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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 enclosure 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 enclosure experiments, produced two alternate stable states that depended on initial forb abundance. Enclosure 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, Frellich and Lorimer 1985, Tilghman 1989, Anderson and Katz 1993). However, testing the alternate-stable-states hypothesis requires either a comparison of enclosure 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 enclosure 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.

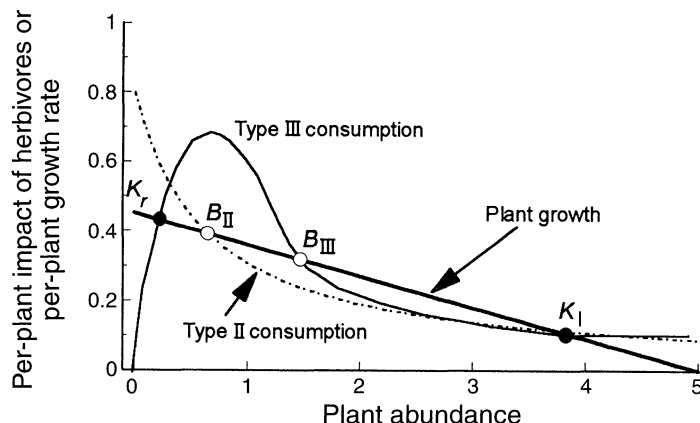
These recent analyses suggest that the original model presented by Noy-Meir (1975), which assumes a drastic simplification of the real-world complexities inherent in plant–herbivore systems, can still provide useful insights into a system's underlying behavior. Plant growth may be described quite simply for species such as forbs, which do not grow beyond the reach of ungulate herbivores. In the simplest form of the Noy-Meir

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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_I , 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_r , where the herbivore is *regulating* plant abundance. Adapted from Schmitz and Sinclair (1997).



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

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

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

$$c(V) = cV/(1 + chV) \quad (2)$$

and the Type III functional response described by

$$c(V) = V^2/(1 + chV^2). \quad (3)$$

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_I 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_I 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 enclosure 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-temperate 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 one another 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 enclosure 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 enclosure 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 exclosure 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 senesces 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 exclosure 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 exclosures;

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 exclosures 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 exclosures;

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.

| | No. of replicate enclosure | Summer deer density (photos/wk) | <i>Laportea</i> , 1996 stand average | | | <i>Laportea</i> in 1996 control plots | |
|------------------------|-----------------------------|---------------------------------|--------------------------------------|----------|-------------|---------------------------------------|-------------|
| | | | Stems/m ² | % Grazed | % Flowering | % Grazed | % Flowering |
| Expt. 1, site 1 | 4 | 0.9 ± 0.6 | 19.1 | 3.4 | 35.1 | 2.4 | 32.1 |
| Expt. 1, sites 2 and 3 | 4 | 0.8 ± 0.7† | 8.1 | 1.6 | 38.3 | 0 | 42.6 |
| Expt. 2 | 2 transplants, 2 natural | 2.8 ± 1.1 | 0.03 | 72.4 | 0 | 83.7 | 0 |
| Expt. 3 | 3 | 4.1 ± 1.7 | 3.7 | 24.6 | 27.2 | 41.9 | 35.5 |

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 exclosure–control sets due to its rarity in the understory. Therefore, in August 1994, 26 flowering *Laportea* plants were transplanted into each exclosure 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 exclosure–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 finite rate of change in *Laportea* density for each exclosure 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 ($c(V)/V = 0.24/(1 + 0.64V)$, $r^2 = 0.91$, 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 ($c(V)/V = 0.28/(1 + 0.82V)$, $r^2 = 0.98$, 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, $r^2 = 0.02$, $P = 0.70$).

