EVIDENCE FOR TWO ALTERNATE STABLE STATES IN AN UNGULATE GRAZING SYSTEM

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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 alternate stable states can exist in plant–herbivore systems. We 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 alternate stable states that 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 nonmonotonic relationship between plants and herbivores has direct implications for the conservation and restoration of plant species in systems where herbivores can be managed.

Key words: alternate stable states; fragmented forests; functional response; grazing system stability; Laportea canadensis; maple–basswood forest; Minnesota, southeastern; Odocoileus virginianus; ungulate management; white-tailed deer.

INTRODUCTION

Following Rosenzweig and MacArthur’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 forage availability. Under certain conditions, the stability of plant–herbivore equilibria depends upon both herbivore density and plant abundance such that two alternate 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 only 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 (Graham 1952, Anderson and Loucks 1979, Frelich and Lorimer 1985, Tilghman 1989, Anderson and Katz 1993). However, testing the alternate-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 alternate-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 into a system’s underlying behavior. Plant growth may be described quite simply for species such as forbs, which do not grow beyond the reach of ungulate herbivores. In the simplest form of the Noy-Meir
Fig. 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 \( (K_p) \), where herbivores limit plant density, is possible for both consumption functions. Depending on the steepness of the Type II curve and intrinsic growth rate of the vegetation, an unstable equilibrium is possible \( (B_{II}) \) such that initial plant densities below this level lead to plant extirpation. 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 \( K_s \), where the herbivore is regulating plant abundance. Adapted from Schmitz and Sinclair (1997).

(1975) model, changes in plant abundance are described by

\[
\frac{dV}{dt} = G(V) - c(V)H
\]

where \( V \) = plant abundance, \( G(V) = rV(1-V/K) \) 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 (Holling 1966, Hassell 1978), which predict a wide range of different plant–herbivore equilibria, are the Type II functional response described by

\[
c(V) = cV/(1 + chV)
\]

and the Type III functional response described by

\[
c(V) = V^2/(1 + chV^2).
\]

Following Schmitz and Sinclair (1997), equilibria for Eq. 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 equilibrium occurs at \( K_s \) in Fig. 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 \(<B_{II}\). This case is not biologically trivial if the herbivores have an alternate 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, \( K_s \) and \( K_r \) represent two alternate stable equilibria, while \( B_{III} \) represents an unstable breakpoint where the system undergoes a switch in the stable equilibrium to which it will return following a perturbation.

Testing the predictions of the Noy-Meir (1975) model in the field involves measuring (1) the shape of the herbivore’s functional response at an appropriate spatial scale, and (2) the effect of herbivores on plant density 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 were again allowed to increase, they would no longer be able to regulate plant density.

The potential for alternate stable states to exist as a result of herbivory has clear implications for the management of plant communities where herbivore populations are largely under human control. If the hypothesis is correct, then (1) herbivore impacts to plant species will be most severe where these plants are rare, (2) management of the herbivore population over time can create a state where both the target plant species and herbivores are abundant, and (3) small changes in herbivore density where they are extremely abundant can cause a sudden, dramatic crash in the plant population. None of these dynamics are expected to occur if a monotonic relationship exists between herbivore and plant abundance. Therefore, management decisions concerning both threatened species conservation and plant production (e.g., forest regeneration for timber production) that are based on the assumption of a monotonic relationship may not achieve desired goals or attain the system’s maximum productive potential.

We examined the nature of the relationship between white-tailed deer and a dominant understory forb species, Laportea canadensis, in mature maple–basswood forests. The general objective of the study was to determine whether deer grazing is a reasonable explanation for the development of alternative communities (with and without a lush understory of Laportea), which has been observed among maple–basswood
stands in southeastern Minnesota. Specifically, we: (1) measured the functional response of deer to Laportea density by observing the proportion of stems grazed among stands with varying combinations of Laportea abundance and indices of deer density; (2) conducted exclosure experiments with paired controls to see if trends in Laportea abundance are consistent with predictions of the Noy-Meir (1975) model given the observed functional response; and (3) developed a simple simulation to illustrate how Laportea abundance could change over time, depending on grazing rate and initial plant abundance. Note that development of plant and deer density guidelines for use by forest managers would require very intensive sampling that was beyond the scope of this study. However, we do believe that this study demonstrates the types of data and procedures one would need to develop such guidelines for a given region.

