin county area and 7.8°C in the Rice county area during 1936 - 1960, and average annual precipitation was 73-76 cm in the vicinity of study sites during 1941-1970 (Grimm 1984). The sites contain loamy soils developed from glacial moraines or silty soils developed from loess-covered glacial till (Grimm 1984).

Two study sites (Low deer site 1 and High deer site 1) are located in Hennepin County, MN (45°N, 93° 30'W), and two study sites (Low deer site 2 and High deer site 2) are located 75 Ian to the south in Rice County, MN (44° 15'N, 93° 20'W). In each pair, sites were selected to include one stand supporting a high overwinter deer density and one stand supporting a comparatively low overwinter deer density based on 1993-1994 aerial surveys.

Low deer site 1 is a 16 ha remnant in Elm Creek Park Reserve bordered by cultivated fields, open shrubland, wet meadows, and early successional forest. Selective logging to favor sugar maple occurred before inclusion in the preserve, and no cattle grazing has taken place in the stand; it was described in Rogers (1981) study of maple/basswood/beech forests in the upper Great Lakes States. High deer site 1 (Riley Creek Woods) is a 16 ha stand with steep northeast facing slopes on the south side and more gradual southwest facing slopes on the north. Residential developments occur along the east and south border, early successional forests and an apple orchard on the north and northeast, and cattle pastures on the western edge. Evidence of limited selective logging exists along one edge, and no historic cattle grazing is known to have occurred at the site.

At Low deer site 2 (7-mile Woods), a 16 ha section of the upland Big Woods forest was sampled which is bordered by continuing Big Woods forest, lowland hardwood forest, early successional forest, cultivated fields, and abandoned fields. Moderate selective logging has occurred in parts to favor sugar maple. At High deer site 2 (River Bend Preserve) sampling was conducted in an approximately 8 ha strip of Big Woods forest surrounded by early successional forest, old fields, and lowland hardwood forest. The stand was never logged, and the understory was grazed by cattle until 20 years ago.

METHODS

Deer densitv estimation

In each stand, 46-50 fixed sampling points were established in a systematic grid (50 m spacing at the 16 ha sites, 25 m spacing for the 8 ha site) immediately following snowmelt in March, 1995. Deer pellet groups were counted and cleared within a 4 m radius of each point at all sites during March 14-20, 1995. Pellet groups were then recounted on the cleared plots during 10 - 15 May, 1995. Because leaf-fall in October uniformly covers the ground, March pellet group counts represent accumulation only for the late fall and winter months, providing an index of overwinter deer density. Re-counts of the same plots in May estimated early spring use of this forest type. Counts were converted to estimates of deer/km2 based on a 150 day deposition period (overwinter) and 58 day deposition period (early spring) assuming 13 pellet groups produced/deer/day

(Eberhardt & van Etten 1956, van Etten 1959). Density differences among sites were compared using likelihood ratio tests for log-linear models (Agresti 1996).

At the two southern study sites, deer presence was also estimated with automated camera stations for the period 1 April - 15 June, thus providing records for one month' beyond when pellet counts are no longer feasible due to concealment by vegetation and rapid pellet decomposition. Deer use of the maple-basswood forest was measured using three cameras triggered by passive infra-red monitors per site (Non-typical Engineering, Green Bay, Wisconsin, USA). The two sites were stratified into 3 equal areas. In each area, monitors were placed at a new randomly located position every 7 days, and data were summarized as deer photographed/week. Selected locations that directed the infra red beam across a deer trail were discarded to avoid sampling deer that were only passing through the stands rather than using the stand for cover or foraging.

Plant community sampling

Densities of all woody species stems < 1 m high and all herbaceous species, and the amounts of each species removed by deer, were sampled during spring (27 April - 4 May), early summer (5 - 11 June), and late summer (12 - 19 August), 1995, using the same systematic plot grids established for pellet counts. Spring sampling was conducted at the time of leaf-out for woody species, so only herbaceous species were monitored in this season. Observations in May 1995 indicated that the spring (27 April - 4 May) survey was conducted too early to fully sample the extent of spring grazing. Spring ephemerals were therefore re-sampled the following year during 13 - 15 May, 1996, at the two southern sites (most spring ephemerals were absent from the northern sites). Pellet group counts conducted at the two southern sites in April, 1996, using the same sampling grids as in 1995 showed no significant changes in deer density between years at either site.

In each sampling period, the number of available "units" of each species was counted in a 1 m^2 area around each sampling point for most species and a 6 m2 area for species with low abundance. The number of grazed "units" of each species was counted within a 6 m2 area of each sampling point. A unit was defined as individual leaves for species with basal leaves only such *as Erythronium* and *Allium*, individual plants for species with a single stem supporting the mass of leaves such as *Trillium* and *Laportea*, and clusters of leaves and stems for caespitose species such as *Carex* following Anderson (1994). The number of basal leaves plus upright stems *was* counted for species with a rosette of basal leaves and a central stem such as *Viola pubescens, Hydrophyllum,* and *Geum*, and a unit was an entire plant for the annual *Galium* spp. Stems and basal leaves less than 1 cm in length were not included in counts. Identification of herbaceous units ("stems" hereafter) grazed by deer rather than other mammalian herbivores was based upon the roughness and height of stem cuts. These criteria were verified based on regular examinations of bite points on stems immediately following direct, close-range observations of grazing deer throughout 1994 and 1995. Stems grazed by lagomorphs or rodents were extremely rare. Due to the low abundance of Trillium spp. at both high deer density sites, supplemental monitoring was conducted on marked individuals.

All nomenclature follows Gleason & Cronquist (1991). Non-flowering Trillium could not be identified to species; flowering stems at sites Low deer site 2 and high deer sites were primarily *T. cernuum, T. flexipes* and hybrids, while at Low deer site 1 were primarily *T. grandiflorum. Smilax* cf. *ecirrata* may include *Smilax herbacea. Galium* spp. was primarily *Galium aparine* at all sites, and included *Galium triflorum. Carex* spp. included *Carex pedunculata* at all sites.

Foraging selectivity analyses

Given the objective of examining potential impacts on the plant community, I analyzed the proportion of grazed stems for each species relative to the proportion of grazed stems in the total herbaceous plant community: The proportion of grazed stems for each species ("grazing intensity" hereafter) was calculated using a ratio estimator equal to the total number of grazed stems of that species divided by the total number of grazed + ungrazed stems of that species in all plots at a given site. Because stems occurring within a single plot are not independent of one another with respect to deer foraging, selective foraging cannot be assessed with typical categorical data analyses. I therefore used

Cochran's (1977) jacknife technique to correct the ratio estimators to reduce bias and to calculate the variance for each ratio.

Species were designated as "preferred" or "unpreferred" when a significantly greater or lower proportion of available stems respectively were removed as compared to the overall proportion of the herbaceous plant community grazed at a given site in a given season. Unless otherwise stated, all comparisons are based on Wilcoxon rank sum tests applied to the jacknife pseudovalues calculated for the estimates of the proportion grazed for each species, with significance accepted at the a = 0.05 level. For any species occurring at a given site in < 5 plots, the uncorrected ratio estimator is reported without statistical inference. This analysis differs from foraging preference calculations which examine representation in the herbivore's diet (browsed stems of a species/browsed stems of all species) relative to availability of that species in the environment. The same i summation terms are used, but the ratios calculated in our analyses relate to the impact on each plant species rather than the contribution of each plant species to the herbivore's diet.

Spatial patterns of grazing

When establishing the permanent plot grids, x-y coordinates for each plot were recorded. Spatial autocorrelation analyses, using the formulas of Sokal & Oden (1978), i were used to examine 1) the spatial scale of patches of preferred forage species within the understory community and 2) the spatial pattern of deer grazing relative to these plant community patterns. This technique determines whether plots within a given proximity are more or less likely to be similar than expected under a random spatial distribution. Patchiness was examined on spatial scales from a 50 m radius to a 200 m radius by 50 m distance classes (i.e. the spacing between plots). Analyses were not conducted for High deer site 2 due to its smaller size and shorter spacing between plots.

RESULTS

Seasonal deer densities

Late winter pellet counts confirmed that overwintering densities were significantly higher at High deer 1 compared to Low deer 1 (likelihood ratio test OG2=21.23, d.f. = 1, P<0.001, Fig. 1), and at High deer 2 compared to Low deer 2 (likelihood ratio test, AG2=95.27, d.f =1, P<0001). Spring pellet counts were a relatively insensitive measure of spring deer density, but were important in demonstrating a large decline in deer use of this habitat between winter and spring (Fig. 1). Infra-red deer activity monitors provided a more sensitive index of deer density during spring and early summer. During April 1June 15, the number of deer photographed/week was significantly higher at High deer site 2 than Low deer site 2 (OG2=14.6, df.= 1, P<0.001, Fig. 1).

Grazing intensity and selectivity

The plant community in the understory layer experienced selective herbivory in: spring, early summer, and late summer. Grazing occurred throughout the spring and summer, with no decrease in the proportion of stems grazed during the summer months (Fig. 2). For the early and late summer samples at all sites, a significantly greater proportion of total available stems (woody and herbaceous species combined) that were grazed or browsed consisted of herbaceous stems as compared to the foliage of woody' species (Wilcoxon rank sum tests, P<0.01 for all comparisons, Fig. 2). Since the biomass of a given deer bite may vary widely among species and growth forms, comparisons here are simply of forage removal events, which relate directly to effects on the plant community, rather than to amount of biomass consumed.

The overall intensity of grazing on herbaceous species in these communities was relatively low at all sites in all seasons (0.2% - 8.6% of herbaceous stems) except at High deer site 1 late summer (27.2% of herbaceous stems). Overall grazing intensity in all seasons was significantly higher at high versus low deer density sites (Wilcoxon rank sum tests, P<0.01 for all comparisons, Fig. 2). At each site, deer exhibited selective foraging patterns. At the southern study sites, the spring ephemeral forb species experienced extremely low grazing intensity at Low deer site 2, while the percent grazed was an order of magnitude greater at site High deer site 2 (Fig. 2). However, the three genera experiencing the highest grazing intensities at high deer density, *Allium, Erythronium,* and *Isopyrum*, only had 6-8%a of stems removed (Table 1). Two species - *Cardamine concatenata* and *Aplectrum hyemale* -- were of extremely low abundance and were not adequately sampled by the plot grids. Regular observations of the patches present indicated that these species were never grazed during the spring. Sedge species besides *Carex springelia* (grouped as *Carex spp.)* initiate growth immediately following snowmelt and experienced high grazing intensity, while *Carex springelia,* which initiates growth later in spring, experienced a lower grazing intensity (Table 1).

Spring ephemerals occurred at low diversity and density at the two northern study sites, and the three dominant species at the southern sites *(Claytonia virginica, Isopyrum biternatum,* and *Erythronium* spp.) were not present. Spring grazing intensity at these sites was low (Fig. 2), and spring grazing at High deer site 1 was predominantly on emerging basal leaves of *Hydrophyllum virginianum.*

In early summer, consistently high grazing intensities were observed for *Trillium spp., Cryptotaenia canadensis,* and *Uvularia grandiflora.* Other non-clonal forbs such as *Smilacina racemosa, Sanguinaria canadensis, Polygonatum biflorum, Impatiens* cf. *pallida,* and *0smorhiza* spp. also experienced high grazing intensity at 1 or more sites (Table 2). However, the relative rarity of these species at some study sites resulted in small sample sizes that either precluded statistical inferences or resulted in no observations of grazing within the total area sampled. For both pairs of study sites, *Trillium* spp., *Uvularla grandiflora, Smilacina racemosa,* and *Sanguinaria canadensis* were significantly less abundant at the high deer density site (Wilcoxon rank sum test, $P<0.05$ for all comparisons), or were not detected at the high deer density sites due to their rarity. In early summer, the grazing intensity on 14 species was either significantly lower than the overall herbaceous community or zero at all sites where they occurred (Table 2). *Phryma leptostachya* had an extremely low abundance that was not adequately sampled by the plot grids, but grazing was incidentally observed on this species outside of plots. *Arisaema* *triphyllum,* a non-clonal, forest interior forb species with similar growth form to the preferred species described above, experienced consistently low grazing intensities at all sites and occurred at significantly higher densities at the sites experiencing high grazing intensity (Wilcoxon rank sum, $P<0.001$ for density comparisons).

Only four species experienced consistent, significantly high grazing intensities in late summer, and among these only *Trillium* was preferentially grazed in both summer samples. In late summer, grazing shifted to three dominant species in the late-summer understory community: *Laportea canadensis, Impatiens pallida,* and *Solidago flexicaulis. Circaea lutetiana* also experienced high grazing intensities at all sites when it was common, but at High deer site 1 the proportion grazed was significantly lower than the overall herb community (Table 3).

Spatial patterns of grazing

No positive spatial aggregation patterns were detected at the 100 m distance class or greater for the total forb community or total grazed stems at any study site. However, significant aggregation at the 50 m distance class was detected at all 3 sites analyzed. At site Low deer site 2, where the overall forb community was significantly aggregated at the 50 m distance class in both summer samples, overall deer foraging intensity was not aggregated on the same spatial scale. The opposite pattern was observed at High, deer site 1 where deer foraging was significantly aggregated at the 50 m distance class, but the overall forb community did not show a similar degree of aggregation (Table 4). *Laportea canadensis,* a highly preferred forage species that was abundant at all three sites, was significantly aggregated at the 50 m distance class at all three sites in both early and late summer. Grazing on this species was highly aggregated on the same spatial scale as availability at High deer site 1, but a lesser degree of aggregation in grazing was observed at the two low deer density sites (Table 4).

DISCUSSION

Studies of deer impacts on woody species have shown that intense, selective browsing can dramatically alter forest canopy composition by preventing the escape of high use browse species (e.g. Anderson & Loucks 1979, Frelich & Lorimer 1985, Tilghman 1989, Anderson & Katz 1993), and by impacting the reproductive strategies of particular species (Allison 1990a,b). In the understory forb community, the potential for grazing to alter community composition is increased since plants are always within reach of deer and grazing only occurs during the growing season. Key factors relating to deer impacts on forest understory communities include 1) overall grazing intensity, 2) selectivity of foraging on different species, 3) response of foraging selectivity to the availability of preferred species, 4) individual plant responses to herbivory in terms of growth, reproduction and underground resource storage, and 5) changes in competitive relationships among species, particularly due to increased light availability within the ground layer following grazing.

Grazing intensity an selectivity

The first three factors were directly addressed by the objectives of this study. Although the overall intensity of grazing by deer in these old-growth maple-basswood remnants was relatively low in spring and summer, consistently higher grazing intensities occurred throughout the growing season at the sites supporting a high density of deer. Local deer concentrations occur where populations are not managed, either because of the area's status as a nature preserve (High deer site 2) or due to the proximity of residential neighborhoods (High deer site 1). In contrast, at the low deer density sites where extremely low grazing intensities were observed, deer are hunted by local landowners on a yearly basis (Low deer site 2) or through bi-annual special hunts organized by the county park system (Low deer site 1).

Consideration of agricultural phenology in the surrounding landscape and reports from reserve managers suggested that the greatest deer impacts would occur in early spring when ephemeral forb species present one of the first photosynthetically active sources of food to deer. However, even at high deer density, only 7.7% of the stems of the most intensively grazed spring ephemeral species were removed (Table 1). The availability of alternative forage sources in early spring such as alfalfa, clover, and old fields combined with limitations imposed on deer consumption of spring ephemerals due to their low stature and small per plant leaf size may be responsible for the low observed grazing intensity in forests during spring.

During early and late summer, the overall intensity of grazing was distributed unevenly across the herbaceous community. Consistent use of species from the Liliaceae family in early summer was observed (*Trillium, Uvularia, Smilacina* and *Polygonatum*, e.g. 12-14 % of *Trillium* grazed at high deer sites) supporting Miller et al.'s (1992) suggestion that high white-tailed deer densities throughout the United States may be disproportionately impacting this group due to dietary preferences. Results presented here correspond with qualitative observations by Balgooyen & Waller (1995) that *Trillium cernuum, Trillium grandiflorum, Sanguinaria canadensis, Smilacina racemosa*, and *Uvularia sessilifolia* am commonly grazed by deer in northern Wisconsin, and with documented impacts on *Trillium grandiflorum* in Illinois (Anderson 1994). Thus, early summer selectivity patterns appear to be consistent within a broader region than considered in this study. In late summer, a distinct shift in selective grazing was observed which focused on four species approaching anthesis (*Laportea canadensis, Solidago flexicaulis, Impatiens biflora flora*, and *Orcaea lutiana* e.g. 33-99% of Laportea grazed at high deer sites). In both early and late summer, deer also exhibited clear avoidance of particular species such as *Arisaema triphyllum*, a long-lived non-clonal forb with the same morphology and phenology as the liliaceaous species, and *Eupatorium rugosum*, which has the same morphology and phenology as the preferred late-summer forbs. These grazing patterns indicate that deer have the potential to cause significant shifts in the species composition of forests without completely defoliating the understory..

Comparison of grazing intensity between the two high deer density sites revealed two important patterns. First, high overall grazing intensity was only observed when a preferred species was the dominant member of the herbaceous community, as occurred at high deer site 1 in late summer (27.2% of herbaceous stems grazed) where *Laportea canadensis is* abundant. Secondly, when preferred forage species were rare, higher grazing was observed on less preferred species (i.e. reduced selectivity) but more grazing intensity on the preferred species was not as low as may be expected based on their rarity in the community. In particular, intensive sampling for *Trillium* spp. at high deer density sites showed that a high proportion of these plants were grazed despite their extreme rarity in the overall community.

Herbivore and forb population dynamics

Experimental defoliation of several forest herbs has been shown to reduce seed production in the following growing season (Rockwood & Lobstein 1994). In addition, partial leaf removal of *Trillium grandiflorum* has been shown to reduce allocation of carbohydrates to rhizomes (Lubbers & Lechowitz 1989). Complete defoliation due to deer is expected to accentuate these effects, and grazing eliminates the current year's reproduction for plants which produce flowers at the terminal end of the stem. In addition to direct impacts on a species' population dynamics, alteration of the relative amounts of seed production between forb species due to selective herbivory could disrupt any ongoing spatial dynamics based on different forb propagation strategies (Struik & Curds 1962, Thompson 1980, Tilman 1994).

Compared to the Iiliaceous species, deer impacts on other preferred species may be less severe due to leaf regrowth following a grazing event (e.g. *Laportea, Impatiens,* and *Circaea) or* continued growth from ungrazed basal leaves (e.g. *Osmorhiza* spp. arid *Viola pubescens*). In addition, *Laportea* and *Impatiens* individuals grazed early in the growing season may still regrow and flower in that season (pers. obs.). However, such responses were not observed for species such as *Sanguinaria canadensis* and *Caulophyllum thalictroides.* These variable responses could be particularly important in determining the sensitivity of a given species to the degree of herbivory it experiences. For example, the regrowth potential of *Laportea canadensis* should be a critical determinant of whether this species can remain as a dominant member of the understory in forests such as High deer site 1 given the observed level of grazing.

Implications for community structure in fragmented forests

All of the factors discussed above indicate that persistent high densities of deer sites will change the composition of the understory communities. The observed disproportionate grazing intensities on species such as *Trillium* and *Uvularia* clearly indicate that high local deer densities can reduce the relative abundance of certain forbs in spite of low overall herbivory levels in the spring and summer. The high proportion of grazed *Laportea canadensis* stems at high deer densities may have the greatest consequences for the overall summer community. *Laportea is* reported as the dominant late-summer forb species in upland, mesic forests of the midwestern United States (Curtis 1959,1981), and forms a relatively continuous layer 20-100 cm in height in broad patches. The species is a well-adapted competitor in the forest understory (Menges 1983); however, herbivory intensities observed in this study will probably reduce its abundance and increase light availability for other summer forbs.

Within-stand forb distribution analyses showed that aggregation patterns of all forb species combined did not correspond to overall deer foraging patterns. However, I found that the spatial pattern of grazing on the understory forb community where deer density was high followed the patchy distribution of *Laportea* itself. In contrast, no correlation was observed between deer grazing patterns and the within-stand distribution of *Laportea* at low deer density sites. These within-stand patterns suggest that landscape features occurring at spatial scales greater than the forest stand play an important role in determining growing season foraging patterns where lower deer densities occur. Key features likely include the distribution of agricultural crops, native plant communities, and residential developments in the surrounding landscape. At higher deer density, foraging patterns become consistently more responsive to within-stand forage distribution (Table 4).

In the southern Minnesota farmland region, productivity of white-tailed deer populations is about as high as known anywhere within the species' vast range (Harder 1980). Such high productivity in the midwest is attributed to the availability of crops such as corn, soybeans, and alfalfa (Nixon et al. 1991, Murphy 1970). The low overall levels of herbivory observed within forest remnants of the agricultural region suggests that understory plants are not a critical dietary component upon which such high deer productivity depends, although the stands may provide an important source of thermal insulation during winter months.

Because deer in a landscape with small fragmented forest patches can obtain growing season forage in surrounding lands, chronically high herbivory rates on preferred understory herbaceous species could be maintained over the long term in the absence of management to limit deer density. Given the selective foraging patterns of deer and small sizes of remnant maple-basswood forests in Minnesota, deer clearly have the potential to alter the understory composition of remaining forests in this region. The type of impact described here is closely tied to the composition of the landscape (Chapter 5). In areas containing greater relative proportions of forested as compared to agricultural land, the degree of selectivity and the dependence of deer on the forest understory community can be expected to change, possibly resulting in a more evenly distributed impact on all forest herbaceous species. The combination of 1) high local densities of deer not dependent on growing season forage in native forest communities and 2) the selective foraging patterns documented in this agricultural region of Minnesota, indicates that white-tailed deer populations must be an important consideration in both the conservation and restoration of forest remnants in midwestern and eastern North America.

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Table 1. Availability and percent grazed of spring ephemerals at the two Rice Co. study sites sampled during 13-15 May, 1996. For each site, * indicates species with a significantly lower percent grazed than the overall herb community, ** indicates no significant difference between the proportion of a species grazed and the overall grazing intensity on the herb community, and *** indicates species with a significantly greater percent grazed than the overall herb community, tested at the α=0.05 level. Grazing intensity on early-spring emergent sedge species measured during 27-31 April, 1995, is also reported, with statistical comparisons to the overall proportion of forbs + sedges grazed at that point in the 1995 growing season. Species are listed in order of their relative abundance averaged over all sites.

	Low Deer 2		High Deer 2	
Spring ephemeral species (1996)	Percent Grazed	Available (stems/m^2)	Percent Grazed	Available (stems/m^2)
Erythronium spp.	***0.86	94.7	**7.71	30.0
Isopyrum biternatum	*0.13	23.4	**6.84	79.4
Claytonia virginica	*0.10	16.1	*0.84	5.8
Dicentra cucullaria	*0.19	7.3	*4.34	0.1
Anemone quinquefolia	0.0	0.7	0.0	0.4
Allium tricoccum	0.0	1.3	**6.46	0.3
Aplectrum hyemale	0.0	0.2	--	0.0
Cardamine concatenata	--	0.5	--	0.5
All spring ephemerals	0.67	142.11	7.05	116.2
Sedge species (early spring 1995)				
Carex springelia	0	1.2	***6.09	0.6
Carex spp.	0	0.2	***42.7	3.6

Table 2. Availability and percent grazed of the most common herbaceous species sampled during June 5 -11, 1995. Preferred and unpreferred species were grazed to a significantly greater or lower degree respectively than the overall herb community at all sites where statistical comparison was possible. For each site, * indicates species with a significantly lower percent grazed than the overall herb community, ** indicates no significant difference between the proportion of a species grazed and the overall grazing intensity on the herb community, and *** indicates species with a significantly greater percent grazed than the overall herb community. In each category, species are listed in order of their relative abundance averaged over all sites. For species occurring in fewer than 5 plots at a given site, the observed proportion of grazed stems is reported without an indication of statistical significance.

	Low deer 1		High deer 1		Low deer 2		High deer 2	
Preferred	Percent Grazed	Stems/m^2	Percent Grazed	Stems/m^2	Percentt Grazed	Stems/m^2	Percent Grazed	Stems/m^2
Cryptotaenia canadensis	15.97	0.10	--	0.00	***7.08	1.78	6.60	0.20
Trillium spp.	***1.70	1.03	***12.60[a]	0.007	***14.94	0.15	***14.40[b]	0.002
Viola sororia	--	0.0	--	0.00	--	0.0	***4.97	0.66
Uvularia grandiflora	***4.02	0.21	***10.96	0.06	***3.91	0.16	--	0.0
Athyrium filix-femina	--	0.0	***21.73	0.15	--	0.0	--	0.0
Variable preference ranking between sites								
Laportea canadensis	*0.13	24.04	***12.54	3.89	***0.82	5.91	33.33	0.02
Geranium maculatum	0.0	0.05	**7.07	0.15	***1.73	3.60	*1.60	18.90
Viola pubescens	***0.79	0.46	*3.20	0.27	*0.17	16.67	***6.03	0.45
Asarum canadense	--	0.0	30.7	0.13	0.04	8.64	6.98	0.62
Osmorhiza spp.	0.0	0.69	--	0.00	***1.55	5.47	100.00	0.03
Thalictrum dioicum	0.0	0.13	***10.05	0.37	***0.85	5.18	0.0	0.16
Circaea lutetiana	0.0	0.05	***13.02	0.94	*0.17	1.73	***9.80	2.44
Geum canadense	--	0.0	0.0	0.01	0.0	1.56	***7.74	2.94
Phlox divaricata	7.71	0.21	--	0.00	**0.70	1.42	0.0	0.38
Caulophyllum thalictroides	***1.13	0.33	***9.11	0.91	0.0	0.51	2.11	0.23
Impatiens cf. *pallida*	--	0.0	0.0	0.28	***3.35	1.43	0.0	0.02
Sanicula spp.	--	0.0	--	0.00	*0.35	0.78	--	0.0
Sanguinaria canadensis	***1.87	0.15	--	0.10	***1.14	0.32	***6.33	0.07
Smilacina racemosa	***4.34	0.23	--	0.04	0.0	0.21	***4.56	0.09
Smilax cf. *echirrata*	0.0	0.02	25.00	0.01	0.0	0.04	7.27	0.04
Polygonatum cf. *biflorum*	0.0	0.09	--	0.00	0.0	0.004	**3.14	0.06

Table 2 (continued).

Unpreferred or ungrazed								
Solidago flexicaulis	0.21	0.26	30.56	0.01	0.0	0.13	*2.09	0.22
Phryma leptostachya	0.0	0.03	--	0.00	0.0	0.06	--	0.0
Hydrophyllum virginianum	*0.13	5.32	*5.06	0.35	*0.03	13.84	*1.06	6.28
Hepatica acutiloba	0.0	1.28	--	0.00	*0.14	4.56	0.0	3.26
Hackelia virginiana	0.0	0.007	0.0	0.04	0.0	0.11	0.0	0.007
Poaceae	--	0.0	0.0	0.04	0.0	0.44	0.0	0.34
Galium spp.	0.0	2.68	0.0	0.09	0.0	4.22	0.0	2.22
Eupatorium rugosum	--	0.0	--	0.00	--	0.0	0.0	0.70
Carex spp.	0.0	0.02	0.0	0.29	0.0	1.44	0.0	2.14
Adiantum pedatum	--	0.0	0.0	0.15	0.0	1.64	--	0.0
Arisaema triphyllum	0.0	0.03	0.0	1.22	0.0	0.13	*1.27	0.30
Anemone quinquefolia	--	0.0	0.0	0.05	0.0	0.71	0.0	1.12
Amphicarpaea bracteata	0.0	0.37	*4.94	0.21	0.69	0.82	--	0.0
Total herb community	0.30	37.93	8.61	10.30	0.65	85.54	2.85	51.30

[a] Percent grazed based on marked plants occurring in 34 50x4m strip plots

[b] Percent grazed based on a census of all known *Trillium* individuals at the site (n=97), each marked in late summer 1994 or spring 1995.

Table 3. Availability and percent grazed of the most common herbaceous species at four forest stands during late summer, 1995. Preferred and unpreferred species were grazed to a significantly greater or lower degree respectively than the overall herb community at all sites where statistical comparison was possible. For each site, * indicates species with a significantly lower percent grazed than the overall herb community, ** indicates no significant difference between the proportion of a species grazed and the overall grazing intensity on the herb community, and *** indicates species with a significantly greater percent grazed than the overall herb community. In each category, species are listed in order of their relative abundance averaged over all sites. For species occurring in fewer than 5 plots at a given site, the observed proportion of grazed stems is reported without an indication of statistical significance.

	Low deer 1		High deer 1		Low deer 2		High deer 2	
Preferred	Percent Grazed	Stems/m²	Percent Grazed	Stems/m²	Percent Grazed	Stems/m²	Percent Grazed	Stems/m²
Laportea canadensis	***2.16	20.09	***33.18	3.26	***1.26	5.61	98.96	0.16
Solidago flexicaulis	3.19	0.24	0.0	0.01	***32.25	0.18	***56.99	0.69
Impatiens cf. *pallida*	--	0.0	***31.30	0.14	***2.2	0.85	--	0.01
Trillium spp.	***2.87	0.31	--	0.0	***8.16	0.04	***32.3*	0.002
Variable preference ranking between sites								
Circaea lutetiana	--	0.03	*5.64	0.44	***1.30	1.24	***33.35	1.9
Geranium maculatum	0.0	0.11	0.0	0.06	0.29	0.93	**8.27	4.34
Caulophyllum thalictroides	29.2	0.09	*24.24	0.11	0.0	0.13	13.6	0.07
Uvularia grandiflora	***19.00	0.12	0.0	0.03	***27.09	0.13	--	0.0
Sanguinaria canadensis	0.0	0.07	0.0	0.01	***4.44	0.08	0.0	0.02
Smilacina racemosa	0.0	0.08	31.56	0.01	0.0	0.08	0.0	0.01
Smilax cf. *ecirrata*	52.50	0.02	33.33	0.01	0.0	0.05	50.0	0.01
Unpreferred or ungrazed								
Asarum canadense	--	0.0	0.0	0.11	0.0	7.65	0.0	0.5
Hepatica acutiloba	*1.19	1.26	--	0.0	0.0	3.39	*1.95	2.36
Viola pubescens	0.0	0.23	0.0	0.09	0.08	4.41	0.0	0.48
Thalictrum dioicum	1.5	0.23	0.0	0.23	0.0	3.39	1.7	0.78
Hydrophyllum virginianum	*0.66	0.64	0.0	0.04	0.0	1.02	0.42	1.38
Geum canadense	--	0.0	--	0.0	0.0	0.57	*0.67	2.28
Carex spp.	--	0.0	0.0	0.16	0.0	1.15	0.0	1.90
Viola sororia	--	0.0	0.0	0.07	--	0.0	*6.29	2.14
Adiantum pedatum	--	0.01	0.0	0.15	0.0	1.24	--	0.0
Cryptotaenia canadensis	0.0	0.02	--	0.0	0.0	1.20	0.0	0.06
Amphicarpa bracteata	0.0	1.04	*0.72	0.16	--	0.02	--	0.0
Osmorhiza spp.	0.0	0.38	--	0.0	*0.92	0.39	--	0.0

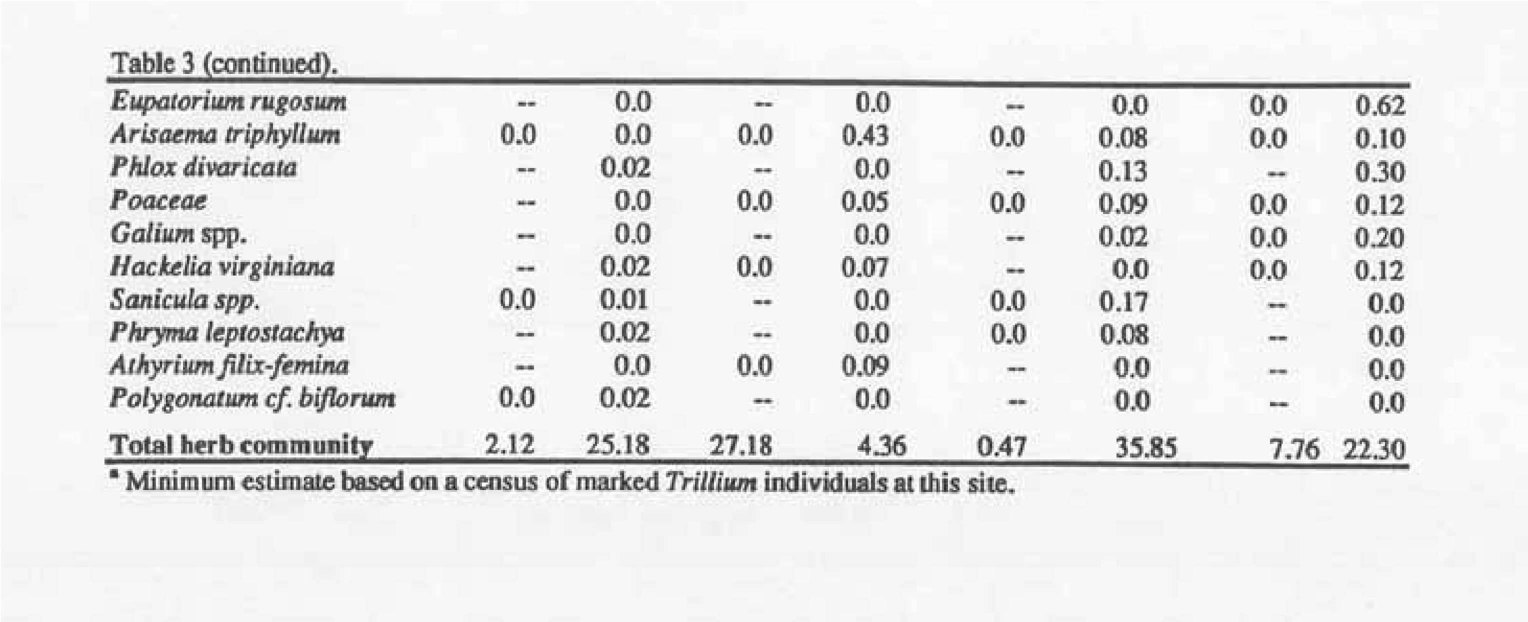

Table 3 (continued).

Eupatorium rugosum	--	0.0	--	0.0	--	0.0	0.0	0.62
Arisaema triphyllum	0.0	0.0	0.0	0.43	0.0	0.08	0.0	0.10
Phlox divaricata	--	0.02	--	0.0	--	0.13	--	0.30
Poaceae	--	0.0	0.0	0.05	0.0	0.09	0.0	0.12
Galium spp.	--	0.0	--	0.0	--	0.02	0.0	0.20
Hackelia virginiana	--	0.02	0.0	0.07	--	0.0	0.0	0.12
Sanicula spp.	0.0	0.01	--	0.0	0.0	0.17	--	0.0
Phryma leptostachya	--	0.02	--	0.0	0.0	0.08	--	0.0
Athyrium filix-femina	--	0.0	0.0	0.09	--	0.0	--	0.0
Polygonatum cf. biflorum	0.0	0.02	--	0.0	--	0.0	--	0.0
Total herb community	2.12	25.18	27.18	4.36	0.47	35.85	7.76	22.30

[a] Minimum estimate based on a census of marked *Trillium* individuals at this site.

Table 4. Comparison of the spatial distribution of grazing to forb availability based on autocorrelation analyses. Significant spatial correlation at the α=0.05 level, indicating a patchy distribution on the scale of a 50 m radius circular area, occurs when (standard normal deviate - 95% critical value) is ≥ 0. ** indicates highly significant positive spatial aggregation, i.e. (standard normal deviate - 95% critical value) > 0.025, * indicates a marginally significant positive aggregation, i.e. $0.025 \geq$ (standard normal deviate - 95% critical value) ≥ 0, and - indicates no significant aggregation.

	Overwinter	Early Summer: Overall community		Early Summer: *Laportea canadensis*		Late Summer: Overall community		Late Summer: *Laportea canadensis*	
Site	Deer/km^2 ± 95%CI	Available	Grazed	Available	Grazed	Available	Grazed	Available	Grazed
H1	11.3 ± 6.1	-	-	**	*	-	-	**	-
R1	5.3 ± 4.3	**	-	**	**	**	-	**	*
H2	23.8 ± 12.5	*	**	**	**	-	**	**	**

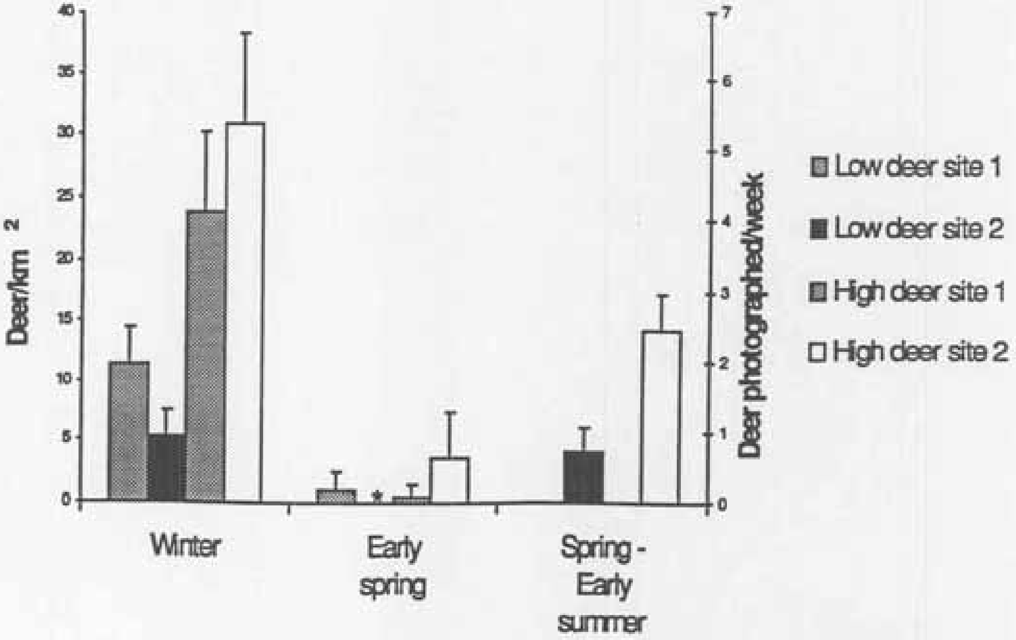

Figure 1. Comparison of seasonal deer densities among the four study sites. Relative densities during winter (October - March) and early spring (late March - mid-May), 1995, were estimated from pellet counts for all study sites. Relative deer use of Rice county study sites during spring and early summer (April 1 - June 15) was measured with passive infra-red activity monitors. Error bars indicate ±1 SE. Deer/km^2 conversions from pellet counts are based on a 150 day and 58 day pellet deposition period in winter and spring respectively, and the assumption of a 13 group/deer/day deposition rate. * No groups counted within forty-six 4 m radius plots.

