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Effect of Herbivore Exclosure Caging on the Invasive Plant *Aliaria petiolata* in Three Southeastern New York Forests

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ABSTRACT. We examined effects of herbivore exclosures on non-native *Alliaria petiolata* (Bieb.) Cavara and Grande, and on the native herb layer, to determine if selective herbivory by mammals (particularly white-tailed deer) may facilitate *A. petiolata* invasion. The study was done from 1996 to 2000, in one urban forest without deer (New York Botanical Garden Forest), and two suburban forests (Kitchawan Preserve and Mt. Holly Sanctuary), both in a region with > 50 deer km^{-2}. Each forest had four pairs of 4-m^2 plots, with one of each pair caged to exclude deer. No significant differences developed in percent cover of native plants between uncaged and caged plots. At Mt. Holly, *A. petiolata* cover in caged plots averaged nearly twice its cover in uncaged plots, with a similar trend at Kitchawan but not at NYBG. Individual *A. petiolata* size in caged plots at Mt. Holly averaged more than three times that in uncaged plots. Herbivory on *A. petiolata* was 30 to 40 times more frequent in uncaged plots in both forests with deer, but only one plant showed herbivory at NYBG. We attribute *A. petiolata* cover and size differences between caged and uncaged plots to deer herbivory, noting that Mt. Holly appeared most heavily browsed. We suggest that interactions between deer and invasive species could change as densities of both increase, and that these interactions should be considered in forest management.

INTRODUCTION

Alliaria petiolata (Bieb.) Cavara and Grande (Brassicaceae), commonly known as garlic mustard, is one of the most important non-native herbaceous plants threatening native woodland plants in eastern deciduous forests of North America (McCarthy 1997; Nuzzo 1993a; Schwartz and Heim 1996; Yost et al. 1991). In southeastern New York, where this study was done, *A. petiolata* is a biennial, with germination and growth of a basal rosette of leaves in the first spring and summer, persistent foliage and some new growth throughout the winter, followed by further growth, flowering, and fruiting the subsequent spring and summer. It grows under closed forest canopy and along forest edges, and exhibits wide ecological amplitude for light levels and soil moisture, which may be due to high phenotypic plasticity (Byers and Quinn 1998; J. A. Morrison, unpublished data). *Alliaria petiolata* has been a component of the North American flora at least since it was first recorded on Long Island in 1868, and it has spread exponentially since then. It is now found throughout 30 northeastern states and southeastern Canada (Cavers et al. 1979; Nuzzo 1993b). It can spread

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rapidly once introduced to a site, with apparent displacement of native herbaceous species within ten years (Anderson et al. 1996, Nuzzo 1994).

Researchers focus mostly on attributes of the plant itself to understand why *A. petiolata* is invasive. Its high reproductive capacity, autogamy, and competitive ability, for example, have been addressed by various studies (Anderson et al. 1996; Baskin and Baskin 1992; Byers and Quinn 1998; Cavers et al. 1979; Cruden et al. 1996; McCarthy 1997; McCarthy and Hanson 1998; Nuzzo 1991, 1993a; Nuzzo et al. 1991; Yost et al. 1991). Underlying ecological changes that may promote its spread have received little attention, however, even though there is growing recognition of the need for broader ecosystem understanding for management of plant invasions (Hobbs and Humphries 1995).

One ecological factor that may be important in *A. petiolata* invasion, but has not been investigated experimentally in the field, is herbivory by mammals, particularly white-tailed deer (*Odocoileus virginianus* Zimmerman). White-tailed deer have increased dramatically since the early twentieth century in the successional, fragmented forests of the northeastern United States (Anderson 1997; McShea et al. 1997; Porter and Underwood 1999). For example, Knox (1997) estimates pre-colonial density of fewer than 4 deer km^{-2} in the eastern United States, in contrast with densities of 6 to 12 deer km^{-2} in much of Virginia by 1988. Alverson et al. (1988) suggest pre-colonial estimates of 4 deer km^{-2} in northern Wisconsin, compared with up to 9 deer km^{-2} in 1988. Deer density can be much greater in some areas. In northern Westchester County, New York, where we conducted part of our study, density is estimated at more than 50 deer km^{-2} (Glenn Cole, Regional Wildlife Manager, New York State Department of Environmental Conservation, Region 3, personal communication).

White-tailed deer at their current densities have become a keystone species, significantly altering the composition of forest ecosystems and leading to alternate stable states in many forests of eastern North America (Alverson and Waller 1997; DeCalesta 1997; Healy 1997; Schmitz and Sinclair 1997; Stromayer and Warren 1997; Waller and Alverson 1997). Deer herbivory can affect plant growth, fitness, and competitive ability of food plants, especially where deer densities are high due to a lack of natural predators, where active management increases deer populations, or where hunting is limited because of proximity to towns (McShea et al. 1997; Philips and Maun 1996). Selective herbivory by dense deer herds damages trees of certain species, potentially leading to long-term changes in forest composition (Horsley and Marquis 1983; Stewart and Burrows 1989; Strole and Anderson 1992; Tilghman 1989). In addition, deer eat more-palatable herbaceous flora (Williams et al. 2000), allowing less-palatable herb species to increase (Alverson et al. 1988; Waller and Alverson 1997).