Although conservation of Laportea is not a major concern, the dynamics of this relatively abundant species may provide insight into how deer affect other species of conservation concern (e.g., Miller et al. 1992, Balgooyen and Waller 1995, Waller and Alverson 1997). Equally important is the conservation of a rare community—old-growth maple–basswood forests—within which deer have the potential to change community dynamics by reducing or eliminating species of major importance such as Laportea.

Study System

The study took place on three counties in southeastern Minnesota; Rice County (44°15’ N, 93°20’ W), Hennepin County (45° N, 93°30’ W), and Wright County (45°10’ N, 93°50’ W). The landscape comprises small remnant old-growth forest stands embedded in a mosaic of agricultural crops, pastures and old fields, wetlands, second-growth forests, and residential developments. The local agricultural crops are corn (Zea mays), soybeans (Glycine max), and alfalfa (Medicago sativa). The region experiences a continental, cold-tomperate humid climate with warm summers and cold winters.

This study area was searched for stands (study sites) with the following characteristics. First, each site had old-growth forest with 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). Oaks (Quercus rubra and Q. alba) were also canopy members, and ironwood (Ostrya virginiana) was an important subcanopy species. Second, sites contain loamy soils developed from glacial deposits or silty soils developed from loess-covered glacial till (Grimm 1984). Third, all study sites were a minimum of 5 km apart and are therefore considered independent of each other with regard to growing-season deer herbivory and plant growth. Eleven study sites were found that met these criteria. Surveys of understory vegetation were conducted, and indices of deer populations were developed at all 11 study sites to obtain information on the functional response of deer to Laportea abundance (objective 1). The exclosure experiments necessary to shed light on objective 2 were conducted at five of the 11 sites, selected to include two with relatively high local deer densities and three with relatively low deer densities. Details of these experiments are given in the Methods.

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 may be important in areas of high deer density. During the growing-season, deer in these landscapes consume primarily agricultural crops (Nixon et al. 1991, personal observations). Deer also consume forest forbs during the growing season, concentrating on a few highly preferred forb species (Augustine 1997). The extremely high productivity of deer populations in the midwestern United States (Harder 1980) is attributed to the availability of crops such as corn, soybeans, and alfalfa (Murphy 1970, Nixon et al. 1991), so 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 ability.

In many remnant maple–basswood stands, the wood nettle Laportea canadensis is the dominant mid- to late summer understory forb species (Rogers 1981). Laportea is a clonal, perennial herb that commonly occurs in the understory of upland, mesic, deciduous forests in midwestern and northeastern North America (Menges 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 m 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 significantly greater degree than the overall understory community during mid- to late summer (Augustine 1997).

Methods

Measuring the functional response of deer to Laportea

The functional response could potentially be examined on the scale of a deer’s immediate environment when foraging (~1–10 m²), on the scale of entire forest
stands (5–30 ha), or at any intermediate level. Because Eq. 1 is a nonspatial model, selecting an appropriate spatial scale at which to measure the functional response of deer is critical for testing model predictions. We examined the functional response at the stand scale (i.e., the stand was the sampling unit) because old-growth maple–basswood forests exist as isolated fragments in southern Minnesota and we were interested in the impact of deer on Laportea persistence within any given fragment. In other words, are deer contributing to the development of alternate communities among the 11 stands studied here?

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 each stand and an estimate of the number of deer responsible for this consumption.