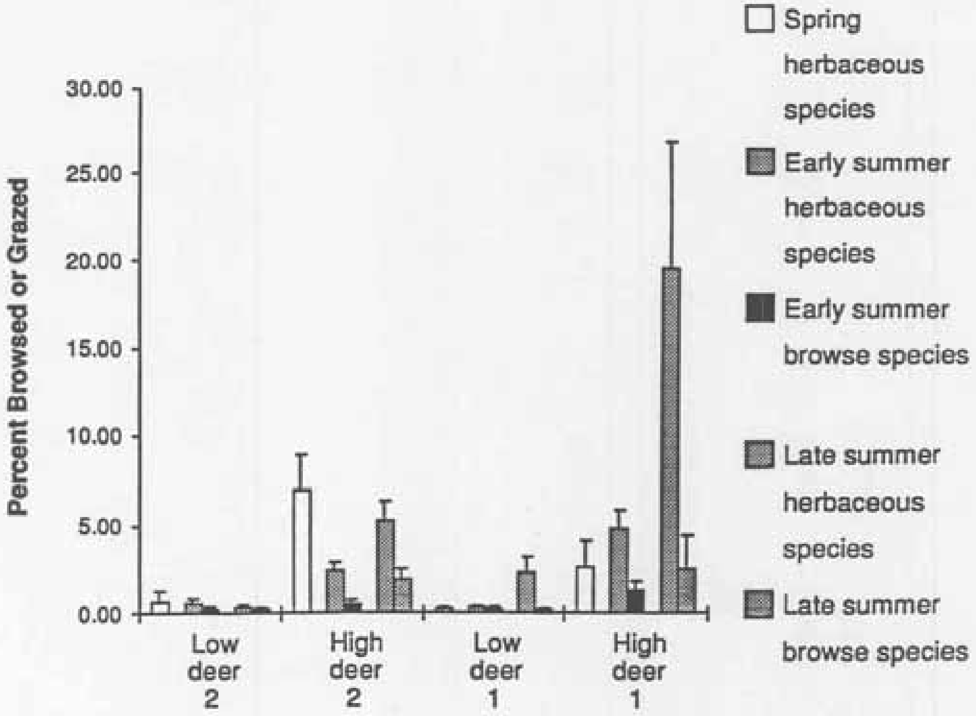

Figure 2. Seasonal patterns of deer foraging on herbaceous and woody species in the understory (0-1 m layer) of four Big Woods forests. Percentages grazed or browsed are based on the total availability of herbaceous + woody species stems in the understory. R2 and H2 are high deer density sites. Error bars indicate ±1 SE.

EFFECTS OF WHITE-TAILED DEER *ON* THE SIZE STRUCTURE *AND* REPRODUCTIVE POTENTIAL OF *TRILLIUM* POPULATIONS

Abstract: The effects of grazing by white-tailed deer on populations of Trillium spp. were examined in remnant, old-growth patches of the highly fragmented Big Woods forest ecosystem in southeastern Minnesota. The highest summer grazing intensity was observed where deer occur at high overwinter concentrations, while significantly lower grazing intensity was observed where deer occur at low overwinter density. Grazing was focused on large, reproductive plants such that at high deer density sites Trillium population structure was skewed toward small plants and deer consistently caused > 50% induction in reproduction during the growing season. No significant impact of current year herbivory on reproduction in the following year was detected. However, flowering rates at one site containing high overwinter deer densities for at least the past 5 years suggests that the cumulative effects of grazing over several years can reduce reproduction in subsequent years. Transplant experiments with *Trillium grandiflorum* also found significant deer impacts on growth and reproduction where deer occur at high density. 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, local deer management should be a consideration in the conservation and restoration of fragmented forest communities in eastern North America.

INTRODUCTION

A large body of research has recognized that 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 (e.g. Leuthold,1996; Zimov et al., 1995; Anderson & I-Ducks 1979; Spatz & Mueller-Dombois,1973; Harper, 1969; Howard, 1966). 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 species extirpations in particular forest stands or isolated forest patches (Beak, Cottam & Vogl, 1960; Anderson & Loucks, 1979; Frelich & Lorimer, 1985; Tilghman, 1989). While extensive research has been conducted on winter browsing effects of deer on forest i communities (Graham, 1952; Beals, Cottam & Vogl, 1960; Anderson & Loucks, 1979; Frelich & Lorimer, 1985; Tilghman, 1989; Allison, 1990; Strole & Anderson, 1992; Anderson & Katz, 1993), considerably less attention has been paid to growing season deer i herbivory and potential *effects on* understory herbaceous plant communities (Balgooyen & Waller, 1995; Anderson, 1994; Miller, Bratton & Hadidian, 1992). As managers continue to, face difficult decisions concerning the management of deer populations, often with limited available information, a better understanding of the effects deer exert on native plant communities is needed.

Recently, Alverson, Kuhlmann & Waller (1994) and Alverson, Waller & Solheim (1988) suggested that human-induced changes in the distribution of plant communities can alter plant-herbivore relationships and potentially cause significant herbivore impacts within the new landscape. In Minnesota, dramatic changes in the structure of forest landscapes since European settlement have also resulted in changes in the distribution and abundance of white-tailed deer (Berner & Simon, 1993). In southeastern Minnesota, an approximately 7,750 km? contiguous area of mesic deciduous forest in the presettlement landscape dominated by elms, *Ulrnus americana* and *Ulums rubra,* sugar maple, *Acer saccharum,* and American basswood, *Tilia americana,* (Grimm, 1984; Marschner, 1974; Daubenmire, 1936) has 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). Deer were extirpated or extremely rare in this region of the state from the late 1800's through the 1920's, 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 3 decades deer populations in southeastern Minnesota have increased steadily to current densities (Berner & Simon, 1993; Dexter, 1996).

Recent surveys conducted in four old-growth Big Woods remnants in southeastern Minnesota documented highly selective deer foraging patterns on the understory forb community during the growing season (Chapter 1, Appendix C). Species in the *Trillium* genus were consistently selected at varying levels of *Trillium* abundance and deer density. While studies have suggested that deer can eliminate selected herbaceous species from forest patches (Anderson, 1994; Alverson, Waller & Solheim,1988), this has not been experimentally addressed. The objectives of this study were therefore to examine: 1) the effect of deer herbivory on the size structure of *Trillium* populations at varying local deer densities, 2) the effect of deer herbivory on the reproductive potential of Trillium populations, and 3) the potential impact of deer on forest restoration efforts.

STUDY AREA

Studies were conducted at 3 old-growth maple-basswood stands 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), exhibit an all-aged distribution of tree sizes, and contain large (50-100cm dbh) individuals of the 3 dominant tree species (Appendix B). Green ash *Fraxinus pennsylvanica,* black ash *F. nigra,* hackberry *Celds occidentalis,* bitternut hickory, northern red oak *Quercus* rubra, white oak *Quercus alba,* box elder *Acer negundo,* black cherry *Prunus serodna,* butternut, and black walnut *Juglans nigra,* are less abundant elements of the canopy. Ironwood 0styra *virginiana is* an important subcanopy species. The 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 believed to contain relatively high local deer densities and one site believed to contain a comparatively low local deer density based on 1993-94 aerial counts.

SPECIES DESCRIPTIONS

Trilllum cernuum and *Trillium flexipes* are long-lived, non-clonal, shade tolerant forbs found in the understory of mesic deciduous forests. *T. cernuum occurs* from Newfoundland west to Minnesota and south to Maryland, while *T. flexipes* occurs from central New York to Minnesota and south to Georgia (Gleason & Cronquist, 1991). In Minnesota, specimens have been collected throughout the Big Woods region (Ownbey & Morley, 1991). Both T. *cernuum and T. flexipes occur* at all study sites, as well as individuals with hybrid characteristics. As a result, I considered these species as a single *T. flexipes-T. cernuum* complex.

Trilllum grandiflorum is a long-lived, non-clonal, shade-tolerant herb distributed throughout rich, broad-leaved deciduous forests from the southern Appalachian mountains through the Great Lakes region including Ontario, and east to Maine (Gleason & Cronquist, 1991; Kawano, Ohara & Utech, 1986). In Minnesota, *T. grandiflorumn* has been collected from deciduous forests throughout the central part of the state, and from locations south, east, and west of the Rice County sites included in this study (Ownbey & Morley, 1991). A 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* in 1972 (N. Falkum, pers. comm.), but this forest no longer exists. *T. grandiflorum* does not occur naturally at any of the sites included in this study.

Fragmentation of Big Woods forests in southeastern Minnesota has likely resulted in the loss of understory species from existing stands due to factors such as the historical effects of livestock herbivory, the loss of plant propagules from forest patches to surrounding human-dominated habitats (Tilman et al. 1994), and stochastic events. In addition, the few remaining fragments may not contain an understory community representative of the large, contiguous presettlement forest. Conservation plans for remnant Big Woods forests in southeastern Minnesota therefore focus on restoring forest corridors between existing fragments, and restoring species characteristic of Big Woods forests. To examine the potential impact of deer on forest restoration efforts, I examined deer grazing impacts on transplanted populations of *T. grandiflorum.* This species was chosen because *T. grandiflorum* is palatable to deer (Anderson 1994, Balgooyen and Waller 1995, Chapter 1), 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* transplants were conducted are located toward the southern edge of the species' range, and hence may represent stressful growing conditions where herbivore effects could be especially severe.

Individual *Trillium* plants consist of a single stem (rarely two) supporting a whorl of 3 leaves in the larger size classes, and a single leaf in juvenile plants. *T. grandiflorum* seeds germinate in the spring and produce adventitious roots (no leaves) in the first growing season, the cotyledon leaf develops in the second growing season, and a single leaf is produced in the third growing season Manzawa & Kalisz, 1993). Using annual constriction counts, Hanzawa & Kalisz (1993) found that the minimum age to reproduction for *T. grandiflorum* was 17 years. To my knowledge, studies of *T. cernuum* and *T. flexipes* age structure have not been conducted. In Minnesota, all three *Trillium* species reach anthesis in late May - 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, Ohara & Utech,1986; Ohara & Utech 1988).

METHODS

Study Design

Three separate studies were used to examine the effects of deer on *Trillium* populations. First, I measured deer grazing intensity and examined the effect of grazing on the size structure of Trillium populations at two high deer density sites (High deer sites 1 and 2) and one comparatively low deer density site (Low deer site). Secondly, I used small deer exclosures placed around individual *Trillium* plants to measure the magnitude of deer impacts on *Trillium* growth and reproduction at High deer site 1. Finally, I examined potential deer impacts on plant community restoration efforts by establishing two transplanted populations *of Trillium grandiflorum* at High deer site 2 and the Low deer site, and conducting an experiment using "closures placed around individual transplants at each site.

Deer Density Estimation

Three methods were used to estimate seasonal deer densities at each study site. First, winter deer density was measured using both deer pellet group counts and aerial counts. At each of the 3 study sites, 46-50 permanent sampling points were established in a systematic grid following snowmelt in March, 1995. Deer pellet groups were counted within a 4 m radius of each point at all sites during March 14-20, 1995, and during 1- 12 April, 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 density. Counts were converted to relative estimates of deer/km^2 based on a 150 day deposition period (overwinter) assuming 13 pellet groups produced/deer/day (Eberhardt & van Etten, 1956). Density differences between sites were compared using likelihood ratio tests for log-linear models (Agresti, 1996).

I obtained a second estimate of winter deer density at each study site from aerial counts because the different methods involve different advantages and disadvantages (e.g. see Fuller 1991, White 1992, Jordan et a1. 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 (see Chapter 5). Aerial counts measure the number of deer per 1 km2 of permanent cover in mid-winter, while pellet counts measure the number of deer spending 24 hours/day in 1 km^2 of Big Woods forest during the course of the winter. An analysis of aerial count versus pellet count estimates at 6 Big Woods forests in southeastern Minnesota showed that both methods provide consistent results for deciduous forests except where alternative winter habitat is locally available (Chapter 5).

Deer density during spring and summer was measured at each site using 3 automated cameras attached to infra-red deer monitors (Non-typical Engineering, Green Bay, Wisconsin, USA) which were moved to new randomly located positions every 7 days (Chapter 1). Because only 6 monitors were available, the Low deer site and High deer site 2 were sampled during 1 April - 15 June, 1995, and High deer site 1 was sampled during 1 April -11 August, 1996. Data obtained from camera monitors were analyzed in terms of the number of deer photographed per week.

Grazing Intensity and Effects on *Trillium* Size Structure

Naturally occurring *Trillium cernuum* and *T. flexipes* were sampled at High deer sites 1 & 2 and the Low deer site using permanent, systematically located 50 m transects. A 2 m transect width was sampled at the Low deer site where Trillium was abundant, and a 4 m width was used at High deer sites 1 & 2. 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 non-flowering) of each plant was recorded. Because *Trillium* was extremely rare at High deer site 2, few plants were observed along transects. I therefore conducted extensive understory searches at this site and marked all plants found between April 14 May 15,1995.

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

In 1996, marked plants at each site were surveyed during 5-8 May. Because relatively little deer grazing occurs before this point in the growing season, both reproductive status and length of the emerging leaf bundle of each plant were recorded to obtain at pre-grazing distribution of plant sizes for each population. Plants were re surveyed during 17-20 June, 1996, to obtain the same measurements as the survey in June, 1995, and plants were re-checked 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, *I* deleted one randomly selected plant in the pair from the sample, and all reported sample sizes and analyses are based on this subset of plants.

For Trillium species, Kawano, Ohara & Utech (1986) found that leaf area is a good measure of biomass and hence the growth stage of an individual. I estimated leaf area in the field as:

Plant leaf area = leaf length x leaf width x 0.5 x # of leaves,

and also measured the 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 provides a reliable estimate of individual leaf area.

Response of *Trillium* to Protection from Herbivory

To examine deer impacts on growth and reproduction of a naturally occurring *Trillium* population, High deer site 1 was searched during 9 -10 May, 1995 to find and mark 50 *Trillium* with leaf length >_ 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, and were checked for deer grazing on 17 August, 1995 and 26 July, 1996.

Trillium grandiflorum Transplant Experiments

I transplanted 120 *Trillium grandiflorum* rhizomes to the Low deer site and 120 rhizomes to High deer site 2 in August, 1994. Individuals were planted along transects at a minimum spacing of 3 m to insure that each represents an independent observation. At both sits, 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, 1995,1112 May, 1996, and 17 18 June, 1996, and were rechecked for deer grazing 26 27 August, 1995, and 25 26 July, 1996.

RESULTS

Deer Densities

Winter deer densities based on pellet group counts were significantly lower at the Low deer site compared to the high deer sites in both seasons of both years (Fig. 1, likelihood ratio tens, $\Delta G^2 > 12.25$, d f.=1, $P < 0.001$ for all comparisons). Pellet group counts in 1995 showed winter concentrations of 24-31 deer/km^2 at High deer sites 1 and 2 compared to 4 deer/km^2 at the Low deer site (Fig. 1). Aerial counts showed an overwinter concentration of 25-36 deer/km^2 of permanent cover at High deer sites 1 and 2, and 11 deer/km2 at the Low deed site (Fig. 1). The pellet count estimate at High deer site 1 was significantly lower in 1996 than 1995 (Fig. 1), but aerial counts conducted in both years at this site showed 4 constant density (23.4 and 25.3 deer/km2). The change in pellet density was likely due to a local shift in habitat use of deer during the more severe winter conditions in 1996 to several conifer patches and a large south facing slope next to High deer site 1. Therefore, the combined winter deer density estimates show a high local overwinter concentration at High deer sites 1 and 2 during the study period relative to the Low deer site.

The automated cameras provided a sensitive index of growing season density, and showed that growing season deer density was approximately 3 times higher at High deer site 2 as compared to the Low deer site in 1995 (ΔG^2=14.6, d.f.=1, P<0.001), and 4 times higher ',in 1996 at High deer site 1 than the 1995 index for the Low deer site (ΔG^2= 31.3, d.f.=1, P<0.0001, Fig. 1).

Winter aerial counts were conducted intermittently at High deer site 2 and the Low deer site over the past 8 years and every winter for the past 5 years at High deer site 1 (J. Moriarty and J. Vorland, pers. comet.),. High deer site 1 and 2 differ, in that only at High deer site 1 have high densities been present for at least the past 5 years. The current density at High deer site 2 is the result of a rapid increase between 1989 and 1993. Overwinter densities at the Low deer site have been low over the past 8 years.

Grazing Intensity and Effects on *Trilllum* Size Structure

I examined grazing intensity and population size structure for a sample of 143, 28, I and 76 marked plants in 1995 and 164, 47, and 90 marked plants in 1996 at the Low deer site, High deer site 1, and High deer site 2 respectively. Significant differences in the intensity of deer grazing among sites were observed in both 1995 and 1996 (Table 1, X^2=32.15 and 27.04 respectively, d.f.=2, P<0.0001). The highest grazing intensity occurred at High deer site 2 in both years, and was 2 5 times higher than overall grazing intensities at both the Low deer site and High deer site 1. No significant differences in overall grazing intensity were detected between the low deer site and High deer site 1 in 1995 or 111996 (Table 1, X^2=0.29, P=0.59; X^2 =0.6, P=0.80). Most grazing on *Trillium* occurred between early May and the second sampling period in late June. The exception to this pattern was at High deer site 2 in 1995 when a large proportion of plants was grazed after the June sampling date (Table 1). In addition to deer grazing, plants can be defoliated by lepidopteran larvae which feed on and occasionally sever the base of the stem. At the Low deer site, High deer site 1, and High deer site 2 respectively, lepidopteran damage was observed for 0.0, 0.0, and 6.6 % of plants in 1995 and 0.0, 0.6, and 4.4% of plants in 1996.

I 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 measured in June after anthesis (weighted regression, r^2=0.96, F=239, p<0.0001). Early May leaf bundle length measurements were used to construct a pregrazing plant size distribution (<1% were grazed before May sampling), and late June leaf area estimates were used to construct a post grazing size distribution for each of the 3 populations. The June size distributions do not include plants grazed by deer because all grazed plants were 100% defoliated.

No significant differences were detected in the size class distributions of the 3 populations based on the early May leaf bundle length measurements (1 tailed K-S statistics$\leq$0.06, P$\geq$0.8 for all comparisons, Fig. 2). By late June (post anthesis and postgrazing) significant differences in the size distributions of the three populations were observed (Fig. 2). At High deer site 1, the population consisted predominantly of individuals with leaf area less than 80 cm^2, which differed significantly from the Low deer site (K-S statistic=0.28, P=0.05). The distribution at High deer site 2 was shifted toward an increased frequency of smaller plants in the population, but was not statistically different from the other sites (K-S statistics < 0.21, P > 0.26). Although no early May measurements were made on plants in 1995, the distribution of plant sizes in late June, 1995, was similar to that observed in 1996: the distribution at High deer site 1 contained significantly more small plants than the Low deer site (K-S statistic = 0.59, P=0.0005), and High deer site 2 was shifted toward smaller plants but was not statistically different from the Low deer site (K- statistic=0.04, p=0.88).

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 before being influenced by the within season effects of grazing. In early May of 1995 and 1996, they flowering rate at High deer site 1 (4% and 15%) was significantly lower than both the Low deer site (27% and 34%) and High deer site 2 (32% and 38%) ($X^2 \geq 7.0$ p ≤ 0.0081 for all comparisons). No difference was detected in the May flowering rate between High deer site 2 and the Low deer site in either year ($X^2 \leq 0.6$, $P \geq 0.40$). Over the course of the growing season, flowering plants experienced a higher grazing rate than the overall population (flowering and non flowering plants) at all three study sites (Table 1). A significantly higher proportion of reproductive plants was grazed at High deer site 2 compared to the Low deer site in both years (Table 1, $X^2=7.57$ and 7.14, $P<0.007$). The sample of reproductive plants was extremely small at High deer site 1 due to their rarity; 4 of 8 marked reproductive plants were grazed in 1995 and 10 of 13 marked reproductive plants were grazed in 1996. The 1996 grazing rate was significantly higher than the proportion of reproductive plants grazed at the Low deer site (Table 1, $X^2=6.42$, $p=0.01$).

Impacts of grazing in 1995 on *Trillium* reproduction in 1996 were examined by comparing 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% flowering in 1996, N=25 vs. 90% flowering in 1996, N=44 respectively, $X^2=1.67$, $P=0.20$ ($Z=1.09$, $P=0.28$). Given the sample sizes for this comparison, there was a 90% chance of detecting a 0.35 difference in flowering rates at the alpha = 0.1 level.

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

Response of *Trillium* to Protection from Herbivores

The exclosure experiment conducted at High deer site 1 showed a dramatic response of *Trillium* to release from herbivory after only 2 growing seasons. At the beginning of the experiment in May, 1995, plant size was similar for exclosed ($X = 43.86\text{cm}^2$) versus unexclosed ($X = 45.49\text{cm}^2$) plants (paired t test, $t=0.54$, $p=0.3$) and 28% of the plants in both experimental groups were flowering.

Within a growing season, plants can be defoliated by deer, mechanical damage to the stern, and lepidopertan larvae. During both growing seasons, the proportion of plants that were not defoliated by the late June sample was significantly higher for plants protected from deer as compared to unprotected plants (Fig. 3, 1995: X^2 7.71, P=0.006, 1996: X^2=22, P<0.0001). These differences reflect the observation that 36% and 44% of the unprotected sample were grazed by deer in 1995 and 1996 respectively. For protected and unprotected plants combined, 12% and 8% experienced lepidopteran damage in 1995 and 1996 respectively.

In 1996, after one year of protection from deer herbivory, leaf area of unprotected plants in early May was significantly lower than the leaf area of paired protected plants (26.8cm^2 vs. 37.1cm^2, t=2.72, P=0.007). Measurements in May were not possible for all unprotected plants because 25% were grazed before the sampling period, and size comparisons were based on individuals which could be measured. Flowering rates of protected versus unprotected plants diverged over the course of the study (Fig. 3) such that by June, 1996, the flowering rate of protected plants was 19 times greater than the rate for unprotected plants (X^2=27.0, p<0.0001).

Trillium grandiflorum Transplant Experiments

In early May, 1995, 58 unprotected and 19 protected transplants emerged at the Low deer site, and 56 unprotected and 18 protected transplants emerged at High deer site 2 following overwinter mortality at both sites. At this time, mean plant leaf area was similar inside vs. outside exclosures at both sites (t<1.20, p>0.24). At High deer site 2, 10% of Unprotected plants were grazed before any measurement could be taken in early May, and these were not used in calculations of initial mean plant size or flowering rate: In 1995, deer grazing intensity on unprotected plants was significantly greater at High deer site 12 compared to the Low deer site (Table 2,X^2=14.9, P<0.0001). No deer grazing on transplants was observed after the late June check. The overall proportion of transplants damaged by lepidopteran larvae was also significantly greater at High deer site 2 (31.1 % vs. 7.9%, X^2=12.92, d.f.=1, P=0.0003). However, at High deer site 2, the proportion of transplants retaining leaves through anthesis was significantly greater for protected (available to lepidopteran larvae only) vs. unprotected (available to deer and lepidopteran larvae) plants (X^2=7.4, d.f.=1, P=0.007). No significant difference was detected between protected and unprotected plants at the Low deer site (X^2=0.09, d.f.=1, P=0.76).

Following one year of protection from deer herbivory, mean leaf area in early May 1996 at High deer site 1 was significantly greater for protected than unprotected plants (t^2=2.49, p=0.027). Grazing intensity decreased from 1995 to 1996 at High deer site 2 and increased at the Low deer site such that in 1996 then was no significant difference in the proportion of unprotected Trillium grazed (X^2=0.99, p=1.0). In 1996 at high deer site 1, 35% of the unprotected plants disappeared due to unknown causes between May and June while only 15% disappeared at the low deer site, possibly resulting in a greater underestimate of deer grazing intensity at high deer density. All observed deer grazing occurred before the late June check. 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 versus outside at both low deer density (Table 2, X^2=4.94, p=0.03) and high deer density (X^2=2.86, p=0.09).

Flowering rates of transplants were similar inside versus outside exclosures at the beginning of the experiment in early May, 1995, at both low deer density (94% vs. 84%, X^2=1.34, p=0.25) and high deer density (78% vs 80%, X^2=0.04, p=.84). No significant difference was detected between the proportion of transplants flowering in the post anthesis (sample (late June) for protected vs. unprotected plants at the Low deer site in 1995 (Table 2, X^2=0.00, d.f.=1, P=0.97) or in 1996 (52.9% vs. 38.2%,X^2=1.16, P=0.28). At High deer site 2, in spite of considerable damage by lepidopteran larvae in the 1995 growing season, a significantly greater proportion of transplants was flowering at anthesis inside vs. outside deer exclosures in 1995 (X^2=4.32, d.f.=1, P=0.04) and in 1996 (X^2=5.1, d.f.= 1. P=0.02).

DISCUSSION

Deer Impacts on Natural *Trillium* Populations

The effect of deer herbivory on an understory forb population depends on both the grazing, rate on that species and the response of individual plants to defoliation. For long-lived perennials such as *Trillium*, the response of an individual to herbivory must be considered in terms of re-growth and reproduction in the season when herbivory occurs, and growth and reproduction in subsequent growing seasons. Deer impacts on individual *Trillium* are especially severe since a single bite results in 100% defoliation and removal of the flower or fruit from reproductive plants, no re-growth occurs within that growing season, and *Trillium* do not reproduce clonally. Our observations of naturally occurring *Trillium* populations in forest stands supporting high relative deer densities clearly showed that deer dramatically reduce the reproductive output of the population during the growing, season by grazing large, flowering plants. Similar observations for *T. grandiflorum* in Illinois (Anderson, 1994) and observations in northern Wisconsin (Balgooyen & Waller, 1995) suggest that *Trillium* spp. are of relatively high preference across a large geographic region.

The impact of grazing was reflected in the changes in size structure of the *Trillium* populations (Fig. 2). At low deer density, despite considerable grazing rates including the removal 'of an estimated 36% of flowering plants, the population still contained a relatively high proportion of plants in the large size classes (leaf area > 120 cm^2). At High deer site 2, where the highest grazing rates were observed, smaller plants dominated the size distribution such that plants >120 cm^2 leaf area were rare. The post-grazing size distribution was even more skewed at High deer site 1 such that large size classes are missing, and most plants are smaller than 80 cm^2 leaf area.

In all *T. cernuum- flexipes* populations monitored, more than 85% of ungrazed, flowering plants developed fruits. This rate of pollination is higher than observed for *T. flexipes* elsewhere (Ohara & Utech,1988), indicating that pollinators were not limiting reproduction. In the absence of other compensatory sources of seed and juvenile plant mortality, our results indicate that deer at high densities are directly reducing population recruitment by >50%, and such extreme impacts are consistent across years and study sites. Many factors may *have led to the low Trillium densities at high deer density sites, including patchy* Trillium distributions at the time of forest fragmentation, stochastic events, historic livestock grazing at High deer site 2, and elevated deer densities.

Regardless of historic impacts on the populations, the documented levels of grazing strongly suggest that high localized deer densities are preventing *Trillium* populations from recovering. The exclosure experiment at High deer site 1 supported this conclusion and demonstrated that changes in plant size and reproductive rates for unprotected plants are dramatically reversed when plants are protected from deer for only 2 years (Fig. 3).

In addition to the within growing season reduction in *Trillium* reproduction, herbivory can further impact populations if defoliation of a plant in one growing season reduces reproduction in subsequent years. I found no significant difference in 1996 flowering rates, for ungrazed versus grazed plants that were reproductive in 1995. This result suggests that a single herbivory event does not have long term effects on *Trillium* reproduction. Partial defoliation (50%) of *Trillium grandiflorum* without removing the flower results in the allocation of resources to sexual reproduction at the expense of underground carbohydrate storage within a growing season, and hence 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 reserves normally expended on seed production since deer remove the flower in addition to all foliage. This result suggests that *Trillium* individuals can be highly resilient to deer grazing impacts 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.

The cumulative effects of herbivory over several growing seasons on reproductive success could not be directly assessed within the time period of this study. However, comparison of the *Trillium* populations at the 2 high deer density sites shows that while both populations are currently experiencing high grazing intensities on large, reproductive plants, the populations contain a significantly proportion of flowering plants in early May before most deer grazing takes place. This likely reflects differences in deer densities over the past 5 - 8 years. At High deer site 2, high densities have only been present for the past 2 - 3 years following a rapid increase in the local deer population between 1989 and 1993. At High deer site 1, aerial counts show a consistently high and slightly increasing local deer density from 1992 - 1996. Lower pre grazing flowering rates at this site suggest that cumulative, long term grazing impacts occur when high local deer densities are maintained for at last 5 years.

Although no baseline demographic data is available for *T. cernuum* or *T. flexipes* populations, population structure of *T. flexipes* based on size class analysis (Ohara & Utech, 1;1988) is similar to that observed for *T. grandiflorum* (Kawano, Ohara & Utech, 1986). For a *T. grandiflorum* population in Michigan, Hanzawa & Kalisz (1993) found that individuals ranged from 1- 30 yrs old and the minimum age of reproductive plants was 17 years. Based on constriction counts, several reproductive plants at High deer sites 1 and 2 were >25 years old (personal observations). This suggests that if high grazing intensities continue for more than 15 - 20 years, deer can drive a local population to extinction. Conversely, the long generation time of understory forbs such as *Trillium* species will severely limit that rate at which population densities can increase following a reduction in local deer density.

In addition to direct impacts of grazing on *Trillium*, community level grazing pattern may affect *Trillium* establishment, growth, and survival. Previous work showed that *Trillium* spp. are grazed to a greater degree than many common forb species, such as *Hydrophyllum virginianum* and *Arisaema triphyllum*, (Chapter 1). At both high deer density sites, *Trillium* was extremely rare in the overall understory (Table 1), but deer still exerted high grazing intensity on this genus. Species with phenological patterns similar to *Trillium*, occur at comparatively high densities in the forest understory and likely compete for light land establishment sites. The selective pattern of deer grazing strongly suggests that increased *Trillium* foliage removal will not lead to compensatory increases in ground level light availability and hence increased survivorship of *Trillium* seeds or juvenile stages. Equally important was the observation that high grazing intensities are maintained on reproductive *Trillium* individuals even where they occur at low densities and hence are extremely rare in the overall plant community.

This community level grazing pattern can result in strong negative deer impacts on particular species such as *Trillium* while other forb species remain abundant. This is in contrast to the common situation where 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. This study shows that deer can be exerting significant effects on understory plant communities while the overall groundlayer remains green

Deer Impacts on Plant Community Restoration

The fragmentation and disturbance of forests throughout the eastern United States, and particularly in the Big Woods region of Minnesota, has likely resulted in the local loss of understory species from many existing forest patches as a result of historical land use practices (logging and livestock grazing), land use practices in the surrounding landscape, local species' distributions at the time of fragmentation, stochastic events, and elevated deer densities. While many Big Woods remnants have been protected from direct human impacts, deer can still affect efforts to restore the native plant community. The transplant experiments with *Trillium grandiflorum* showed that, as with naturally occurring *Trillium* populations, grazing impacts where deer occur at high overwinter density include a large within g0owing season reduction in flowering rates and survivorship, and across years a decline in plant size compared to protected transplants.

A second major factor affecting transplant survival and reproduction was high levels of I stem damage by lepidopteran larvae at High deer site 2, indicating that under reduced deer densities, other sources of mortality and damage could inhibit transplant success. However, these experiments clearly show that at high deer density, significant additive deer impacts occur even when other important factors are affecting transplant survival and reproduction (High deer site 2, protected vs. unprotected plants). Because our objective was to measure deer impacts, I did not assess whether factors such as seed production, germination and subsequent survivorship would be sufficient at either site for successful *T. grandiflorum* establishment. The observed levels of deer grazing, *Trillium* survival and flowering rates, and changes in plant size over the 2 years at the Low deer site show that given suitable conditions for *T. grandiflorum* establishment, deer at low overwinter density are not expected to be a significant factor affecting transplant success.

Conclusions

In the highly fragmented Big Woods landscape in southeastern Minnesota, deer are dispersed throughout the agricultural landscape during the growing season, and often concentrate in deciduous forest stands during the winter. Higher growing season deer densities are observed at forested sites where high overwinter deer concentrations also occur. (fur combined studies show the deer cause large, significant reductions in *Trillium* reproduction and survivorship during the growing season at sites supporting high overwinter deer concentrations (25-35 deer/km^2). Levels of herbivory observed at 2 sites in southeastern Minnesota suggest that deer can lead to the local extirpation of sensitive, forbs such as *Trillium* in remnant Big Woods forests. The most significant impacts tin population structure were observed where deer have occurred at high overwinter concentrations for at least 5 years. Significantly lower grazing intensities and higher *Trillium* flowering rates are observed where deer occur at low (4 - 11 deer/km^2) overwinter concentrations, but long term monitoring will be needed to determine whether this level of herbivory does not lead to *Trillium* population declines. Transplant experiments with *Trillium grandiflorum* showed that deer grazing can cause significant, additive impacts on reproduction, within season survival, and growth of restored plant populations at sites supporting high deer densities. In contrast, significant deer impacts on transplant success were not observed at low deer density.

Other research showing that ungulate herbivory can have positive effects on forb populations (e.g. Paige & Witham, 1987; Paige, 1992) and can be an important factor maintaining community structure (e.g. McNaughton, 1983) has been interpreted as an indication of along co-evolutionary history for the plant herbivore interaction. The results presented here suggest that the relationship between deer and forest communities in southeastem Minnesota has undergone a rapid change in response to landscape fragmentation and changing deer densities over the past 150 years, such that grazing can lead to tie local extirpation of sensitive plant species. As a result, this study provides evidence that management of deer populations in parks and preserves must be an important consideration for the conservation and restoration of fragmented forest communities throughout eastern North America.

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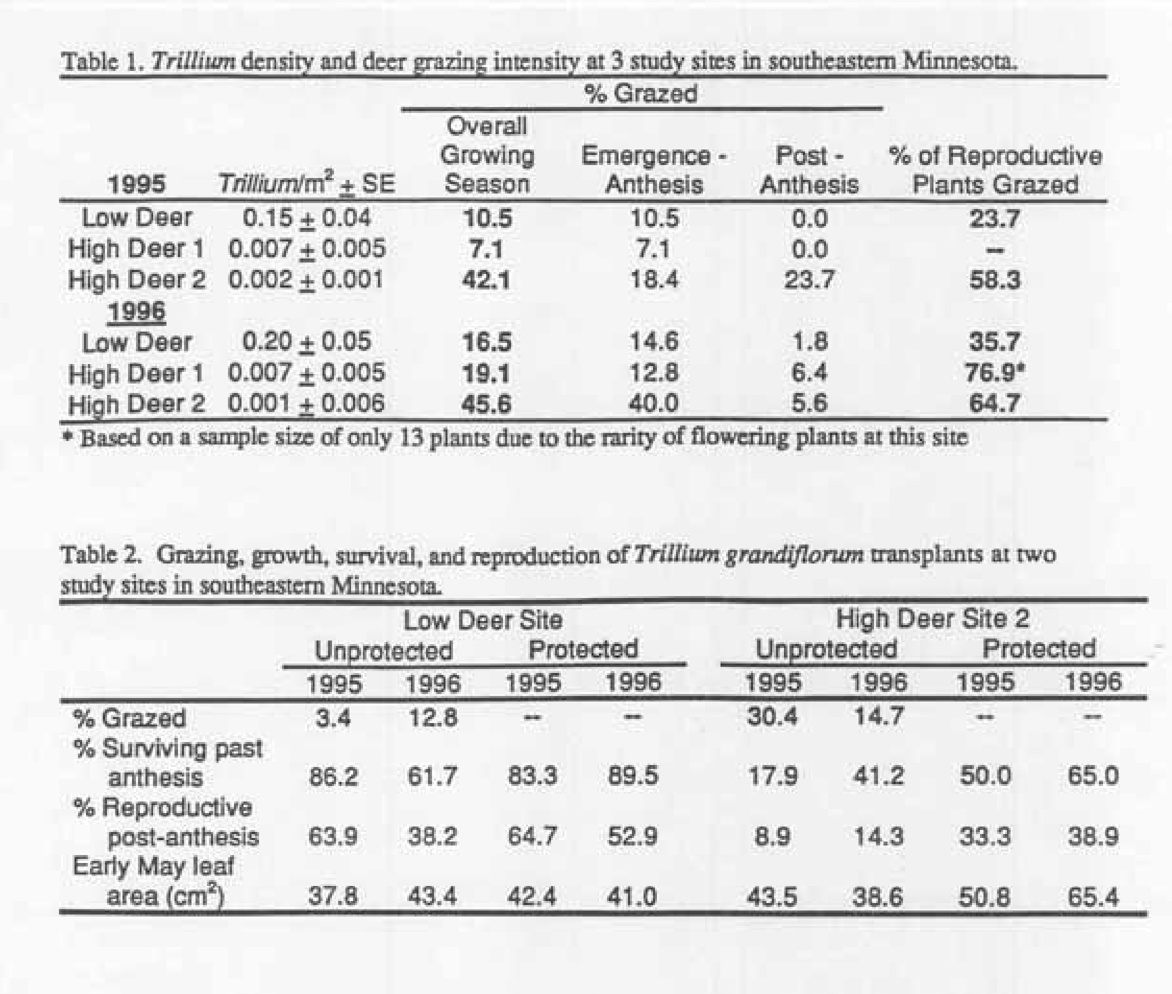

Table 1. *Trillium* density and deer grazing intensity at 3 study sites in southeastern Minnesota.

		% Grazed			
1995	*Trillium*/m² ± SE	Overall Growing Season	Emergence - Anthesis	Post - Anthesis	% of Reproductive Plants Grazed
Low Deer	0.15 ± 0.04	**10.5**	10.5	0.0	**23.7**
High Deer 1	0.007 ± 0.005	**7.1**	7.1	0.0	**--**
High Deer 2	0.002 ± 0.001	**42.1**	18.4	23.7	**58.3**
1996					
Low Deer	0.20 ± 0.05	**16.5**	14.6	1.8	**35.7**
High Deer 1	0.007 ± 0.005	**19.1**	12.8	6.4	**76.9***
High Deer 2	0.001 ± 0.006	**45.6**	40.0	5.6	**64.7**

* Based on a sample size of only 13 plants due to the rarity of flowering plants at this site

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

	Low Deer Site				High Deer Site 2			
	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 (cm²)	37.8	43.4	42.4	41.0	43.5	38.6	50.8	65.4

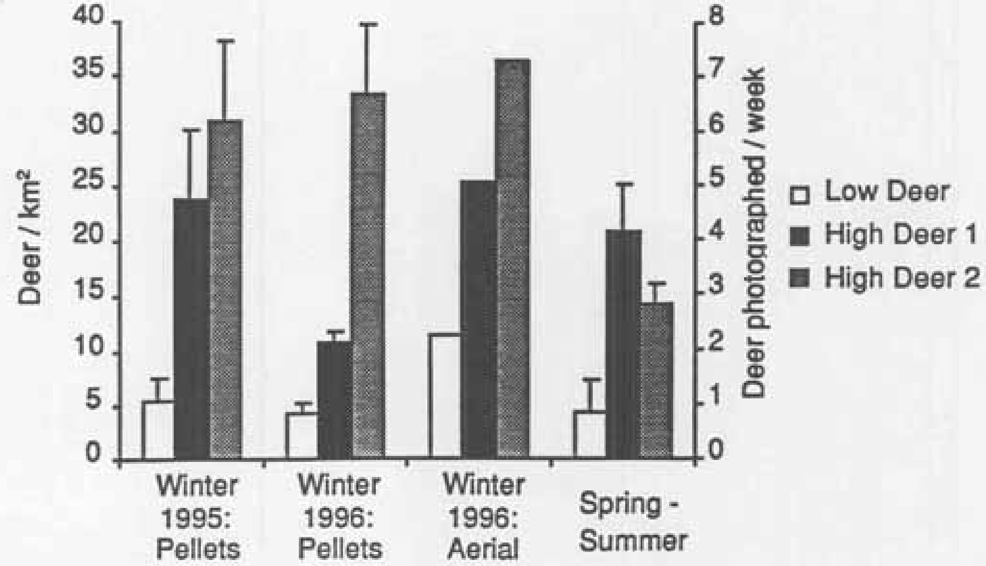

Figure 1. Comparison of seasonal deer densities among three study sites in southeastern Minnesota. Winter density estimates based on pellet-group counts were converted to an estimate of deer/km^2 + 1 SE using a value of 13 pellet-groups/deer/day. Aerial counts are expressed as deer/km^2 of permanent winter cover. Spring-summer relative deer density estimates are expressed as the number of deer photographed/week ± 1 SE and were measured at high deer 1 and low deer sites in 1995 and high deer 2 in 1996 using passive infra-red camera monitors.