Whether or not a plant species is eaten or avoided by selective herbivores like deer can be very important for its success, and can be considered a potential influence on the invasiveness of a species. Several studies suggest that deer avoid *A. petiolata* in favor of more palatable species, and it is tempting to attribute the invasiveness of *A. petiolata*, in part, to this selective herbivory (Anderson et al. 1996; Williams 1996). A lack of herbivory is often suggested as an explanation for why certain non-native species become invasive. This "enemy release hypothesis" (Keane and Crawley 2002) primarily concerns herbivory by insects and pathogens that specialize on a host plant in its native range and help to regulate its population size. When a host plant is introduced to a new region it is possible for these specialists to be left behind, resulting in plant population release, and invasiveness. The hypothesis also predicts that generalist herbivores will have greater effects on native rather than non-native plants, but there is no obvious reason why even selective generalists like

deer should avoid non-native species per se. Because food plant choice by deer is partly frequency-dependent (Brown and Doucet 1991), it is even plausible that deer may switch to an invasive species if it becomes very abundant while native species become scarce. Field experiments are needed to explore whether non-native species are avoided by generalist herbivores, and whether preference for native food plants is frequency-dependent.

We investigated how *A. petiolata* responded to protection from herbivory by comparing caged and uncaged plots of vegetation dominated by *A. petiolata* in three southeastern New York forests (two with deer, one without). We compared changes in percent cover of *A. petiolata* and other vegetation over four years in caged and uncaged plots, and also measured differences in *A. petiolata* size and herbivory rate. We hypothesized that, within a forest, there would be no difference between caged and uncaged plots for *A. petiolata* cover, size, or herbivory rate if deer did not eat *A. petiolata*. Alternatively, if deer did eat *A. petiolata*, then cover would be less, plants would be smaller, and herbivory greater in uncaged plots relative to caged plots, but only in the forests with deer.

Our hypotheses address direct effects of herbivores on *A. petiolata*. It is also possible for herbivores to have indirect effects on plant cover and size (Damhoureyeh and Hartnett 1997). For example, smaller size and lower cover of *A. petiolata* in caged plots could be caused by increased competition from native plants released from herbivory. In addition, herbivory is only one of the complex ways that deer can affect plant cover and size and lead to differences in caged and uncaged plots (Waller and Alverson 1997). Trampling can damage plants, but may also create disturbed microsites for recruitment. Nutrient addition from deer scat may favor certain plant species, particularly invaders (Stohlgren et al. 1999). Our experiment does not directly assess all deer affects, but our results can be interpreted in reference to them.

STUDY AREAS

We conducted the caging experiment in three forests. The 16-ha New York Botanical Garden (NYBG) Forest, located in the Bronx, New York City, is an old-growth, never clearcut forest remnant, completely surrounded by a highly urbanized landscape. The latest published vegetation survey, from 1985, showed that canopy dominants were, in order of importance, *Tsuga canadensis* (L.) Carriere, *Quercus rubra* L., *Acer rubrum* L., *Betula lenta* L., *Fagus grandifolia* Ehrh., *Liquidambar styraciflua* L., *Prunus serotina* Ehrh., *Liriodendron tulipifera* L., and *Fraxinus americana* L. (Rudnicky and McDonnell 1989). There has been high mortality of *T. canadensis* since that survey due to the hemlock woolly adelgid (J. A. Morrison, unpublished data). Deer are not present in the NYBG Forest.

The other two forests are Westchester County's 84-ha Kitchawan Preserve, in Kitchawan, New York, and The Nature Conservancy's 86-ha Mt. Holly Sanctuary, near Cross River, New York. Both preserves consist of second-growth deciduous forest with closed canopy, located in northern Westchester County. Kitchawan is 42 km north of NYBG and Mt. Holly is 15 km northeast of Kitchawan. Both forests are contiguous with tracts of privately held forest fragments embedded in a suburban matrix of mixed land use, including houses, lawns, and forest. No formal canopy study has been done at either Westchester site, but common canopy trees at Kitchawan are *A. saccharum, B. lenta, Fraxinus pennsylvanica* Marshall, *P. serotina*, and *Quercus* spp. Common trees at Mt. Holly are *A. rubrum, B. lenta, P. serotina*, and *Quercus* spp. (J. A. Morrison, personal observation). Common herb layer species in the three forests are shown in Table 1. White-tailed deer are not present in the

NYBG Forest, but Kitchawan and Mt. Holly fall within the northern Westchester region, with estimated density of more than 50 deer km^{-2}. Mt. Holly in particular has the appearance of a forest strongly impacted by deer, with a clearly defined browse line and a nearly barren herb layer in many places (J. A. Morrison, personal observation).

METHODS

At NYBG and Kitchawan, in July 1996, we established four pairs of 4-m^2 plots, with each plot surrounded by an additional 0.5-m walkway. We originally established four pairs at Mt. Holly also, but two pairs had to be eliminated due to a new property line demarcation. We established two new pairs at Mt. Holly in May 1997; initial data collected from the two older pairs were dropped from the study. We chose locations for plots by searching each forest for four areas where *A. petiolata* occurred in stands large enough to accommodate the plots. A plot pair was situated within each stand so that each plot had similar *A. petiolata* densities. One plot plus walkway, per pair, was randomly assigned to a caging treatment (described below). Distances between the outer edge of the walkways of caged and uncaged plots, within a pair, ranged from 0.5 to 2 m. Distances between the four stands within a forest ranged from 10 to 500 m.

We censused the herb layer vegetation in all plots, prior to cage installation, between July 10 and 25, 1996, except in the two new plots at Mt. Holly, which we initially censused between May 28 and June 10, 1997. We divided each 4-m^2 plot into sixteen 0.25-m^2 subplots with a quadrat frame, and by careful visual estimates assigned a percent cover interval score for each species in each subplot, as follows: < 5%, 5-10%, 11-20%, 21-30%, 31-40%, 41-50%, 51-60%, 61-70%, 71-80%, 81-95%, > 95%. This method allowed us to census all plots within a short enough time interval to avoid large phenological differences from one plot to another. Dividing plots into 16 smaller subplots allowed us to be more accurate in our visual rankings. We were able to stand in the walkway on all sides of the 4-m^2 plot and lean over each subplot to make estimates, thus avoiding trampling the estimated vegetation. To obtain total percent cover per species per 4-m^2 plot, we converted interval scores to interval midpoints, summed across all 16 subplots, and divided by 16. Total percent cover for all native species combined was calculated by adding the values for all native species. In a few cases this resulted in more than 100% cover in a plot due to overlapping layers of foliage. Species names and native status were assigned according to Gleason and Cronquist (1991). Specimens of species not readily identified in the field were brought to the lab for identification and are stored at The College of New Jersey. Specimens of some uncommon species lacked sufficient characters for identification; they were assumed to be native.