The most efficient method for estimating deer density is the overwinter pellet count, which was done at all 11 study sites. Pellet counts were conducted immediately after snowmelt during 1–12 April 1996, in 45–50 plots at each study site. Although there is no doubt that these pellet count data provide an index of relative deer density among sites, one should confirm two things about this index. First, the index should be highly correlated with actual numbers of deer among sites. This was confirmed by aerial counts done during winter leaf-off conditions of high visibility at six of the 11 sites (Augustine 1997). Second, the winter deer density estimate should also provide an index of density during the growing season. Infrared camera monitors were used to measure growing-season density at four of the sites where enclosure experiments were conducted (Augustine 1997). There were three monitors placed randomly at each site. Monitors were moved to new random points every 7 d throughout the growing season. Deer density is expressed as number of deer photographed per week. Data from camera monitors, direct observations of deer during field work, and conversations with local wildlife managers indicated that winter density was closely correlated with summer deer density, except at one 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 winter pellet-group deer density estimates, and a separate analysis using only the four study sites with growing-season camera monitor deer density estimates was also done. If the functional response curve for the growing-season camera data is similar to that using the winter pellet counts, then the accuracy of the more widely available pellet data will be verified.

The abundance and proportion of grazed Laportea was sampled in each stand using uniformly spaced 6-m² plots in which the number of Laportea stems was counted. Each stem was recorded as being ungrazed, recently grazed, or old-grazed. When deer bite a plant, ~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 senescence and eventually falls off, leaving only a necrosis scar. Recently grazed stems were those with the bite point still present, while old-grazed stems were those with only a necrosis scar. The bite point typically falls off within 25–35 d, so recently grazed stems approximate a 30-d grazing rate. All sites were sampled during 3–14 August 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. The number of plots used at each site was based on surveys conducted in 1995. At one site where Laportea was extremely low in abundance, all known plants in the stand were censused 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) jackknife technique. For each study site, we calculated the proportion grazed per deer as (proportion of Laportea stems recently grazed)/(estimated deer density), where calculations were made both for winter deer density based on pellet-group counts (deer per square kilometer), and growing-season density based on photographic records (number of deer photographed per week).

Effects of deer herbivory on Laportea

Effects of deer herbivory on Laportea populations were tested by means of deer enclosure experiments. Four such experiments could potentially be carried out, involving the following conditions:

Expt. 1. Sites where deer density is relatively low for our region, but Laportea abundance is relatively high, in which case deer are assumed not to be regulating Laportea abundance and there should be no difference in Laportea growth inside and outside enclosures;

Expt. 2. Sites where deer density is high but Laportea abundance is very low, in which case deer are assumed under the Noy-Meir model to be regulating Laportea abundance and enclosures should show a dramatic impact on Laportea growth;

Expt. 3. Sites where deer density and Laportea abundance are both relatively high for our region, in which case deer are predicted under the Noy-Meir model not to dramatically reduce Laportea abundance, and there should be only limited impacts on growth between Laportea inside and outside enclosures;

Expt. 4. Sites where both deer density and Laportea
Table 1. Conditions at sites used in this 1994–1996 study of the relationship between white-tailed deer (*Odocoileus virginianus*) and the forest herb *Laportea canadensis* in old-growth forest stands in southeastern Minnesota.

<table>
<thead>
<tr>
<th>Expt.</th>
<th>No. of replicate enclosure</th>
<th>Summer deer density (photoc/wk)</th>
<th>Laportea, 1996 stand average</th>
<th>Laportea in 1996 control plots</th>
</tr>
</thead>
<tbody>
<tr>
<td>1, site 1</td>
<td>4</td>
<td>0.9 ± 0.6</td>
<td>19.1</td>
<td>2.4</td>
</tr>
<tr>
<td>1, sites 2 and 3</td>
<td>4</td>
<td>0.8 ± 0.7†</td>
<td>8.1</td>
<td>35.1</td>
</tr>
<tr>
<td>2</td>
<td>2 transplants, 2 natural</td>
<td>2.8 ± 1.1</td>
<td>0.03</td>
<td>83.7</td>
</tr>
<tr>
<td>3</td>
<td></td>
<td>4.1 ± 1.7</td>
<td>3.7</td>
<td>41.9</td>
</tr>
</tbody>
</table>

Note: Growing-season deer density is based on records of infrared camera monitors at each site (mean no. deer photographed/wk, with 95% CI).