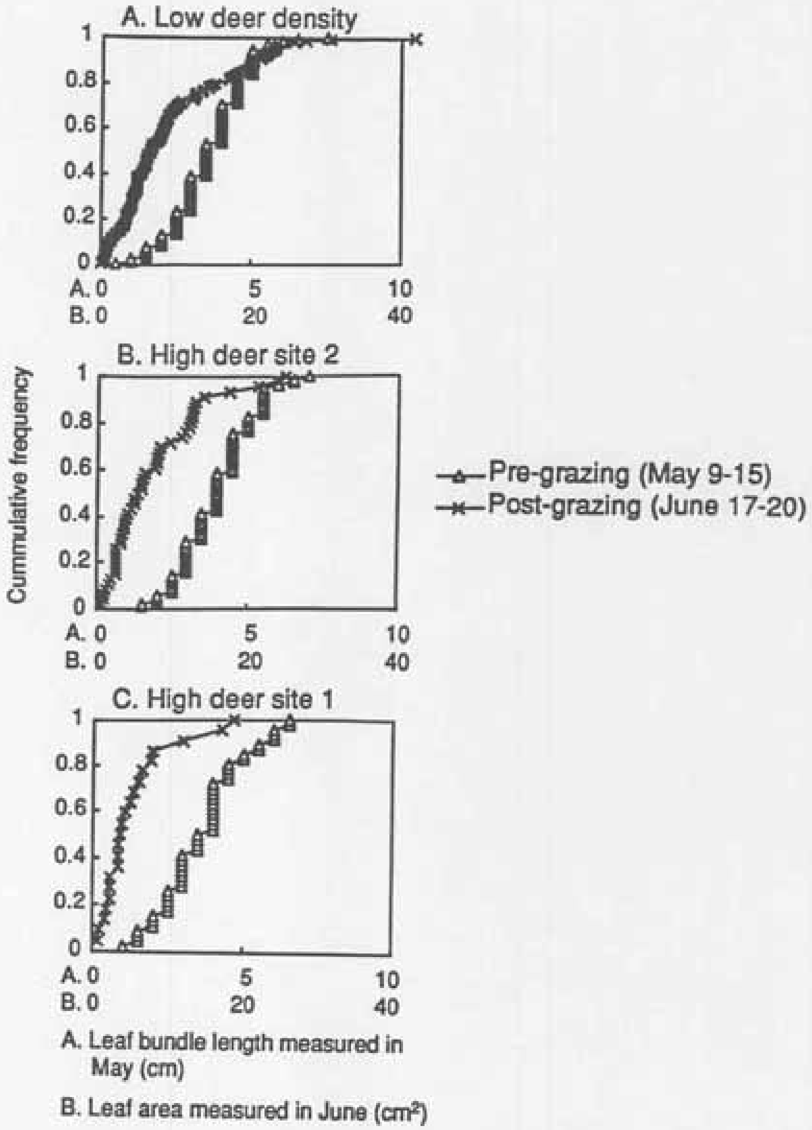

Figure 2. Cumulative frequency distributions of plant sizes for three *Trillium* populations experiencing different levels of deer herbivory. The early-May distribution is based on the length of emerging leaf bundles (cm) while the late-June distribution is based on estimated leaf area (cm^2) of ungrazed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

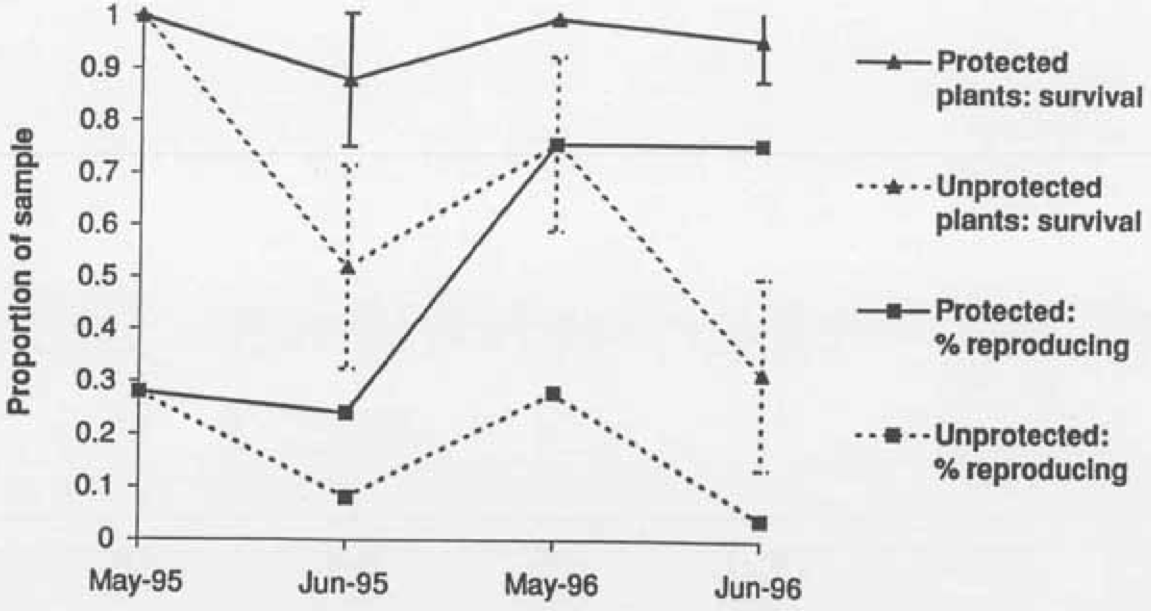

Figure 3. Trends in the flowering rate and within-growing season survival of protected versus unprotected *Trillium* at High deer site 2.

EFFECTS OF WHITE TAILED DEER ON THE UNDERSTORY PLANT COMMUNITY OF REMNANT BIG WOODS FORESTS

Abstract: Effects of white tailed deer herbivory on the understory herbaceous community of remnant Big Woods forests in southeastern Minnesota were examined using exclosure experiments. At study sites with low relative deer density, no differences in plant community composition were detected between exclosures and control plots after two years of protection from deer herbivory. At sites with growing season deer densities 3 - 4 times higher, major deer effects were observed after only 2 years of protection from herbivory at one study site, while less severe effects were observed at a second study site. Changes at the first site included increased density and flowering rates of late-summer forb species characteristic of mature, mesic deciduous forests (*Laportea canadensis* and *Circaea lutetiana*) inside exclosures and increased density and flowering rates of species more commonly associated with dry mesic forests of the prairie forest transition zone (*Eupatorium rugosum* and *Hackelia virginana*) in grazed control plots. In addition, a significant increase in the density of one spring ephemeral genus, *Erythronium* spp., was observed in exclosures while density in control plots remained relatively constant. In contrast, plat the second high deer site where a palatable, late summer forb (*Laportea canadensis*) is abundant, no changes in community composition were observed inside exclosures, and deer had less severe effects on *Laportea* and *Circaea* flowering rates. Results show that high deer densities can dramatically alter understory herbaceous plant communities in fragmented forests, but that deer effects may depend on the initial condition of the plant community.

INTRODUCTION

Although considerable research has documented the effects of winter browsing by white tailed deer on the tree species composition of forests (e.g. Tilghman 1989, Anderson & Loucks 1979, Graham 1952), researchers have not experimentally examined the effects of growing season herbivory on understory herbaceous plant communities. Observations of deer grazing patterns (chapter 1), forest surveys comparing areas with varying evels of deer (Anderson 1994, Balgooyen and Waller 1995), and a survey of park and preserve managers in the United States (Miller et al. 1992) suggest that elevated deer densities may be exerting major effects on forest understory herb communities. These impacts are predicted to be especially severe in highly fragmented forests where the increased amounts of forest edge also increase the accessibility of forest understory plants to deer (Alverson et al. 1988).

In southeastern Minnesota, an approximately 7,750km^2 region of contiguous, mesic, deciduous forest dominated by *Ulmu*s spp., *Acer saccharum*, and *Tilia americana* (Grimm 0984, Daubenmire 1936) was converted primarily to agricultural and residential land uses following European settlement, with only scattered stands on the order of 5 32 ha remaining (Jokes 1980, Vasilevsky & Hackett 1980). To complement forest surveys documenting the intensity and selectivity deer grazing in the understory of these forest remnants (chapter 1), the impacts of deer herbivory on the understory herbaceous community were examined using exclosure experiments. The objectives of this study were to determine the response of the understory community to release from herbivory given different local densities of deer, and to relate the measured response of the plant community to patterns of deer grazing intensity and selectivity.

STUDY AREA

Exclosure studies were conducted at 5 old growth maple basswood forest sites with a closed, homogeneous canopy containing overstory trees >50 cm dbh. The canopy layer is dominated by sugar maple (*Acer saccharum*), elm (*Ulmus americana* and *U. rubra*), and American basswood (*Tilia americana*). Ironwood (*Ostrya Virginiana*) is an important subcanopy species. Three sites are located in Rice County, MN (44° 15'N, 93° 20'W), and two sites are located in Hennepin County, MN (45°N, 93° 30'W). Sites were selected which included three with relatively low deer densities (Low deer sites 1, 2, and 3), and two with relatively high deer densities (High deer sites 1 and 2). Detailed descriptions of the sites are given in Chapter 1, with exception of Low deer site 3. This site is an approximately 8 ha upland stand east of the Cannon River within the Cannon River Wilderness Park. The stand is dominated by sugar maple (Appendix B), and is surrounded by agricultural fields, residences, and oak aspen forests. The two high deer density sites differed in the abundance of preferred forbs species (Chapter 1); in particular, High deer site 1 had a relatively high density of *Laportea canadensis* while High deer site 2 had ate extremely low density of *Laportea*.

METHODS

Deer Density Estimation

Growing season deer density at four of the five study sites was measured using automated cameras attached to passive infra red deer monitors as described in Chapter 1. Camera monitors were used at High deer site 2 and Low deer site 2 during 1 April - 15 June, 19195, and at High deer site 1 and Low deer site 1 during 1 April - 11 August, 1996. Data from cameras were analyzed in terms of the number of deer photographed per week. Deer density measurements for a separate study (chapter 5) using pellet group counts and aerial counts indicated that deer density at Low deer site 3 was similar to densities at Low deer sites 1 and 2.

Exclosure Experiments

Exclosure experiments were used to examine the effect of deer herbivory on the understory forb community at each study site. Within a given stand, canopy gaps created by individual windfalls result in a mosaic of regenerating tree patches of different ages. In order to locate deer exclosures and control plots at all study sites in areas with similar characteristics, releves were conducted to identify patches of forest with (1) a closed, homogenous overstory with the bases of most tree crowns 8 m above the forest floor, (2) overstory trees >50cm dbh present, (3) sugar maple, elm. and basswood dominant in the overstoy and oaks not dominant (relative basal area < 0.30) (4) well drained soils, and (5) an understory herbaceous community representative of the overall forest. In areas of each forest meeting these criteria, sets of 3 10 m^2 plots were established (Table 1) such that the 3 plots inn each set were as similar to one another in terms of herbaceous plant composition as possible. One randomly selected plot in each set was protected with a welded wire exclosures, and the other 2 plots were marked with permanent stakes as controls. Exclosures were designed to allow access by small mammalian herbivores, including lagomorphs.

At High deer site 2, the rarity of Laportea canadensis, a dominant forb at many Big Woods stands, resulted in this species being absent from all exclosure/control plots. To further examine the effects of deer on Laportea, and its effect on other forb species in the understory, 26 flowering Laportea plants were transplanted into 2 of the 10 m^2 exclosures and into one control plot paired to each of these exclosures in August, 1994. In addition, 2 smaller 1 m^2exclosures, each with a control plot, were established in the largest naturally occurring patch of Laportea at the site. This patch is located in a canopy gap and does not fully represent the conditions of the other exclosure control sets under a uniform canopy.

The number of grazed, ungrazed, and reproductive units of all forb species was recorded in exclosures and controls when plots were established in August, 1994. Grazed, ungrazed and flowering units of all herbaceous species were subsequently censused at all sites during 25 May - 6 June and 5-10 August in 1995, and 30 May - 4 June and 29 July - 2 August in 1996. Two exclosure/control sets at High deer site 1 were not established until April, 1995, so that plants were protected for 2 full growing seasons but data are only available for 1995 and 1996.

The effects of deer on spring ephemeral forb species were examined at High deer site 2 and Low deer sites 2 and 3 for *Isopyrum biternatum*, *Erythronium* spp., and *Claytonia virginica*. Five other spring ephemeral species were also present at these sites

(Chapter 1), but were relatively uncommon and not examined in the exclosure study. At High deer site 1 and Low deer site 1, *Isopyrum, Erythronium* and *Claytonia* were not presents and other spring ephemeral species were extremely rare. During 22 - 25 April, 1995, and 1- 4 May, 1996, all exclosures and control plots at the Rice County study sites were sampled with 30 0.25 M^2 subplots using a stratified random sampling procedure.

Statistical Analysis

Analyses of the exclosure experiments are separated into three sections. First, the effects of deer on the 3 dominant spring ephemeral species were analyzed using ANOVAs. Second, I the overall forb community was examined using ordination methods to summarize changes in early summer and late summer community composition over time. Finally, I specifically examined the effects of deer the on abundance and flowering rates of two common late summer forb species*, Laportea canadensis* and *Circaea lutetiana*.

1) *Springy ephemeral species*:

Effects of deer exclusion on the 3 dominant spring ephemeral species at Rice county bites were examined using a 3 way ANOVA, testing the significance of the deer by year interaction term. Because exclosures and controls were established in August, 1994, it was not possible to ensure that initial densities of spring ephemerals were similar for exclosures and paired controls. At the High deer site 2, one control with an Erythronium density a order of magnitude greater than all other controls and exclosures was excluded from the analysis for that species. This had no effect on the statistical significance of results, but affected the estimate of mean Erythronium density in control plots for both years. At Low deer sites, only two exclosures and four controls contained an abundant spring ephemeral community, and statistical tests were not performed due to the sample size. At High deer site 2, changes in Claytonia density and flowering were also not analyzed ,statistically because this species only occurred in 2 exclosures and 4 controls.

2) *Early and late summer community composition*:

Data from the early summer (early June) and late summer (early August) sampling .periods, were summarized with Bray Curtis (polar) ordinations (Beals 1984), using the variance regression method for endpoint selection and the Sorensen coefficient as the measure of distance between plots (McCune & Mefford 1995). Two sets of species were examined with ordinations: "early summer" and "late summer" species (Tables 2 & 3). Species "were grouped into these categories based on phenology and morphology, and extremely rare species were excluded from analyses. Ordinations were conducted using both the raw data for each species (with the units for each species given in Tables 2 & 3), and after relativizing each species according to its maximum density such that

$$r_{ij}= d_{ij}/d_{maxj}$$

where r_{ij} is the relativized value for species i in plot j, dij is the density of species i in plot j, and d_{maxj} is the maximum observed density for species i in all plots. Ordinations were first conducted using the data collected from all exclosure (n=16) and control (n=32) plots at the be beginning of the experiment for both early summer and late summer species. These ordinations were used only to recognize among site differences in understory composition at the beginning of the experiment, and not to examine factors responsible for these differences. Ordinations were then applied to the data collected from all plots in 1995 and 1996 (early summer species) or in 1994, 1995 and 1996 (late summer species). Changes in the community composition of a plot over time were measured by changes in the location of that plot along the first 3 ordination axes during the course of the experiment. To examine the effect of deer exclusion on plant community composition, the distance in ordination space between an exclosure and its paired control plots at the beginning of the experiment was compared to the distance between the exclosures and controls after 2 years of Protection from herbivory, where:

Distance between an exclosure and paired controls = $\sqrt{}(\sum(E_j – C_j)^2$

where E_j is the location of the exclosure along ordination axis j, and C_j is the mean location along ordination axis j of the two control plots paired to that exclosure. Changes in the distance between exclosures and controls between the beginning and end of the experiment were analyzed for each study site using paired t-tests. Data from the four exclosure- control sets at Low deer sites 2 and 3 were analyzed together.

3) *Deer impacts on* Circaea *and* Laportea:

Effects of deer on the abundance and flowering rate of *Laportea canadensis* and *Circaea lutetiana* were examined for all exclosure control sets where these species occurred (Table 1). Flowering data for these species were collected during the August sampling period each year. The finite rate of increase within each plot was calculated as the number of stems in 1996 divided by the number of stems in 1994. For *Laportea* at Low de deer sites 1,2 and 3, and *Circaea* at High deer site 2, differences between controls and exclosures were analyzed using paired t tests. Due to the small sample sizes, differences between exclosures and controls were not analyzed statistically for *Laportea* at the High deer sites.

RESULTS

Deer Density

Results from the camera monitors showed that deer densities were approximately 4 times higher at High deer site 1 than Low deer site 1 ($\Delta G^2 = 45.9$, df.=1, $P<0.0001$, Table 1) and 3 times higher at High deer site 2 than Low deer site 2 ($\Delta G^2 = 14.6$, d.f.=1, $P<0.001$, Table 1).

Spring Ephemeral Species

At High deer site 2, deer exclusion had no effect on the density of *Isopyrum* ($F = 2.30$, df. 1, $P = 0.13$) or Claytonia ($F=0.31$, d.f.=1, $P = 0.58$) over the two year period (Table 4). *Erythronium* densities increased to a significantly greater degree inside exclosure~ than outside exclosures ($F = 14.97$, df. 1, $P < 0.001$).

No changes in *Isopyrum* flowering rates were observed between 1995 and 1996 for both exclosures and control plots at High deer site 2 (Table 4, t <1.17 , P >0.28). *Erythronium* flowers were rare (< 1/300 stems) and no pattern with respect to deer exclusion was observed. *Claytonia* flowering rates were similar between years inside and outside exclosures at both high and low deer density (Table 4).

Early and Late-Summer Community Composition

Among site differences in the initial composition of experimental plots were examined because most upland understory species are long lived perennials, and hence initial species composition could be the primary factor determining long term plant community changes. The early summer ordination of plots explained 42.3% of the variation in species composition with the first 3 axes, and variation along axes 1 and 2 displayed the main among site differences (Fig. 1). Based on non relativized data, plots at Low deer 1 were characterized by high *Trillium* abundance, several plots at Low deer sites 2 and 3 were dominated by high *Asarum* abundance, and High deer 1 plots contained high relative abundance of *Arisaema*. Examination of ordination axes 2 versus 3 differentiated a cluster of plots from High deer 2 characterized by high *Geranium* abundance and a cluster from High deer 1 with high *Arisaema* abundance, while other plots from these sites and all plots from Low deer sites contained a community dominated by *Hepatica, Galium*, and *Hydrophyllum*, which sometimes included *Viola sorroria, Viola pubescens,* and *Anemone quinquefolia*.

Changes in species composition in most exclosure and control plots between 1995 and 199§ were small, and no consistent pattern with respect to deer exclusion was observe (Figs. 2 3, Table 5). At High deer 2, one exclosure contained large, flowering plants of *Osmorhiza* spp. by the first early summer census period (89 % and 100%' flowering in 1995 and 1996 respectively). No seed bearing *Osmorhiza* plants occurred in the exclosure when constructed in August, 1994. Control plots only contained 1 *Osmorhiza* plant and hence were not directly comparable for this species. Based on sampling, conducted in 6 m^2 plots distributed over the entire forest (Chapter 5, Appendix C), the overall flowering rate for *Osmorhiza* spp. outside exclosures at High deer 2 was 40.7%, and 42.6% of plants had greater than 50% of the leaf area grazed by deer.

Flowering plants observed outside exclosures at High deer 2 had a maximum of 2 flower umbels her plant, while *Osmorhiza* plants inside the exclosure increased from a mean of 1.5 umbels/flowering plant in 1995 to 4.9 umbels/flowering plant in 1996.

The late summer ordination of plots at the beginning of the exclosure experiment (1994 for all plots except 2 exclosure control sets established in 1995) showed differences among and within study sites, mainly due to differences in the abundance of *Laportea canadensis* (negatively correlated with axes 1 and 2) and Circaea lutetiana (positively correlated with axis 1, negatively correlated with axis 2) (Fig. 4). Four general types of plots were 1) dominated by *Laportea canadensis* with a low abundance of or no other late summer species, 2) dominated by *Laportea* and *Circaea*, and 3) lacking *Laportea* with a high abundance of *Circaea* and *Eupatorium,* and 4) lacking both *Laportea* and *Circaea* High deer site 2 was characterized by the latter type of community lacking *Laportea*, while Low deer sites and High deer site 1 contained both *Laportea* dominated and *Laportea*-*Circaea* plots.

Changes in the species composition of exclosures at High deer site 2 between 1994 and 199 differed significantly from changes in control plots, while differences were not observe between exclosures and controls at High deer site 1 or the Low deer sites (Table 6). While a divergence in species composition of exclosures and controls was observed in all exclosure control sets at High deer site 2, the two sets with Laportea transplants showed a different pattern than the sets without transplants. The former were characterized by a large increase in both *Laportea* and *Circaea* density, such that by 1996 the plots were similar in species composition to exclosure control sets at Low deer site 2 (Fig. 5a). In contrast, the paired controls experienced a slow decline in *Laportea* density and small changes in Circaea density (Fig. 5a). The other two exclosures at this site changed in the negative direction along ordination axis 3 while the four associated control plots changed in the positive direction along axis 3 (Fig. 5b). This axis was positively correlate with *Hackelia, Hesperis*, and *Eupatorium* abundance, three species which are avoided by deer. Hackelia was not present in any plots at the beginning of the experiment, but seedlings invaded control plots in 1995 and flowering plants were observed in 1996. At High deer site 1, a large increase in small (<10 em) *Caulophyllum thalictroides* stems vas observed in one control plot while *Caulophyllum* density in the paired exclosure remained constant. This increase in *Caulophyllum* in the control plot resulted in a large increase in mean ordination distance between exclosures and controls at this study site, and could have resulted from patchy dispersal of *Caulophyllum* seeds by birds. Because such a dramatic change occurred in only one exclosure control set, a statistically significant change in exclosure control distance was not detected (Table 6). The ordination based on non relativized data, which gave greater weight to more abundant species such as *Laportea* and *Circaea,* showed no change in mean distance between exclosures and controls at this site (Figs 7 & 8, Table 6).

Deer impacts acts n *Laportea* and *Circaea*

The exclosure experiments conducted at low deer density showed that deer had no detectable effects on changes in either Laportea density or flowering rates during the period monitored (Fig. 7). No difference in the finite rate of change in Laportea density over the two year period was detected (X =1.78 inside exclosures vs. 1.80 outside exclosures, paired t test, t = 0.08, P = 0.93). Deer exclusion also had no detectable effect on changes in Laportea flowering rates during the experiment (18% vs. 20% in 1994, and 34.9% vs. 37.8% in 1996 for exclosures and controls respectively, 2 way ANOVA, F=0.38, P=0.58).

At High deer site 2, where Laportea availability within the stand is extremely low, the transplant experiment showed that deer are exerting a severe limitation on *Laportea* growth and reproduction. Laportea density in the exclosures with transplants increased exponentially, while controls showed a slow decline (Fig. 8b). For the exclosures and controls with natural *Laportea*, differences in density were not as great (Fig. 8b), but plants differed dramatically in size between treatments with > 50% of protected plants being 40-100 cm tall, while all unprotected plants were < 40 cm. The most significant differences were in flowering rates which reached a mean of 40.196 for both natural and transplanted Laportea in exclosures, and either remained at 096 (natural) or declined from 100% to 0% (transplants) in unprotected plots (Fig. 9b).

At High deer site 1, where Laportea occurs at much higher abundance, deer exerted less severe impacts on Laportea growth and reproduction compared to High deer site 2. A greater finite rate of increase in density was observed for unprotected than protected plants in two exclosure control sets, and similar rates of increase were observed in a third set (Fig. 8a). Exclosures and controls contained a similar proportion of flowering plants in the year when plots were first censused (X =28.4% vs. 28.2%). Flowering rates were consistently higher in exclosures than control plots at the end of the experiment (X =66.7% vs. 35.5%, Fig. 9a).

In contrast to *Laportea canadensis, Circaea lutetiana* was relatively rare at Low deer site , and more common at the High deer sites (Chapter 1). *Circaea* density and flowering rates showed no apparent differences between exclosures and controls at low deer density. At High deer sites, no statistically significant differences in the finite rate of increase (λ) were observed between exclosures and controls (High deer 1: t=0.55, P=0.64; High deer 2: t=0.75, P=0.5). However, the observed trend was a slightly greater Circaea increase in controls (λ=2.4) than exclosures (λ= 2.1) at High deer site 1, in contrast to a greater increase inside exclosures (λ =2.1) than controls (λ =1.9) at High deer site 2 (Fig. 10).

Circaea flowering rates showed a dramatic response to protection from herbivory in just 2 rowing seasons. At High deer site 2, deer exclusion resulted in a significant increase from 0.0% in 1994 to 26.0% in 1996 in exclosures as compared to 0.6% in 1994 and 2.1% in 1996 in controls (2 way ANOVA, F=14.8, P=0.004, Fig. l 1b). Differences between Circaea flowering rates in exclosures and controls at High deer site 1 were highly variable (Fig. 11a), and the effect of deer exclusion on flowering rates was only marginally significant (2 way ANOVA, F=4.25, P=0.085).

A consistent trend of increasing *Laportea* and *Circaea* density during the study period, and a large increase in flowering rates between 1994 and 1995, was observed at all Low deer sites (Fig. 7) and at High deer site 1 (Fig. 9a), suggesting that growing conditions over the region were unusually favorable for *Laportea* and *Circaea* in 1995. Growing conditions in 1995 included above average temperatures and precipitation (USDC 1995), high humidity during June and July, and an early spring snowmelt.

DISCUSSION

Spring ephemeral species

One objective of this study was to test the hypothesis that deer have a strong negative impact on spring ephemeral forbs because these species present one of the first photosynthetically active forage sources available to deer following snowmelt in April and early May. However, forest surveys (Chapter 1, Appendix C) demonstrated relatively low grazing intensity on spring ephemeral forbs at all forest sites surveyed, and spring pellet counts on permanent, cleared plots showed approximately a 10 fold decline in the use of mature forests by deer from winter to spring (Chapter 1). Exclosure experiments showed no effect of grazing on the abundance or flowering rate of dominant spring ephemerals, except for *Erythronium* spp. where deer occur at high density. These results must be interpreted in light of the magnitude of the deer effect detected by the exclosures, the time span of the experiment, and the availability of alternative forage in the surrounding landscape.

Where deer occur at high density, protection of the spring ephemerals from herbivory resulted in an increase in *Erythronium* density, suggesting that deer may be exerting a limiting effect on the *Erythronium* population. Equally important is the fact that *Erythronium* did not decline in grazed control plots. Because the growing season for spring ephemeral species is limited to a short period between snowmelt and canopy tree leaf out, re-growth following the loss of leaf tissue to deer is not possible. Furthermore, removal of the majority of an individual's above ground tissue by a single deer bite is expected to have a significant impact on that individual's ability to reproduce clonally in the following growing season. Thus, any limiting effect of deer herbivory on the overall population of a spring ephemeral species is likely to be detected within the short time span of this !experiment However, high deer densities are a recent development at this study site (Chapter 2), and determining whether deer will cause *Erythronium* to decline will require long term monitoring.

Early end late-summer forb communities

The ordination analysis of "early summer" species included species with a wide range of growth forms and life history characteristics. Species in the Liliaceae family (*Trillium, Polygonatum, Smilacina*, and *Uvularia*) as well as *Sanguinaria* canadensis and *Smilx ecirrata* are all long lived perennials which art unlikely to show major changes in density over a 2 year period Understanding deer effects on these species requires an analysis of individual responses to herbivory in terms of growth and reproduction, as applied ",to Trillium spp. in chapter 2. Other, more abundant species such as *Hydrophyllum, Hepatica, Viola* spp. and *Galium* spp. have a growth form which may be more responsive to the effects of herbivory over a short time span. The lack of a detectable difference between the composition of protected versus unprotected plots at High deer sites is consistent with results from forest surveys showing these species are not grazed to a significantly greater degree than the overall forb community (Chapter 1). Significant changes in the early summer community due to deer herbivory arc only likely to develop over a longer time period as changes in the abundance of long lived species occur.

Ordination analyses and examination of deer effects on flowering rates of particular species only showed consistent, dramatic effects of deer on the late summer community at High deer site 2. The statistical analysis of ordination results did not test for a specific kind of plant community shift (i.e. did not test for directional changes), which is appropriate for the scale of the exclosures used in the experiment. Because understory forbs often have a patchy distribution on a scale greater than 10 m^2, the effect of deer exclusion may be strongly dependent on initial species composition in and immediately surrounding a given 10 m^2 plot. This was true for both early summer analyses where a dramatic increase in *Osmorhiza* was observed in only 1 exclosure, and in the late summer analyses where effects were strongly influenced by transplants. The fact that all exclosures at High deer site 2 diverged from control plots in species composition after only two growing seasons shows that deer are having a dramatic effect on the overall forb community From a conservation standpoint, the type of shifts in plant community composition caused by deer, and the reason for a concomitant lack of severe deer impacts at High deer site 1 are of particular interest.

Examining the effects of deer with respect to plant community conservation requires a clear statement of conservation objectives. Since conservation efforts for Big Woods forests in Minnesota are focused on preserving representative patches of a once abundant forest type, the observed effects of deer herbivory can be examined relative to both the composition of sites with low deer density examined in this study, and the reported groundlayer composition of mesic hardwood forests of this region based on more extensive forest surveys. I

Analyses of deer impacts on *Laportea* and *Circaea* flowering rates at High deer site 2 suggests these two species will not be able to persist at the site under current grazing intensities. The late summer ordination analysis for this site also showed that following protection from herbivory, the late summer understory community became increasingly similar to the composition of plots at sites with low deer density, primarily due to increasing *Laportea* density (Fig. 5a). Both *Laportea* and *Circaea* are listed by Curbs (1059, Table VI 3) as the two most common late summer forb species in southern mesic deciduous forests of Wisconsin. In addition, a survey of 10 Big Woods stands in eastern Minnesota found *Circaea* and *Laportea* to be the only two abundant late summer forb species (Rogers 1981). Similarly, *Osmorhiza claytoni* is listed by both Rogers (1981) and Curtis (1959) as one of the most common early summer forbs in mature, mesic deciduous forest of Wisconsin and Minnesota Thus, deer herbivory at High deer site 2 appears to be eliminating forb species characteristic of Big Woods forests.

Thre second type of species composition shift observed at High deer site 2 was an increase in *Hackelia, Eupatorium*, and *Hesperis* in controls relative to changes in these species within paired exclosures (all 3 species are positively correlated with ordination axis 3, Fig. 6a). These species were ungrazed or significantly undergrazed compared to the overall fort community. In Wisconsin forests, both *Hackelia* and *Eupatorium* reach their maximum presence in southern dry mesic forests (Curtis 1959) which are more often associated with prairie forest transition areas and hence historically were likely to experience higher deer grazing intensities than interior mesic forests (Alverson et al. 1988). This type of deer effect is clearly due to selective foraging, and contrasts with observations in more forested regions of the United States where summer deer impacts are often recognized by the complete removal of understory vegetation (McShea and Rappole 1992, Diamond 1992). These results indicate that management of deer densities within parks arid preserves is necessary to successfully conserve remnants of highly fragmented forest communities such as Big Woods forests.

Although exclosures detected dramatic deer effects at High deer site 2, no significant changes in species composition were observed between exclosures and controls at High deer site 1. Changes in *Laportea* (Fig. 8) and *Circaea* (Fig. 10) abundance were not observed, and changes in community composition were insignificant. At this site, protection from deer herbivory did allow *Laportea* (Fig. 9a) and *Circaea* (Fig. l la) flowering rates to increase in exclosures compared to controls, but flowering rates in controls were only slightly lower than flowering rates at low deer density sites (Fig. 7b vs. 9a; Chapter 4). Deer densities at this study site have been high for at least the past 5 years, suggesting that the current level of herbivory may have a limiting effect on dominant forbs such as *Circaea* and *Laportea*, but is not driving these species to local extinction. While longer term monitoring is necessary to confirm this conclusion, understanding the differing results from High deer site 1 and 2 can provide key insights into the effect of deer management on fragmented forests. This issue is addressed in greater detail in chapter 4.

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Table 1. Summer deer density and numbers of exclosure-control sets constructed at study sites in southeastern Minnesota. A "set" consist of one 10 m^2 exclosure paired to two 10 m^2 control plots. In addition to the 4 sets of 10 m^2 exclosure-control plots at High deer site 2, two 1 m^2 exclosures with paired controls were established in a patch of naturally occurring *Laportea* at the site.

Study site	Summer Deer Density (photos/wk)	Number of Exclosure-control sets	Exclosure-control sets with *Laportea*	Exclosure-control sets with *Circaea*	Sets with spring ephemeral species
High deer site 1	4.1 ± 1.7	4	3	3	--
High deer site 2	2.8 ± 1.1	4	transplants: 2 (10 m^2) natural: 2 (1 m^2)	4	4
Low deer site 1	0.9 ± 0.6	4	4	--	--
Low deer sites 2 & 3	0.8 ± 0.7[a]	4	4	2	2

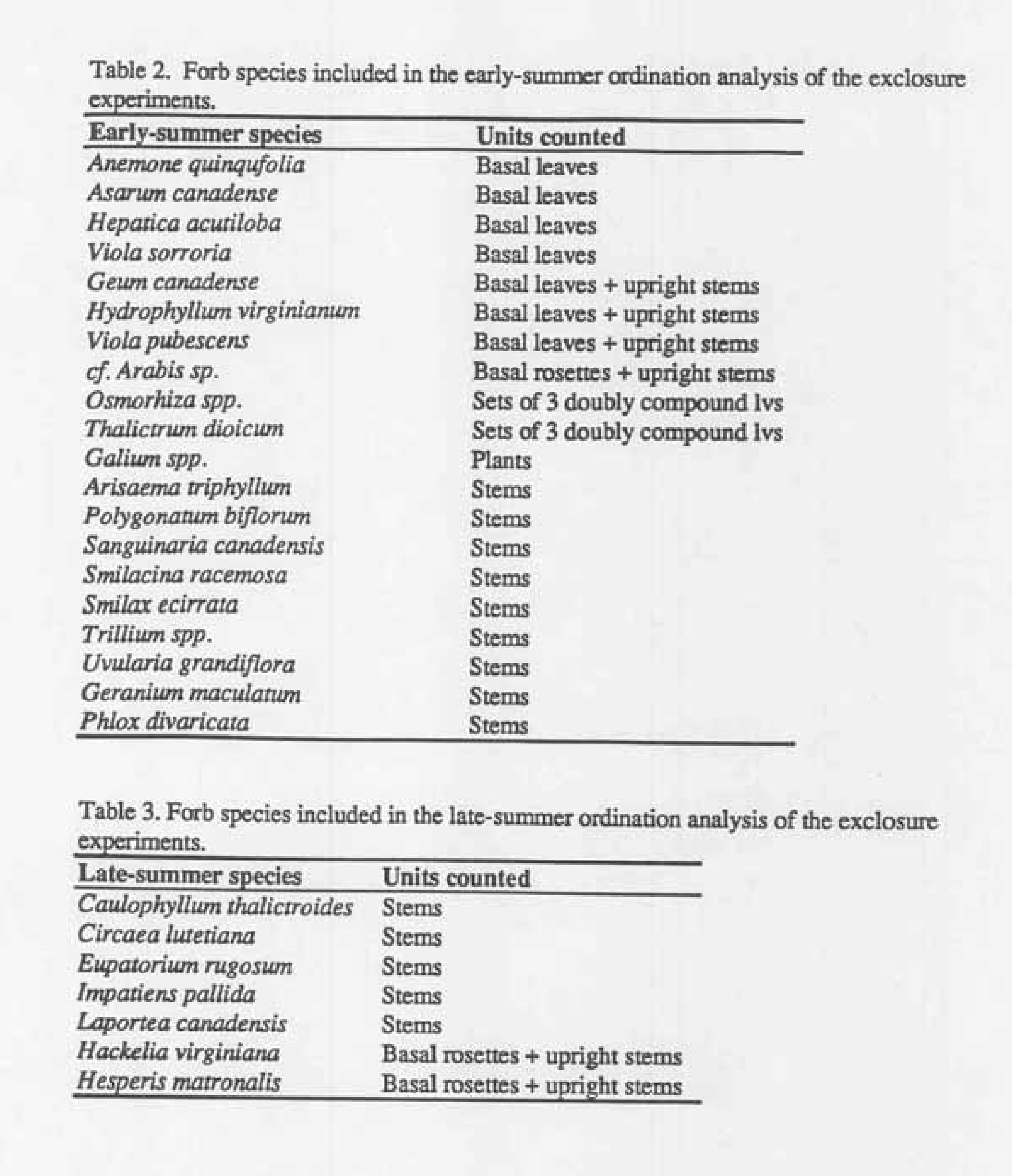

Table 2. Forb species included in the early-summer ordination analysis of the exclosure experiments.

Early-summer species	Units counted
Anemone quinqufolia	Basal leaves
Asarum canadense	Basal leaves
Hepatica acutiloba	Basal leaves
Viola sorroria	Basal leaves
Geum canadense	Basal leaves + upright stems
Hydrophyllum virginianum	Basal leaves + upright stems
Viola pubescens	Basal leaves + upright stems
cf. Arabis sp.	Basal rosettes + upright stems
Osmorhiza spp.	Sets of 3 doubly compound lvs
Thalictrum dioicum	Sets of 3 doubly compound lvs
Galium spp.	Plants
Arisaema triphyllum	Stems
Polygonatum biflorum	Stems
Sanguinaria canadensis	Stems
Smilacina racemosa	Stems
Smilax ecirrata	Stems
Trillium spp.	Stems
Uvularia grandiflora	Stems
Geranium maculatum	Stems
Phlox divaricata	Stems

Table 3. Forb species included in the late-summer ordination analysis of the exclosure experiments.