We installed the cages after the initial censuses in July 1996 or June 1997 (for the two plot pairs added at Mt. Holly). Cages were square, with an open top, made with flexible plastic fencing stapled to 2-m cedar posts at each corner. The fencing at Kitchawan and Mt. Holly was strong black polypropylene netting, with filaments 1 to 2 mm wide and a 36-cm^2 opening between filaments (manufactured by Deerbusters, Inc., Frederick, Maryland). The fencing was staked along the cage bottom; small animals such as voles, birds, or chipmunks could move in and out of the plots through the open top or through the fencing at the forest floor. The netting used at NYBG was a finer plastic of 0.5 to 1-mm width, with a 4-cm^2 opening. It was loosely staked at the bottom so that small animals could enter the plot under the netting as well as through the open top. Stronger netting was required in the

Westchester County sites where deer are abundant but its extra expense was not justified at NYBG.

The cages excluded larger animals, such as white-tailed deer or eastern cottontail rabbits (*Sylvilagus floridanus* [Allen]). In another study, rabbits were able to chew gates through similar fencing material (J. Courteau, personal communication), but we observed no such gates in any of our cages. Our study focused on deer exclusion because of the overabundance of deer in suburban forests but we have observed rabbits on the NYBG grounds near the forest and presumably they are present in the other two forests also (but were not observed by us). Differences between caged and uncaged plots in the NYBG Forest could be attributed to exclusion of rabbits, while differences in the two suburban forests could be attributed to deer or rabbit exclusion.

The very thin filaments of the caging material allowed free movement of air and no appreciable shading and neither type of fencing was considered likely to alter microsite conditions inside cages compared to uncaged plots. We documented light and temperature in the plots. Using an AccuPAR 2000 (Decagon Devices, Inc., Pullman, Washington), we measured photosynthetically active radiation (PAR) in caged and uncaged plots. Measurements were taken in all pairs of plots at Mt. Holly and Kitchawan on September 17, 2000. At NYBG, two pairs of plots were measured on September 20, 2000 (the two other pairs of plots had been eliminated by treefall and flooding during the previous year). The AccuPAR was configured to first read full-sun PAR from a nearby light gap or forest edge, and then, at the plot in the forest, collect and average measurements from 10 points along a 1-m probe over 30 seconds. The probe was held over a plot at waist height at four regularly spaced positions, ensuring that no shade was cast by the operator. We used the averages of the four probe positions to obtain percent of full-sun PAR transmitted to the plot and found no significant difference between caged and uncaged plots (mean percent [*SE*]: caged, 5.01 [0.023]; uncaged, 2.97 [0.009]; one-tailed *t*-test for paired comparisons, $t = 1.21$, $P = 0.13$, $N = 10$). We measured one-time temperature in caged and uncaged plots at Mt. Holly and Kitchawan at the same time PAR data were collected and found no difference (mean degrees C [*SE*]: caged, 17.87 [0.895]; uncaged, 17.81 [0.886]; one-tailed *t*-test for paired comparisons, $t = 1.00$, $P = 0.18$, $N = 8$).

We censused the plots twice more, from May 28 to June 3, 1998, and May 21 to May 29, 2000, following the same procedure described above. *Alliaria petiolata* is a biennial, so plants were either in rosette form or flowering form during the censuses; we combined both forms when estimating cover. We did not quantify rosette and adult forms separately, but field notes indicate that most of the *A. petiolata* in 1996, 1998, and 2000 was in flowering form in all plots except for one uncaged plot at NYBG that was dominated by rosettes. Censusing the same plots every two years allowed us to see *A. petiolata* stands at the same life history stage during each census, with the exception of the two new plot pairs at Mt. Holly established in 1997. The May/June census dates in 1998 and 2000 were earlier in the growing season than the July 1996 census but *A. petiolata* rosettes have largely finished their spring growth by the end of May and do not change size appreciably though July. Flowering adults have cauline leaves, but these leaves are present and fully expanded by late May and are retained through July (Anderson et al. 1996) at our sites (J. A. Morrison, personal observation). Therefore we were confident that plots in different treatments were not affected differently by the census dates.

We analyzed percent cover of *A. petiolata* and total percent cover of all native plant species with repeated measures analysis of variance (von Ende 1993) using PROC GLM of

SAS v. 6 (SAS Institute 1990). There were a few other non-native species present, but they contributed little to total percent cover in these plots, and so were not included in the present study (the exception was *Polygonum cuspidatum* Sieb. and Zucc., but it occurred in only one set of plots at NYBG). Between-plot effects were caging and stand, and within-plot effects were time, time × caging, and time × stand.

The percent cover measures were analyzed separately for each forest because of differences in the duration and timing of data collection, However, because the experiments tested the same hypotheses we determined the significance of F statistics with the Simes-Hochberg method (Simes 1986; Hochberg 1988), a sequential Bonferroni correction. At Kitchawan, four pairs of plots were in the experiment from 1996 through 2000. At Mt. Holly, two pairs of plots were added one year later than the others. At NYBG, repeated measures analysis of all four pairs could be done only through 1998 because one pair of plots was destroyed by flooding and another by a fallen tree in 1999.