† Density measured at site 2 only; *Laportea* data averaged for both sites.

Abundance are relatively low, in which case deer are assumed not to be regulating *Laportea* abundance, and there should be no significant differences in *Laportea* abundance between the inside and outside of exclosures. In practice, Expt. 4 could not be carried out because the low deer/low *Laportea* combination does not occur at any site in our study area.

To carry out the first three experiments, 13 exclosures were built, each 10 m² in area and paired with two adjacent control plots of equal size. The exclosures were capable of keeping out deer but not smaller herbivores such as lagomorphs and rodents. We used eight replicates (four at one study site and two at each of two other study sites) in Expt. 1, two replicates at one study site for Expt. 2, and three replicates at one study site for Expt. 3 (Table 1). In order to have exclosures and paired controls situated in essentially the same environmental setting at all study sites, all plots were established in areas of the forest with (1) a closed, homogenous overstory with the bases of most tree crowns 8 m above the forest floor, (2) overstory trees >50 cm dbh present, (3) sugar maple, elm, and basswood dominant in the overstory and oaks not dominant (relative basal area <0.30), and (4) an understory herbaceous community representative of the overall forest. At the site used for Expt. 2 (high deer density and low *Laportea* abundance), *Laportea* was not originally present in the enclosure–control sets due to its rarity in the understory. Therefore, in August 1994, 26 flowering *Laportea* plants were transplanted into each enclosure and one of its control plots. This transplant experiment should verify that growth of *Laportea* was not limited by some unknown environmental factor at the site. In addition, two smaller 1-m² exclosures, 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 enclosure–control sets under a uniform canopy.

Growing-season deer density estimates based on infrared camera monitors showed that the study sites used in Expts. 2 and 3, testing the effects of high deer density, contained densities 3–4 times greater than those used for Expt. 1, which tests whether low deer density can regulate *Laportea* abundance (Table 1).

The number and flowering status of all *Laportea* stems were recorded in exclosures and controls when plots were established in August 1994. The number and flowering status of *Laportea* stems were subsequently censused at all sites during 5–10 August in 1995, and 29 July–2 August in 1996. The relative rate of change in *Laportea* density for each enclosure and control plot was calculated as (number of stems in 1996)/ (number of stems in 1994).

Predicted trends in *Laportea* density

Trends in *Laportea* populations predicted by a discrete version of Eq. 1 were used in a simple simulation to illustrate how equilibrium *Laportea* abundance depends on both deer density and initial *Laportea* density (objective 3). The difference equation was parameterized using the fitted functional response curve based on the growing-season deer density index (photographs/week), 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/km² (based on pellet counts) showed an abruptly saturating Type II functional response to *Laportea* availability (c(V)/V = 0.24/(1 + 0.64V), r² = 0.91, Fig. 2A). When examined for the four sites where growing-season deer density was measured with camera monitors, the proportion of *Laportea* consumed per deer photographed/week showed a nearly identical Type II functional response curve (c(V)/V = 0.28/ (1 + 0.82V), r² = 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, r² = 0.02, P = 0.70).
**Fig. 2.** (A) The per-plant impact, measured as the proportion of available *Laportea* stems grazed per 10 overwintering deer/km², vs. *Laportea* availability for 11 forests in southeastern Minnesota with the fitted functional response curve \( c(V)/V = 0.24/(1 + 0.66V) \). (B) The per-plant impact, measured as the proportion of available *Laportea* stems grazed per deer photographed per week vs. *Laportea* availability for four forests with the fitted functional response curve \( c(V)/V = 0.26/(1 + 0.88V) \).

*Laportea* density varied from 0.01 to 19.1 stems/m² and the percentage grazed varied from 1.0% to 72.4% among sites. Overwinter deer densities varied from 0.7 to 33.4 deer/km². In addition to the differences in *Laportea* density between the two high-deer-density sites used for Expts. 2 and 3, there was a bimodal distribution of *Laportea* density among study sites with moderate deer densities (7–15 deer/km² in winter; \( n = 5 \) sites). Two sites contained <0.1 stems/m² averaged over the entire stand, no sites contained 0.1–1.0 stems/m², and 3 sites contained >1 stem/m². All study sites with low deer density (<7/km²) contained >1 *Laportea* stem/m².