Late-summer species	Units counted
Caulophyllum thalictroides	Stems
Circaea lutetiana	Stems
Eupatorium rugosum	Stems
Impatiens pallida	Stems
Laportea canadensis	Stems
Hackelia virginiana	Basal rosettes + upright stems
Hesperis matronalis	Basal rosettes + upright stems

Table 4. Density and flowering rates inside and outside exclosures for the 3 most common spring ephemeral species at two Big Woods sites in Rice County. Reported densities are stems/$0.0625m^2$. * Indicates a significantly greater increase in density within exclosures compared to controls.

	Erythronium		*Isopyrum*				*Claytonia*			
	Density		Density		Percent Flowering		Density		Percent Flowering	
Year	Exclosures	Controls	Exclosures	Controls	Exclosures	Controls	Exclosures	Controls	Exclosures	Controls
High deer site 2										
1995	1.65	1.30	8.25	5.30	25.1	23.4	7.50	8.01	33.1	28.9
1996	*4.33	1.73	8.29	7.91	24.6	26.9	9.47	9.01	27.7	29.2
Low deer site 2										
1995	4.65	9.77	1.42	3.84	24.2	40.8	6.50	2.55	21.0	23.7
1996	4.48	15.62	1.04	1.70	21.4	26.2	7.73	4.14	25.3	36.1

Table 5. Changes in the mean ordination distance between exclosures and paired control plots for 20 early-summer forb species at four study sites in southeastern Minnesota. Distances between exclosures and controls in each year were calculated using equation (2) based on Bray-Curtis ordinations using the Sorensen coefficient and variance-regression endpoint selection.

	Mean Distance between Exclosures and Controls			
Site	1994	1996	Paired t	p (2-tailed)
Non-relativized Data (Figure 2-3)				
High deer 2	0.10	0.09	0.82	0.470
High deer 1	0.22	0.24	0.75	0.509
Low deer 2 & 3	0.14	0.15	0.16	0.886
Low deer 1	0.14	0.20	2.45	0.092
Relativized Data (Ordination results not shown)				
High deer 2	0.14	0.10	1.17	0.325
High deer 1	0.28	0.32	-0.62	0.578
Low deer 2 & 3	0.22	0.21	0.30	0.782
Low deer 1	0.21	0.20	0.77	0.497

Table 6. Changes in the mean ordination distance between exclosures and paired control plots for seven late-summer forb species at four study sites in southeastern Minnesota. Distances between exclosures and controls in each year were calculated using equation (2) based on Bray-Curtis ordinations using the Sorensen coefficient and variance-regression endpoint selection.

	Mean Distance between Exclosures and Controls			
Site	1994[a]	1996	Paired t	*P* (2-tailed)
Non-relativized Data (Figures 5-8)				
High deer 2	0.22	0.40	2.99	**0.058**
High deer 1	0.15	0.17	0.83	0.468
Low deer 2 & 3	0.09	0.09	0.02	0.982
Low deer 1	0.06	0.04	1.32	0.278
Relativized Data (Ordination results not shown)				
High deer 2	0.19	0.39	5.00	**0.015**
High deer 1	0.13	0.27	1.61	0.206
Low deer 2 & 3	0.14	0.10	0.81	0.479
Low deer 1	0.11	0.06	1.03	0.379

[a] 1995 data used for 2 exclosure-control sets at High deer 1 not constructed until April, 1995.

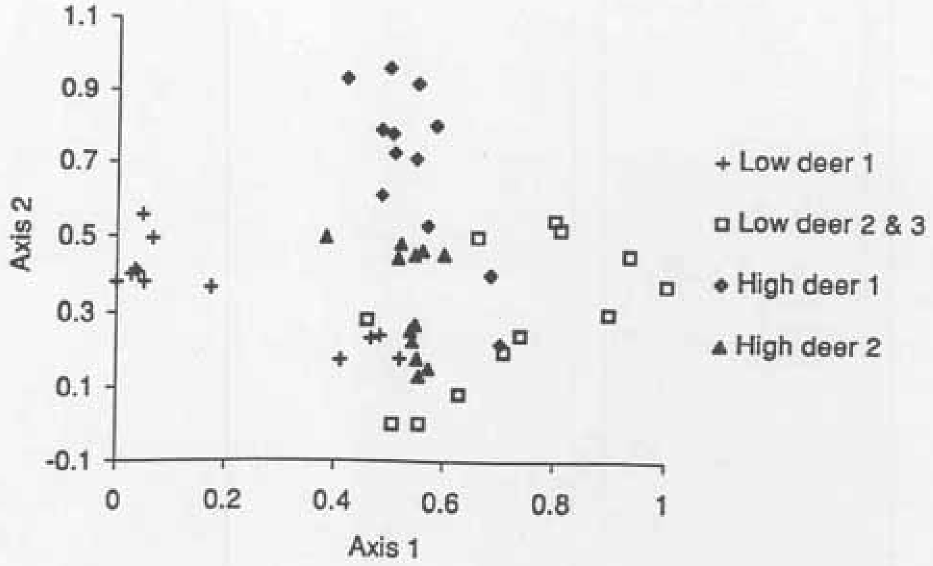

Figure 1. Bray-Curtis ordination of plots from all study sites based on 1995 early-summer species composition.

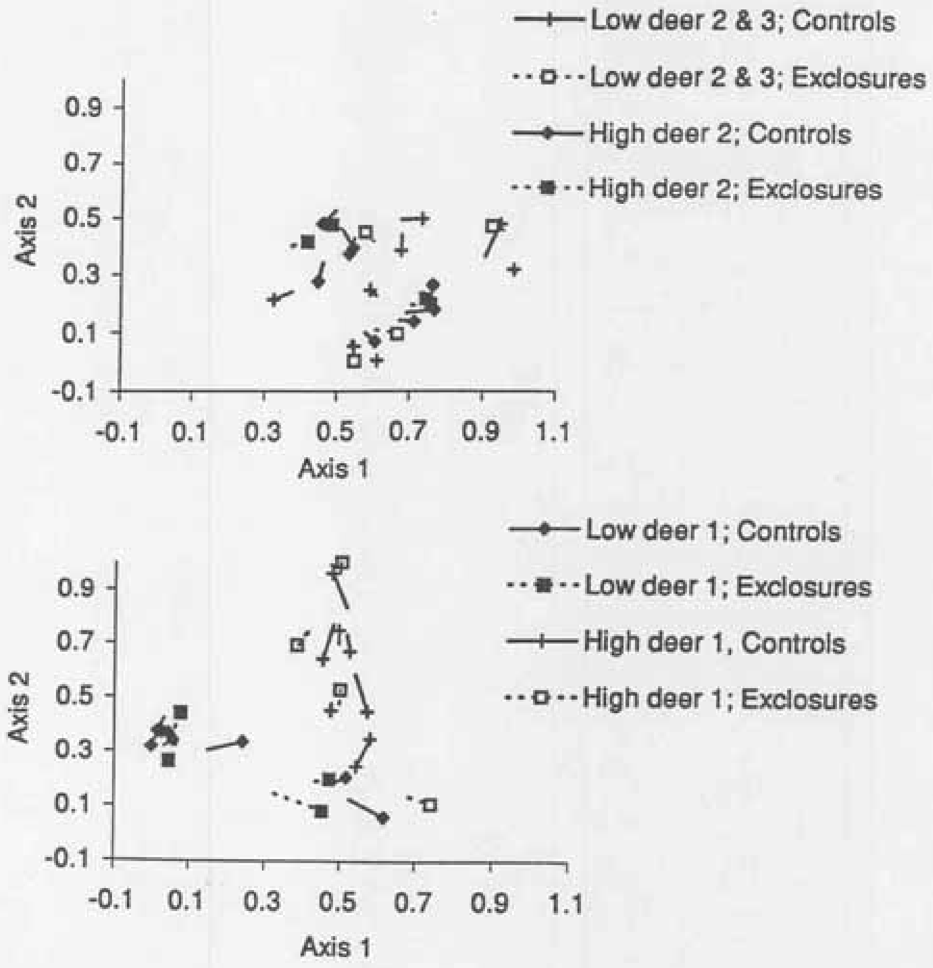

Figure 2. Changes in early-summer species composition of exclosure and control plots along ordination axes 1 and 2 from 1995 to 1996. Each exclosure or control plot is represented by a vector beginning at the 1995 ordination location (no symbol) and ending at the 1996 ordination location (shown with a symbol). The ordination was conducted using all plots from all study sites (High and Low deer).

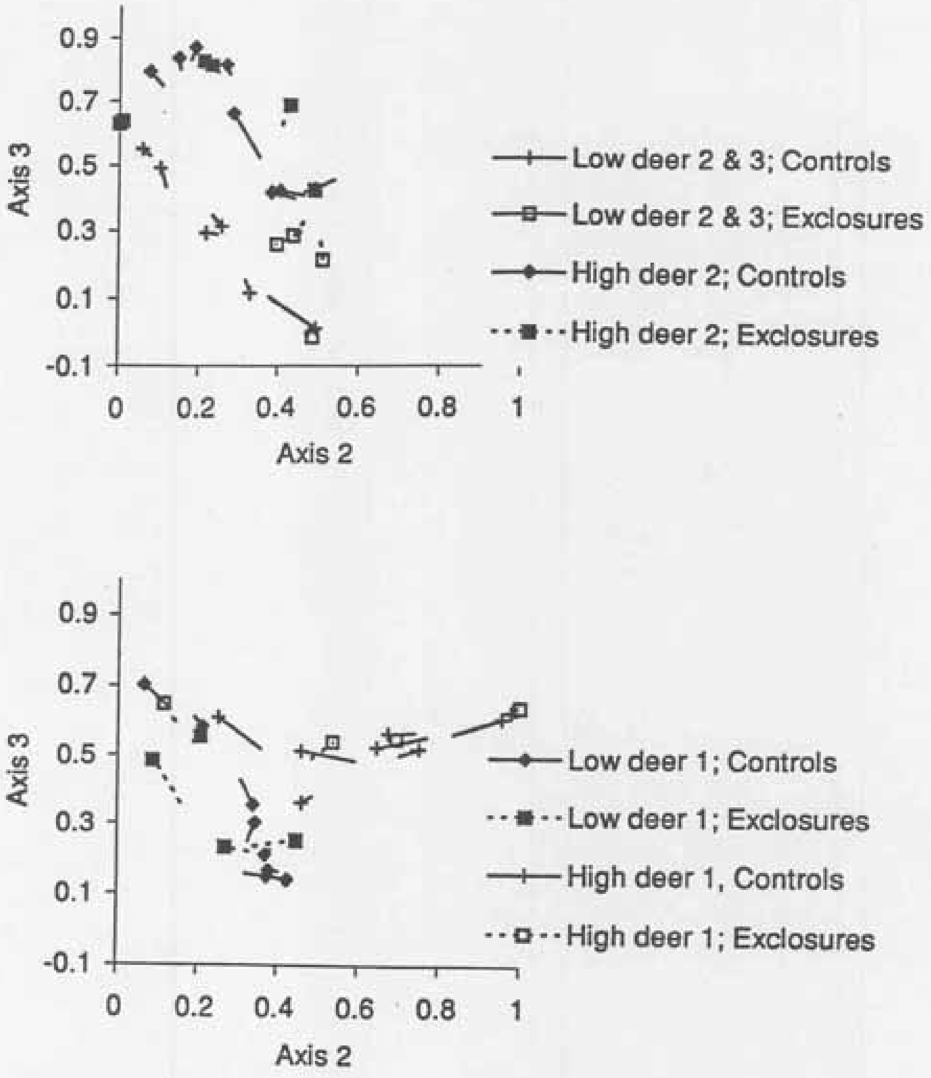

Figure 3. Changes in early-summer species composition of exclosure and control plots along ordination axes 2 and 3 from 1995 to 1996. Each exclosure or control plot is represented by a vector beginning at the 1995 location (no symbol) and ending at the 1996 location (shown with a symbol). The ordination was conducted using all plots from all study sites.

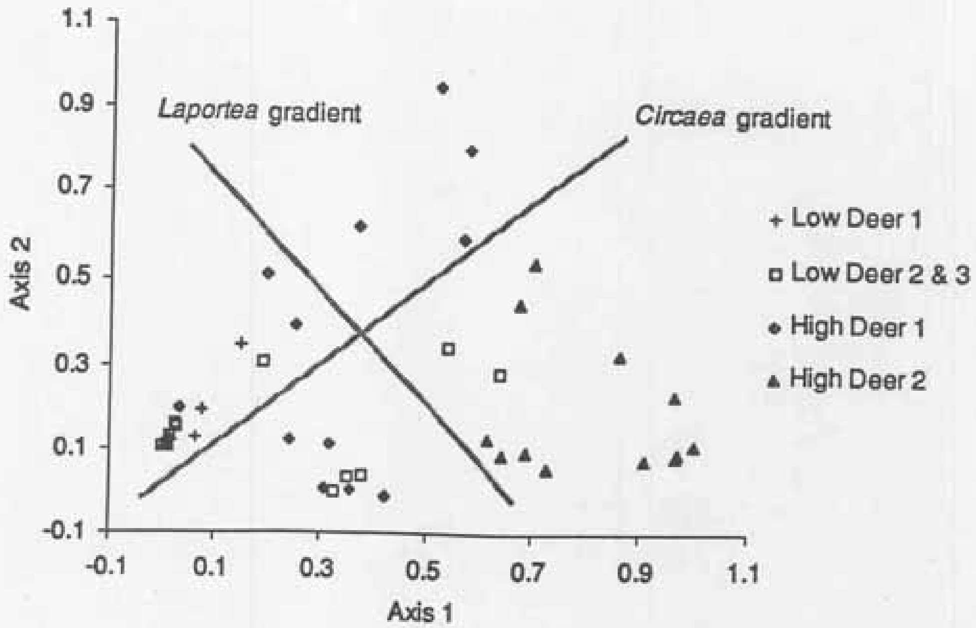

Figure 4. Bray-Curtis ordination of pre-manipulation, late-summer species composition of plots from all study sites. The gray lines run perpendicular to a gradient of changing density of the two dominant late-summer species with the greatest influence on ordination results. These lines divide the forb community into four regions where plots in the left quadrant have high *Laportea* density with no *Circaea*; the right quadrant is a region of low *Laportea* density with high *Circaea*; the lower quadrant contains mixed dominance of *Laportea* and *Circaea*, and the upper quadrant contains low *Laportea* and *Circaea* density. Pre-manipulation data was collected for all exclosure and control plots in August, 1994, except for 2 enclosure-control sets (6 plots) at High deer site 1 which were first censused in August, 1995.

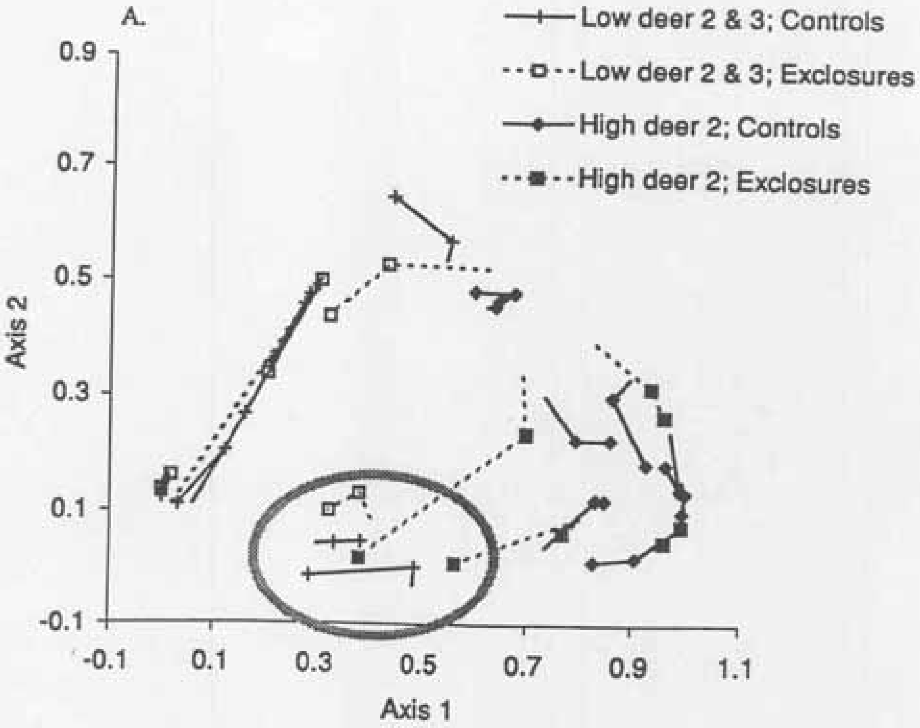

Figure 5a. Changes in late-summer species composition of exclosure and control plots at High deer site 2 and Low deer sites 2 and 3 along ordination axes 1 and 2 from 1994 to 1996. Each exclosure or control plot is represented by a vector from the 1994 ordination location (no symbol) to the 1995 and 1996 ordination locations (shown with a symbol). The gray ellipse delineates a distinct group of plots containing a community dominated by both *Laportea* and *Circaea* which occurred at low deer sites 2 & 3 throughout the study, and in two exclosures from High deer site 2 at the end of the experiment. The ordination was conducted using all plots from all study sites (including sites in (b)).

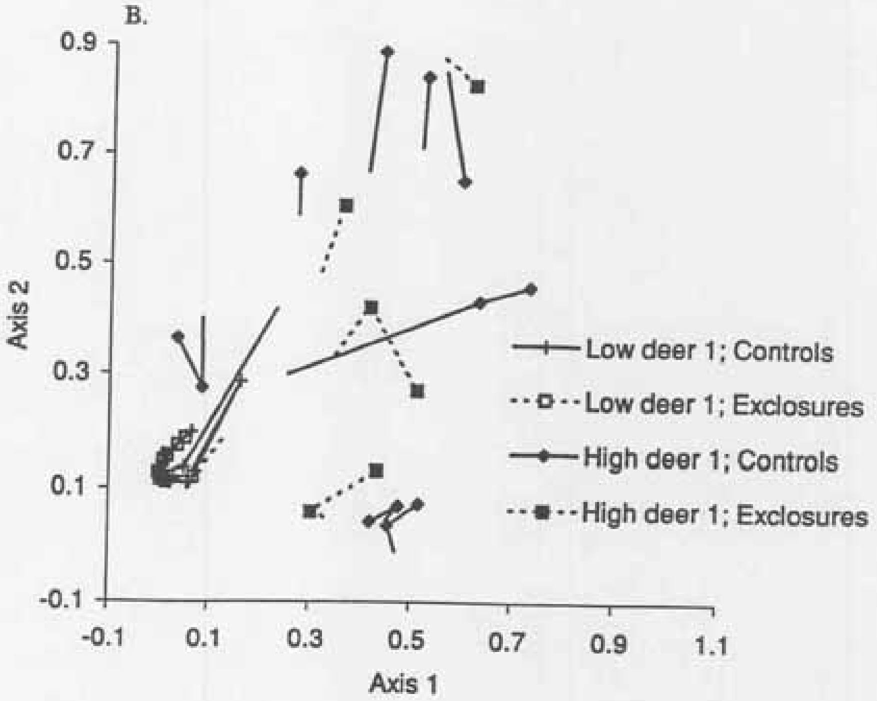

Figure 5b. Changes in late-summer species composition of exclosure and control plots at High deer site 1 and Low deer site 1 along ordination axes 1 and 2 from 1994 to 1996. Notation follows Figure 5. The ordination was conducted using all plots from all study sites (including sites in (a)).

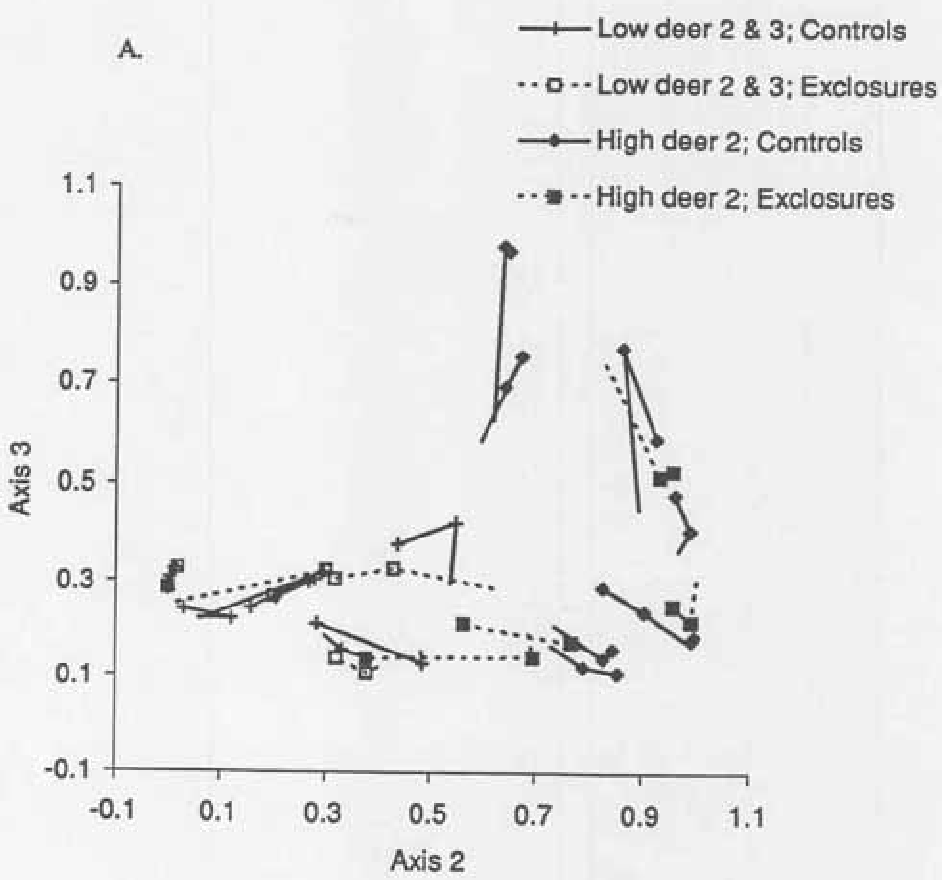

Figure 6a. Changes in late-summer species composition of exclosure and control plots at High deer site 2 and Low deer sites 2 and 3 along ordination axes 2 and 3 from 1994 to 1996. Notation follows Figure 5. The ordination was conducted using all plots from all study sites (including sites in (b)).

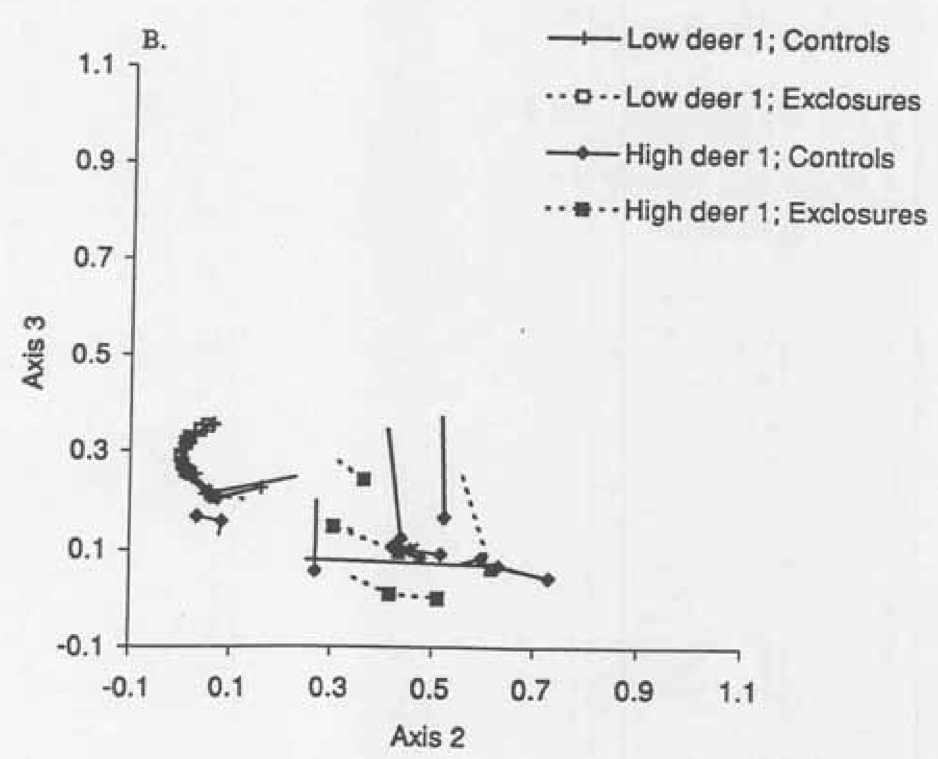

Figure 6b. Changes in early-summer species composition of exclosure and control plots at High deer site 2 and Low deer sites 2 and 3 along ordination axes 1 and 2 from 1994 to 1996. Notation follows Figure 5. The ordination was conducted using all plots from all study sites (including sites in (a)).

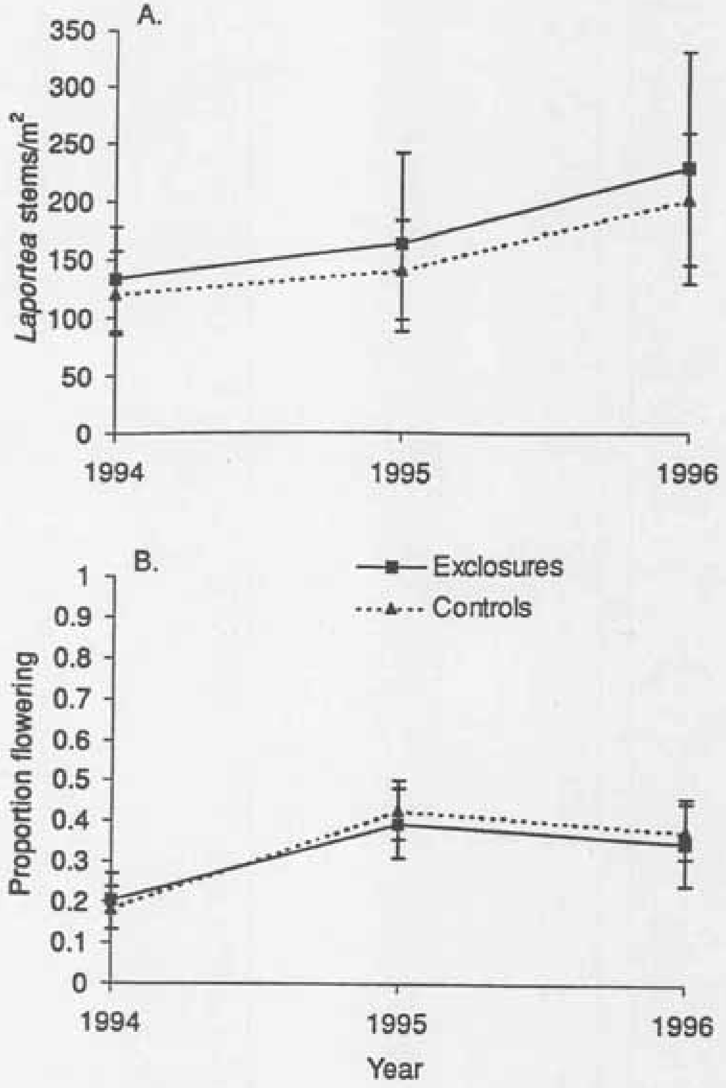

Figure 7. Average trends for (a) *Laportea* density and (b) *Laportea* flowering rates over three years measured in 8 deer exclosures and 16 control plots at Low deer study sites in southeastern Minnesota.

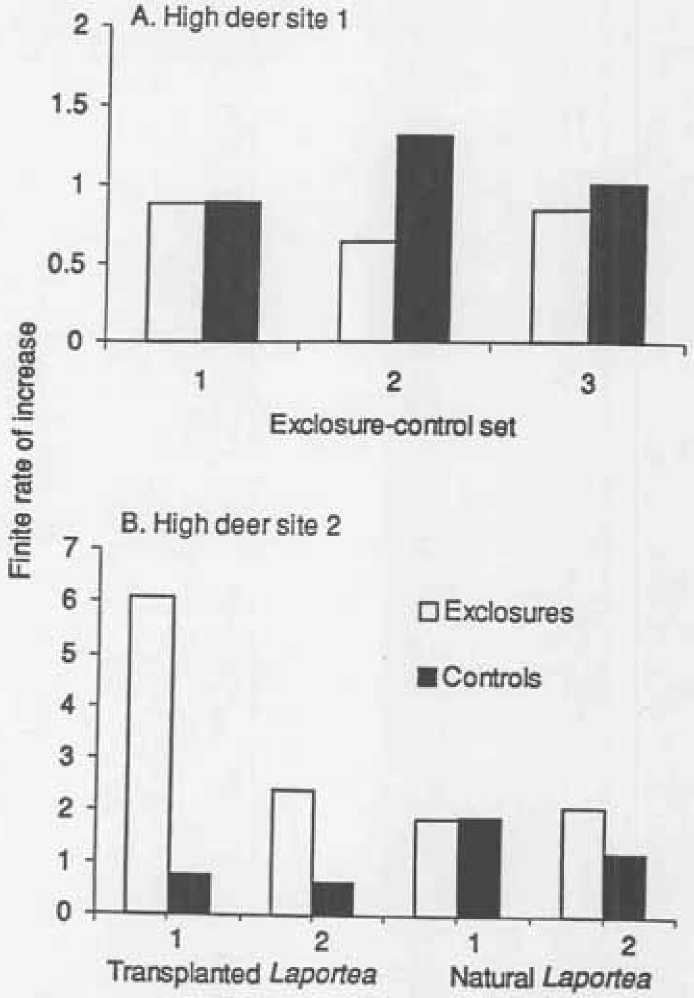

Figure 8.

a) Finite rate of increase in *Laportea* density for 3 exclosure-control sets at High deer site 1. Rates of increase are (# of stems in 1996)/(# of stems in 1994) for the first two exclosure/control sets and (# stems in 1996)/(# stems in 1995) for the third set.

b) Finite rate of increase in *Laportea* density for 2 exclosure-control pairs with transplanted individuals and 2 exclosure-control pairs with naturally occurring individuals at High deer site 2. The latter two exclosure/control pairs are located in the only large *Laportea* patch remaining at this site. Rates of increase are (# of stems in 1996)/(# of stems in 1994).

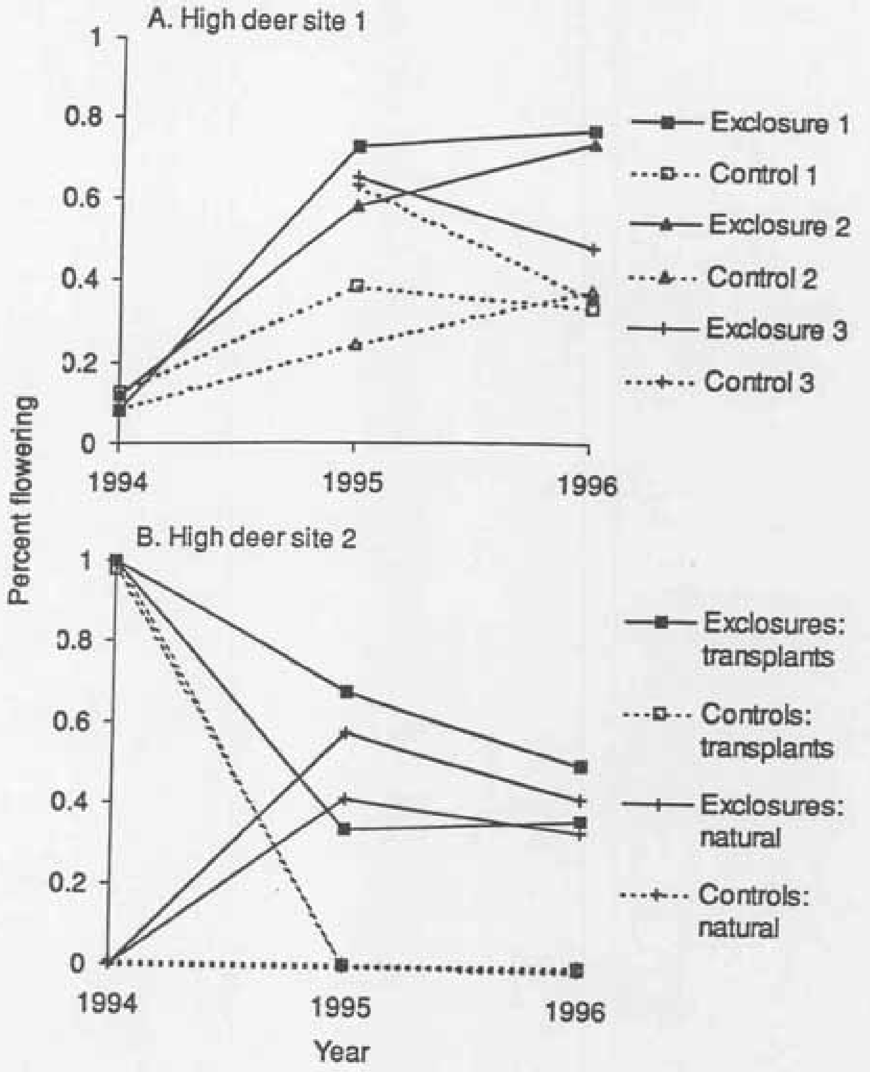

Figure 9

a) Trends in *Laportea* flowering rates for 3 exclosure-control sets at High deer site 1.

b) Trends in *Laportea* flowering rates for transplanted and naturally occurring *Laportea* in exclosures and control plots at High deer site 2. All transplanted individuals were flowering when planted in 1994.

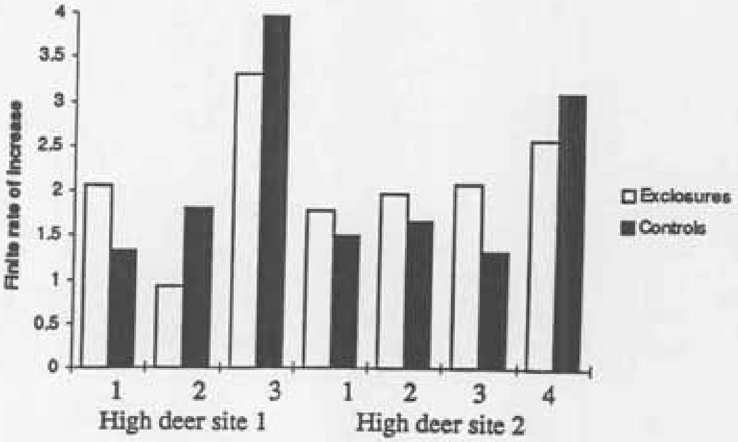

Figure 10. Finite rate of increase in *Circaea* density for exclosure-control sets at High deer sites. Rates of increase are (# of stems in 1996)/(# of stems in 1994) except for exclosure-control set 3 at High deer site 1 which is (# stems in 1996)/(# stems in 1995).

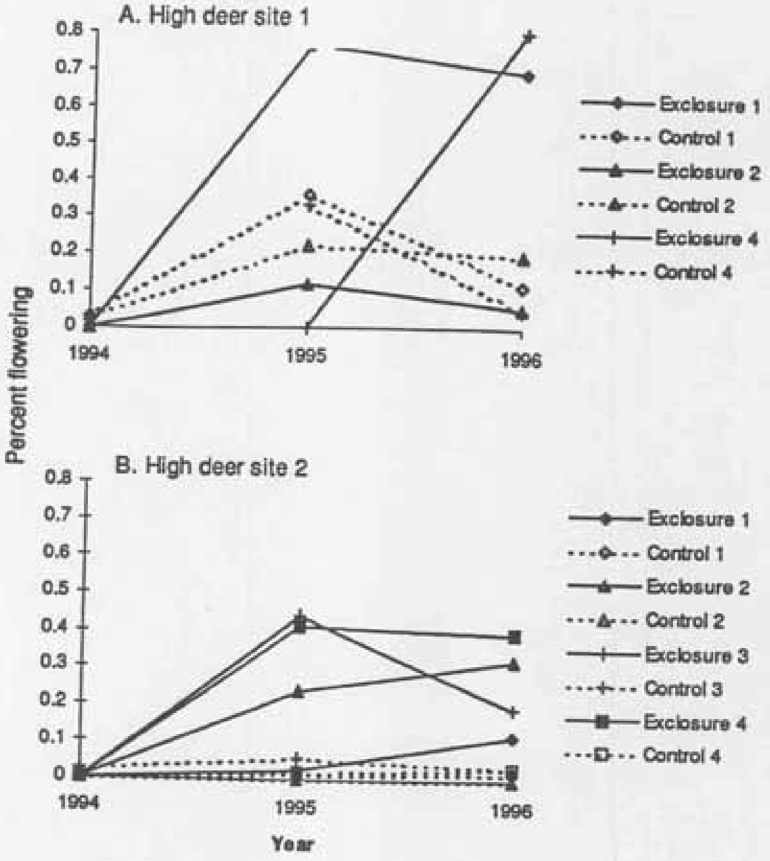

Figure 11.

a) Trends in *Circaea* flowering rates in exclosures and controls at High deer site 1.

b) Trends in *Circaea* flowering rates in exclosures and controls at High deer site 2.

EVIDENCE FOR TWO ALTERNATIVE STABLE STATES IN AN UNGULATE GRAZING SYSTEM

Abstract: Simple models describing plant herbivore interactions predict complex dynamics that depend on both herbivore density and plant abundance. The predictions of such models depend critically on the functional response of herbivores to forage availability, but few field studies have examined these responses or tested the hypothesis that alternative stable states can exist in plant herbivore systems. I examined interactions between white tailed deer, *Odocoileus virginianus*, and a dominant forb species, *Laportea canadensis*, in the understory of deciduous forests by measuring the functional response of deer to this forb and by conducting exclosure experiments under different deer and forb densities. Deer consumption of *Laportea*, measured at the scale of a forest stand, showed a Holling Type II functional response where the proportion of stems consumed has a steeply declining monotonic relationship to stem abundance. At high deer density, the deer forb interaction, as measured by exclosure experiments, produced two alternative stable states which depended on initial forb abundance. Exclosure experiments also identified a lower deer density at which herbivory has no detectable effect on *Laportea* populations. This potential for a non-monotonic relationship between plants and herbivores has direct implications for the conservation and restoration of plant species in systems where herbivores can be managed.

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INTRODUCTION

Following Rosenzwieg and McArthur's (1963) graphical approach to analyzing predator prey interactions, Noy-Meir (1975) and May (1977) examined its applicability to ungulate grazing systems. These theoretical analyses showed that even simple models involving "plant biomass" and a single herbivore can generate complex dynamics. In these models, the critical feature determining the system's predicted behavior is the way in which the herbivore's consumption rate responds to changes in plant biomass. Under certain conditions, the stability of plant herbivore equilibria depends upon both herbivore density and plant biomass such that two alternative stable states can exist for a single herbivore density (Noy-Meir 1975, May 1977).