We assigned all pre-caging measurements a 1996 date in the Mt. Holly analysis, even though two plot pairs were initially measured in 1997. Combining the 1996/1997 initial census dates is reasonable ecologically because the data from both years describe the vegetation before the caging treatment was begun. Our focus is the comparison of percent cover change between caged and uncaged plots, and the 1997 plots were equally divided between caged and uncaged treatments.

We also measured size of adult, flowering *A. petiolata* individuals inside and outside of cages during the June 1998 census. Ideally, we wanted a size measurement that would capture individual biomass, since our observations of uncaged plants suggested that they were smaller overall, with both shorter stems and smaller leaves. We could not measure destructively, however, so we opted to measure stem length of adult plants. We measured the degree to which stem length reflects plant biomass by destructively sampling additional *A. petiolata* plants along transects in each forest (81 plants total) and correlating stem length with aboveground dry mass, obtained after harvesting and drying plants to constant weight at 60° C (Pearson's $r = 0.79$, $P < 0.01$).

We measured size of all adult *A. petiolata* individuals within each plot, or up to 32 plants per plot, sampling in a systematic manner by dividing the plot into an 8 × 4 grid and measuring the plant closest to each grid intersection point. We collected size data from all four pairs of plots at Mt. Holly and from three pairs at Kitchawan (one was inadvertently not sampled) and at NYBG (one had only rosettes at the 1998 census). We tested for difference in plant size between caged and uncaged plots in each forest with t-tests for paired comparisons, using the mean plant size per plot as the tested variable to avoid pseudoreplication (sample sizes in Table 2).

In September 2000, we scored *A. petiolata* plants for presence or absence of herbivory inside and outside of cages. We observed all plants in the plots and in the 0.5-m walkway surrounding the plots, noting whether rosettes had any bitten petioles with missing leaves, or no bitten petioles and all leaves present. We used G-tests for independence (Sokal and Rohlf 1981) for each forest data set to determine if the frequency of bitten plants inside cages differed from the frequency outside of cages.

Table 1. Mean percent cover estimates of 10 most abundant herb layer plant species in *Alliaria*-dominated 4-m^2 plots (N = 8) at start of experiment before caging. Plots were censused in July 1996, except for four at Mt. Holly that were added and censused in June 1997. *SE* = standard error.

	mean % cover	*SE*
Mt. Holly		
Alliaria petiolata (Bieb.) Cavara & Grande	29.92	3.82
Eupatorium rugosum Houttuyn.	3.21	2.21
Carex sp.	1.68	0.86
Oxalis sp.	1.53	0.81
Berberis thunbergii DC	0.59	0.47
Fraxinus americana L.	0.43	0.20
Arisaema triphyllum (L.) Schott	0.40	0.30
Polygonum sp.	0.40	0.18
Acer rubrum L.	0.27	0.10
Celastrus orbiculatus Thunb.	0.19	0.10
Kitchawan		
Alliaria petiolata (Bieb.) Cavara & Grande	15.86	1.84
Acer saccharum Marshall	4.73	1.26
Fraxinus americana L.	4.65	1.84
Galium sp.	2.15	1.52
Parthenocissus quinquefolia (L.) Planchon	1.91	0.92
Polystichum acrostichoides (Michx.) Schott	1.52	0.91
Carex spp.	1.50	0.87
Lindera benzoin (L.) Blume	1.29	0.39
Arisaema triphyllum (L.) Schott	0.94	0.49
fern	0.94	0.94
NYBG		
Alliaria petiolata (Bieb.) Cavara & Grande	44.31	6.46
Polygonum cuspidatum Sieb. & Zucc.	14.15	8.36
Circea lutetiana L.	2.62	1.97
Impatiens capensis Meerb.	1.88	1.34
Phellondendron amurense Maxim.	1.67	1.05
Acer negundo L.	1.57	1.57
Solanum sp.	1.13	1.13
Fraxinus americana L.	1.06	0.93
Commelina communis L.	0.90	0.81
Viola sp.	0.90	0.56

RESULTS

Percent Cover

Over the course of the experiment at Mt. Holly, percent cover of *A. petiolata* decreased significantly in uncaged plots relative to caged plots (Fig. 1). This is shown by the significant

Table 2. Number of plant size measurements of *Alliaria petiolata* used to calulate average plant size per plot in caged and uncaged plots.

Forest	plot treatment	number of plots measured	number of plant size measurements in each plot
Mt. Holly	caged	4	32, 32, 21, 31
	uncaged	4	16, 14, 17, 23
Kitchawan	caged	3	32, 28, 32
	uncaged	3	31, 31, 32
NYBG	caged	3	32, 32, 32
	uncaged	3	32, 32, 12

caging effect, and in the marginally significant time × caging interaction in the repeated measures analysis (Table 3A). Before caging, those plots assigned to the caging treatment had, by chance, somewhat lower average *A. petiolata* percent cover compared to plots assigned to the uncaged treatment, but over four years the caged plots ended up with significantly higher percent cover (Fig. 1). In Kitchawan Preserve (Table 3B) and in the NYBG Forest (Table 3C), percent cover of *A. petiolata* was not significantly different in caged and uncaged plots, although at Kitchawan the trend was toward lower cover in uncaged plots (Fig. 2), and at NYBG there was no consistent trend across the four years (Fig. 3).

Native plant percent cover showed no significant differences between caged and uncaged plots at Mt. Holly (Table 3A, Fig. 1), Kitchawan (Table 3B, Fig. 2), or NYBG (Table 3C, Fig. 3). No consistent trend of differences in native plant cover between caged and uncaged plots was evident.