**Effects of deer on *Laportea* populations**

Exclusion Expt. 1, conducted at low-deer-density sites, showed that deer had no detectable effects on trends in either *Laportea* density or percentage flowering during the period monitored (Fig. 3). No difference in the finite rate of change in *Laportea* density over the 2-yr period was detected (mean \( \lambda = 1.78 \) inside exclosures vs. \( \lambda = 1.80 \) outside exclosures, paired \( t \) test, \( t = 0.08, P = 0.93 \)). No significant effects of deer exclusion on changes in the proportion of stems flowering between the beginning and the end of the experiment were detected (repeated-measures ANOVA, df = 1, \( P = 0.97 \)).

In Expt. 2, where *Laportea* availability within the stand is extremely low and deer density is high, the transplant experiment showed that deer herbivory is 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. 4A). For the exclosures and controls with natural *Laportea*, differences in density were not as great (Fig. 4A), 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 high. The most significant differences were in percentage flowering, which showed a mean of 40.1% for both natural and transplanted *Laportea* in exclosures, and either remained at 0% (natural) or declined from 100% to 0% (transplants) in unprotected plots (Fig. 5A).

In Expt. 3, where *Laportea* occurs at much higher...
abundance, deer exerted less severe impacts on *Laportea* growth and reproduction compared to Expt. 2. A greater finite rate of increase in density was observed for unprotected than protected plants in two of the replicate exclosure–control pairs, and similar rates of increase were observed in a third replicate (Fig. 4B). Exclosures and controls contained a similar proportion of flowering plants in the year when plots were first censused (mean = 28.4% vs. 28.2%). The percentage of stems flowering was consistently higher in exclosures than control plots at the end of the experiment (mean = 66.7% vs. 35.5%, Fig. 5B), but percentage flowering in control plots was still similar to percentage flowering at low-deer-density sites (Table 1).

While control plots represent only a small fraction of the area experiencing grazing pressure within a stand, the percentage of *Laportea* stems flowering and the intensity of grazing by deer recorded in control plots at each study site were similar to estimates for the entire forest stand based on the systematic plot sampling (Table 1).

A consistent trend of increasing *Laportea* density throughout the study period and a large increase in percentage flowering between 1994 and 1995 were observed at all low-deer-density sites (Fig. 3B) and at the high-deer-density site for Expt. 3 (Fig. 5B), suggesting that growing conditions over the region were unusually favorable for *Laportea* in 1995. Growing conditions in 1995 included above average temperatures and precipitation (U.S. Department of Commerce 1995), high humidity during June and July, and an early spring snowmelt.

**Predicted trends in *Laportea* density**

Given the Type II functional response of deer to *Laportea* availability, a discrete version of Eq. 1 as applied to *Laportea* is given by

\[ V_{t+1} = V_t \times \left( \exp \left( 1 - \frac{K}{V} \right) - \frac{cH}{1 + cV} \right) \]  

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 index of summer deer density (Fig. 2A), \( H \) is in units of deer photographed/week.

Predicted changes in *Laportea* density over time illustrate that the population can increase to a high-density equilibrium for all initial *Laportea* densities when deer density is on the order of two individuals pho-
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 forests forage selectively on understory forbs (Augustine 1997). As a result, where Laportaea availability is low, a high proportion of the available stems are consumed by deer, but where Laportaea is abundant, the same absolute amount of consumption results in a much lower overall proportion of the forb population being grazed.