Recently, Schmitz and Sinclair (1997) pointed out that while many studies show that ungulate herbivores can have dramatic effects on plant communities, such studies have compared areas with and without herbivores and hence are designed to test the hypothesis that ungulates have a measurable effect on some aspect of the plant community. For example, in eastern North America, a large body of research has demonstrated that white tailed deer at high densities can inhibit regeneration of particular tree species (Tilghman 1989, Anderson and Loucks 1979, Anderson and Katz 1993, Frelich and Lorimer 1985, Graham 1952). However, testing the alternative stable states hypothesis requires either a comparison of exclosure experiments between areas with natural differences in plant abundance, or large scale manipulations of plant density. One natural experiment in East Africa suggests that while elephants do not cause trees to decline in density where they occur in a woodland state, if fires drive tree densities to low levels, elephants can then regulate tree regeneration and maintain the system in a grassland state (Dublin et al. 1990). For forest ecosystems, Schmitz and Sinclair (1997) suggest that results from exclosure experiments manipulating white tailed deer (*Odocoileus virginianus*) densities (Tilghman 1989) and an observational analysis of moose (*Alces alces*) forest interactions (Brandner et al. 1990) are consistent with the alternative stable states hypothesis.

These recent analyses suggest that the original model presented by Noy-Meir (1975), which assumes a drastic simplification of the real world complexities inherent in plant herbivore systems, can still provide useful insights to a system's underlying behavior. In the forest examples cited by Schmitz and Sinclair (1997), the interaction only applies to juvenile stages of the tree species which are available to ungulate herbivores, and analyzing all stages of tree population dynamics would require an age or size structured approach (e.g. Dublin et al. 1990). Plant growth may be more simplistically described for species such as forbs which do not grow beyond the reach of ungulate herbivores. In the Noy-Meir (1975) model, dynamics of the plant biomass are described by:

$$\frac{dV}{dt}=G(V)- c(V)H \qquad (1)$$

where V = plant biomass, $G(V) = rV(1 - V / K)$ is the logistic growth function with r = intrinsic rate of increase and K = carrying capacity, c(V) is the herbivore functional response, and H is a constant herbivore density. Noy-Meir (1975) showed that model , predictions depend critically on the shape of the herbivore's functional response to plant availability. Two general shapes commonly observed in natural systems (Hassell 1978, Holling 1966) which predict a wide range of different plant herbivore equilibria are the type 11 functional response described by

$$c(V)=cV/(1+c \text{ x } h \text{ x } V) \qquad (2)$$

and the type III functional response described by

$$c(V)= cV^2/(1 + c \text{ x } h \text{ x } V^2). \qquad (3)$$

Following Schmitz and Sinclair (1997), equilibria for equation (1) can be shown as points where $G(V)/V = c(V)H/V$ (Fig. 1). Multiple stable states are possible for type II and type III responses, depending on their exact shape in relation to the intrinsic rate of increase (r) and carrying capacity (K) of the plant in the absence of herbivores. For the case of a type II functional response, a stable equilibria occurs at K in Figure 1, and, depending on the shape of the functional response, an unstable equilibrium or "breakpoint" can occur at B_{II}. In the latter case, a second stable state is predicted where the herbivore extirpates the plant population for initial plant densities less than B_{II}. This case is not biologically trivial if the herbivores have an alternative forage source such that constant herbivore density can be maintained as the plant population under examination declines. A type III functional response curve can intersect the plant growth curve to give three different equilibria (Fig. 1). In this case, K_l and K_r, represent two alternative stable equilibria, while B_{III} represents an unstable breakpoint where the system undergoes a switch in the stable equilibrium to which it will return.

Testing the predictions of the Noy-Meir (1975) model in the field involves two measurements. First, the shape of the herbivore's functional response must be measured at the appropriate spatial scale. Secondly, the effect of herbivores on plant density must be examined at different herbivore and plant densities. Ideally, one would first document the regulating effect of a high herbivore density when plants occur at low density. Then, herbivores would be experimentally reduced and the plant density allowed to recover until it passes a predicted threshold point. At this point, if herbivores are again allowed to increase, they would no longer be able to regulate plant density.

I examined the relationship between white tailed deer and a dominant understory forb species, Laportea canadensis, in mature maplebasswood forests. The objectives of this study were to 1) measure the functional response of deer to Laportea density at the scale of forest stands, and 2) test the predictions of the Noy-Meir (1975) model given the observed functional response.

STUDY SYSTEM

Surveys of understory vegetation were conducted at 11 old growth, maple-basswood stands in Rice County (44° 15'N, 93° 20'W), Hennepin County (45° N, 93° 30'W), and Wright County (45° 10'N, 93° 50'W) in south central Minnesota. Exclosure studies were conducted at 5 of the 11 sites. Each site had a closed, homogeneous canopy dominated by sugar maple (*Acer saccharum*), elm (*Ulmus americana* and *U. rubra*), and American basswood (*Tilia americana*) (> 50% relative dominance by basal area). Ironwood *Ostrya virginiana* is an important subcanopy species. The sites contain loamy soils developed from glacial moraines or silty soils developed from loess-covered glacial till (Grimm 1984). The region experiences a continental, cold temperate humid climate with warm summers and cold winters. The five sites where I conducted exclosure studies were selected to include two with high local deer densities (High deer sites 1 and 2) and three with comparatively low deer densities (Low deer sites 1, 2, and 3).

All stands are a minimum of 5 km apart, and are therefore considered independent of one another with regard to growing season deer herbivory and plant growth. The landscape surrounding each of these forest stands is a mosaic of agricultural crops, pastures and old fields, wetlands, second growth forests, and residential developments. The local agricultural crops are corn, *Zea rays*, soybeans, *Glycine max*, and *alfalfa, Medicago saliva*.

Deer occurred at all study sites, but varied in density as a result of different local management practices. Deer are not currently hunted at the two sites with the highest deer densities, while at other sites deer are either hunted on a yearly basis or have a variable history of hunting pressure. While hunting is the major factor regulating deer densities, other factors such as car collisions and emigration tray be important in areas of high deer density. During the growing season, deer in these landscapes consume primarily agricultural crops (personal observations, Nixon et al. 1991). Deer also consume forest forbs during the growing season, concentrating on a few preferred forb species (Chapter 1, Appendix C). The extremely high productivity of deer populations in the midwestem United States (Harder 1980) is attributed to the availability of crops such as corn, soybeans, and alfalfa (Nixon et al. 1991, Murphy 1970), such that local deer densities are likely unaffected by the availability of forest forbs. Therefore, when examining the deer-forb relationship, local deer density can be viewed as a constant set by management rather than as a function of forb availability.

In many remnant maple basswood stands, the wood nettle *Laportea canadensis* is one of the dominant mid summer understory forb species (Rogers 1981). *Laportea* is a clonal, perennial herb that commonly occurs in the understory of upland, mesic deciduous forests in mid western and northeastern North America (Merges 1983). *Laportea* initiates growth in early summer about the same time as canopy leaf-out, grows throughout the summer, and flowers in early August. Within stands, *Laportea* has a highly clumped distribution (Struik and Curtis 1962) and *Laportea* patches create a distinctive structural layer of vegetation at 0.5 1.0 meters in height. Menges (1983) indicates that *Laportea*'s morphological plasticity, shade tolerance, and clonal reproduction have contributed to its dominant status. At the sites where exclosure experiments were conducted, Laportea is grazed to a greater degree than the overall understory community during mid late summer (Chapter 1).

METHODS

Measuring the functional response of deer to *Laportea*

The functional response could potentially be examined at the scale of a deer's immediate environment when foraging (ca. l - 10 m^2), at the scale of entire forest stands (5 - 30 ha), or at any intermediate level. Because eq. (1) is a non spatial model, selecting the correct spatial scale at which to measure the functional response of deer is critical for testing model predictions. I examined the functional response at the stand scale (i.e. the stand was the sampling unit) because our objective was to examine deer-*Laportea* dynamics at that level.

Determining the shape of the functional response in the field (expressed in Fig. 1 as the per plant impact, or the proportion of plants consumed, for a given herbivore density) required an estimate of both the proportion of *Laportea* consumed within a stand and an estimate of the number of deer responsible for this consumption. I estimated overwinter deer density using pellet group counts at each of the 11 study sites, and confirmed these pellet count estimates at six study sites where aerial counts were also conducted (Chapter 5). Pellet counts were conducted immediately after snowmelt during 1-12 April, 1996, in 45-50 plots at each site.

Infra-red camera monitors were used to measure growing season density at four of the sites where exclosure experiments were conducted. Data from camera monitors showed that winter deer density provides an approximate index of summer deer density, except at 1 site where migratory behavior of deer and hunting practices affected between season deer movements. The functional response of deer to *Laportea* availability was analyzed for all 11 study sites using pellet group deer density estimates, and for 4 study sites using camera monitor density estimates.

The abundance and proportion of grazed *Laportea* was sampled in each stand using uniformly spaced 6 m^2 plots in which the number of *Laporte*a stems was counted

Each stem was recorded as being ungrazed, recently grazed or old grazed. When deer bite a plant, approximately 75-90% of the total leaf area is removed, and a rough cut is left on the central stem at the bite point. This bite point senesces and eventually falls off, leaving only a neucrosis scar. Recently grazed stems were those with the bite point still present, while old grazed stems were those with only a neucrosis scar. The bite point typically falls off within 25-35 days, so recently grazed stems approximate a 30-day grazing rate. All sites were sampled during August 3 14, 1996, using 45-50 plots in stands where *Laportea* was abundant, 94-100 plots where *Laportea* was moderately abundant, and 154-160 plots where *Laportea* was sparse. At one site where *Laportea* was extremely low in abundance, all known plants in the stand were censured and used to calculate the proportion grazed (n=185 stems).

The proportion of available *Laportea* stems newly grazed at each site was calculated using a ratio estimator equal to the total number of newly grazed stems divided by the total number of newly grazed + ungrazed stems in all plots at a given site. Because stems occurring within a single plot are not independent of one another with respect to deer foraging, the ratio estimator was corrected to eliminate first order bias using Cochran's (1977) jacknife technique. For each study site, I calculated:

$$\text{Proportion grazed per deer} = \frac{\text{proportion of } \textit{Laportea} \text{ stems recently grazed}}{\text{estimated deer density}} \tag{4}$$

where calculations were made both for winter deer density based on pellet group counts (deer/km^2), and growing season deer density based on camera monitors (deer photographed/week).

Effects of deer herbivore on *Laportea*

Exclosure experiments were used to examine the effect of deer herbivory on *Laportea* populations (Chapter 3). Here, I specifically examine results from these experiments with respect to *Laportea* growth and flowering rates, relying on data presented in Chapter 3. These experiments provide a unique opportunity to examine the multiple stable states hypothesis because High deer site 1 has a high density of *Laportea* while the High deer site 2 has an extremely low density of *Laportea*. Growing season deer density estimates based on infra red camera monitors confirmed that High deer sites 1 and 2 contained densities 3 4 times greater than Low deer sites 1 and 2, and that growing season densities at the high deer sites were similar or slightly greater at site 1 (Table 1). Low *Laportea* abundance was not observed at any low deer density sites, so this combination could not be examined.

Predicted trends in *Laportea* density

Trends in *Laportea* populations predicted by a discrete version of equation (1) were used to illustrate how equilibrium *Laportea* abundance depends on both deer density and initial *Laportea* density. The difference equation was parameterized using the fitted functional response curve based on the growing season deer density index (photographs/wk), the mean intrinsic rate of increase (r) of low density *Laportea* transplants inside exclosures, and a general estimate of *Laportea* carrying capacity (K) based on the five study sites with the highest *Laportea* density.

RESULTS

Functional response of deer to *Laportea* availability

At the scale of forest stands, the proportion of *Laportea* consumed per 10 overwintering deer/km^2 (based on pellet counts) showed an abruptly saturating type II functional response to Laportea availability ($c(V)/V = 0.24 / (1 + 0.64\ V)$, $r^2 = 0.91$, Fig. 2a). When examined for the four sites where growing season deer density was measured, the proportion of Laportea consumed per deer photographed/week showed a nearly identical type II functional response curve (c(V)(V = 0.28 / (1 + 0.82 V), r^2 = 0.98, Fig. 2b). To examine whether the shape of the functional response may also depend on herbivore density, residuals from the fitted functional response curve based on pellet count data were graphed against the deer density estimate for each site. This plot showed no apparent pattern (linear regression, r^2=.02, P = 0.70).

Laportea density varied from 0.01 to 19.1 stems/m^2 and the percent grazed varied from 1.0% to 72.4% among sites. Overwinter deer densities varied from 0.7-33.4 deer/km^2.

Effects of deer herbivory on *Laportea*

Results and statistical analyses for trends in Laportea density and flowering rates from the exclosure experiments at each study site are presented in chapter 3 (Figs. 7 9). In summary, deer at low density had no detectable effects on trends in either *Laportea* density or flowering rates during the period monitored (Chapter 3, Fig. 9). The two high deer density sites differed in the impact of deer on *Laportea.* At High deer site 2, where *Laportea* availability is extremely low, deer suppressed growth and eliminated sexual reproduction of transplanted *Laportea* (Chapter 3, Fig. 8b,9b) while *Laportea* density increased exponentially in exclosures (Chapter 3, Fig. 9b). Flowering rates of natural and transplanted *Laportea* reached a mean of 40.1 % inside exclosures, and either remained at 0% (natural) or declined to from 100% to 0% (transplants) in unprotected plots (Chapter 3, Fig. 9b). In contrast, at High deer site 1, deer exerted less severe impacts on *Laportea* growth and reproduction. Flowering rates were consistently higher in exclosures than controls (Chapter 3, Fig. 9a), but flowering rates in controls were only slightly lower than rates at Low deer sites (Table 1), and deer did not cause a decline in *Laportea* density (Chapter 3, Fig. 8a).

Predicted trends in *Laportea* density

Given the type II functional response of deer to *Laportea* availability, a discrete version of equation (1) as applied to *Laportea* is given by:

$$V_{t+1} = V_t \times \exp\left(r\left(\frac{1-V}{K}\right) - \frac{c \times H}{1 + c \times h \times V}\right) \qquad (5)$$

where V_t = Laportea density in year t, r = 0.72, K = 11 stems/m^2, c=0.28 and h=2.92. Since c and h are from the fitted functional response curve based on the summer deer density index, H is in units of deer photographed/wk. The estimated intrinsic rate of increase is likely a maximum for Laportea in upland, closed canopy forest since it is based on patches of large, flowering transplants which could increase through both clonal and seed reproduction.

Predicted changes in *Laportea* density overtime illustrate that the population can increase to a high density equilibrium for all initial Laportea densities when deer density is on the order of 2 photographed/wk (Fig. 3a). With an increased deer density (3 photographed/wk) initial *Laportea* densities above 0.1 stems/m^2 can still increase to a high density equilibrium but initial densities below this level lead to extirpation (Fig. 3b). With even higher deer density (4 photographed/wk), the predicted breakpoint shifts such that initial *Laportea* densities below 0.6 stems/m^2 lead to extirpation (Fig. 3c).

DISCUSSION

When analyzed on the scale of a forest stand, deer clearly showed a steeply saturating type II functional response to *Laportea* availability (Fig. 2). This pattern of consumption is possible because *Laportea* most likely represents a small portion of the diets of deer because large patches of high quality forage such as soybeans, corn, and, alfalfa are present in the landscape surrounding these forests. For example, rumen content analyses conducted in a similar agriculturally dominated landscape found 84% of the summer diet to consist of agricultural products (Nixon et al. 1991). Within such a landscape, yearling and adult does in particular use permanent cover, such as mature forests, during resting periods and make daily trips on the order of 0.5 km to crop fields during summer months (Nixon et al. 1991). Forests also provide cover for fawns while adult does are foraging, and serve as travel corridors. Deer moving through these forest stands forage selectively on understory forbs (Chapter 1). As a result, a relatively high proportion of *Laportea* is consumed when availability is low, while a lower proportion is consumed where *Laportea* is abundant.

Given such a functional response curve, the Noy-Meir model predicts three possible plant herbivore interactions depending on herbivore density. First, at low herbivore density, consumption only balances plant growth at high plant density, resulting in a stable plant herbivore equilibrium where plant densities are nearly identical to the carrying capacity of the plant population in the absence of herbivores. Second, if the consumption curve lies entirely above the plant growth curve, herbivores will always extirpate the plant population. Third, for a range of intermediate herbivore densities, consumption will balance plant growth at two different plant densities. While the equilibrium at high plant density is stable, the intersection at low plant density is unstable and plant densities below this level will lead to plant extirpation (Noy-Meir 1975, May 1977). For plant densities above this point, growth exceeds consumption, and the plant population can increase to the high density equilibrium.

As predicted, the effects of deer herbivory on *Laportea* abundance were undetectable in the exclosure experiments at Low deer sites. These sites all contained abundant *Laportea*. The combination of low deer with low *Laportea* density did not occur in any surveyed forests, and hence could not be examined. Whether low deer densities can lead to *Laportea* extirpation for extremely low initial *Laportea* abundance was therefore not tested, but the absence of such stands and the shape of the fitted functional response curve indicates that only a single stable equilibrium occurs with low deer densities (Fig. 3a). The opposite situation, in which a high deer density can drive *Laportea* to extinction for all initial *Laportea* densities, is unlikely to occur due to the steeply saturating functional response curve (Fig. 2). A qualitative comparison of this curve to the rate of *Laportea* increase at low density (in the absence of grazing) suggests that deer densities on the order of at least double the highest observed density in southeastern Minnesota are required to drive *Laportea* to extinction for all initial plant densities.

Results from the two high deer density sites support the prediction that two alternative states are possible for a given deer density. Where *Laportea* is rare, deer are causing severe reductions in *Laportea* growth and biomass, and are prohibiting sexual reproduction. The likely explanation for why *Laportea* still exists at the site is that high deer densities only developed recently; aerial counts conducted over the past 8 years show that the current level of deer resulted from a rapid increase between 1989 and 1993 (J. Vorland *personal communication*). The documented grazing intensity at this site suggests that if deer remain at current densities, they will extirpate *Laportea* in this locale. In contrast, *Laportea* at a similar forest site with a similar or slightly higher growing season deer density did not experience these severe impacts on growth and reproduction. Aerial counts conducted at this site show deer densities have been consistently high for at least the last 5 years (J. Moriarty *personal communication*), suggesting that long term deer-*Laportea* coexistence is possible where high herbivore densities occur with high Laportea abundance. *Laportea* reproduction in exclosures clearly increased following protection from herbivory, but *Laportea* in control plots maintained relatively high flowering rates and could respond to apparently favorable growth conditions with a rapid increase in density. Collectively, these observations support the Noy-Meir (1975) hypothesis that two stable ecosystem states are possible depending both on herbivore density and initial plant density (Fig: 3b,c).

Model applicability

Central assumptions which must be considered in applying the Noy-Meir model include the presence of only one herbivore and one plant species, constant plant growth conditions and herbivore density over time, and the continuous logistic function used to describe plant growth.

Because the Noy-Meir model assumes only one plant species, he cautioned that predictions may not be applicable to communities with plant species that vary widely in growth rates and palatability. The understory community in mature maple-basswood forests does not appear to violate this critical assumption, because *Laportea*, the dominant late summer forb species (Rogers 1981), can respond to herbivory with rapid regrowth, and other species with similar phenological patterns and morphology (e.g. *Circaea lutetiana, Impatiens pallida, Solidago flexicaulis*) are also palatable (Chapter 1, Appendix C). However, two relatively rare forb species are ungrazed and may have some level of chemical defense (*Hackelia virginiana* and *Eupatorium rugosum*). Including a competition term that is a function of herbivore density in the logistic growth equation of the Noy-Meir model does not change the qualitative predictions, but does greatly reduce the range of conditions over which a high palatable plant high herbivore density equilibrium can occur. The long term effects of unpalatable species should depend on the regrowth rate of the plant species under study, and the costs of chemical defense incurred by unpalatable competitors measured in terms of their growth rate.

Environmental conditions affecting *Laportea* growth appeared to vary considerably over the time span of this study, and these changes could alter the exact plant density at which the plant herbivore system switches to a new equilibrium. In this study, *Laportea* density at the two high deer density sites differed by two orders of magnitude (0.03 vs. 3.7 stem/m^2) such that the unstable system breakpoint could vary across a wide range of plant densities and still be detected. Under field conditions, predictions of when plant and herbivore densities are near an unstable equilibrium could be strongly affected by temporal variability. Furthermore, factors which change herbivore densities over time (e.g. biennial or triennial deer control hunts) could regularly switch the system between regions where an unstable equilibrium does or does not occur, but these fluctuations will only be important when the plant species occurs at low density (Fig. 3).

A critical assumption of general predator prey and plant herbivore models such as equation (1) is that the shape of the herbivore's functional response does not depend on its own density. This may not apply over a spectrum from very low herbivore abundance to a very high level where the herbivore is forage limited As individuals become increasingly constrained by nutrition, consumption of a plant species may become less responsive to forage availability, changing from a type III to type II and possibly approaching a type I response (i.e. less steeply saturating type II response). Under such circumstances, the range of herbivore densities where multiple stable equilibria occur will be more restricted than if the functional response does not change with herbivore density.

This assumption could not be directly assessed in this study due to limitations on the number of stands that could be sampled, but regression of the residuals around the functional response curve on overwinter deer density showed no pattern, suggesting that for the range of deer densities observed in southeastern Minnesota, the shape of the functional response curve is not dependent on deer density. Further consideration of this assumption, and its implications for plant herbivore dynamics, is needed

I

Perturbations and stable states

The previous discussion indicates that two different stable plant herbivore equilibria are possible when deer occur at high densities, determined by initial plant density. Deer do not change the system's state by pushing plant density past a critical breakpoint, but rather can drive the plant population to a new equilibrium once some other perturbing factor causes plant density to cross the breakpoint. For example, Dublin et al. (1990) showed that in East Africa, elephants do not cause woodlands (high tree density state) to switch to grassland (low tree density state), but rather elephant herbivory interacts with perturbations caused by fires.

In southeastern Minnesota, two different factors may affect within stand *Laportea* density and interact with deer density. The current forests are small fragments of an approximately 7,000 km^2 region of contiguous maple basswood forest which existed prior to European settlement (Grimm 1984, Daubenmire 1936). Due to *Laportea*'s patchy distribution, the extreme degree of fragmentation which occurred following European settlement, leaving stands on the order of 5-32 ha (Vasileskey 1977), could by chance result in a proportion of forest fragments containing low *Laportea* density. In addition, many forest fragments currently protected in parks and preserves were originally grazed by domestic livestock. This was true for High deer site 1 in this study, which may explain the low *Laportea* density prior to the increase in deer density. Since cattle can be stocked at high densities and are unable to select between different patches in the landscape, they can drive even abundant forbs to low density.

Results from this study suggest that following a major reduction in *Laportea* density in a stand, deer at high densities can eliminate the species from the forest and prevent any successful recolonization (Fig. 3b,c). The existence of such a situation has clear implications for restoration of native plants within fragmented forests, since reintroduction efforts often involve the introduction of a species at low overall density. For example, transplanting 5000 individuals to a 15 ha forest stand would still give a density (0.03 stems/m^2) of the order where high deer densities are predicted to eliminate *Laportea* (Fig. 3b,c). A temporary deer reduction to permit the transplants to increase in density may therefore result in a successful restoration. Recognizing this potential for non monotonic relationships between plant populations and managed herbivores such as deer can improve our understanding of the effects of herbivores in remaining parks and preserves and the success of management efforts which involve manipulations of plant and herbivore populations.

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Table 1. A comparison of grazing intensity and flowering estimates for *Laportea canadensis* in control plots from the exclosure experiment and estimates for the entire stand based on systematic plots sampling. The number of exclosure-control sets constructed at each site and the estimated growing season deer density based on infra-red camera monitors (deer photographed/week ± 95% CI) are also presented. Growing season camera sampling was conducted in 1995 at High deer 2 and Low deer 2, and in 1996 at High deer 1 and Low deer 1.

Study site	Number of exclosure-control sets	Summer Deer Density (photos/wk)	1996: Stand Average % Grazed	1996: Stand Average % Flowering	1996: Experimental Control plots % Grazed	1996: Experimental Control plots % Flowering
High deer site 1	3	4.1 ± 1.7	24.6	27.2	41.9	35.5
High deer site 2	transplants: 2 natural: 2	2.8 ± 1.1	72.4	0	83.7	0
Low deer site 1	4	0.9 ± 0.6	3.4	35.1	2.4	32.1
Low deer site 2 & 3	4	0.8 ± 0.7[a]	1.6	38.3	0	42.6

[a] Density measured at site 2 only, *Laportea* data averaged for both sites

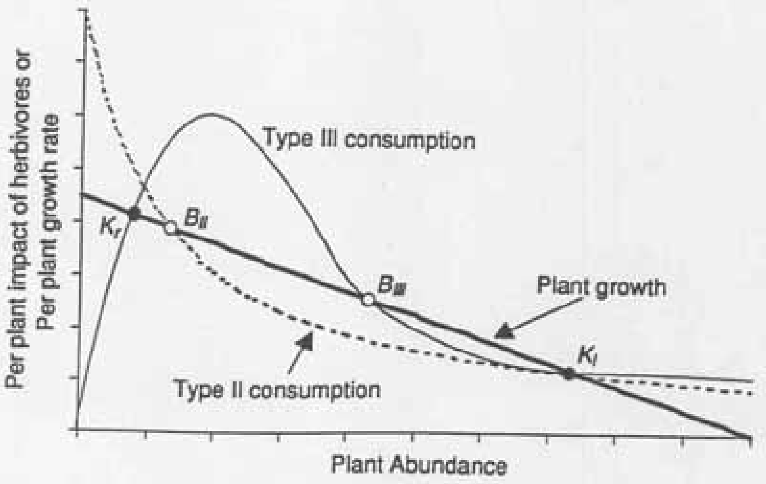

Figure 1. Plant-herbivore equilibria predicted by the Noy-Meir (1975) model (eq. 1) given type II and type III plant consumption functions and a fixed herbivore density. A high plant density equilibrium (K_l) is possible for all consumption functions. Depending on the steepness of the type II curve or intrinsic growth rate of the vegetation, an unstable equilibrium is possible (B_{II}) such that initial plant densities below this level lead to plant extinction. An unstable equilibrium is also possible for a type III consumption curve (B_{III}), but in this case plant densities below this level lead to a stable, low plant density equilibrium where the herbivore is regulating plant biomass (K_r).

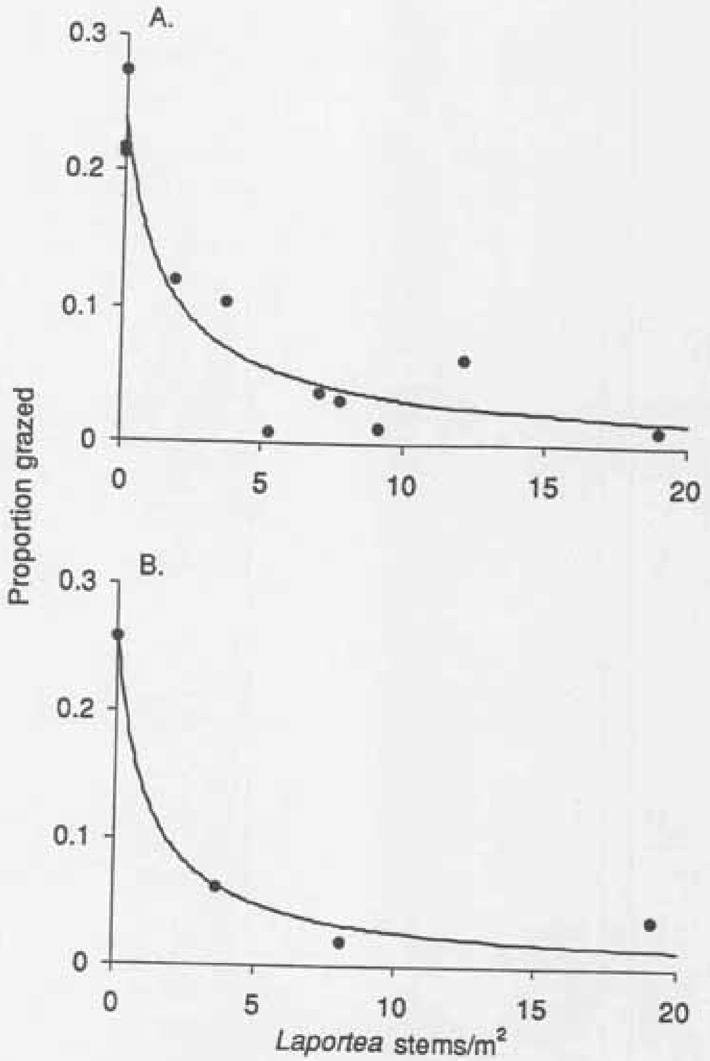

Figure 2. (A) The per plant impact, measured as the proportion of available *Laportea* stems grazed, of 10 overwintering deer/km^2 versus *Laportea* availability for 11 forests in southeastern Minnesota with the fitted functional response curve ($c(V)/V = 0.24 / (1 + 0.66\ V)$). (B) The per plant impact of 1 deer photographed/week versus *Laportea* availability for 4 forests with the fitted functional response curve ($c(V)/V = 0.26 / (1 + 0.88\ V)$).

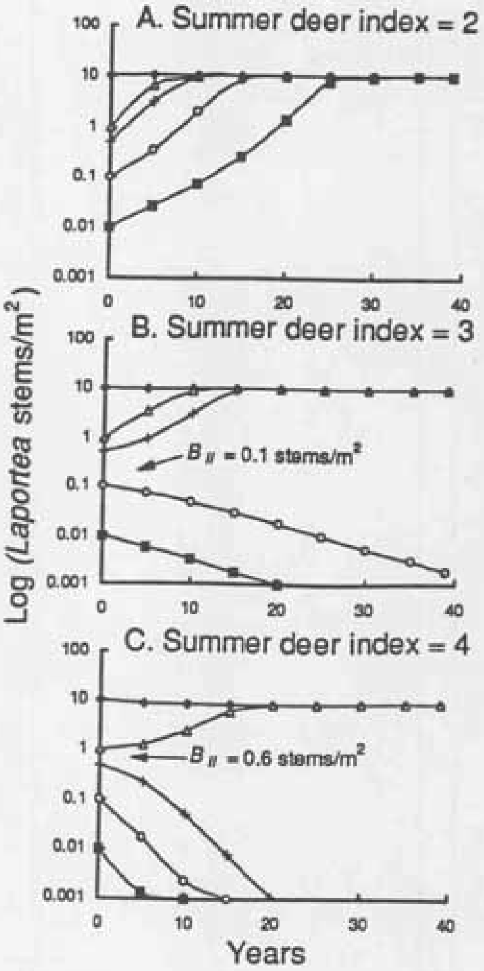

Figure 3. Predicted changes in *Laportea* density over time based on equation (5) given different deer densities and initial *Laportea* densities. Deer density is assumed to remain constant over time.

PREDICTORS OF WHITE TAILED DEER GRAZING INTENSITY IN FRAGMENTED DECIDUOUS FORESTS

Abstract: White tailed deer, *Odocoileus virginianus*, can cause major changes in the composition and structure of forest communities by browsing tree saplings and by grazing understory forbs. However, the magnitude of these effects can vary widely among forests as a result of differences in deer management and the availability of forage sources. I examined the predictability of growing season deer grazing intensity in fragments of old growth maple basswood forest based on local winter deer density, composition of the landscape surrounding each forest fragment, and characteristics of forb populations within the forest. A survey of 11 sites in southeastern Minnesota showed that in early summer, grazing intensity on six palatable forb species was most highly correlated with the availability of alfalfa within a 1.5 km radius of the stand. Further analyses showed that winter deer density and forb flowering rate within the stand were also important in explaining a significant amount of variation in grazing intensity among forests. Most of the among site variation in grazing intensity on five palatable late summer forb species could be explained either by the availability of row crops, alfalfa, and fields within a 1.5 km radius of the stand, or by a combination of winter deer density and forb abundance within the stand. Multiple regression also showed that all three factors combined (landscape composition, winter deer density, forb abundance within the stand) are significant predictors of late summer grazing by white tailed deer. These results indicate that landscape composition surrounding protected old growth forest remnants is an important determinant of deer impacts on understory vegetation and should be considered in addition to winter deer density indices in deer management decisions. In addition, results demonstrate that winter deer density is only a useful indicator of deer grazing impacts on late summer forb species when considered in combination with the abundance of palatable forbs in a given forest.

INTRODUCTION

Over the past 150 years, much of the deciduous forest region of the upper-midwestern United States has been converted to an agriculturally dominated landscape (Cole et al. 1997). In the upper Great Lakes States (Minnesota, Wisconsin, and Michigan), this transition has resulted in the loss of approximately 98% of old growth or old semi hardwood forests, with mostly small, scattered woodlots remaining in the southern regions of these states (Frelich 1993). During and following forest fragmentation, many factors may have altered the species composition of remaining stands such as the historical effects of livestock herbivory, the loss of plant propagules from forest patches to surrounding human-dominated habitats (Tilman et al. 1994), and stochastic events. The transition to an agricultural landscape also altered the distribution and abundance of native large mammalian herbivores. White tailed deer were originally extirpated in many areas of the mid western United States following conversion to agriculture in the 1800s, but populations recovered in the 1900s following protective hunting laws (e.g. Bemer and Simon 1993). Today, deer can attain high local densities in parks and preserves designed to protect remaining fragments of deciduous forest, with significant potential consequences for forest plant communities (e.g. Alverson et al. 1988, Miller et al. 1992, Anderson and Katz 1993, Anderson 1994, Chapter 1).

In southeastern Minnesota, an approximately 7,750km^2 region of contiguous, mesic, deciduous forest dominated by *Ulmus* spp., *Acer saccharum,* and *Tilia americana*, often referred to as "Big Woods" forest (Grimm 1984, Daubenmire 1936), was converted primarily to agricultural and residential land uses following European settlement. Only scattered stands on the order of 5 32 ha remain today (Jakes 1980, Vasilevsky & Hackett 1980). Although deer in agricultural landscapes forage primarily on crops, deer also consume understory forest vegetation during the growing season, and use forests for cover, parturition sites, and travel corridors (Nixon et al. 1991). Previous surveys documented selective foraging on understory forb species in Big Woods forests during early and late summer (Chapter 1), and exclosure studies demonstrated that deer herbivory can negatively impact species characteristic of Big Woods forests such as *Trillium* spp. in early summer (Chapter 2), and *Laportea canadensis* and *Circaea lutetiana* in mid late summer (Chapter 3).

In the parks and preserves protecting Big Woods forests in Minnesota, managers use winter deer density estimates, personal observations, and comments from area residents in deciding whether and how often to control local deer densities. In deciduous forests, several techniques such as pellet-group and aerial counts exist for assessing local winter deer density, but growing season density is difficult to assess due to dense vegetation. Because deer dispersal and migration can result in significant seasonal shifts in density (Nixon et al. 1991, Chapter 1), whether winter deer densities provide a useful indicator of summer grazing intensity within a given forest patch is unknown. The objective of this study was to examine the predictability of spring and summer deer grazing intensity within Big Woods forests based on 3 types of information that managers may be able to obtain: local winter deer density, the composition of the landscape surrounding the forest patch, and the abundance of palatable forb species within the forest patch. In particular, I focused on palatable understory forb species such as *Trillium* spp., *Laportea canadensis*, and *Circaea lutetiana,* which deer have been shown to negatively affect in Big Woods forests (Chapters 2 & 3).

STUDY AREA

Understory surveys were conducted at 12 Big Woods forests located in Rice County (44° 15'N, 93° 20'W), Hennepin County (45°N, 93° 30'W), and Wright County i (45° 10'N, 93° 50'W) in southeastern Minnesota (Appendix A). Due to the extreme degree of forest fragmentation in this region, most remaining old growth stands (and all study sites) are 5-32 ha, but larger patches of old growth stands mixed with second-growth forest exist. Selected sites are among the highest quality remnants of old growth maple basswood forest in Minnesota, although most have experienced occasional selective logging or grazing by domestic livestock. Two sites are privately owned, while the rest are protected in state, county and city parks, or through the state Scientific and Natural Areas program. Due to the close proximity of two stands included in the study (Woodrill and Wolsfeld Woods SNAs), data from these stands were combined and all analyses are based on 11 study sites.

All sites are dominated by sugar maple, American basswood, and elms (>50% of relative dominance by basal area), exhibit an all aged distribution of tree sizes, and contain large (50 100cm dbh) individuals of the 3 dominant tree species (Appendix B). Sites contain loamy soils developed from glacial moraines or silty soils developed from loess-covered glacial till (Grimm 1984). The region experiences a continental, cold temperate humid climate with warm summers and cold winters. Annual average temperatures were 6.7 7.0°C in the Hennepin county area and 7.8°C in the Rice county area during 1936 1960, and annual average precipitation was 73-76 cm in the vicinity of study sites during 1941-1970 (Grimm 1984).

The landscape surrounding each Big Woods stand is a mosaic of agricultural crops, pastures and old fields, wetlands, second growth forests, and residential developments. The predominant agricultural crops, corn Zea mays, soybeans, *Glycine max*, and alfalfa, *Medicago sativa*, are grown in the vicinity of all study sites.

Deer occur at all study sites, but vary in density as a result of different local management practices. Deer are not currently hunted at the two sites with the highest deer densities, while at other sites deer are either hunted on a yearly basis, or have a variable history of hunting pressure. While hunting is the major factor regulating deer densities, other factors such as car collisions and emigration may be important in areas of high deer density.

METHODS

Deer density estimation

In southeastern Minnesota, park and wildlife managers typically obtain information on local deer densities from winter aerial counts. In addition, pellet group counts offer an inexpensive method for estimating winter density in deciduous forest stands since leaf fall in October creates a relatively uniform layer of litter, such that early spring counts represent pellet group accumulation for the late fall and winter months.

Winter deer density was measured at all Big Woods stands in this study using pellet group counts conducted immediately following snowmelt during 1- 12 April, 1996, in 45-50 4 m^2 plots. Counts were converted to an estimate of overwintering deer/km^2 as described in Chapter 1. In addition, aerial counts were conducted in January, 1996, using a fixed wing Piper Supercub aircraft at four sites and a Robinson R-22 helicopter at two sites. Aerial counts were conducted by two deer managers closely familiar with the local landscape who have counted these sites for at least the past 5 years. Data reported are based on the number of deer observed uncorrected for visibility. These counts are a primary consideration in decisions to conduct special deer hunts in protected areas (J. Vorland and J. Moriarty, pers. comm). For each site, the area flown included the Big Woods stand sampled for understory forbs and a surrounding mosaic of second growth forest, shrubland, and wetlands. For some sites, the aerial count included floodplain forests or a wetland/shrubland mosaic extending > 3 Ian from the Big Woods study site. For this study, winter deer densities based on aerial counts were calculated from the number of deer observed within the area flown that was also within a 3 lam radius of the center of the Big Woods stand. Densities from area counts were expressed as deer/km2 of winter cover, with the area of winter cover for each site calculated as described below.

Understory plant community sampling

I surveyed the abundance and proportion grazed of 8 spring ephemeral forb species and 16 summer forb species (Table 1) using systematic plot sampling. Spring ephemerals were surveyed at the 6 most southern study sites during 10-16 May, 1996, and summer forb species were surveyed at all 11 study sites during 10-20 June and 3-14 August, 1996. At each site, forbs were counted in 46-50 6 m^2 circular plots, using 50 m spacing at 8 sites, and 25 m spacing at the 3 smallest study sites. For species with low abundance at a given site, additional sampling was conducted using shorter spacing between plots (80-96 and 145-250 6 m^2 plots for moderately rare and rare species respectively). In each plot the number of grazed, ungrazed, and flowering plants were counted!, where a `plant' was defined as any group of photosynthetic tissues connected above ground only. The only exception was for spring ephemerals with basal leaves only (*Allium, Erythronium*, and *Aplectrum*) where the number of basal leaves was counted Species for which a deer bite does not remove all leaves on a plant were counted as grazed if > 50% of the leaf area was removed. Flowering plants were only counted for a given species in the sampling period closest to when the species reaches anthesis.