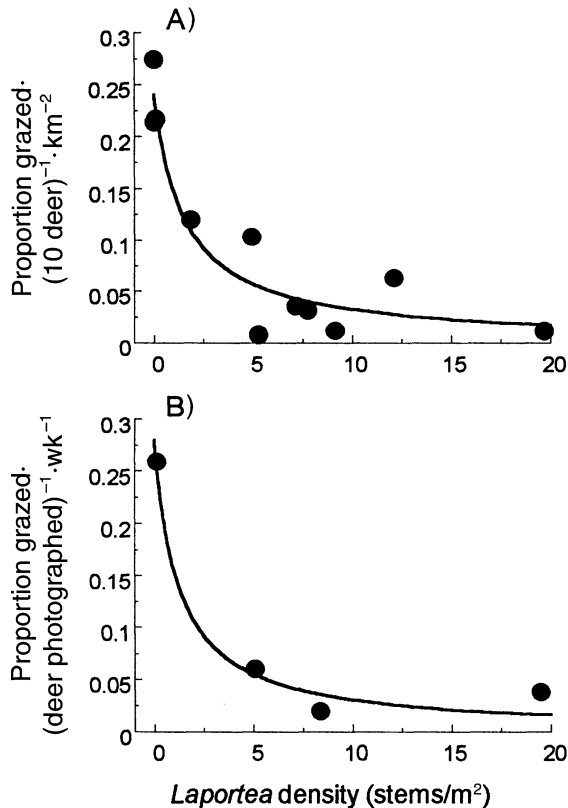


FIG. 2. (A) The per-plant impact, measured as the proportion of available *Laportea* stems grazed per 10 overwintering deer/km², vs. *Laportea* availability for 11 forests in southeastern Minnesota with the fitted functional response curve ($c(V)/V = 0.24/(1 + 0.66V)$). (B) The per-plant impact, measured 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; $n =$ five 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

Exclosure 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

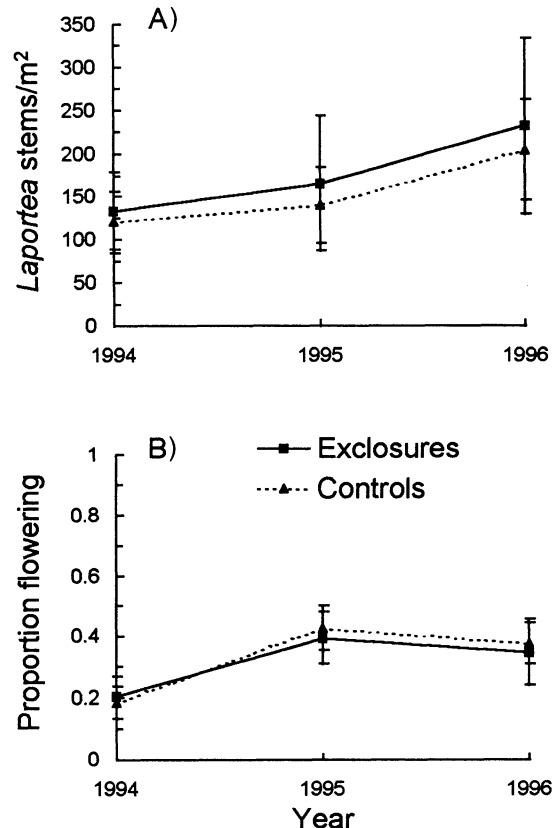


FIG. 3. Results of exclosure Expt. 1 (low deer density and high *Laportea* abundance). Average trends over a 3-yr period for (A) *Laportea* density and (B) percentage of *Laportea* stems flowering. Data show means and 95% confidence intervals.

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

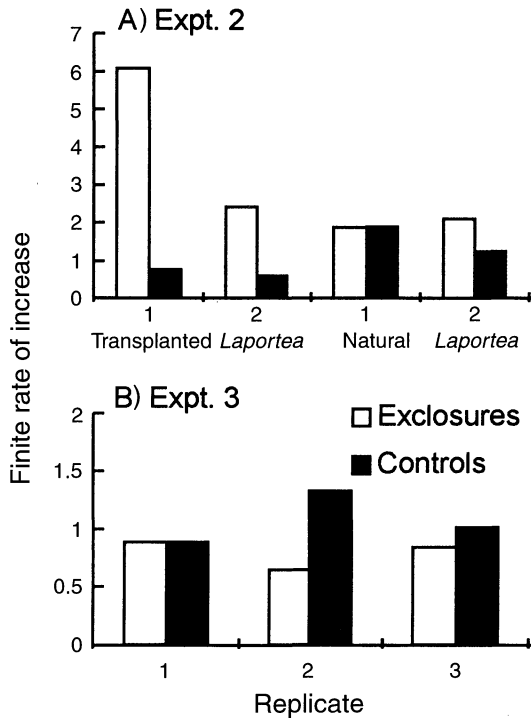


FIG. 4. The finite rate of increase in *Laporteia* density for enclosure experiments with high deer density. (A) High deer density and low *Laporteia* abundance (Expt. 2). (B) High deer density and high *Laporteia* abundance (Expt. 3). Rate of increase is calculated as (number of stems in 1996)/(number of stems in 1994).

abundance, deer exerted less severe impacts on *Laporteia* 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 enclosure–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 *Laporteia* 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 *Laporteia* 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