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 single 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 Laportaea abundance were undetectable in enclosure Expt. 1, at sites with low deer density. These sites all contained abundant Laportaea. The combination of low deer with low Laportaea density did not occur in any surveyed forests, and hence could not be examined. Whether low deer densities can lead to Laportaea extirpation for extremely low initial Laportaea abundance was therefore not tested, but the absence of such stands and the shape of the fitted functional response curve indicate that only a single stable equilibrium occurs with low deer densities (Fig. 6A). The opposite situation, in which deer at high density can drive Laportaea to extinction for all initial Laportaea 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 Laportaea 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 Laportaea to extinction for all initial plant densities.

Results from Expts. 2 and 3, with high deer density, support the prediction that two alternate states are possible for a given deer density. At the site where Laportaea 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 this site is that high deer densities only developed recently; aerial counts conducted over the past 8 yr show that the current level of deer population resulted from a rapid increase between 1989 and 1993 (J. Vorland, personal communication). The documented grazing intensity 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 yr (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. Combined with the bimodal distribution of Laportea density among study sites with moderate deer density, these results support the Noy-Meir (1975) hypothesis that two stable ecosystem states are possible depending both on herbivore density and initial plant density (Fig. 6B, C).

Central assumptions that must be considered in applying the Noy-Meir model include the continuous logistic function used to describe plant growth, the presence of only one herbivore and one plant species, and constant plant growth conditions and herbivore density over time. The former two assumptions appear to be met in this system where clonally reproducing Laportea populations have minimal age and size structure, and deer are the only large, mammalian herbivore. Differences in environmental conditions among years appeared to affect Laportea growth, and these changes could cause the exact plant density at which the plant–herbivore system switches to a new equilibrium to vary over time. In this study, Laportea density at the two high-deer-density sites differed by two orders of magnitude (0.03 vs. 3.7 stems/m²) such that the unstable system breakpoint could vary across a wide range of plant densities and still be detected, but exact predictions of this breakpoint are not possible. In addition, factors that 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. 6).

Perturbations and stable states

The previous discussion indicates that two different stable plant–herbivore equilibria determined by initial plant density are possible when deer occur at high densities. 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 ~7000-km² region of contiguous maple–basswood forest that existed prior to European settlement (Daubenmire 1936, Grimm 1984). The patchy distribution of Laportea within the forest and its limited dispersal ability, combined with the extreme degree of fragmentation that occurred following European settlement in the late 1800s, leaving stands on the order of 5–32 ha (Vasilevsky and Hackett 1980), could by chance result in a proportion of forest fragments containing low Laportea density. In addition, many forest fragments currently protected in parks and reserves were grazed by domestic livestock several decades ago. This was true for the site of Expt. 2 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 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. 6B, 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 a low initial density. For example, transplanting 5000 individuals to a 15-ha forest stand would still yield a density (0.03 stems/m²) of the order where high deer densities are predicted to eliminate Laportea (Fig. 6B, C). A temporary deer reduction to permit the transplants to increase in density might therefore result in a successful restoration.

In addition, our results suggest that appropriate ungulate population densities will differ among protected areas depending on the abundance of plant species of management concern. Given that white-tailed deer may be exerting geographically widespread effects on palatable understory species (Miller et al. 1992, Balgooyen and Waller 1995, Waller and Alves 1997), where such species occur at low density they may be under greatest threat of extirpation due to herbivory. However, if deer can be reduced until populations recover above a threshold density at which their consumption by deer is saturated, then intensive deer population regulation may no longer be necessary. These results must be extended with caution to other species since Laportea persistence under
relatively high deer densities may be in part due to its capacity for regrowth after tissue loss. Slow-growing, long-lived plant species may therefore have a much higher threshold density at which deer no longer suppress population growth.

While our results do not prove the alternate-stable-states hypothesis, they are clearly inconsistent with a monotonic relationship between herbivore and plant abundance. This suggests that greater attention needs to be paid to the alternate-stable-states hypothesis through both adaptive management strategies in parks and preserves (Lancia et al. 1996) and through carefully controlled research designs that involve more than simply excluding herbivores and documenting changes in the plant community. Recognizing this potential for relationships between plants and managed herbivores such as deer that are not monotonic can subsequently improve the success of management efforts that involve manipulations of plant and herbivore populations.

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