In the August sampling season, I distinguished between recently grazed and old grazed stems for species with stems that regrow rather than completely senescing after being grazed. The definition of recently grazed was based on the condition of the bite point, defined for each species based on regular observations of marked plants with simulated grazing in 1995 and 1996, such that the recently grazed stems represent approximately a 30-day grazing rate. Late summer grazing calculations are based on recently grazed stems only. In spring, no grazed stems are believed to have senesced prior to sampling. Stems of *Trillium* and *Sanguinaria* grazed in the first week of spring may have senesced prior to sampling in June, but no other grazed stems are believed to have been missed in this sampling period.

For analyses, species were grouped based on growth form and observed patterns of deer herbivory. One distinct morphological group consisted of non clonal forbs with a single, ce central stem and no capacity for regrowth following herbivory, and included *Sanguinaria canadensis, Arisaema triphyllum, Smilax* cf. *ecirrata*, and four species in the Liliaceae family. Summary statistics for groups of species were based only on plots in which all of those species were counted. At two sites where *Trillium* spp. was extremely rare, supplemental data on deer grazing intensity were collected using marked individuals. *Trillium* sp. includes *Trillium grandiflorum, Trillium cernuum*, and *Trillium flexipes*, and *Osmorhiza* spp. includes *Osmorhiza longistylus* and *Osmorhiza claytonii.* All nomenclature follows Gleason and Cronquist (1991).

Composition of the landscape surrounding Big Woods forests

To examine whether the landscape surrounding remnant Big Woods forests affects deer ' g intensity within a stand, composition of the landscape within a 3 Ian radius area of each study site was mapped during ground surveys conducted 25 May - 5 June, 1996, using color infra red aerial photographs taken in April, 1991 and 1992 as a base template. Maps derived from the ground surveys were digitized using a geographical information system (GIS: Arc/Info 3.4.2b, 1996); land use was classified into 12 categories of relevance to deer habitat use and foraging patterns (Table 1).

While deer may undergo long distance dispersal and migratory movements between winter and summer ranges, movements within a home range during the growing season are usually local. For example, in an agricultural landscape similar to the region examined in this study, Nixon et al. (1991) reported that the mean distance moved between bedding sites and crop fields during summer months was 565 m for females and 721 m for males. To examine the effects of the availability of alternative forage sources such as 'row crops and forage crops (alfalfa and clover) in the landscape immediately surrounding Big Woods stands on spring and summer deer grazing intensity within the forest, I calculated the proportion of total land area (total km^2 - km^2 in open water) within a 1.5 km radius of each study site occupied by these agricultural field types. For the study sites where aerial deer counts were conducted, GIS coverages were also used to calculate', the total area of permanent cover (deciduous and coniferous forest, shrubland, and wooded wetland) within the intersection of a 3 km radius of the center of the study site and the total area flown. Forested residential areas only occupied a small portion (7 ha) of the area flown at one study site, and were not included as winter cover.

Statistical Analysis

The relationship between grazing by white tailed deer in Big Woods stands and winter deer density, forb availability within the stand, demographic condition of forb populations within the stand, and availability of alternative forage patches in the surrounding landscape was examined using multiple linear regression analyses (Weisberg 1985). In each analysis, regression models were fitted for all possible combinations of predictors. Comparison of the significance of overall regression F-tests, the coefficients of variation, and t-statistics for the significance of individual predictors were used in model selection. All reported models showed no evidence of non constant variance, non-linearity, or non-normality based on the diagnostics outlined by Weisberg (1985: 128163), although the small sample size limited the power of the tests for non normality.

RESULTS

Deer Density

Winter deer densities based on pellet counts varied from 0.7 - 33.4 deer/km^2 among study sites. Inspection of the relationship between aerial count estimates and pellet count estimates at sites where both were conducted (n=6) identified one study site where i results from the two methods were inconsistent (see Fig. 1). At this site, pellet counts were believed to have underestimated density due to a local shift in winter deer habitat use. During the severe winter conditions of 1995-96, deer likely increased use of two nearby conifer stands and an adjacent south facing shrubland. An aerial count and pellet counts were also conducted at this study site during the more mild winter of 1994-95. The aerial count, which samples a larger area than the pellet counts, gave a similar estimate between the two years, while the pellet count estimate was dramatically lower in 1995-96 (Fig. 1). Using the 1995 deer density estimates for this site, a strong linear relationship is observed between pellet count and aerial count deer density estimates (Aerial deer/km^2 =1.064 (Pellet deer/km^2) 3.270; F=12.7, P=0.02, r^2=0.76, Fig. 1). Thus, pellet counts appear to provide a reliable estimate of local overwinter deer density in Big Woods forests, except during winters with high snow depths where alternative winter habitat is, locally available. Analysis of the landscape within a 3 km radius of the 5 study sites where aerial counts were not conducted indicated that pellet counts were not likely to have under-estimated local deer density due to the presence of alternative winter habitat. In subsequent analyses, the 1995 pellet count estimate was used for the one site where the 1996 result was a known underestimate.

Seasonal Grazing Patterns

Understory surveys for this study supported previous observations of selective foraging in all seasons (Chapter 1). In spring, grazing intensity on spring ephemeral forbs. (6 forests surveyed) was extremely low at 4 forests (0.01-1.5%), occurred at the greatest intensity (7.1 %) at the highest deer density site, and was mainly focused on *Erythronium* spp. (0.6- 7.7% grazed among sites) In early summer, the sampled species included a group of 7 non-clonal species which initiate growth in spring, have a single, central stem, and flower in early June. Grazing in early summer was focused on 6 of these species (*Sanguinaria, Smilacina, Smilax, Polygonatum, Trillium*, and *Uvularia*) while 1 species was consistently avoided (*Arisaema triphyllum*). The range of grazing intensities observed among sites was 1.0-37.0% for the most palatable species (*Trillium* spp.), 1.29-6% for, all six palatable species combined, and 0.0-4.1 % for *Arisaema.* Other sampled species included *Geranium maculatum* and *Osmorhiza* spp. which have short stems or basal leaves in spring, allocate increasing amounts of growth to multiple, tall stems in summer, and flower in mid-June, and seven species which initiate growth in early summer and dominate the late summer forb community. Both *Geranium* and *Osmorhiza* experienced generally low grazing intensity, except *Osmorhiza* was heavily grazed at the highest deer density site (42.6%) in early summer. Of the seven late summer dominant species, five experienced high grazing intensity in late summer (0.4-35.5%). These species were either approaching anthesis during the August sampling dates (*Circaea lutetiana, Laportea canadensis, Impatiens biflora, Solidago,flexicaulis*), or flower in early summer but remain green and develop fruits in late summer (*Caulophyllum thalictroides*). Two other late, summer species, *Eupatorium rugosum* and *Hackelia virginiana*, were avoided by deer (0.0% grazed) in late summer at the sites where they occur. Estimated grazing intensities for all species surveyed in each season am listed in Appendix C.

Predictors of grazing intensity in fragmented forests

Spring

Grazing intensity was relatively low in spring at most study sites, and grazing focused on *Erythronium* spp. Regression analysis showed that only winter deer density was a significant predictor of the proportion of *Erythronium* stems grazed (F=14.3, P=0.01, r^2=0.78), primarily because the highest grazing intensity occurred at the highest deer density site (Fig. 1). Neither deer density nor alfalfa availability was related to the small level of variability in grazing intensity between the 5 other study sites.

Early summer

Analysis of early summer grazing intensity focused on the six palatable, non-clonal, single stemmed species. A stepwise regression analysis including winter deer density, alfalfa availability within 1.5 km of the site, abundance of the six species within the stand, and mean flowering rate of the six species indicated that alfalfa availability alone was the most important predictor of grazing intensity within a stand (F=5.14, P=0.05). However, alfalfa availability only explained a small proportion of the variability in grazing among sites (r^2=0.36, Fig. 3). The scatterplot of alfalfa availability versus percent grazed showed 4 strong inverse linear relationship, with one clear outlier (Fig. 3). This forest was unusual in the extremely low abundance (0.09 stems/m^2) and low flowering rate (1.9%) of these forts. Excluding this forest, the regression of alfalfa availability on percent grazed was highly significant (F=15.4, P=0.004, r^2= 0.66, Fig. 3).

Examination of the outlier forest led to further analysis of the effect of flowering rate and deer density on grazing intensity. If sites with current high deer densities also had high densities for the past several years, cumulative grazing impacts could reduce the flowering rate of sensitive species (Chapter 2). This in turn leads to a lower overall grazing intensity on such forb populations because deer primarily graze the large, flowering plants (Anderson 1994, Chapter 2). Therefore, sites with high deer density are also likely to have low flowering rates, and these two counteracting factors could result in an intermediate level of grazing within a given forest. Such interactions may by difficult to detect with a multiple regression analysis using the small sample of forests in this study.

Examination of the relationship between winter deer density and grazing intensity showed, that at sites with > 20 deer/km^2 (n=3), low grazing intensity never occurred, while considerable variation was observed at lower deer density sites (Fig. 4). To examine the effect of deer density categorically, sites were given a deer density rank of 1 if winter deer density was > 20 /km^2 and 0 for lower overwinter density. Similarly, the two sites with the lowest flowering rate of palatable, non-clonal, single stemmed forbs were assigned a categorical flowering rate rank of 0 with all other sites equal to 1. When the effects of deer density and forb flowering rate are examined with this categorical approach, all three variable's are significant predictors of grazing intensity where: Percent grazed = 2.72 -1.07 (Alfalfa) + 3.39 (Deer density rank) + 5.27 (Flowering rate rank) (F=15.7, P=0.002, r^2=0.87; Alfalfa: P=0.001, Deer rank: P=0.009, Flowering rank: P=0.003).

Among the six species analyzed previously, *Trillium* spp. was consistently the most highly preferred in early summer (Chapter 1). For all sites where *Trillium* spp. occur (n=10), 4 stepwise regression analysis including winter deer density (from pellet counts), alfalfa availability in the surrounding landscape, *Trillium* abundance (stems/m^2), and *Trillium* availability rate suggested that winter deer density alone was the most significant predictor of grazing intensity (F=6.79, P = 0.031, = 0.46). However, inspection of the scatterplot of percent grazed versus alfalfa availability again showed a strong inverse relationship with one obvious outlier (Fig. 5). Excluding the outlier forest, alfalfa availability is a highly significant predictor of grazing intensity (F=27.5, P=0.001, r^2=0.80, Fig. 5). This outlier was the highest deer density site. *Trillium* flowering rates were not unusually low at any site, and no relationship between grazing and flowering rate or *Trillium* abundance was observed.

A multiple linear regression including both winter deer density and alfalfa availability was significant overall (F=5.4, P=0.04, r^2=0.61), with deer density as the most important predictor (P=0.04) and alfalfa as only a marginally significant predictor (P=0.10) This result was due to the influence of one forest where high overwinter density (28.7/km^2) and low alfalfa availability was associated with only a 12.6% grazing rate on *Trillium*. Overwintering deer at this site are believed to include a high proportion of migratory individuals as well as deer using the site during fall and early winter due to its temporary protection from hunting in 1995-96 (J. Moriarty, pers. comm.). As a result, summer deer density may be lower than expected based on winter counts. Multiple regression excluding this forest found both winter deer density and alfalfa availability to be highly significant predictors of grazing intensity on *Trillium* spp. (F=11.4, P=0.009, r^2=0.79; Deer density: P=0.008, Alfalfa: P=0.03).

The degree of selective foraging by deer in early summer is exemplified by the contrast between the high observed grazing intensities for *Trillium* spp. at certain study sites and the consistent avoidance of a morphologically and phenologically similar forb, *Arisaema triphyllum* (Fig. 5). Grazing intensity on this species was consistently near zero at all sites except the highest deer density site where 4.1% was grazed (Fig. 5).

Late Summer

Late summer analyses were first conducted for the group of five palatable late summer orbs. Inspection of the data suggested that grazing intensity may be non-linearly related to, several predictors. The test of the need to transform the response described by Box and Cox (1964) was conducted with each of the three predictors separately. All three suggested a 0.15-0.35 power transformation, so analyses were conducted with a 0.25 power transformation of grazing intensity. Flowering rates of late summer species were not used as indicators of population demography or mean plant size because the species vary widely in life history strategies from the long lived, primarily clonal *Solidago* to the annual *Impatiens*, and observed flowering rates of species such as *Laportea* may reflect current growing season growth conditions and grazing impacts mom than historical impacts on mean plant size.

Multiple regression analyses show that most of the variation in grazing intensity on late summer palatable species can be explained by winter deer density, the abundance of palatable orbs within a stand, and the availability of row crops, alfalfa, and fields in the surrounding landscape (F=22.0, P=0.0006, r^2==0.90), where deer density and row crop + alfalfa +1 field availability are highly significant predictors (P=0.016 and 0.012 respectively), and forb abundance is marginally significant (P=0.06). A combination of' winter deer density and palatable forb abundance within the stand explains much of the variability in grazing intensity (F=12.3, P=0.004, r^2=0.75; deer density: P=0.009, forb abundance: P=0.007), but an equally valid explanation for a similar level of variation is provided by the availability of row crops + alfalfa + fields as the only predictor (F=26.4, P=0.0006, r^2=0.75) or to a slightly lesser degree, by the availability of row crops + alfalfa only (F=10.8, P=0.01, r^2=0.53) (Figs. 6 7).

Analyses were also conducted for one of the most intensively grazed late summer species, *Laportea canadensis*. The Box-Cox procedure again indicated the need to transform the response, and a 0.25 power transformation was selected. Multiple linear regression analyses with winter deer density, Laportea abundance, and availability of row crops, alfalfa, and fields in the surrounding landscape showed all three are significant predictors of grazing on *Laportea* (F=21.4, P=0.0007, r^2=0.90; Deer density: P=0.013, *Laportea* abundance: P=0.036, Row crops + alfalfa + fields: P=0.024). As with all late summer palatable species combined, most of the variation in grazing on Laportea can be explained by the combination of winter deer density and Laportea abundance (F=14.7, P=0.002, r^2=0.79), by the availability of row crops + alfalfa + fields alone (F=21.89, P=0.OO1, r^2=0.71) or to a slightly lesser degree by the availability of row crops + alfalfa alone (F=9.85, P=0.01, r^2=0.52) (Figs. 8 9).

DISCUSSION

Understanding how management can influence the effects of large mammalian herbivore on plant communities is critical for the successful conservation of ecosystems where nave predators have been extirpated or protected patches of native plant communities are so small that wildlife population dynamics operate within a much larger landscape In the midwestern United States, many conservation efforts are focused on protecting remaining forest fragments in parks and preserves, but high levels of white tailed deer herb ivory have the potential to dramatically alter forest plant communities (Chapters 2 4, Anderson 1994, Alverson et al. 1988, Tilghman 1989). In protected forests of southeastern Minnesota, local deer populations are either managed through hunting, or no deer management policy exists. While deer management is often justified on the grounds of limiting impacts on native vegetation, management decisions are typically based on estimates of winter deer density with little knowledge of how winter deer density relates to summer grazing on understory vegetation.

Winter deer density

The regression relating winter deer density estimates based on pellet counts to estimates from aerial counts showed that estimates from the two methods are strongly correlated (Fig. 1). The two methods provide slightly different measures of deer density: pellet counts measure the number of deer spending 24 hours/day in 1 km^2 of Big Woods forest during the course of the winter, while aerial counts measure the number of deer using 1 km^2 of permanent cover in mid winter. Thus, aerial counts can potentially give a slightly higher overall density estimate. Analyses presented here are based on the pellet count density estimates for all study sites; the same level of observed grazing intensity is expected to occur for an approximately similar aerial count winter density as related in the regression equation (Fig. 1).

Grazing patterns and predictors

This study documented considerable variability in grazing intensity on preferred understory forb species among forest stands, as well as important seasonal foraging patterns. Spring grazing intensity was significantly correlated with winter deer density, but was generally low and only reached a level of 7.7% on the most heavily grazed species (*Erythronium* spp.) at the highest deer density site. Short term exclosure studies indicate that this level of grazing may have a limiting effect on *Erythronium* density (Chapter 3), but longer term studies are needed to determine if such a low level of grazing can cause *Erythronium* populations to decline. Adequate availability of alternative forage sources in early spring such as alfalfa, clover, and old fields combined with limitations imposed on deer consumption of spring ephemerals due to their low stature and small per plant leaf size may be responsible for the low observed grazing intensity in forests during spring. In early summer, grazing intensity on a group of six palatable forb species was highly correlated with the availability of alfalfa fields in the immediately surrounding landscape. Deer herbivory may have the greatest impact on these species because a deer bite removes most or all leaves of an individual, their growth form prohibits any post-grazing growth within a growing season, and a deer bite eliminates reproduction for an individual in that year. For example, other studies have shown that high grazing intensity dramatically reduces reproductive rates and alters population structure of *Trillium* spp. and indicate that herbivory sustained at such levels can drive populations to local extinction (Chapter 2). The primary growing season of these forbs coincides with the period when row crop fields are still bare soil, but alfalfa fields provide a source of high protein forage. Thus, in agriculturally dominated regions, the composition of forest plant communities can be closely linked to farming practices in the landscape immediately surrounding parks and preserves.

However, variability in grazing within forest stands is not adequately explained by landscape composition alone, as shown by the significance of a multiple regression including alfalfa availability and a categorical ranking of deer density and forb flowering rate. First, low grazing intensity was never observed at sites with winter deer densities >20 deer/km^2 (Fig. 4), such that increased alfalfa availability may not dramatically reduce grazing deer densities remain high. Conversely, management to reduce deer densities is not predicted to reduce grazing on sensitive forest forbs unless alternative forage sources such as alfalfa are available in the surrounding landscape. Grazing intensity may also be lower for a population with low flowering rates which consists mainly of small plants (Fig. 3), but such a population will also be more sensitive to low grazing intensity. Therefore, from a management perspective, information on flowering rates may not be necessary to gauge the impact of a given deer population on understory forbs. However, if surveys are conducted to directly assess grazing intensity, results indicate that an index of mean plant size, such as flowering rate, should be considered as a potential factor influencing overall grazing intensity in a given forest. Collectively, these results show that where conservation or restoration of native forest communities is an objective, deer management should focus not only deer density, but also on alternative forage sources such as alfalfa in the surrounding landscape.

During June through August, row crops such as corn and soybeans develop and provide an abundant source of deer forage throughout much of the agricultural region of Minnesota. Fields, which in this study included a broad array of grass dominated plant communities (Table 2), may also increase in forage availability as old field forbs develop and mowing or grazing of pastures, hay fields, and golf courses stimulates plant growth. Grazing surveys showed that palatable late summer forbs such as *Laportea* and *Circaea,* which have similar phenology to row crops, still experience high grazing intensity in certain forests. Results from this study identified two different factors which could be the cause of the variability in late summer grazing intensity among Big Woods forests. First, the availability of alternative forage in the surrounding landscape, whether quantified as the abundance of row crops, alfalfa, and fields or simply as row crops and alfalfa, was a highly significant predictor of grazing intensity alone (Figures 6, 8). This result indicates that forests expected to experience high versus low grazing intensity can be distinguished by characteristics of the surrounding landscape only, such that changes in winter deer density will have little effect on summer grazing.

However, the abundance of late summer palatable forbs within a forest and winter deer density combined were significant predictors of grazing intensity in a multiple regression model which explained the same amount of variation in grazing intensity as landscape composition. The strong relationship between forb abundance and grazing intensity (Figures 7b, 9b) was only observed after controlling for the correlation with winter deer density (Figures 7a, 9a), suggesting that higher summer deer densities occurred at sites where winter density was high. The linear relationship between forb abundance and a 0.25 power transformation of grazing intensity (Figures 7b,9b) corresponds to a concave, exponentially declining relationship with the untransformed grazing intensities: grazing intensity was much higher than expected from deer density alone at extremely low forb density sites, decreased rapidly with increasing forb abundance, and remained at a consistently lower level than expected based on deer density alone at moderate to high forb abundance sites. This kind of relationship has been categorized as a "type II" function al consumer response (sensu Holling 1966, see

Chapter 4). The essential feature is that forage availability reaches a level where deer consumption is saturated such that overall grazing intensity on the plant population declines. Palatable late summer forb abundance varied widely among forests (0.1-20 stems/m^2), in contrast to the six early-summer palatable forbs which only varied from 0.1 2 stems/m^2 and for which no effect of forb abundance was detected. This explanation for grazing variability based on winter deer deity and forb abundance indicates that forests expected to experience high grazing intensity on late summer species can be identified based only on within site characteristics. The observation that winter deer density was a much more significant predictor of grazing intensity when included in a regression model with forb abundance has clear management implications since decisions to control deer populations are often based solely on estimates of deer density.

Distinguishing between the relative importance of winter deer density, within stand forb abundance, and characteristics of the surrounding landscape as predictors of late summer grazing intensity is difficult because I could only sample existing forest characteristics rather than manipulate them experimentally. While the sample included a wide range of variation in all three predictors of interest, forests surrounded by more residential developments, and hence fewer agricultural fields, are typically areas where hunting is restricted and higher deer densities occur. Thus, much of the grazing variability explained by winter deer density was also explained by agricultural crop availability.

Results from exclosure experiments conducted at two of the forests in this study (Chapter 3 & 4) shed light on the relative effect of agricultural crop availability vs. within-stand forb abundance. The two sites contained similarly high summer deer densities, but differed dramatically in *Laportea* abundance (Chapter 4). While extremely high grazing intensity (72%) and significant impacts on plant growth and reproduction occurred at the low *Laportea* density site, much lower grazing intensity (25%) and less severe impacts on growth reproduction occurred at the high *Laportea* density site (Chapter 3 & 4). The forest experiencing higher grazing intensity had mom row crops and alfalfa (18 vs. 10%) and a similar amount of fields (18 vs. 21%) within a 1.5 km radius compared to the forest with lower grazing intensity. Thus, in areas with similar landscape characteristics, within-stand forb abundance can be a critical determinant of deer grazing impacts. The availability of agricultural crops in the surrounding landscape still appears to be an additional important determinant of grazing intensity since including this variable in a multiple regression model that already included winter deer density and forb abundance explained significantly mom among forest variability, and all three factors combined were significant predictors of grazing intensity both for all palatable late summer forbs and for *Laportea canadensis* alone.

Collectively, results from this study indicate that both landscape composition surrounding fragmented forests and winter deer density should be considered in decisions of how to manage deer populations to reduce impacts on native plant communities. Currently, decisions made by parks managers concerning whether to control local deer populations, goal deer densities, and the frequency of special deer hunts am often based on winter deer density estimates and personal knowledge of park conditions. However, if the surrounding landscape is undergoing changes such as increased row cropping or increased conversion to residential neighborhoods, managers should recognize that the relationship between local deer density and the plant communities that a park is designed to protect may change significantly in response to these landscape changes. In addition, these results show that deer impacts on late summer understory species depend on forb abundance within a forest in addition to deer density and landscape composition, such that sites where historical factors have resulted in low current densities of palatable forb species way be especially sensitive to grazing by white tailed deer.

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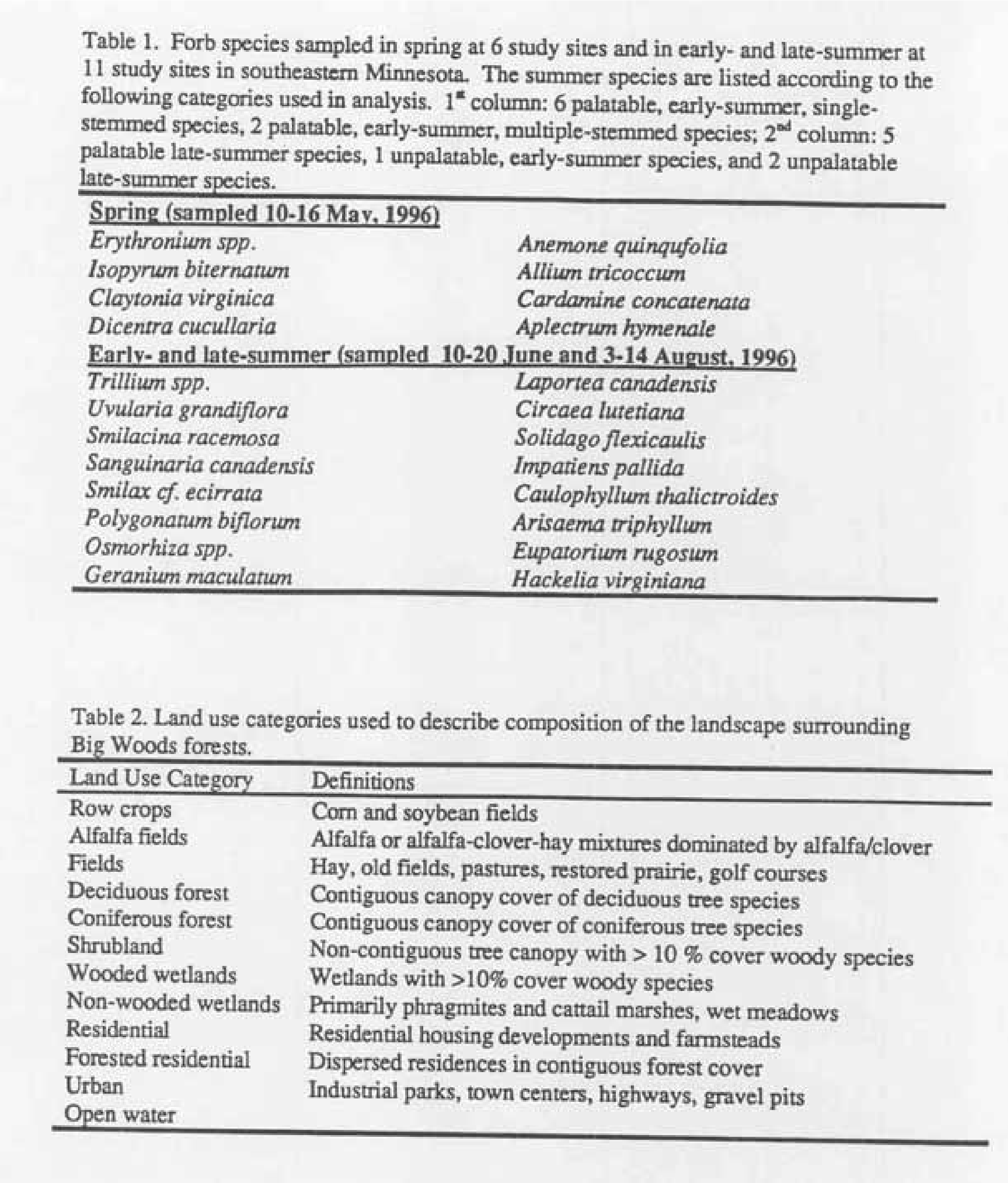

Table 1. Forb species sampled in spring at 6 study sites and in early- and late-summer at 11 study sites in southeastern Minnesota. The summer species are listed according to the following categories used in analysis. 1st column: 6 palatable, early-summer, single-stemmed species, 2 palatable, early-summer, multiple-stemmed species; 2nd column: 5 palatable late-summer species, 1 unpalatable, early-summer species, and 2 unpalatable late-summer species.

Spring (sampled 10-16 May, 1996)	
Erythronium spp.	*Anemone quinqufolia*
Isopyrum biternatum	*Allium tricoccum*
Claytonia virginica	*Cardamine concatenata*
Dicentra cucullaria	*Aplectrum hymenale*
Early- and late-summer (sampled 10-20 June and 3-14 August, 1996)	
Trillium spp.	*Laportea canadensis*
Uvularia grandiflora	*Circaea lutetiana*
Smilacina racemosa	*Solidago flexicaulis*
Sanguinaria canadensis	*Impatiens pallida*
Smilax cf. ecirrata	*Caulophyllum thalictroides*
Polygonatum biflorum	*Arisaema triphyllum*
Osmorhiza spp.	*Eupatorium rugosum*
Geranium maculatum	*Hackelia virginiana*

Table 2. Land use categories used to describe composition of the landscape surrounding Big Woods forests.

Land Use Category	Definitions
Row crops	Corn and soybean fields
Alfalfa fields	Alfalfa or alfalfa-clover-hay mixtures dominated by alfalfa/clover
Fields	Hay, old fields, pastures, restored prairie, golf courses
Deciduous forest	Contiguous canopy cover of deciduous tree species
Coniferous forest	Contiguous canopy cover of coniferous tree species
Shrubland	Non-contiguous tree canopy with > 10 % cover woody species
Wooded wetlands	Wetlands with >10% cover woody species
Non-wooded wetlands	Primarily phragmites and cattail marshes, wet meadows
Residential	Residential housing developments and farmsteads
Forested residential	Dispersed residences in contiguous forest cover
Urban	Industrial parks, town centers, highways, gravel pits
Open water	

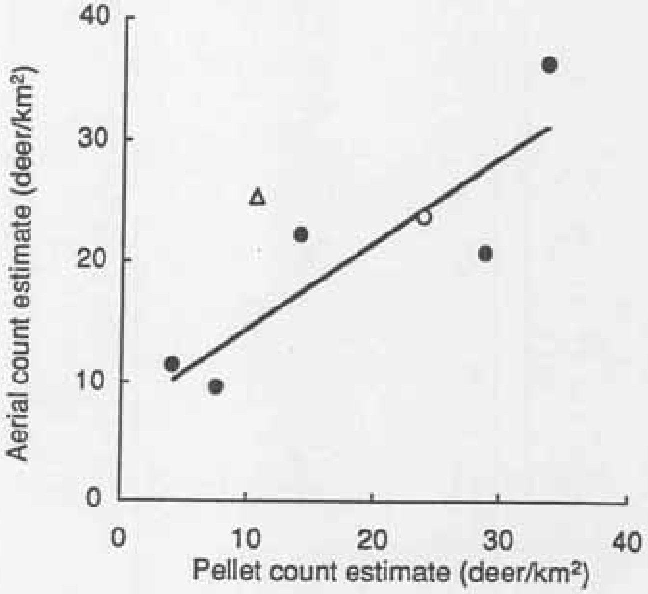

Figure 1. The correlation between winter deer density estimates based on pellet counts versus aerial counts. Solid circles represent observations for five study sites for the 1995-96 winter, and the open triangle represents the 1995-96 density estimates for a sixth site where pellet counts are believed to have underestimated winter density due to a local shift in deer habitat use. The open circle represents the 1994-95 pellet and aerial count density estimates for this latter site, and shows deer densities were nearly constant between years while the pellet count density was significantly lower in 1996. Using the 1994-95 winter estimate for this site, a significant linear relationship is observed between estimates based on the two methods (all circle symbols; Aerial count deer/km^2 = 0.714(Pellet count deer/km^2) + 7.27; F=12.7, P=0.02, r^2=0.76).

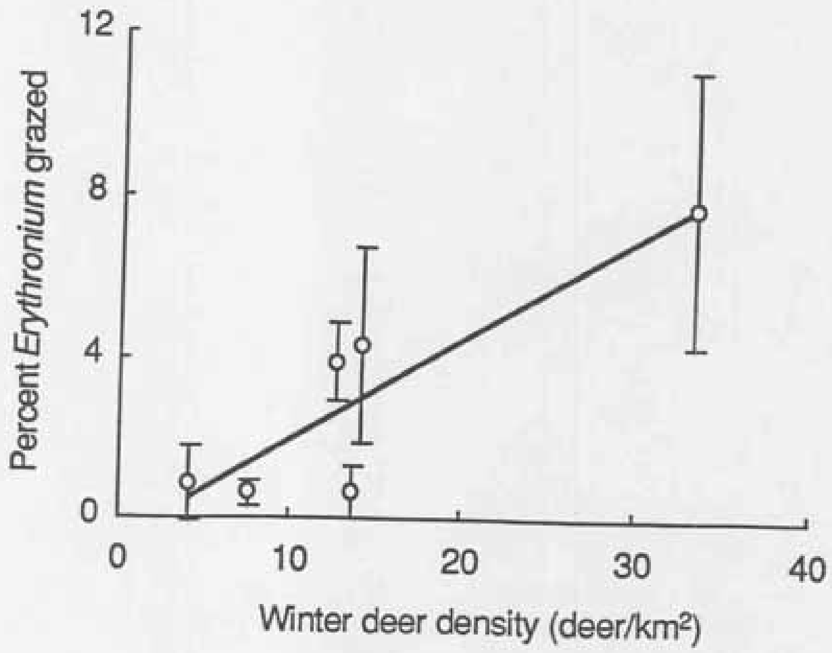

Figure 2. The relationship between the percent of *Erythronium spp*. grazed within six Big Woods stands and winter deer density based on pellet group counts. Error bars indicate ± 1 SE for each forest.

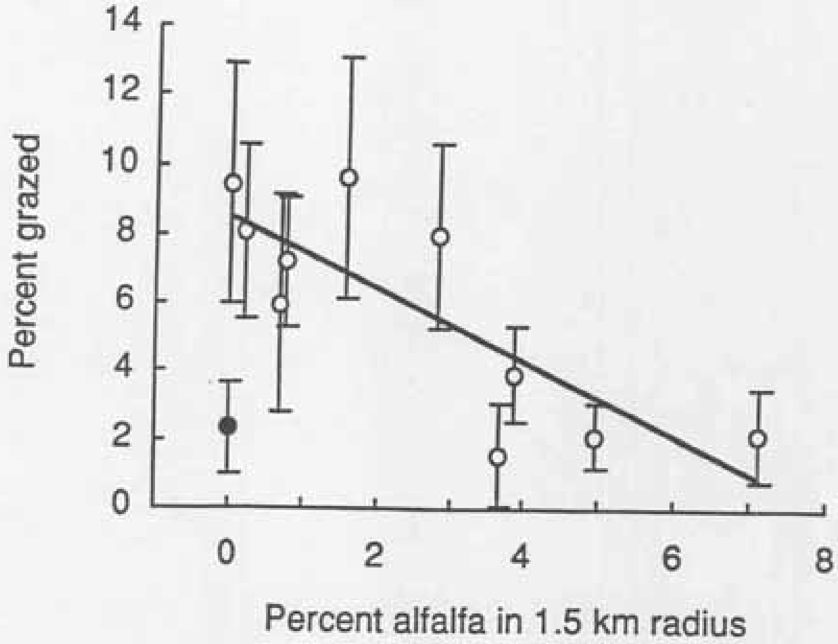

Figure 3. The relationship between grazing intensity on six palatable, early-summer forb species in 11 Big Woods stands and the percent of the landscape within a 1.5 km radius of each stand occupied by alfalfa fields. Error bars indicate ± 1 SE for each forest.

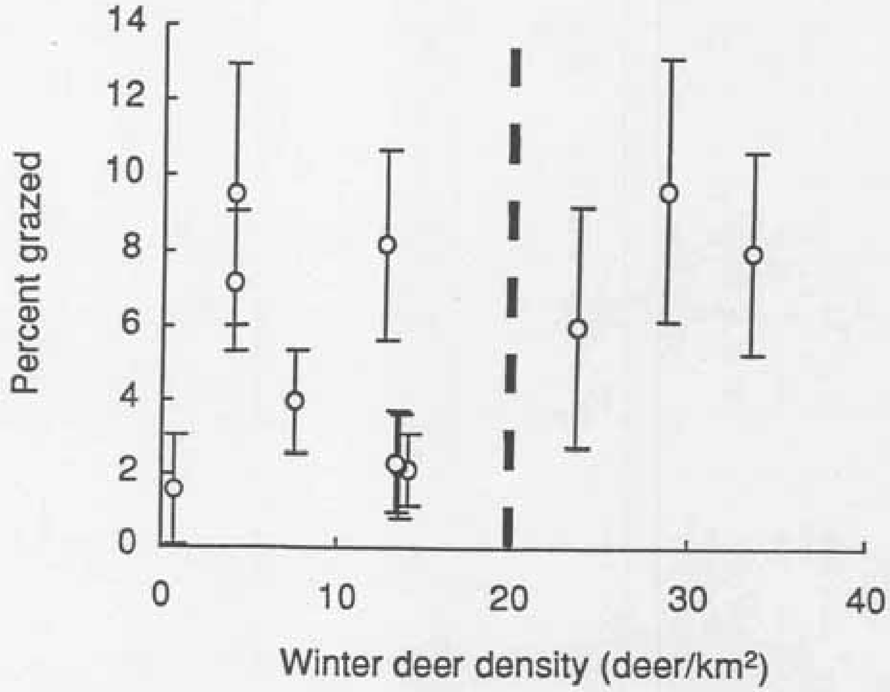

Figure 4. The relationship between grazing intensity on six palatable, early-summer forb species in 11 Big Woods stands and winter deer density based on pellet group counts. Error bars show ± 1 SE.

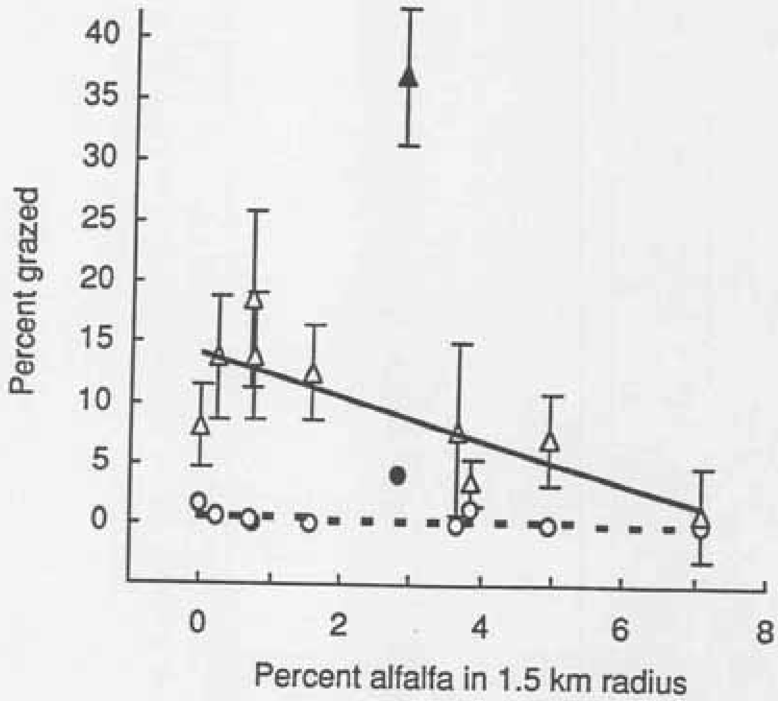

Figure 5. The relationship between the percent of *Trillium spp* (triangles) and *Arisaema triphyllum* (circles) grazed at 11 Big Woods sites and the percent of the landscape within a 1.5 km radius of each stand occupied by alfalfa fields. *Trillium spp.* was the most highly preferred forb in early summer, while *Arisaema* was avoided. Grazing intensity for both species was much higher than expected based on alfalfa availability at the highest deer density site (solid symbols). For the remaining study sites, alfalfa availability was a highly significant predictor of grazing on *Trillium* (open triangles; F=15.4, P=0.004, r^2= 0.66) while grazing intensity was consistently close to zero for *Arisaema* and was unrelated to alfalfa availability (open circles; F=0.48, P=0.51). Error bars show ± 1 SE.