Alliaria petiolata Size

Individual *A. petiolata* plants were significantly larger in caged plots than in uncaged plots at Mt. Holly (Fig. 4; *t*-test for paired comparisons: Mt. Holly, $t = 3.19$, $df = 3$, $P = 0.05$). At Kitchawan, sizes were similar in caged and uncaged plots (Fig. 4; $t = 0.68$, $df = 2$, $P = 0.57$). At NYBG, they were more variable and not significantly different (Fig. 4; $t = 1.18$, $df = 2$, $P = 0.36$).

Herbivory

Herbivory on *A. petiolata* plants occurred with significantly greater frequency in uncaged plots, compared to caged plots, at both Mt. Holly (Fig. 5; $G_{adj} = 132.13$, $df = 1$, $P < 0.001$) and Kitchawan (Fig. 5, $G_{adj} = 46.87$, $df = 1$, $P < 0.001$). At Mt. Holly, 27% of the 255 uncaged plants and 0.82% of the 488 caged plants observed had bitten petioles. At Kitchawan, bitten petioles were present in 8% of the 562 uncaged plants and 0.21% of the 460 caged plants. The NYBG plants did not experience herbivory either inside or outside of cages, except for one out of 332 uncaged plants observed (the *G*-test of independence for NYBG data was not needed, or possible, because the frequency of observations for one level of the herbivory factor was so low across both levels of the caging factor).

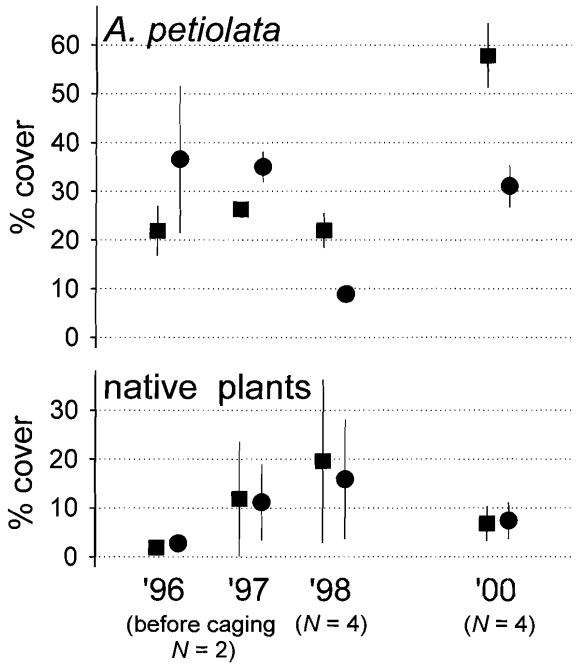

Figure 1. Mt. Holly Sanctuary: estimated percent cover (mean ± *SE*; small error bars are hidden by the symbol) in 4-m^2 plots that were caged to prevent herbivory (squares) or uncaged (circles).

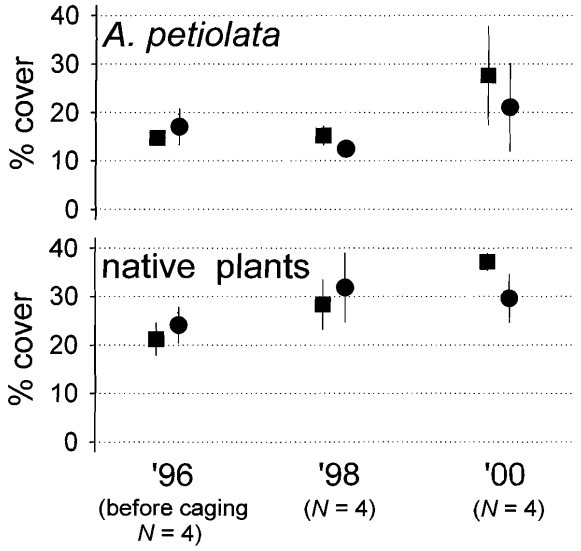

Figure 2. Kitchawan Preserve (see Fig. 1 caption).

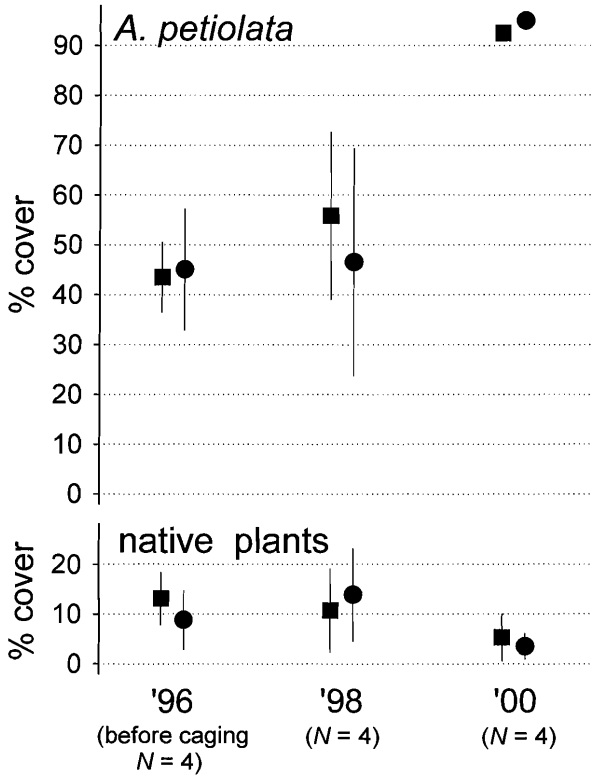

Figure 3. NYBG Forest (see Fig. 1 caption).