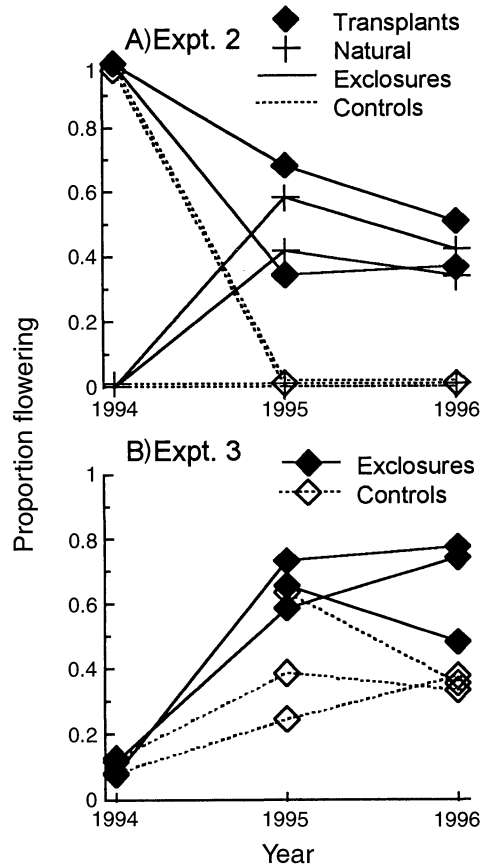


FIG. 5. Trends in the percentage of *Laporteia* stems flowering under high deer density. For Experiment 2, all transplanted individuals were flowering when planted in 1994, and “Natural” refers to exclosures and control plots with plants that occurred naturally at the site.

growing conditions over the region were unusually favorable for *Laporteia* 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 *Laporteia* density

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

$$V_{t+1} = V_t \times \left(\exp \left[r \left(1 - \frac{K}{V} \right) - \frac{cH}{1 + chV} \right] \right) \quad (4)$$

where V_t = *Laporteia* density in year t , $r = 0.72$, $K = 11$ stems/m², $c = 0.28$, 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 *Laporteia* density over time illustrate that the population can increase to a high-density equilibrium for all initial *Laporteia* densities when deer density is on the order of two individuals pho-

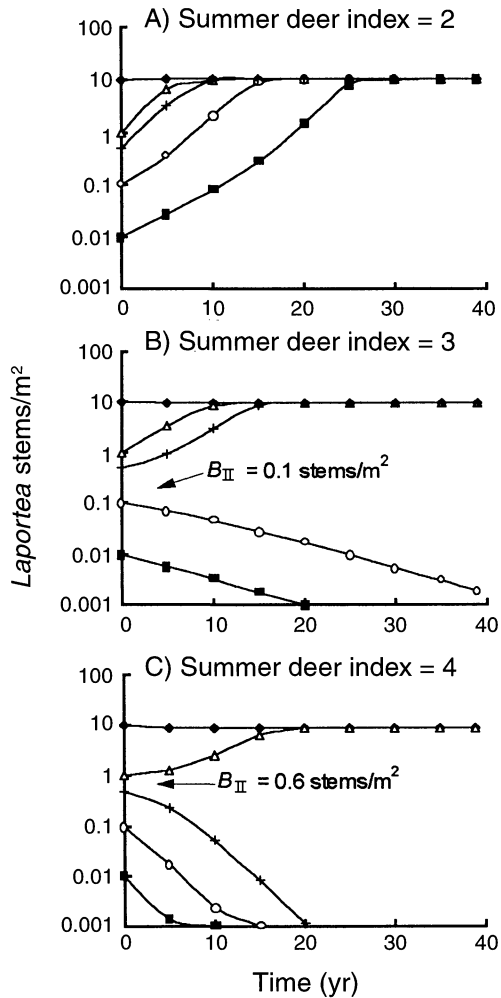


FIG. 6. Predicted changes in *Laportea* density over time based on Eq. 4 given different deer densities and initial *Laportea* densities. Deer density is assumed to remain constant over time. Note the logarithmic scale.

tographed per week (Fig. 6A). With an increased deer density (three deer photographed per week) initial *Laportea* densities >0.1 stems/m² can still increase to a high-density equilibrium but initial densities below this level lead to extirpation (Fig. 6B). With even higher deer density (four deer photographed per week), the predicted breakpoint shifts such that initial *Laportea* densities <0.6 stems/m² lead to extirpation (Fig. 6C).

DISCUSSION

When analyzed on the scale of a forest stand, deer grazing intensity 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 due to the availability of large patches of high quality forage such as soybeans, corn, and alfalfa 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 forests forage selectively on understory forbs (Augustine 1997). As a result, where *Laportea* availability is low, a high proportion of the available stems are consumed by deer, but where *Laportea* 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 *Laportea* abundance were undetectable in enclosure Expt. 1, at sites with low deer density. 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 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 *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 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 *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 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 stem/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 den-

sities. 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 preserves 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 Alverson 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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