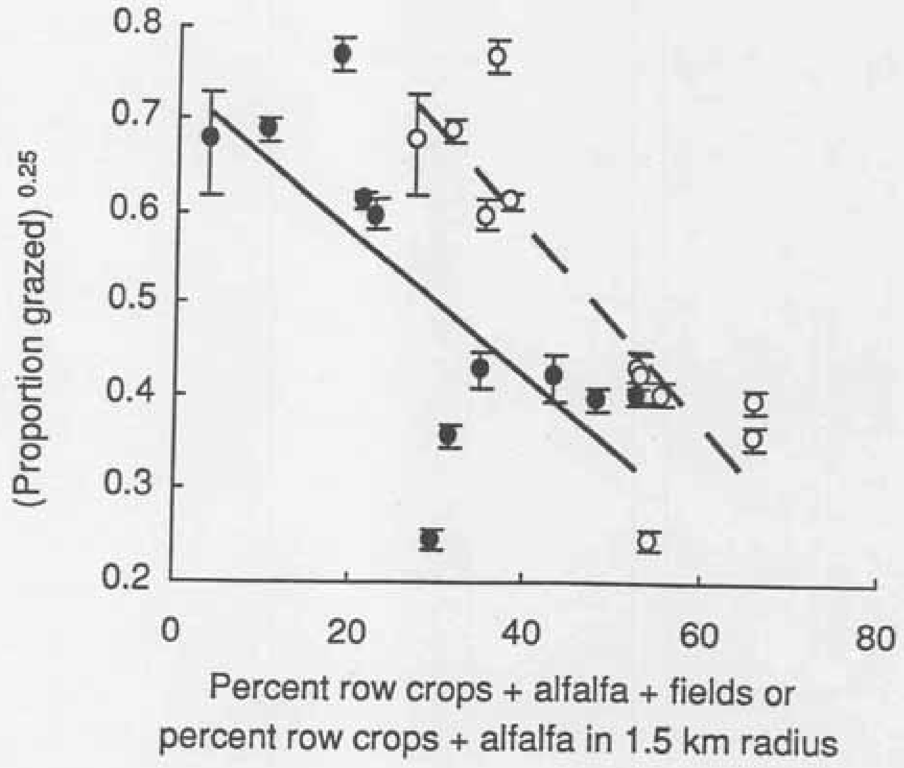

Figure 6. The relationship between grazing intensity on five late-summer palatable forb species and two closely related measures of alternative forage availability within a 1.5 km radius of the stand: percent row crops, alfalfa, and fields (open circles; r^2=0.75, P<0.001) and the percent row crops and alfalfa only (closed circles; r^2=0.53, P=0.01). Error bars show ± 1 SE.

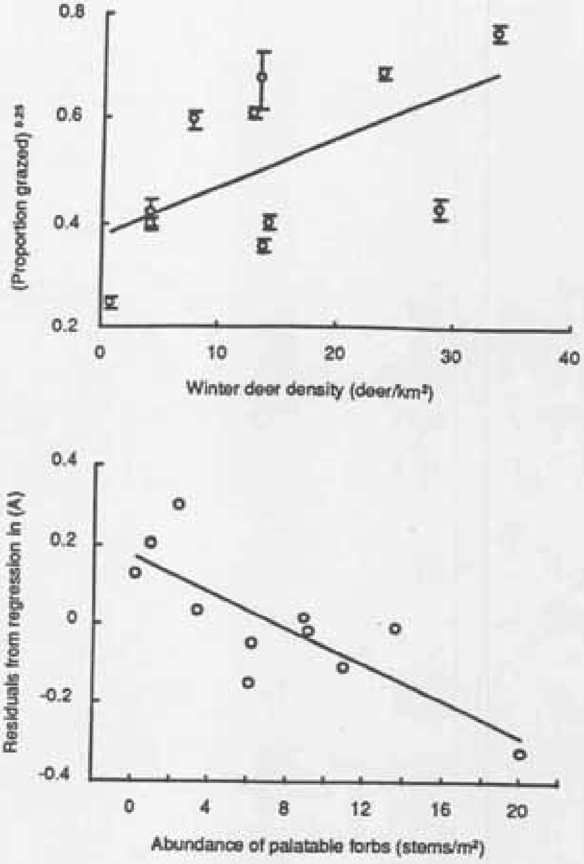

Figure 7. (A) The relationship between grazing intensity on five late-summer forb species in Big Woods stands and winter deer density, and (B) the residuals from (A) as a function of palatable forb abundance within the stand. The multiple linear regression using these two predictors explained 75% of the variability in grazing intensity (Winter deer: *P*=0.009; Forb abundance: *P*=0.007).

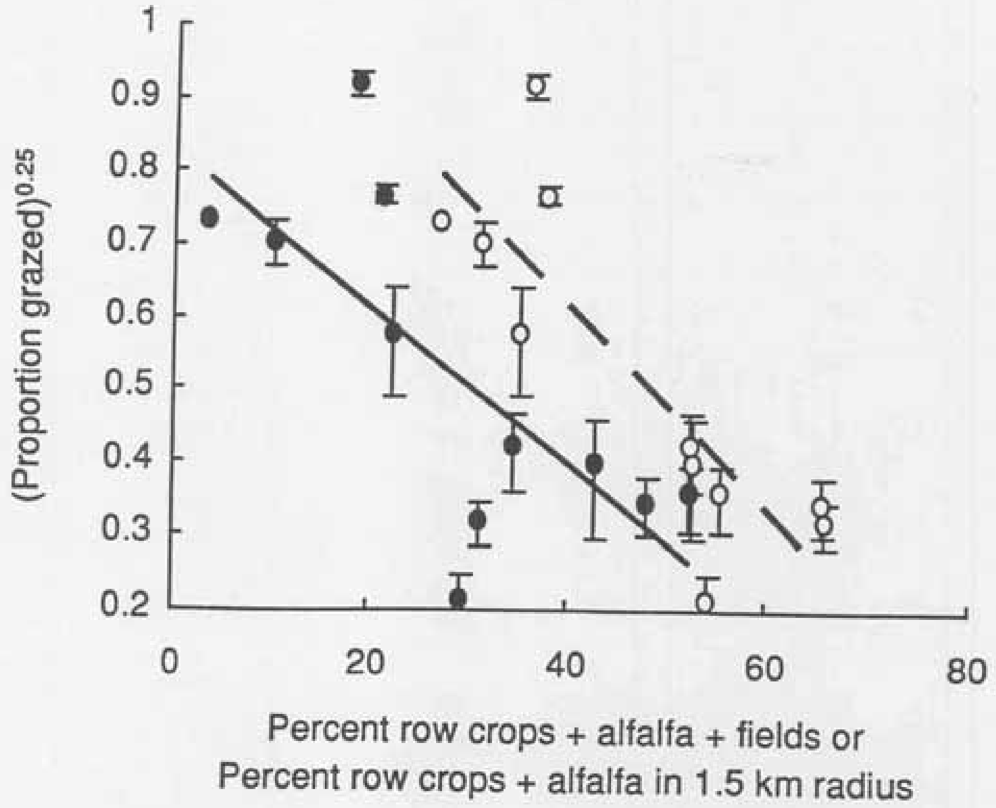

Figure 8. The relationship between grazing intensity on *Laportea canadensis* and two closely related measures of alternative forage availability within a 1.5 km radius of the stand: percent row crops, alfalfa, and fields (open circles; r^2=0.75, P<0.001) and the percent row crops and alfalfa only (closed circles; r^2=0.53, P=0.01). Error bars show ± 1 SE.

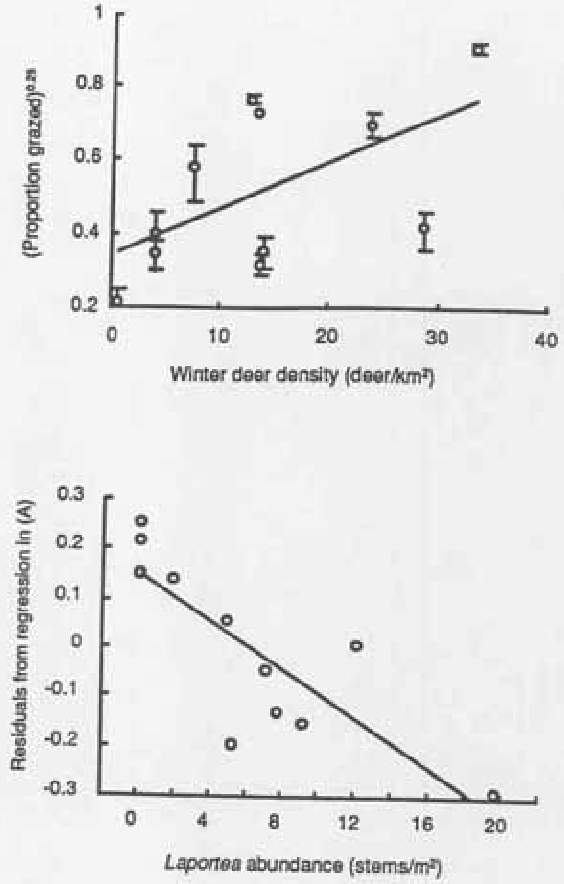

Figure 9. (A) The relationship between grazing intensity on Laportea canadensis in 11 Big Woods stands and winter deer density, and (B) the residuals from (A) as a function of palatable forb abundance within the stand. The multiple linear regression using these two predictors explained 79% of the variability in grazing intensity (Winter deer: P=0.005; *Laportea* abundance: P=0.004).

APPENDIX A. STUDY SITE LOCATIONS AND OWNERSHIP

Table 1. Locations and current ownership of the 12 Big Woods sites included in this study. All sites were used in chapter 5, with the exception that data from Woodrill and Wolsfeld Woods SNAs were pooled and treated as a single site.

Thesis reference: Chapters 1-4	Common Site Name **Hennepin Co., MN**	Ownership/Management	Location
High Deer Site 1	Riley Creek Woods	City of Eden Prairie	sec. 29, T.166N,R.22W
Low Deer Site 1	Taylors Woods	Hennepin County Parks	sec. 16,T.120N,R.22W
	Woodrill	Scientific and Natural Area (DNR)	sec. 36,T.188N,R.23W
	Henry Woods	Private	sec. 24, T.120N,R.23W
	Schmidt Woods	Private	sec. 25, T.120N,R.25W
	Wolsfeld Woods	Scientific and Natural Area (DNR)	sec. 27,T.166N,R.23W
	Rice Co., MN		
High Deer Site 2	River Bend Nature Preserve	City of Fairibault, MN	sec.4,T.109N,R.20W
Low Deer Site 2	Seven Mile Woods	Private and Rice County Parks	sec.12,T.100N,R.20W
Low Deer Site 3	Canon River Wilderness Park	Rice County Parks	sec.26 and 34,T.111N,R.20W
	Nerstrand Big Woods SP	State Park (DNR)	sec.9,T.110N,R.19W
	Townsend Woods	Scientific and Natural Area (DNR)	sec.18,T.109N,R.22W
	Trout Lily Preserve	The Nature Conservancy	sec.20,T.110N,R.20W

Table 2. Specific notes on the area sampled at each study site.

Common Site Name	Area Sampled
Riley Creek Woods	16 ha stand owned by Eden Prairie
Taylors Woods	16 ha stand on east side of Diamond Creek
Schmit Woods	22 ha stand owned by Mr. Bernard Schmit adjacent to SE corner of Crawford Woods SNA,
Henry Woods	All of approx. 16 ha stand owned by Mr. Lloyd Henry
Woodrill	All upland forest from 100 m east of B. Dayton residence to approx 200 m east of Bufflehead Lake
Wolsfeld Woods	From the Wolsfeld Woods SNA Management Plan (1981, MNDNR office files, St. Paul, MN) sampling included sections W4, W6, W 1/2 of W7, SE 1/3 of W8, and E 2/3 of W10
River Bend Nature Preserve	Stand bounded by "Owl trail" on north, east & west, and the mature/second growth border on the south
Seven Mile Woods	Mature forest of Caron Park and adjacent mature, upland forest owned by Mr. Alan Grannis
Canon River Wilderness Park	Stand extending between Hwy 3 and Cannon River floodplain; excluding creek bed
Nerstrand Big Woods SP	From Mason (1994) sampling included parcels 10, 22, 23, 24, and W 1/2 of 31, excluding creek bed vegetation
Townsend Woods	All upland forest in SNA
Trout Lily Preserve	Approx. 5 ha mature, upland forest on south side of creek dividing the preserve, including cemetery inholding

APPENDIX B. CANOPY COMPOSITION OF STUDY SITES IN SOUTHEASTERN MINNESOTA

1NTRODUCTION and METHODS

The region of pre-settlement Big Woods forest in southeastern Minnesota appears to have been relatively homogeneous over a large area in terms of tree species composition, being dominated by elms, sugar maple, and basswood, with many other less frequent but regularly occurring species (Grimm 1984). The "Big Woods" sites included in this study span a large geographical area, have been subject to varying levels of human disturbance, and include sites located in a forest prairie transition area where mature forests have only developed since European settlement. Because the canopy layer significantly affects understory forb communities by controlling light levels and nutrient recycling (Curtis 1959), I examined the degree of similarity between study sites in terms of canopy tree composition and tree size class distributions. All sites were sampled at 46 50 systematically located points using the point centered quarter method. At one site, the Nature Conservancy's Trout Lily Preserve, only 42 points were sampled due to the stand's small size. Trees were defined as woody stems ≥ 10 cm diameter at breast height (dbh). At each sampling point, the area was divided into quarters along the cardinal axes, and in each quarter the distance to the nearest tree, the tree species, and its dbh were recorded. Based on these data, I calculated the mean density of trees at each site, the relative dominance (Table 1), relative density (Table 2), and mean dbh (Table 3) of the tree species in each stand and the frequency distribution of trees in 10 cm dbh size classes within each stand (Fig. 1).

RESULTS

All sites are dominated by shade tolerant sugar maple, basswood, and elms with sugar maple dominating the 1050 cm size classes. Relative density of these species is greater than 60% and relative dominance is greater than 55% at all sites (Tables 1 2). Elms are rare, but a few large individuals of both *Ulmus americana* and *U. rubra* were encountered at study sites, and elm regeneration (10-20cm dbh trees) was consistently encountered at most study sites. Elms were particularly abundant in the 10-20 cm dbh size class at River Bend where sugar maple in this size class was correspondingly rare. Red and white oak are abundant in the large size classes (>50 cm dbh) at several sites and comprise a significant proportion of the basal area, but oak regeneration was not observed at any sites. At most sites, ironwood is an important subcanopy species.

The size class distribution of trees at the majority of the study sites showed a distribution representative of all aged forests. Large tines (>50 cm dbh) comprise a significant proportion of the trees at all study sites. River Bend and Wolsfeld Woods SNA, and to a lesser extent Townsend Woods SNA, showed a greater degree of recent (10-20 cm dbh) regeneration and a corresponding lack of tress in the 20-40 cm dbh size classes. This pattern is most distinct at River Bend and may be due to the presence of cattle prior to the 1970's. Whether Townsend Woods has been grazed in the past is unknown. The Nature Conservancy's Trout Lily Preserve, which is located in the prairie forest transition zone of the pre-settlement landscape (Grimm 1984), has a distinctly different tree size distribution where the 20-50 cm dbh classes are dominant. This more even-aged stand may have developed from an oak savanna following fire suppression after European settlement. Other study sites in the former prairie forest transition zone (River Bend, Nerstrand State Park, 7-mile Woods, Cannon River Wilderness Area) are in locations afforded some degree of fire protection by streams and topography, and may have contained a more mesic forest community before European settlement led to complete fire protection and the development of maple basswood dominated forests. Size class distributions at most study sites have also been affected by occasional selective tree removals for firewood and to promote sugar maple syrup production.

LITERATURE CITED

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Grimm, E. (1984). Fire and other factors controlling the Big Woods vegetation of Minnesota in the mid nineteenth century. *Ecol. Monogr.*, 54, 291-311.

Table 1. Relative dominance of tree species at 12 Big Woods stands in southeastern Minnesota based on point-centered quarter sampling. Trees were defined as any woody plant > 10 cm dbh.

	Hennepin/Wright County Sites						Rice County Sites					
	Riley Creek	Taylor's Woods	Woodrill	Henry's Woods	Schmidt Woods	Wolsfeld Woods	River Bend	7 mile Woods	Cannon River	Nerstrand State Park	Townsend Woods	Trout Lily Preserve
Acer saccharum	0.68	0.90	0.41	0.92	0.61	0.65	0.60	0.60	0.62	0.44	0.31	0.63
Tilia americana	0.11	0.01	0.17	0.03	0.22	0.17	0.16	0.24	0.24	0.23	0.28	0.11
Ostrya virginiana	0.005	0.000	0.003	0.007	0.004	0.02	0.02	0.005	0.009	0.008	0.032	0
Quercus rubra	0.15	0.07	0.24	0	0.07	0.10	0	0.02	0.07	0.14	0.29	0.17
Ulmus americana	0	0.006	0.003	0.01	0.007	0	0.07	0.01	0.01	0.001	0.06	0
Fraxinus nigra	0.004	0.007	0	0.01	0.01	0.006	0.01	0.008	0.02	0.02	0.02	0.05
Quercus alba	0	0	0.13	0.02	0.07	0.05	0.05	0.05	0.02	0.07	0	0.01
Carya cordiformis	0.002	0.000	0.008	0	0	0	0.02	0.02	0.003	0.001	0	0.006
Ulmus rubra	0.04	0	0.005	0.005	0	0	0.009	0.001	0	0.001	0	0.007
Celtis occidentalis	0.001	0	0	0.001	0	0	0.01	0.004	0.002	0	0.001	0.008
Fraxinus pennsylvanica	0	0.006	0.03	0.002	0.002	0	0.003	0.01	0	0.04	0	0.008
Juglans cinerea	0.01	0	0	0	0	0	0.002	0	0.009	0	0	0
Juglans nigra	0	0	0	0	0	0	0.01	0	0	0.02	0	0.005
Quercus macrocarpa	0	0	0	0	0.01	0	0	0.004	0	0	0	0
Acer negundo	0	0	0	0	0	0	0.02	0.015	0	0	0	0
Prunus serotina	0	0	0	0	0	0	0.02	0	0	0	0	0
Acer rubra	0	0	0	0	0.000	0	0	0	0	0	0	0
Fraxinus americana	0	0	0	0	0	0	0	0	0	0.01	0	0
Betula papyrifera	0	0	0	0	0.002	0	0	0	0	0	0	0
Populous grandidentata	0	0	0	0	0.002	0	0	0	0	0.01	0	0

Table 2. Relative density of tree species and total tree density at 12 Big Woods stands in southeastern Minnesota based on point-centered quarter sampling of trees > 10 cm dbh.

	Hennepin/Wright County Sites						Rice County Sites					
	Riley Creek	Taylor's Woods	Woodrill	Henry's Woods	Schmidt Woods	Wolsfeld Woods	River Bend	7 mile Woods	Cannon River	Nerstrand State Park	Townsend Woods	Trout Lily Preserve
Acer saccharum	0.82	0.91	0.69	0.77	0.67	0.68	0.29	0.69	0.69	0.59	0.46	0.71
Tilia americana	0.06	0.02	0.09	0.05	0.15	0.09	0.09	0.10	0.14	0.13	0.18	0.07
Ostrya virginiana	0.03	0.005	0.02	0.05	0.05	0.17	0.15	0.04	0.05	0.04	0.16	0
Quercus rubra	0.05	0.03	0.11	0	0.03	0.04	0	0.02	0.04	0.08	0.13	0.10
Ulmus americana	0	0.02	0.005	0.05	0.04	0	0.21	0.03	0.02	0.005	0.03	0
Fraxinus nigra	0.005	0.005	0	0.05	0.01	0.005	0.06	0.02	0.02	0.02	0.04	0.04
Quercus alba	0	0	0.07	0.005	0.03	0.03	0.02	0.04	0.02	0.07	0	0.006
Carya cordiformis	0.005	0.005	0.02	0	0	0	0.05	0.03	0.01	0.005	0	0.03
Ulmus rubra	0.02	0	0.005	0.03	0	0	0.03	0.005	0	0.005	0	0.02
Celtis occidentalis	0.005	0	0	0.01	0	0	0.05	0.01	0.02	0	0.01	0.006
Fraxinus pennsylvanica	0	0.005	0.005	0.005	0.005	0	0.005	0.005	0	0.04	0	0.006
Juglans nigra	0	0	0	0	0	0	0.01	0	0	0.02	0	0.01
Juglans cinerea	0.005	0	0	0	0	0	0.005	0	0.005	0	0	0
Quercus macrocarpa	0	0	0	0	0.005	0	0	0.005	0	0	0	0
Acer negundo	0	0	0	0	0	0	0.03	0	0	0	0	0
Prunus serotina	0	0	0	0	0	0	0.02	0	0	0	0	0
Acer rubra	0	0	0	0	0.005	0	0	0	0	0	0	0
Fraxinus americana	0	0	0	0	0	0	0	0	0	0.01	0	0
Betula papyrifera	0	0	0	0	0.005	0	0	0	0	0	0	0
Populous grandidentata	0	0	0	0	0.005	0	0	0.01	0	0.01	0	0
Trees / ha	345.3	394.6	369.3	349.7	259.8	344.7	427.6	439.2	294.4	374.9	291.0	330.5

Table 3. Mean dbh of tree species at 12 Big Woods stands in southeastern Minnesota based on point-centered quarter sampling of trees > 10 cm dbh.

	Hennepin/Wright County Sites						Rice County Sites					
	Riley Creek	Taylor's Woods	Woodrill	Henry's Woods	Schmidt Woods	Wolsfeld Woods	River Bend	7 mile Woods	Cannon River	Nerstrand State Park	Townsend Woods	Trout Lily Preserve
Acer saccharum	27.6	30.3	25.2	34.7	35.9	31.4	41.9	27.6	31.2	26.0	28.2	35.2
Tilia americana	44.6	30.0	49.0	21.4	45.9	51.6	36.2	42.9	46.7	43.4	48.0	44.9
Ostrya virginiana	13.3	10.0	15.8	12.8	12.6	13.7	11.9	12.1	15.1	15.3	16.6	0
Quercus rubra	59.1	70.1	51.9	0	56.3	62.8	0	39.7	47.9	43.1	58.8	52.2
Ulmus americana	0	23.7	30.0	14.9	16.6	0	16.5	19.3	24.9	12.0	16.3	0
Fraxinus nigra	31.0	54.5	0	15.1	36.3	42.0	14.5	23.0	32.3	41.3	26.6	40.2
Quercus alba	0	0	50.2	61.0	60.7	53.7	55.7	37.6	43.8	31.5	0	59.0
Carya cordiformis	19.0	13.5	26.0	0	0	0	18.3	24.6	18.3	12.0	0	17.9
Ulmus rubra	45.5	0	35.5	15.2	0	0	16.7	10.0	0	12.0	0	21.4
Fraxinus pennsylvanica	0	49.5	87.0	21.5	25.5	0	23.0	44.0	0	31.4	0	46.7
Celtis occidentalis	14.0	0	0	13.0	0	0	14.4	18.5	13.5	0	14.8	0
Juglans cinerea	50.0	0	0	0	0	0	22.0	0	48.5	0	0	0
Juglans nigra	0	0	0	0	0	0	34.5	0	0	33.3	0	25.3
Quercus macrocarpa	0	0	0	0	57.0	0	0	27.0	0	0	0	0
Acer negundo	0	0	0	0	0	0	24.4	38.0	0	0	0	0
Prunus serotina	0	0	0	0	0	0	25.6	0	0	0	0	0
Acer rubra	0	0	0	0	11.0	0	0	0	0	0	0	0
Fraxinus americana	0	0	0	0	0	0	0	0	0	38.8	0	0
Betula papyrifera	0	0	0	0	23.0	0	0	0	0	0	0	0
Populous grandidentata	0	0	0	0	28.0	0	0	0	0	35.3	0	0

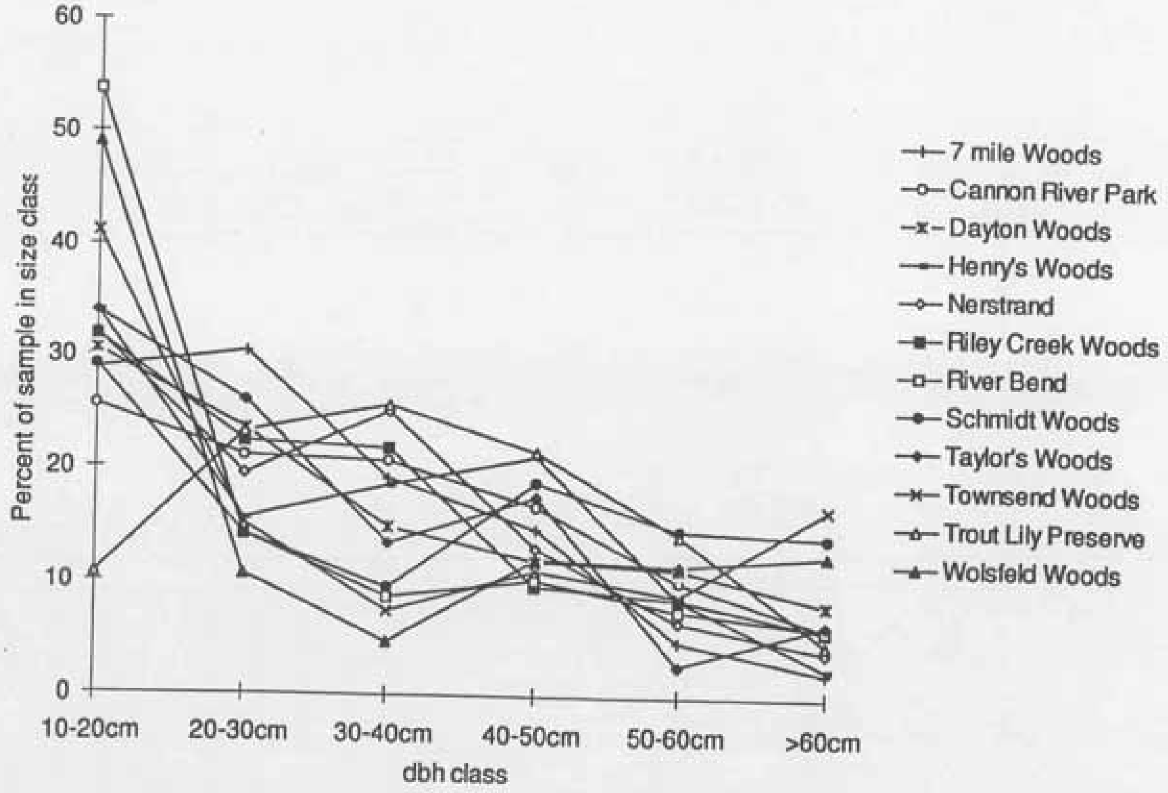

Figure 1. The size class frequency distribution of trees, by 10 cm dbh size classes, for 12 Big Woods stands in southeastern Minnesota. Data is based on point-centered quarter sampling of trees > 10 cm dbh at each stand.

APPENDIX C. ABUNDANCE, PERCENT GRAZED, AND PERCENT FLOWERING OF SELECTED UNDERSTORY FORB SPECIES IN 12 BIG WOODS STANDS IN SOUTHEASTERN MINNESOTA

METHODS Results presented here are based on understory forest surveys conducted in 1996 during spring (10-16 May) at 6 Big Woods forests and early summer (10-20 June) and late summer (3-14 August) at 12 Big Woods forests in southeastern Minnesota. Data was summarized for each species surveyed and for groups of species relevant to deer grazing impacts on the understory forb community. Flowering rates are presented for each individual species in the sampling period closest to when it reaches anthesis, and are only presented for groups species when all included species have similar reproductive strategies. A detailed description of the survey methods is given in Chapter 5.

Table 1. Abundance, percent grazed, and percent flowering for eight spring ephemeral forb species at six Big Woods stands in southeastern Minnesota.

Site	All species				*Erythronium spp.*						*Isopyrum biternatum*					
	Stems/m^2		% Grazed		Stems/m^2		% Grazed		%Flowering		Stems/m^2		% Grazed		%Flowering	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
7mile	142.11	30.14	0.67	0.57	94.75	28.69	0.86	0.91	0.30	0.16	23.43	9.46	0.13	0.17	27.45	1.48
Cannon River	110.14	19.36	1.49	0.65	22.87	7.70	4.27	2.43	4.18	1.30	61.27	16.42	0.95	0.68	24.17	1.96
Nerstrand	130.61	18.09	0.01	0.00	107.44	18.48	0.62	0.30	1.29	0.41	12.59	4.14	0.05	0.06	32.19	2.00
River Bend	116.22	13.24	7.06	1.96	30.04	9.06	7.72	3.42	1.82	1.93	79.42	12.03	6.84	2.81	26.43	3.31
Trout Lily	93.07	20.54	3.95	0.69	63.93	19.69	3.88	0.94	0.21	0.12	12.12	6.11	4.38	1.85	18.17	7.17
Townsend	119.97	19.58	0.16	0.09	16.33	6.64	0.65	0.66	1.38	0.42	0.07	0.07	--	--	--	--

	Allium tricoccum						*Anemone quinquefolia*						*Aplectrum hyemale*					
	Stems/m^2		% Grazed		%Flowering		Stems/m^2		% Grazed		%Flowering		Stems/m^2		% Grazed		%Flowering	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
7mile	1.33	0.36	0.00	0.00	0.00	0.00	0.72	0.22	0.00	0.00	3.03	1.03	0.19	0.14	0.00	0.00	26.68	12.16
Cannon River	0.67	0.25	0.00	0.00	0.00	0.00	0.43	0.20	0.00	0.00	4.05	4.08	0.00	0.00	--	--	--	--
Nerstrand	0.85	0.21	0.00	0.00	0.00	0.00	2.35	0.59	0.00	0.00	3.61	1.08	0.00	0.00	--	--	--	--
River Bend	0.27	0.12	6.46	1.69	0.00	0.00	0.41	0.20	0.00	0.00	4.31	0.86	0.00	0.00	--	--	--	--
Trout Lily	0.04	0.02	0.57	4.48	0.00	0.00	0.64	0.33	1.55	1.21	0.00	0.00	0.00	0.00	--	--	--	--
Townsend	0.14	0.06	4.22	6.31	0.00	0.00	0.04	0.03	--	--	--	--	0.004	0.004	--	--	--	--

	Claytonia virginiana						*Cardamine concatenata*						*Dicentra cucullaria*					
	Stems/m^2		% Grazed		%Flowering		Stems/m^2		% Grazed		%Flowering		Stems/m^2		% Grazed		%Flowering	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
7mile	16.15	9.20	0.10	0.21	36.66	5.25	0.53	0.36	--	--	--	--	7.28	3.03	0.19	0.13	1.66	0.60
Cannon River	12.90	5.66	0.03	0.03	25.69	2.09	0.26	0.18	0.40	0.23	3.80	0.32	11.85	2.82	0.41	0.33	3.14	0.78
Nerstrand	0.20	0.13	--	--	--	--	3.70	1.52	0.00	0.00	2.63	1.51	3.49	1.18	0.51	0.49	5.65	2.43
River Bend	5.78	2.44	0.84	0.51	36.87	7.62	0.49	0.49	--	--	--	--	0.11	0.05	4.34	2.54	3.03	2.79
Trout Lily	14.30	5.27	1.09	0.48	34.03	3.42	1.62	0.85	0.00	0.00	6.29	2.58	0.43	0.23	0.00	0.00	9.51	6.19
Townsend	0.00	0.00	--	--	--	--	0.36	0.15	0.00	0.00	14.34	3.72	91.42	17.43	0.08	0.05	2.62	0.49

Table 2. Abundance and percent grazed of 16 forb species (Chapter 5, Table 1) sampled during 10-20 June at 12 Big Woods stands in southeastern Minnesota. "Palatable early-summer species" consisted of *Geranium maculatum, Osmorhiza spp., Polygonatum biflorum, Sanguinaria canadensis, Smilacina racemosa, Smilax cf. ecirrata, Trillium spp.*, and *Uvularia grandiflora* and "Palatable, early-summer, single-stemmed species" consisted of the same group excluding *Geranium* and *Osmorhiza*. Flowering rates are also reported for these two groupings since all species included flower in early summer (June).

	All species				All palatable early-summer species						Palatable, early-summer, single-stemmed species					
	Stems/m^2		% Grazed		Stems/m^2		% Grazed		% Flowering		Stems/m^2		% Grazed		% Flowering	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
7mile Woods	19.5	3.9	1.1	0.47	3.7	0.8	2.32	1.01	8.29	3.08	0.8	0.1	7.15	1.87	10.75	3.17
Cannon River	18.7	2.5	1.4	0.49	1.7	0.4	1.34	0.58	18.44	3.82	1.0	0.1	2.10	0.96	20.14	3.47
Woodrill	0.8	0.1	0.2	0.17	0.1	0.0	1.24	1.41	0.61	0.71	0.1	0.0	1.25	1.39	0.61	0.70
Henry Woods	15.5	2.3	8.4	3.69	1.0	0.2	9.17	3.00	13.15	2.93	0.8	0.2	9.45	3.48	11.24	2.86
Schmidt Woods	9.8	1.7	0.7	0.32	1.2	0.4	0.67	0.62	10.83	4.76	0.5	0.1	1.57	1.50	8.23	3.36
Nerstrand S.P.	11.3	1.4	1.3	0.35	7.5	1.1	1.02	0.30	4.25	1.24	1.2	0.1	3.89	1.39	10.35	1.89
River Bend	20.4	7.3	7.5	2.02	10.1	4.2	6.94	2.20	2.00	1.21	0.2	0.0	7.90	2.69	3.08	1.45
Riley Creek	7.9	1.6	5.2	1.79	0.4	0.1	4.44	2.43	0.00	0.00	0.3	0.1	5.93	3.19	0.00	0.00
Trout Lily Pres.	3.0	0.7	1.9	0.49	0.3	0.0	7.93	2.47	4.75	1.40	0.3	0.0	8.08	2.55	4.84	1.43
Townsend Woods	9.2	2.0	0.4	0.19	1.5	0.2	1.31	0.77	17.49	2.98	0.8	0.2	2.17	1.36	4.54	2.12
Taylor's Woods	24.1	2.3	2.3	0.70	2.2	0.4	8.62	3.13	19.18	3.00	1.9	0.4	9.59	3.50	15.15	2.80
Wolsfeld Woods	2.7	0.3	0.4	0.16	0.2	0.1	1.28	1.32	2.00	1.74	0.1	0.0	3.07	3.60	3.21	3.84

Table 3. Abundance, percent grazed, and percent flowering for 10 early-summer flowering forb species, measured during 10-20 June, 1996, at 12 Big Woods stands in southeastern Minnesota.

	Arisaema triphyllum						*Caulophyllum thalictroides*						*Geranium maculatum*					
	Stems/m²		% Grazed		% Flowering		Stems/m²		% Grazed		% Flowering		Stems/m²		% Grazed		% Flowering	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
7mile	0.17	0.05	0.00	0.00	8.70	2.88	0.35	0.10	0.58	0.60	8.43	3.51	1.88	0.48	1.20	0.82	1.13	0.55
Cannon River	0.09	0.05	0.00	0.00	9.63	4.52	0.12	0.04	1.74	1.96	45.85	5.77	0.50	0.18	0.00	0.00	0.35	0.39
Woodrill	0.62	0.08	0.00	0.00	8.00	0.99	0.00	0.00	--	--	--	--	0.00	0.00	--	--	--	--
Henry	0.99	0.32	1.41	0.85	2.63	1.30	0.06	0.02	17.41	8.40	15.35	4.77	0.00	0.00	--	--	--	--
Schmidt	0.59	0.29	0.00	0.00	5.14	2.33	0.03	0.01	0.00	0.00	5.82	7.00	0.04	0.03	--	--	--	--
Nerstrand	0.43	0.07	0.60	1.23	4.65	2.16	0.16	0.05	0.00	0.00	19.90	7.25	5.12	0.79	0.41	0.15	2.37	1.13
River Bend	0.79	0.21	4.06	1.64	2.42	0.68	0.04	0.04	--	--	--	--	9.92	4.19	6.83	2.25	1.95	1.21
Riley Creek	1.06	0.24	0.31	0.34	4.00	1.23	0.39	0.11	3.44	1.74	4.23	2.02	0.08	0.04	0.00	0.00	2.22	2.92
Trout Lily	0.76	0.13	0.46	0.33	3.91	0.73	0.01	0.01	--	--	--	--	0.00	0.00	--	--	--	--
Townsend	0.03	0.01	0.00	0.00	25.72	8.40	0.04	0.02	0.00	0.00	25.18	15.43	0.01	0.01	--	--	--	--
Taylors	0.05	0.02	0.00	0.00	34.53	23.71	0.14	0.05	1.29	0.00	16.61	0.00	0.03	0.02	--	--	--	--
Wolsfeld	1.83	0.23	0.14	0.10	5.35	0.72	0.24	0.05	0.00	0.00	38.11	7.16	0.14	0.07	0.00	0.00	1.18	1.08

	Osmorhiza spp.						*Polygonatum biflorum*						*Sanguinaria canadensis*					
	Stems/m²		% Grazed		% Flowering		Stems/m²		% Grazed		% Flowering		Stems/m²		% Grazed		% Flowering	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
7mile	0.51	0.10	0.99	0.69	54.13	6.47	0.02	0.01	5.53	6.35	0.00	0.00	0.24	0.05	2.88	2.08	20.71	6.60
Cannon River	0.30	0.08	1.40	1.02	51.55	8.99	0.08	0.02	0.00	0.00	2.50	2.29	0.41	0.07	0.00	0.00	29.23	4.24
Woodrill	0.00	0.00	--	--	--	--	0.00	0.00	--	--	--	--	0.00	0.00	13.75	7.70	6.68	5.36
Henry	0.16	0.07	6.50	7.68	20.56	11.76	0.03	0.02	0.00	0.00	15.73	12.79	0.27	0.13	18.32	13.58	7.48	4.26
Schmidt	0.69	0.34	0.16	0.31	10.08	12.59	0.14	0.05	0.00	0.00	8.51	7.39	0.05	0.02	0.00	0.00	40.68	28.95
Nerstrand	0.14	0.04	0.99	1.05	9.44	4.68	0.09	0.03	1.08	1.18	0.00	0.00	0.26	0.06	6.09	3.96	12.28	3.57
River Bend	0.02	0.01	42.62	21.76	40.65	11.38	0.03	0.02	6.16	5.84	0.00	0.00	0.07	0.02	10.19	5.17	6.87	3.01
Riley Creek	0.02	0.01	--	--	--	--	0.01	0.01	0.00	0.00	0.00	0.00	0.16	0.04	1.29	1.37	0.00	0.00
Trout Lily	0.00	0.00	--	--	--	--	0.03	0.01	0.00	0.00	0.00	0.00	0.17	0.03	9.47	3.78	6.22	1.87
Townsend	0.66	0.13	0.25	0.27	33.67	3.45	0.29	0.09	0.00	0.00	0.00	0.00	0.23	0.05	3.38	1.87	13.76	2.75
Taylors	0.20	0.04	2.45	1.41	53.62	6.26	0.08	0.02	0.00	0.00	5.24	3.38	0.20	0.08	8.15	2.87	10.45	6.47
Wolsfeld	0.00	0.00	--	--	--	--	0.01	0.01	0.00	0.00	14.46	21.52	0.03	0.01	3.57	3.74	3.26	3.79

Table 3, continued

	Smilacina racemosa						*Smilax cf. ecirrata*						*Trillium spp.*					
	Stems/m^2		% Grazed		% Flowering		Stems/m^2		% Grazed		% Flowering		Stems/m^2		% Grazed		% Flowering	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
7mile	0.13	0.05	7.98	6.22	1.30	1.75	0.07	0.02	3.14	3.28	1.57	1.64	0.20	0.05	13.81	5.29	10.46	5.08
Cannon River	0.05	0.02	3.01	4.06	3.64	3.99	0.05	0.02	0.00	0.00	4.84	3.97	0.29	0.06	7.15	3.70	29.46	6.43
Woodrill	0.08	0.03	1.44	1.75	0.00	0.00	0.00	0.00	--	--	--	--	0.01	0.01	--	--	--	--
Henry	0.05	0.02	0.00	0.00	0.00	0.00	0.02	0.01	0.00	0.00	0.00	0.00	0.37	0.07	8.09	3.30	18.77	5.04
Schmidt	0.15	0.04	0.00	0.00	2.29	2.37	0.01	0.00	--	--	--	--	0.03	0.01	7.87	7.22	18.26	4.44
Nerstrand	0.09	0.03	1.10	1.27	1.33	1.24	0.05	0.01	1.95	2.08	0.00	0.00	0.39	0.08	3.55	1.98	16.76	4.58
River Bend	0.07	0.02	18.06	6.49	0.00	0.00	0.02	0.01	17.53	10.61	7.53	7.53	0.00	0.00	36.99	5.65	15.07	4.19
Riley Creek	0.06	0.03	3.12	3.33	0.00	0.00	0.06	0.04	5.40	3.14	0.00	0.00	0.01	0.00	18.52	7.48	7.14	5.04
Trout Lily	0.05	0.02	10.39	6.76	0.00	0.00	0.00	0.00	--	--	--	--	0.03	0.02	13.76	5.07	9.01	3.91
Townsend	0.16	0.09	0.69	1.90	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.01	0.00	1.02	3.97	15.10	2.76
Taylors	0.09	0.03	0.00	0.00	2.16	2.02	0.01	0.01	0.00	0.00	0.00	0.00	1.28	0.27	12.59	4.31	18.94	3.95
Wolsfeld	0.04	0.02	4.93	5.84	1.67	2.42	0.01	0.01	--	--	--	--	0.00	0.00	--	--	--	--

	Uvularia grandiflora					
	Stems/m^2		% Grazed		% Flowering	
	Mean	SE	Mean	SE	Mean	SE
7mile	0.25	0.07	1.57	1.19	9.47	3.68
Cannon River	0.18	0.06	1.91	1.53	17.47	3.98
Woodrill	0.00	0.00	18.71	9.37	7.00	6.72
Henry	0.06	0.03	10.86	4.30	5.93	3.09
Schmidt	0.10	0.06	9.40	6.68	4.70	3.34
Nerstrand	0.44	0.07	4.91	1.12	5.95	1.75
River Bend	0.01	0.01	35.96	7.13	2.52	5.66
Riley Creek	0.07	0.02	13.59	9.30	2.56	2.76
Trout Lily	0.00	0.00	--	--	--	--
Townsend	0.14	0.05	6.56	4.38	0.00	0.00
Taylors	0.25	0.09	18.06	5.70	10.13	1.90
Wolsfeld	0.00	0.00	--	--	--	--

Table 4. Abundance and percent grazed of 6 late-summer flowering forb species, measured during 10-20 June, 1996, at 12 Big Woods stands in southeastern Minnesota.