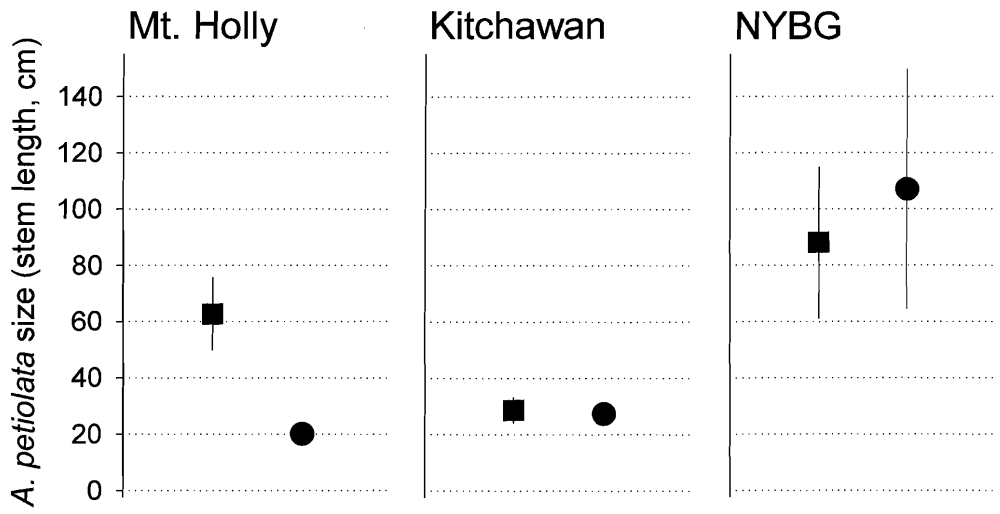

Figure 4. Mean (± *SE*) across plots of average *A. petiolata* size in plots that were uncaged (circles) or caged (squares) for two years (one year for two plots at Mt. Holly) to prevent hebivory (N = 4; small error bars are hidden by the symbol). Size is the sum of stem lengths measured on adult flowering plants.

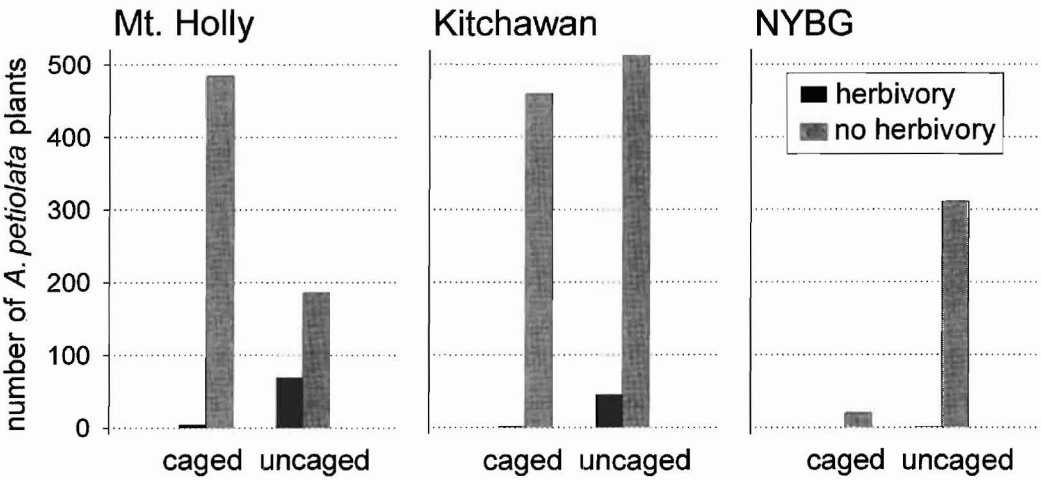

Figure 5. Frequency of *A. petiolata* plants with herbivory (bitten pitioles and missing leaves), inside and outside of cages. Plants were censused in September 2000.

DISCUSSION

We expected that protection from herbivory would have little effect on *A. petiolata* but would have a dramatic effect on the native herb layer in the forests with deer. We had three major grounds for our expectation: the prevalent idea that non-native species gain an advantage, in part, because they lack a suite of herbivores that utilize them as food (Baker 1974; Mack 1985; Keane and Crawley 2002), comments in the literature that deer do not eat *A. petiolata* (Nuzzo 2000; Tilghman 1989), and our observations of thriving *A. petiolata* in forests with deer herds. However, our results were not consistent with this expectation.

We found that native vegetation did not respond to protection from herbivores after four years, but *A. petiolata* did respond under certain circumstances. The following evidence supports this conclusion: (1) there was no difference in percent cover of native vegetation inside and outside of cages over the four years of the experiment; (2) *A. petiolata* cover was higher inside of cages, but only in the two forests with deer, and significantly higher only at Mt Holly, where the native vegetation is especially denuded, potentially providing little food for mammalian herbivores, particularly in the winter; (3) individual *A. petiolata* plants were larger inside cages only in one of the forests with deer, Mt. Holly; and (4) there were much greater herbivory rates on uncaged *A. petiolata* in the forests with deer, especially at Mt. Holly, and hardly any herbivory at NYBG, the forest without deer.