	Circaea lutetiana				*Eupatorium rugosum*				*Impatiens pallida*			
	Stems/m^2		% Grazed		Stems/m^2		% Grazed		Stems/m^2		% Grazed	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
7mile	0.70	0.14	1.74	0.78	0.01	0.01	--	--	5.46	2.22	1.54	1.30
Cannon River	0.38	0.12	1.01	1.01	0.01	0.01	--	--	1.49	0.46	1.19	0.89
Woodrill	0.07	0.03	0.00	0.00	0.00	0.00	--	--	0.00	0.00	--	--
Henry	0.76	0.18	4.64	3.43	0.00	0.00	--	--	4.29	3.65	14.70	1.26
Schmidt	0.16	0.05	1.14	1.28	0.00	0.00	--	--	0.70	0.37	0.00	0.00
Nerstrand	0.83	0.15	0.91	0.91	0.04	0.04	--	--	0.40	0.10	0.00	0.00
River Bend	2.14	0.35	13.72	3.08	0.47	0.18	3.13	2.92	0.03	0.03	--	--
Riley Creek	0.48	0.23	4.92	4.20	0.00	0.00	--	--	0.49	0.17	3.81	2.72
Trout Lily	1.89	0.67	1.23	0.58	0.00	0.00	--	--	0.03	0.02	2.67	3.81
Townsend	0.84	0.38	0.31	0.45	0.00	0.00	--	--	0.18	0.09	0.00	0.00
Taylors	0.03	0.01	0.00	--	0.00	0.00	--	--	0.02	0.02	--	0.00
Wolsfeld	0.32	0.07	1.15	0.54	0.00	0.00	--	--	0.02	0.01	--	--

	Laportea canadensis				*Solidago flexicaulis*				*Hackelia virginiana*			
	Stems/m^2		% Grazed		Stems/m^2		% Grazed		Stems/m^2		% Grazed	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
7mile	8.89	2.32	0.22	0.25	0.23	0.07	8.29	3.53	0.00	0.00	--	--
Cannon River	14.56	2.33	1.38	0.60	0.31	0.10	1.89	1.28	0.00	0.00	--	--
Woodrill	0.00	0.00	--	--	0.00	0.00	--	--	0.00	0.00	--	--
Henry	11.94	2.18	8.24	4.11	0.03	0.03	--	--	0.00	0.00	--	--
Schmidt	6.02	1.12	0.75	0.36	0.26	0.10	13.33	7.07	0.02	0.01	--	--
Nerstrand	1.79	0.58	2.10	1.68	0.40	0.08	5.17	2.25	0.00	0.00	--	--
River Bend	0.10	0.05	25.82	3.60	0.30	0.10	7.99	4.15	0.07	0.03	0.00	0.00
Riley Creek	4.98	1.37	6.39	2.73	0.01	0.01	--	--	0.15	0.07	1.95	2.70
Trout Lily	0.03	0.01	6.25	--	0.01	0.01	--	--	0.00	0.00	--	--
Townsend	6.87	1.39	0.05	0.06	0.08	0.04	1.33	1.22	0.01	0.01	--	--
Taylors	21.29	2.53	1.64	0.64	0.05	0.04	--	--	0.00	0.00	--	--
Wolsfeld	0.03	0.02	--	--	0.01	0.00	--	--	0.00	0.00	--	--

Table 5. Abundance and percent grazed of 16 forb species (Chapter 5, Table 2) sampled during 3-14 August at 12 Big Woods stands in southeastern Minnesota. "Palatable late-summer species" consisted of *Circaea lutetiana, Caulophyllum thalictroides, Impatiens pallida, Laportea canadensis*, and *Solidago flexicaulis*. Flowering rates are not reported for "Palatable late-summer species" grouped together because flowering rates vary widely among species from the annual *Impatiens* to the predominantly clonal *Solidago*.

	All Species				Palatable late-summer species				*Circaea & Laportea*					
	Stems/m^2		% Grazed		Stems/m^2		% Grazed		Stems/m^2		% Grazed		% Flowering	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
7mile	10.65	0.22	2.48	0.71	9.13	0.22	2.50	0.79	7.94	0.23	2.11	0.80	29.94	2.70
Cannon River	11.95	0.21	2.38	0.74	10.96	0.21	2.64	0.84	10.38	0.20	1.85	0.74	28.44	2.62
Woodrill	0.61	0.00	6.11	2.93	0.11	0.00	33.88	11.90	0.09	0.00	39.18	12.69	5.27	3.93
Henry	14.63	0.33	3.01	1.79	13.62	0.33	3.15	1.90	13.07	0.34	2.61	1.74	33.58	3.91
Schmidt	10.33	0.25	0.50	0.22	8.96	0.25	0.38	0.19	8.08	0.25	0.36	0.21	26.70	4.77
Nerstrand	6.33	0.11	8.25	1.96	3.39	0.09	12.64	3.56	2.52	0.09	10.44	3.62	19.60	4.60
River Bend	6.91	0.20	11.85	4.33	2.37	0.06	35.49	6.61	1.61	0.04	39.42	5.82	4.16	1.29
Riley Creek	6.93	0.20	20.07	3.61	6.17	0.20	22.37	4.11	5.70	0.20	22.36	4.12	21.03	3.97
Trout Lily	1.38	0.01	9.91	2.01	0.97	0.01	14.02	2.55	0.86	0.01	14.27	2.62	10.27	3.84
Townsend	7.25	0.25	1.49	0.45	6.14	0.26	1.64	0.53	5.64	0.26	1.36	0.50	16.40	5.18
Taylors	21.12	0.31	3.32	1.47	20.04	0.32	3.40	1.55	19.72	0.33	3.24	1.56	29.85	2.06
Wolsfeld	1.33	0.02	6.78	6.25	0.28	0.00	14.52	7.84	0.25	0.00	15.05	8.18	8.73	3.31

Table 6. Abundance, percent grazed, and percent flowering of seven late-summer dominant species, measured during 3-14 August, 1996, at 12 Big Woods stands in southeastern Minnesota.

	Circaea lutetiana						*Laportea canadensis*						*Impatiens pallida*				*Caulophyllum thalictroides*			
	Stems/m^2		% Grazed		% Flowering		Stems/m^2		% Grazed		% Flowering		Stems/m^2		% Grazed		Stems/m^2		% Grazed	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
7mile	0.82	0.18	4.55	2.52	11.19	3.15	7.16	1.57	1.46	0.62	32.16	2.84	0.21	0.01	2.55	4.44	0.16	0.04	2.63	1.75
Cannon River	0.51	0.21	22.93	10.88	9.30	5.49	9.16	1.40	1.65	0.74	29.08	2.72	0.46	0.02	17.16	7.98	0.13	0.04	2.82	2.95
Woodrill	0.09	0.03	41.31	12.69	5.27	3.93	0.00	0.00	--	--	--	--	0.00	0.00	--	--	0.01	0.01	0.00	0.00
Henry	0.66	0.18	2.18	1.46	12.51	4.53	12.13	2.25	2.58	1.8	34.72	4.23	1.46	0.06	7.33	5.41	0.04	0.02	0.00	0.00
Schmidt	0.15	0.04	3.39	2.95	14.11	7.07	7.76	1.65	0.22	0.16	26.88	4.89	0.27	0.02	0.00	1.28	0.03	0.01	6.43	4.24
Nerstrand	0.61	0.15	6.20	1.72	4.18	1.96	1.91	0.65	11.2	5.5	23.98	5.41	0.32	0.01	14.51	5.64	0.11	0.03	6.29	2.01
River Bend	1.60	0.28	39.58	5.86	4.20	1.30	0.10	0.04	72.4	5.3	0.00	0.00	0.01	0.00	--	--	0.01	0.003	--	--
Riley Creek	0.61	0.15	19.81	5.98	17.32	3.90	4.94	1.20	24.6	4.69	21.15	4.26	0.27	0.01	44.57	13.75	0.25	0.08	9.81	8.56
Trout Lily	0.83	0.17	13.90	2.73	10.28	3.85	0.00	0.00	34.8	2.23	--	--	0.06	0.00	20.82	11.71	0.003	0.00	--	--
Townsend	0.23	0.08	8.07	5.36	34.03	20.02	5.28	1.24	1.04	0.36	19.81	3.66	0.03	0.00	20.25	20.51	0.04	0.02	3.39	2.94
Taylors	0.03	0.02	--	--	--	--	19.69	2.25	3.24	1.55	29.88	2.06	0.00	0.00	--	--	0.11	0.03	5.67	5.48
Wolsfeld	0.24	0.05	15.84	8.44	8.72	3.38	0.01	0.01	--	--	--	--	0.00	0.00	--	--	0.02	0.01	7.21	13.15

	Solidago flexicaulis						*Eupatorium rugosum*						*Hackelia virginiana*					
	Stems/m^2		% Grazed		% Flowering		Stems/m^2		% Grazed		% Flowering		Stems/m^2		% Grazed		% Flowering	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
7mile	0.11	0.03	19.44	5.36	1.94	1.61	0.01	0.01	--	--	--	--	0.00	0.00	--	--	--	--
Cannon River	0.11	0.04	11.83	4.12	1.42	1.76	0.003	0.003	--	--	--	--	0.00	0.00	--	--	--	--
Woodrill	0.00	0.00	--	--	--	--	0.00	0.00	--	--	--	--	0.00	0.00	--	--	--	--
Henry	0.02	0.02	--	--	--	--	0.00	0.00	--	--	--	--	0.04	0.00	--	--	--	--
Schmidt	0.14	0.06	0.00	0.00	0.00	0.00	0.00	0.00	--	--	--	--	0.06	0.01	--	--	--	--
Nerstrand	0.33	0.08	24.17	7.35	1.15	0.77	0.03	0.02	--	--	--	--	0.01	0.00	--	--	--	--
River Bend	0.53	0.15	29.63	7.45	2.16	0.84	0.72	0.26	0.00	0.00	56.76	4.52	0.08	0.00	0.00	0.00	79.16	13.57
Riley Creek	0.00	0.00	--	--	--	--	0.00	0.00	--	--	--	--	0.04	0.00	0.00	--	67.00	13.40
Trout Lily	0.08	0.05	8.29	10.52	0.00	0.00	0.00	0.00	--	--	--	--	0.00	0.00	--	--	--	--
Townsend	0.14	0.08	4.25	3.38	0.45	1.06	0.00	0.00	--	--	--	--	0.00	0.00	--	--	--	--
Taylors	0.08	0.05	--	--	--	--	0.00	0.00	--	--	--	--	0.00	0.00	--	--	--	--
Wolsfeld	0.00	0.00	--	--	--	--	0.00	0.00	--	--	--	--	0.00	0.00	--	--	--	--

Table 7. Abundance and percent grazed of 9 early-summer forbs measured during 4-13 August, 1996, at 12 Big Woods stands in southeastern Minnesota.

	Arisaema triphyllum				*Geranium maculatum*				*Osmorhiza spp.*				*Polygonatum biflorum*				*Sanguinaria canadensis*			
	Stems/m^2		% Grazed		Stems/m^2		% Grazed		Stems/m^2		% Grazed		Stems/m^2		% Grazed		Stems/m^2		% Grazed	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
7mile	0.12	0.00	0.00	0.00	0.65	0.02	3.75	1.30	0.01	0.00	0.00	0.00	0.09	0.00	10.71	14.98	0.62	0.04	2.45	2.63
Cannon River	0.19	0.01	0.00	0.00	0.23	0.01	0.00	0.00	0.24	0.01	0.00	0.00	0.03	0.00	0.00	0.00	0.15	0.00	1.18	1.18
Woodrill	0.39	0.00	0.00	0.00	0.00	0.00	--	--	0.00	0.00	--	--	0.00	0.00	--	--	0.00	0.00	--	--
Henry	0.28	0.01	0.00	0.00	0.00	0.00	--	--	0.07	0.00	1.98	2.96	0.01	0.00	0.00	0.00	0.03	0.00	0.00	0.00
Schmidt	0.33	0.02	0.00	0.00	0.07	0.00	0.00	0.00	0.25	0.01	4.00	3.25	0.09	0.01	--	--	0.07	0.00	0.00	0.00
Nerstrand	0.18	0.01	0.00	0.00	1.80	0.04	3.06	1.09	0.15	0.00	1.27	1.28	0.00	0.00	--	--	0.09	0.00	1.94	2.11
River Bend	0.23	0.01	0.37	0.47	2.23	0.08	4.91	2.53	0.003	0.00	--	--	0.00	0.00	--	--	0.04	0.00	8.34	9.02
Riley Creek	0.55	0.02	1.83	1.99	0.03	0.00	--	--	0.02	0.00	--	--	0.00	0.00	--	--	0.02	0.00	0.00	0.00
Trout Lily	0.30	0.00	0.00	0.00	0.00	0.00	--	--	0.00	0.00	--	--	0.01	0.00	--	--	0.08	0.00	0.00	0.00
Townsend	0.04	0.00	0.00	0.00	0.00	0.00	--	--	0.71	0.02	0.51	0.51	0.06	0.00	6.45	7.10	0.05	0.00	0.00	0.00
Taylors	0.03	0.00	0.00	0.00	0.01	0.00	--	--	0.11	0.00	1.82	1.39	0.03	0.00	0.00	0.00	0.04	0.00	14.38	12.62
Wolsfeld	1.07	0.02	0.31	0.29	0.01	0.00	--	--	0.01	0.00	--	--	0.01	0.00	--	--	0.01	0.00	--	--

	Smilacina racemosa				*Smilax cf. ecirrata*				*Trillium spp.*				*Uvularia grandiflora*			
	Stems/m^2		% Grazed		Stems/m^2		% Grazed		Stems/m^2		% Grazed		Stems/m^2		% Grazed	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
7mile	0.14	0.01	1.07	1.30	0.04	0.01	4.21	4.28	0.07	0.00	5.28	5.90	0.21	0.05	0.98	0.99
Cannon River	0.04	0.00	0.00	0.00	0.03	0.01	5.34	5.52	0.04	0.00	0.00	0.00	0.12	0.03	0.00	0.00
Woodrill	0.06	0.00	1.16	1.12	0.00	0.00	--	--	0.00	0.00	--	--	0.01	0.00	0.00	0.00
Henry	0.04	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.14	0.01	0.00	0.00	0.02	0.01	3.85	4.57
Schmidt	0.22	0.01	0.00	0.00	0.02	0.01	0.00	0.00	0.02	0.00	0.00	0.00	0.13	0.04	12.17	8.77
Nerstrand	0.06	0.00	3.18	2.39	0.06	0.01	8.51	4.71	0.11	0.01	5.60	4.76	0.39	0.07	6.24	2.36
River Bend	0.03	0.00	12.04	7.28	0.01	0.01	26.35	17.40	0.00	0.00	--	--	0.00	0.00	--	--
Riley Creek	0.04	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	--	--	0.05	0.02	7.00	4.07
Trout Lily	0.01	0.00	--	--	0.01	0.00	0.00	0.00	0.01	0.00	--	--	0.00	0.00	--	--
Townsend	0.05	0.00	0.00	0.00	0.03	0.01	0.00	0.00	0.02	0.00	--	--	0.05	0.02	0.00	0.00
Taylors	0.07	0.00	1.16	1.64	0.02	0.01	11.20	8.84	0.31	0.01	4.19	2.35	0.25	0.07	5.72	2.41
Wolsfeld	0.03	0.00	--	--	0.00	0.00	--	--	0.01	0.00	--	--	0.00	0.00	--	--

APPENDIX D. EFFECTS OF DEER AND DEER MANAGEMENT ON TRILLIUM SPP. IN NERSTRAND BIG WOODS STATE PARK

INTRODUCTION AND METHODS

This study used a 7-year deer exclosure, located at Nerstrand Big Woods State Park, to examine changes in *Trillium* population structure. In addition, a hunt conducted at this site between 1995 and 1996 enabled us to examine changes in deer grazing intensity on *Trillium* in response to management. While both the exclosure and the deer hunt represent unreplicated experiments, they provide useful information on deer management and *Trillium* populations for comparison to the results in Chapter 2.

In 1989, a 10x10 m deer exclosure was constructed at Nerstrand Big Woods State Park, Minnesota, in a stand of second growth maple basswood forest (Parcel 8, Section 9 from Mason(1994)). The stand was clear cut between 1937 and 1940 and experienced occasional grazing by sheep until 1945 (Mason, 1994). The current canopy layer is dominated by 20-40 cm dbh trees composed primarily of northern red oak, sugar maple, bitternut hickory, and black ash.

No plant measurements were taken in the exclosure in 1989. In June, 1995, I established two l0x10m control plots adjacent to the north and south sides of the exclosure. *Trillium* in plots included *T. cernuum* and *T. flexipes*; these two species were considered as a single *T. cernuum flexipes* complex. Control plots and the exclosure were divided into a grid of 1001 m^2 plots and stem height, length and width of one randomly selected leaf, deer grazing, other herbivore damage, and reproductive status of one *Trillium* in each plot where the species occurred were recorded on 16-18 June, 1995, and 17-18 June, 1996. No leaf size measurements could be recorded for grazed plants.

To provide a local estimate of deer density, aerial count data provided by Jeanine Vorland (MNDNR) were converted to the number of deer/ km^2 of permanent winter cover as described in Chapter 5. In the fall of 1995, a special deer hunt was held by the state park. The change in grazing intensity on *Trillium* spp. between 1995 and 1996 was therefore analyzed to test whether the reduction in deer density had a measurable effect on this plant population.

RESULTS

No measurements of the understory forb community were taken inside or outside the exclosure at the time of construction in 1989. *Trillium* typically have a patchy distribution on large spatial scales (>50m radius patches); the controls and exclosure are located within a single large *Trillium* patch in the understory, and I assume that population structure within this patch was similar inside and outside at the time of construction. In both 1995 and 1996, the distribution of plant sizes within the unprotected sample contained a significantly greater frequency of smaller plants compared to the exclosure sample (Kolmogorov-Smirnov test statistic=0.36, P=0.0001). Between 1995 and 1996, the relative frequency of large plants in the exclosure population increased significantly (K-S statistic=0.29, P=0.007), while the relative frequency of large plants in the unprotected population increased to a lesser degree (K-S statistic=0.26, 1995>1996: p=0.13) (Fig. 1). In the 1995 growing season, following the highest overwinter deer count in the past 6 years, 29.4% of the unprotected *Trillium* sample was grazed. J, Following a deer hunt within the park in the fall of 1995, grazing intensity on *Trillium* in 1996 declined significantly to 7.6% (X^2=16.1, p=0.0001). From 1995 to 1996, late June flowering rates in the unprotected sample increased from 6.5% to 15.1% (X2=3.66, P=0.056), while flowering rates in the exclosure increased to an even greater degree from 34.2% to 71.4% (X^2=19.1, P<0.0001). Mean stem height of ungrazed *Trillium* outside the exclosure showed no detectable change from 1995 to 1996 following the deer reduction (X =19.2 cm vs. X =19.0 cm, t=0.23, p=0.82).

After 7 years of protection from deer herbivory, *Trillium* density was marginally lower outside the exclosure (X =1.25 plants/m^2, N=200) versus inside the exclosure (X =1.61 plants/m^2, N=100) (Z = 1.18, p=0.24). Due to the variability in *Trillium* density on a scale of 1-2 m, the probability of detecting a 50% difference in density at the α=0.1 level was 0.83.

These results show that 1) deer reductions can have measurable effect on the plant community by reducing grazing intensity on palatable species and consequently allowing higher reproductive rates, and 2) cumulative effects of grazing over many years has a significant effect on *Trillium* population size structure. The results are consistent with those presented in Chapter 2, and again support the conclusion that deer management must be a consideration in the conservation of fragmented forest plant communities. The fact that *Trillium* occur outside the exclosure at a relatively high density (1.25/m^2) suggests that the species tray persist with low moderate deer densities, but long term monitoring or demographic modeling is necessary to determine whether current levels of grazing are causing a slow, long term decline in the population.

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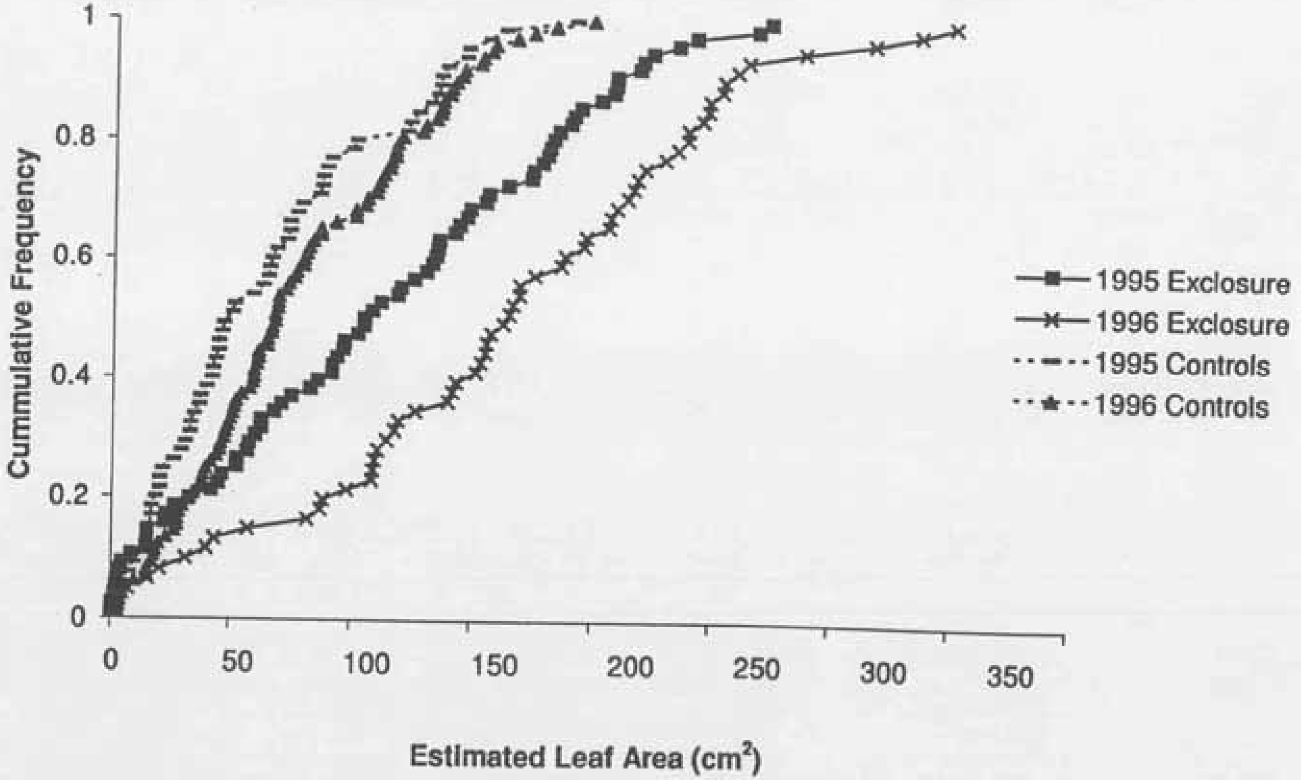

Figure 1. Cumulative frequency distribution of *Trillium* plant sizes inside and outside a 7-year exclosure at Nerstrand Big Woods State Park. Plant size is an estimate of total leaf area based on leaf measurements, and distributions only include ungrazed plants.

APPENDIX E. SIZE STRUCTURE, GRAZING BY WHITE TAILED DEER, AND POLLINATION RATES FOR A YELLOW LADY SLIPPER, *Cyrpripedium calceolus pubescens*, POPULATION

INTRODUCTION and METHODS

I examined intensity of grazing by white tailed deer for a population of *Cypripedium calceolus* pubescens at Nerstrand Big Woods State Park in southeastern Minnesota because discussion with the park manager, surveys of other forests in upper Great Lakes region (Cottam and Curds 1956, Alverson et al. 1988), and a survey of park managers throughout the eastern United States (Miller et al. 1992) suggested that deer herbivory may be an important factor impacting this species. I also monitored flowering and pollination rates because *Cypripedium* spp. cannot be self pollinated (Stoutamire 1967), and hence pollinators have the potential to limit seed set rates.

During June and August, 1994, and May, 1995, extensive understory searches were conducted in the south eastern quarter of section 9 in the state park to find *C. calceolus pubescens* individuals. When one or more plants were found, a permanent PVC stake was place in the center of the group, and the area within a 5 m radius of the stake was carefully searched by two independent observers. If >10 stems were found, then a 10 m radius was searched. All stems were individually marked with a numbered aluminum tag. In 1994, five distinct patches of plants containing 87 stems were marked, and after the 1995 surveys, a total of 18 distinct patches containing 235 stems were marked In 1996, the same 18 patches were monitored, and newly found stems increased the sample to 258. Plants were located in parcels 11, 20, 21, 22, and 24 (Mason 1994) in second growth forest dominated by sugar maple (*Acer saccharum*), red oak (*Quercus rubra*), white oak (*Quercus alba*), basswood (*Tilia americana*), elm (*Ulmus* spp.) and ironwood (*0styra virginiana*). Plants occurred within both a closed canopy, understory environment and in canopy openings in dense patches of sugar maple and prickly ash (*Zanthoxylum americanum*) saplings.

In 1994, I recorded grazing by deer, flowering status, and whether or not stems were developing a fruit. In 1995 and 1996, all marked plants were surveyed in late May (pre-anthesis) to record flowering status and any herbivore damage, and then were revisited in late June (Post-anthesis) to record any herbivore damage, whether or not flowering plants were developing a fruit, and stem height of ungrazed plants. When deer graze a plant, the upper 2-5 leaves and the flower (if present) are usually removed, and 1 or more leaves may remain at the stem base. For several large plants, deer stripped all leaves from the stem in the same way that deer remove foliage from woody plants. Other herbivore damage included feeding on the stem base by lepidopteran larvae, which occasionally severed the stem.

RESULTS

In all three years, low grazing rates by white tailed deer were observed (Table 1). In 1995, grazing was higher for flowering compared to non flowering plants, but in 1996, grazing intensity was similar for flowering and non-flowering plants. The highest flowering, pollination, and grazing rates were all observed in 1994 (Table 1). Data analyzed for marked plants which were surveyed in all 3 years showed the same patterns, indicating that differences between 1994 and 1995-96 were not simply due to the increased number of plants surveyed. Grazing intensity appeared to be unrelated to winter deer density (Table 1). Flowering rates in late June varied from 14-50% per year. Flowering rates reported for five *C. calceolus* populations in coniferous forests in eastern Europe were consistently higher, but were also highly variable, ranging from 25-78% over a six year period (Kull and Kull 1991). Pollination rates were extremely low in 1995 and 1996 (Table 1) compared to pollination rates of 11-33% reported by Kull and Kull (1991), suggesting that pollinators could have a limiting effect on the population. However, pollination rates are characteristically low for *Cypripedium* spp. since they do not offer an energetic reward to pollinators, such that pollination could vary widely between years.

The population contained a similar number of plants in the middle, non flowering height classes (11-25 cm) as the larger, sexually reproductive height classes (≥26 cm), and few small plants (Fig. 1). This structure suggests that seedling recruitment occurs at low rates or episodically, with high survivorship of larger plants, consistent with Curtis' (1943) description of highly specific germination and growth requirements for *Cypripedium* spp. Individuals of *C. calceolus* may be extremely long lived (at least 26 years, Kull and Kull (1991)), but longer term studies have not been conducted No mortality of marked stems was observed during this study. The population size distribution presented here provides a baseline for future comparison to other populations. Observed grazing intensities in this study suggest that deer at current densities in the state park have minimal impacts on *Cypripedium calceolus pubescens*.

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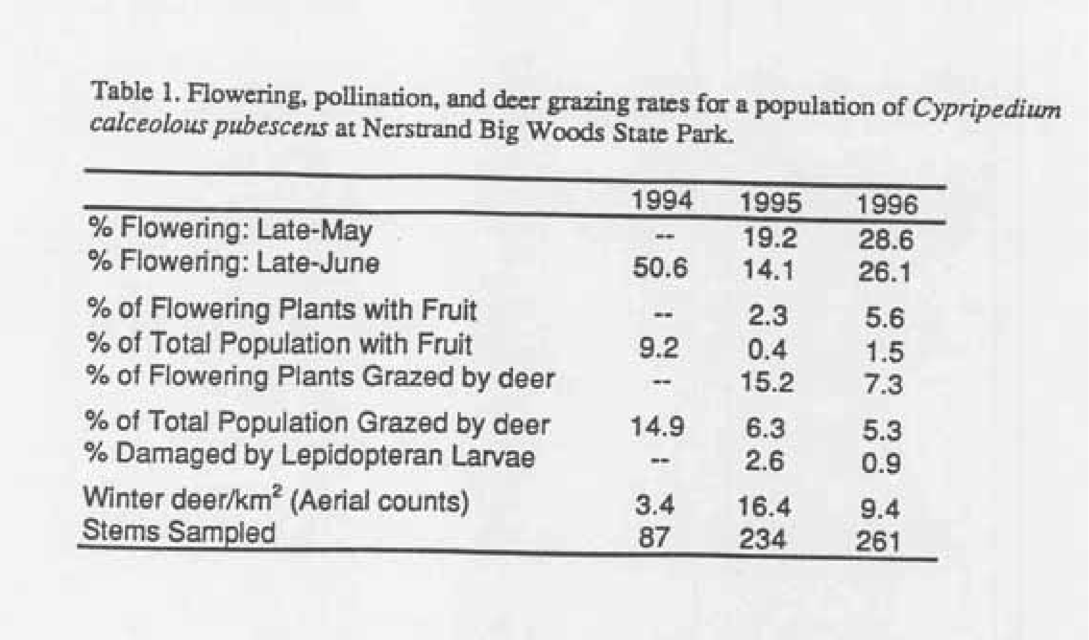

Table 1. Flowering, pollination, and deer grazing rates for a population of *Cypripedium calceolous pubescens* at Nerstrand Big Woods State Park.

	1994	1995	1996
% Flowering: Late-May	--	19.2	28.6
% Flowering: Late-June	50.6	14.1	26.1
% of Flowering Plants with Fruit	--	2.3	5.6
% of Total Population with Fruit	9.2	0.4	1.5
% of Flowering Plants Grazed by deer	--	15.2	7.3
% of Total Population Grazed by deer	14.9	6.3	5.3
% Damaged by Lepidopteran Larvae	--	2.6	0.9
Winter deer/km^2 (Aerial counts)	3.4	16.4	9.4
Stems Sampled	87	234	261

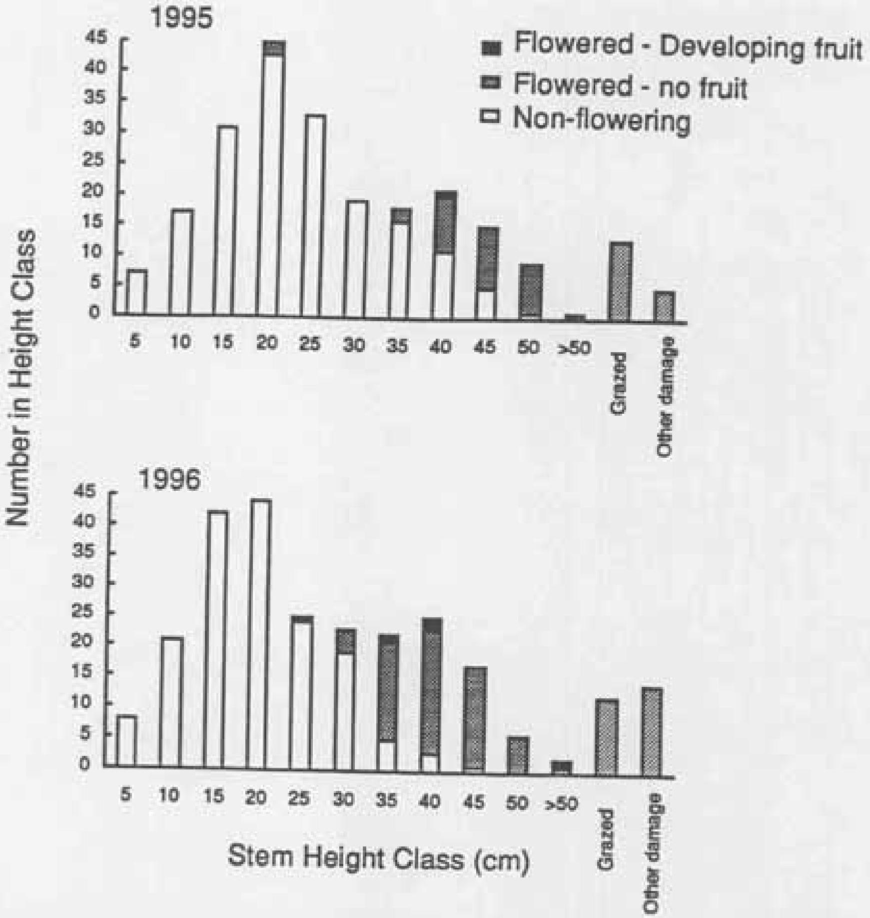

Figure 1. Size structure of a *Cypripedium calceolus pubescens* population at Nerstrand Big Woods State Park. Grazed plants had the upper 2-5 leaves removed by white-tailed deer, and most "other damage" was damage to the stem base caused by lepidopteran larvae.

APPENDIX F. COMMON NAMES OF PLANT SPECIES

Table 1. Common names of herbaceous plant species in this thesis

Scientific Name	Common Name
Adiantum pedatum	Maiden hair fern
Allium tricoccum	Wild leek
Amphicarpa bracteata	Hog peanut
Anemone quinquefolia	Wood anemone
Aplectrum hyemale	Putty root
Arabis sp.	Rock cress
Arisaema triphyllum	Jack-in-the-Pulpit
Asarum canadense	Wild ginger
Athyrium filix-femina	Lady fern
Cardamine concatenata	Cut-leaved toothwort
Carex spp.	Sedges
Caulophyllum thalictroides	Blue cohosh
Circaea lutetiana	Enchanter's nightshade
Claytonia virginica	Spring beauty
Cryptotaenia canadensis	Honewort
Cyrpripedium calceolus pubescens	Large yellow lady slipper
Dicentra cucullaria	Dutchman's breeches
Erythronium spp.	Trout lily
Eupatorium rugosum	White snakeroot
Galium spp.	Bedstraw
Geranium maculatum	Wild geranium
Geum canadense	White avens
Hackelia virginiana	Stickseed
Hepatica acutiloba	Hepatica
Hesperis matronalis	Sweet rocket
Hydrophyllum virginianum	Virginia waterleaf
Impatiens cf. pallida	Jewelweed
Isopyrum biternatum	False rue anemone
Laportea canadensis	Wood nettle
Osmorhiza spp.	Sweet cicily
Phlox divaricata	Wild blue phlox
Phryma leptostachya	Lopseed
Poaceae	Grasses
Polygonatum biflorum	Solomon's seal
Sanguinaria canadensis	Bloodroot
Sanicula spp.	Sanicle/black snakeroot
Smilacina racemosa	False solomon's seal
Smilax ecirrata	Carrion flower
Solidago flexicaulis	Zig-zag goldonrod
Thalictrum dioicum	Early meadowrue
Trillium spp.	Trillium
Uvularia grandiflora	Large-flowered bellwort
Viola pubescens	Yellow forest violet
Viola sororia	Dooryard violet