The lack of response to caging by native vegetation at NYBG can be explained by the absence of deer in the forest and appears to indicate that there is also little herbivore pressure from rabbits. In the forests with deer, however, reasons for the lack of native plant response are less clear. It is possible that some single-species percent cover responses occurred, but if so they were not great enough to affect the overall cover of the native community (a future paper will explore responses of individual species). There was some indication of native cover increase in the 2000 data at Kitchawan (Fig. 2) indicating that a longer time of protection from herbivory may allow natives to recover, but that trend was not observed at Mt. Holly. We did not directly measure herbivory on native species as we

did for *A. petiolata*, but it is unlikely that native vegetation would be avoided by mammalian herbivores; the browse line and barren appearance of the herb layer strongly suggest otherwise, especially at Mt. Holly. We hypothesize that the lack of response by the native community compared to *A. petiolata* may be explained by the fact that the native community was so severely reduced to begin with, while the *A. petiolata* population was comparatively vigorous, with many successfully reproducing individuals. The native species were sparse and small, and perhaps had little resources to draw on for growth after release from herbivory. In addition, many species may have a depleted seed bank due to a history of chronic overbrowsing, in which case recruitment could remain very low even when pro-

Table 3. Repeated measures analyses of variance for percent cover of *Alliaria petiolata* and native species in caged and uncaged 4-m^2 plots situated in four *A. petiolata* stands in each of four sites. Asterisks denote significance based on the Simes-Hochberg sequential Bonferroni procedure, which provides critical values of α' for three tests across the three sites (^{a} = ≤ 0.10; * = ≤ 0.05; ** = ≤ 0.01). The "adjusted *P*" values given for within-plot effects are conservative tests that account for departures from sphericity in the variance-covariance matrix in repeated measures data. **(A)** Mt. Holly: measurements were made shortly before cages were installed in 1996 or 1997 (treated as one date) and also in 1998 and 2000. **(B)** Kitchawan: measurements were made shortly before cages were installed in 1996 and also in 1998 and 2000. **(C)** NYBG: measurements were made shortly before cages were installed in 1996 and again in 1998 (adjusting *P* values is unnecessary when there are only two repeated measures).

Source of variation	*df*	*MS*	*F*	*P* (Bonferroni-adjusted significance level)	Greenhouse-Geisser adjusted *P*	Huynh-Feldt adjusted *P*
(A) Mt. Holly Sanctuary						
Alliaria petiolata						
Between-plot effects						
Caging	1	5.272	23.85	0.016*		
Stand	3	0.956	4.33	0.130		
Error (= caging × stand)	3	0.221				
Within-plot effects					(ϵ = 0.55)	(ϵ = 1.81)
Time	2	16.807	14.74	0.005*	0.025*	0.005*
Time × caging	2	7.616	6.68	0.030^a	0.073	0.030^a
Time × stand	6	0.705	0.62	0.713	0.657	0.713
Error	6	1.140				
Native Species						
Between-plot effects						
Caging	1	0.062	0.18	0.702		
Stand	3	13.704	39.47	0.007*		
Error (= caging × stand)	3	0.275				
Within-plot effects					(ϵ = 0.575)	(ϵ = 1.944)
Time	2	3.066	25.70	0.001**	0.010*	0.001**
Time × caging	2	0.113	0.94	0.440	0.411	0.440
Time × stand	6	2.822	23.65	0.001**	0.009*	0.001**
Error	6	0.051				

(*continued*)

Table 3 (*cont'd*)

Source of variation	*df*	*MS*	*F*	*P* (Bonferroni-adjusted significance level)	Greenhouse-Geisser adjusted *P*	Huynh-Feldt adjusted *P*
(B) Kitchawan Preserve						
Alliaria petiolata						
Between-plot effects						
Caging	1	0.328	0.31	0.618		
Stand	3	1.970	1.84	0.314		
Error (= caging × stand)	3	1.069				
Within-plot effects					(ϵ=0.65)	(ϵ=2.50)
Time	2	2.479	9.49	0.014*	0.035*	0.014*
Time × caging	2	0.405	1.55	0.287	0.298	0.287
Time × stand	6	2.351	8.99	0.009*	0.029	0.009*
Error	6					
Native Species						
Between-plot effects						
Caging	1	0.009	0.01	0.935		
Stand	3	3.064	2.70	0.219		
Error (= caging × stand)	3	1.136				
Within-plot effects					(ϵ=0.694)	(ϵ=2.821)
Time	2	2.390	14.82	0.005*	0.015*	0.005*
Time × caging	2	0.777	4.82	0.057	0.087	0.057
Time × stand	6	0.299	1.85	0.236	0.278	0.236
Error	6	0.161				
(C) NYBG Forest						
Alliaria petiolata						
Between-plot effects						
Caging	1	0.603	1.10	0.372		
Stand	3	17.469	31.73	0.009*		
Error (= caging × stand)	3	0.550				
Within-plot effects						
Time	1	1.899	0.87	0.420		
Time × caging	1	1.186	0.54	0.515		
Time × stand	3	19.59	8.95	0.052		
Error	3	2.188				
Native Species						
Between-plot effects						
Caging	1	0.129	0.47	0.543		
Stand	3	4.849	17.60	0.021*		
Error (= caging × stand)	3	0.275				
Within-plot effects						
Time	1	0.268	5.20	0.107		
Time × caging	1	0.241	4.65	0.120		
Time × stand	3	2.986	57.77	0.004**		
Error	3	0.051				

tected from herbivory. It is possible, however, that the native community did respond to caging with increased recruitment, but our percent cover measure did not detect it. Percent cover is very useful for making accurate yet rapid estimates of biomass per species, which is important in a study like ours in order to avoid large phenological differences between sampling sites. It does not measure numbers of plants, however, so if new individuals recruited but contributed little new biomass, the percent cover of the species may not show any change.

We attribute the differences in *A. petiolata* cover and size between caging treatments to protection from a direct effect of herbivory rather than any indirect herbivory effect or some other cage effect. Indirect effects of herbivory could be lower cover and size in caged plots because of increased competition from plants released from herbivory, or higher cover and size in uncaged plots due to decreased competition from plants subject to herbivory. However, *A. petiolata* cover and size showed the opposite pattern — higher in caged plots relative to uncaged plots — indicating direct herbivory. Disturbance of the herb layer by trampling could be a second direct effect of mammals in our study, but the strikingly lower herbivory rate inside cages suggests that herbivory differences were of primary importance. If there was another cage effect not attributable to mammal exclusion, we would expect to detect it in all three forests. However, differences inside and outside of cages were seen only in the two forests with deer and were more pronounced at Mt. Holly, where deer density was probably highest. We chose the thin filament mesh for use as caging material to minimize any effect on the plant community and, as expected, microsite measurements of light and temperature were no different inside and outside of cages.

We did not detect the animal species responsible for the observed herbivory on *A. petiolata*. It makes sense to attribute the herbivory to deer, because it best explains our results and because of the high density of deer in northern Westchester County (>50 km^{-2}), but it is possible that leaves could also have been taken by rabbits (*S. floridanus*) or voles (for example, *Microtus pinetorum* [Le Conte]). However, if the herbivory we observed was due only to small mammals such as voles, then we should have consistently seen little difference inside and outside of cages because small animals could easily access the caged plots through or under the mesh. There was some herbivory inside cages at Mt. Holly and Kitchawan indicating the presence of small herbivores, but there was significantly more herbivory outside of cages. If the difference was due to rabbits, that would not explain why herbivory on *A. petiolata* was nearly nonexistent at NYBG but common at Kitchawan and Mt. Holly, because we know that rabbits were present at NYBG.

We do have reason to think that deer were browsing more heavily at Mt. Holly. There was a noticeable deer browse line at Mt. Holly and at every visit over four years we observed deer in the forest. Native plant cover measured before the experiment was lower at Mt. Holly than at Kitchawan (Figs. 1 and 2), which is consistent with the almost barren herb layer throughout much of the Mt. Holly forest. Kitchawan did not have a distinct browse line and the herb layer appeared more abundant (J. A. Morrison, personal observation). We did sight deer at Kitchawan but less frequently than at Mt. Holly, even though these forests are not far from each other and are in similar landscapes. We hypothesize that deer may be less prevalent at Kitchawan because many area residents take dogs there, usually allowing them to run unleashed. We saw deer at every visit to Mt. Holly but we saw dogs at nearly every visit to Kitchawan. Our evidence that deer are the animals responsible for herbivory on *A. petiolata* is indirect but compelling. It would be useful to investigate this problem more closely with hand-lens examination of bitten petioles at

regular intervals throughout the year, in order to distinguish the shredded bites of deer from the clipped and nibbled bites of rabbits and voles (Strole and Anderson 1992). Experimental feeding trials would also be helpful.

A key reason for successful invasion by a non-native plant species is commonly thought to be a relative lack of herbivory because of escape from herbivore species found in its native range (Baker 1974; Mack 1985; Keane and Crawley 2002). In fact, the enemy release hypothesis is the premise upon which the scientific discipline of biological control is based (Debach and Rosen 1991; Guretzky and Louda 1997) and a biological control program is being developed for *A. petiolata* (Blossey et al. 2001). The idea applies especially to feeding by highly specialist insect herbivores but it may not apply to herbivores with a broader diet. White-tailed deer have diet preferences leading to avoidance of relatively unpalatable plant species as long as preferred species are available (Alverson et al. 1988; Longhurst et al. 1968; McCullough 1985; Nudds 1980; Short 1975; Strole and Anderson 1992; Vangilder et al. 1982); however, they do not rely on any tightly co-evolved genetic relationship with their host plants. The fact that *A. petiolata* is non-native is probably of little importance in whether it is eaten by deer compared to the fact that it is a member of the mustard family (Brassicaceae) and so contains a suite of secondary chemicals (Chew 1988; Cole 1975; Larsen et al. 1983; Van Etten and Tookey 1979). These bitter compounds can make mustards less palatable to vertebrate herbivores, although cows in Ontario are reputed to eat *A. petiolata* leaves in autumn and spring (Cavers et al. 1979). Anecdotally, *A. petiolata* is considered unappealing to deer (Tilghman 1989).

A. petiolata's life history, on the other hand, could encourage herbivory, especially during the winter, by animals that otherwise would avoid such a chemically defended plant. It germinates in early spring and spends the following winter as a basal rosette of green leaves, even growing new leaf tissue in the winter months (Anderson et al. 1996). In addition, it begins spring growth before nearly all other understory plants and shrubs (J. A. Morrison, personal observation). Fresh *A. petiolata* leaf tissue is thus available to herbivores throughout the winter, when most other foliage is unavailable. If deer make frequency-dependent food choices, a plant species that occurs at very low frequency may be relatively ignored, but may become a primary food as its proportional representation in the flora increases (Brown and Doucet 1991). In addition, deer are predicted to shift to a more generalist diet during winter (Nudds 1980). Whether or not *A. petiolata* has become a primary food for deer at Mt. Holly we cannot say, but our results are consistent with deer including *A. petiolata* in their diet because of a lack of other forage plants below the browse line. If deer do feed on *A. petiolata* at some sites, it is possible that biological control in those sites will have little additional effect because deer already may be suppressing the *A. petiolata* population to a substantial degree.

It appeared that deer ate *A. petiolata* at lower rates at Kitchawan and had less effect on its size and cover than at Mt. Holly. The 8% of uncaged plants with herbivory at Kitchawan was lower than the 27% at Mt. Holly, and this was just a one-time look at herbivory in the fall while there were still other species available as food. It would be of interest to measure and compare herbivory on native species and *A. petiolata* over the course of the year, especially in the winter when most other species have senesced or are perennating underground, unavailable to herbivores. There is so little plant food available to deer at Mt. Holly in the winter that the green foliage of *A. petiolata* rosettes may be their only choice, while at Kitchawan, where the woody vegetation is not as denuded, other foods are available. Another possible explanation for different herbivory rates among sites is

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