Variable effects of large mammal herbivory on three non-native versus three native woody plants

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Abstract

(1) The enemy release hypothesis posits that introduced species leave behind co-evolved pathogens and predators, thereby gaining an advantage over native competitors. On the other hand, introduced plants may encounter biotic resistance from local generalist herbivores such as large mammals.

(2) We conducted a replicated, manipulative field experiment to compare the effects of large-mammal herbivory on growth and survival of three native and three invasive woody species over 2 years. Non-native Acer platanoides, Frangula alnus P. Mill. (=Rhamnus frangula L.) and Elaeagnus umbellata were each paired with a likely native competitor of similar life form and shade tolerance. Seedlings were planted with and without large-mammal exclosures, in open and understory environments.

(3) In the open, E. umbellata grew taller than its paired native only when exposed to herbivory, but F. alnus grew taller than its paired native only within exclosures. The effects of exclosure on growth rate did not differ between A. platanoides and its native congener. In the understory, exposure to browsing reduced height growth rate overall in native species, but not in invasive species.

(4) Browsing increased understory mortality only in the native shrub Viburnum dentatum, and did not affect mortality in the open. Within exclosures, there was a general trade-off between open growth and understory survival, but outside of exclosures, E. umbellata exhibited both greater open growth and greater understory survival than its native competitor.

(5) Although large-mammal herbivory did not consistently favor non-natives, lack of browsing impact played an important facilitating role for E. umbellata in particular.

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1. Introduction

Invasive plants often grow more vigorously or densely in their introduced range than in their indigenous range (Keane and Crawley, 2002; Hinz and Schwarzaender, 2004; Bossdorf et al., 2005). A long-standing and oft-cited explanation for this trend is the enemy release hypothesis, which posits that introduced species leave behind their co-evolved herbivores, parasites or pathogens (Darwin, 1859; Elton, 1958; Maron and Vilà, 2001; Colautti et al., 2004). The enemy release hypothesis is supported by an accumulating body of research indicating that invasive plant species generally experience reduced herbivore loads and attack rates in their introduced ranges, compared with their indigenous ranges (Wolfe, 2002; Colautti et al., 2004; Hinz and Schwarzaender, 2004; Bossdorf et al., 2005; Vilà et al., 2005).

On the other hand, although introduced species may escape their historical enemies, they may also encounter new potential adversaries in their introduced range. Another long-standing principle of invasion ecology, the biotic resistance hypothesis, predicts that the spread of alien species into new habitats may be limited by interactions with resident species (Elton, 1958; Levine et al., 2004). Both enemy release and biotic resistance may influence the invasive success of a given species. Across a large sample of European plant species naturalized to North America, the reported "noxiousness" of an invader was...
positively correlated with the loss of pathogens from its home range, but negatively correlated with the accumulation of new pathogens from its introduced range (Mitchell and Power, 2003).

In particular, although introduced plant species may leave behind co-evolved specialist enemies, they may still be vulnerable to generalist enemies in their new habitats (Memmot et al., 2000; Maron and Vilà, 2001; Keane and Crawley, 2002; Hinz and Schwarzländer, 2004; Levine et al., 2004). Such generalists include small vertebrate seed predators and large vertebrate grazers, as well as generalist arthropods. Although large mammal herbivory can exert strong effects on community composition (Waller and Alverson, 1997; Keane and Crawley, 2002), few quantitative studies have assessed the relative impact of such herbivory on invasive exotics and their native competitors (Maron and Vilà, 2001; Keane and Crawley, 2002; Levine et al., 2004). Moreover, most exclusion experiments assessing the impact of mammal herbivory on exotics have tended to focus on herbaceous rather than woody species (Levine et al., 2004). One study of a woody invader found that exposure to native mammal herbivory had a more negative effect on the growth of the native vine *Lonicera sempervirens* than on its invasive congener *L. japonica*, in part due to compensatory growth by the invader (Schierenbeck et al., 1994). In light of widespread concern about the impact of record high deer populations on tree regeneration in forest systems (Waller and Alverson, 1997), additional research is needed into the effects of large-mammal browsing on native versus non-native woody forest species.

We conducted a manipulative field experiment comparing the effects of mammal browsing on growth and survival of three native and three non-native, invasive woody species in western Massachusetts, to determine the role of local generalists in facilitating or inhibiting the spread of these invaders. We planted seedlings of each species, with and without exclosures, in replicated plots within both open and understory environments. We focused on the seedling and sapling stages of growth because it is during this period that mammal browsing is most likely to exert a controlling influence on establishment. In selecting species for our study, we chose non-native woody invaders of varying life form and shade tolerance, and paired each with a native of similar life form and shade tolerance. We, thus, compare each individual invader with a likely local competitor and take into account differences due to ecological type.

Our exclosures were designed to limit access by mammal browsers such as white-tailed deer (*Odocoileus virginianus*) and porcupine (*Erithizon dorsatum*), both seen frequently at the study site. Because the herbivores excluded by our treatment were generalists, we expected that exposure to browsing would reduce the growth or survival of both non-native and native species to some degree. The enemy release hypothesis predicts that this effect should be greater in natives than in non-natives, however, with the result that non-native invaders should have a greater advantage over their local competitors in the presence of local herbivores. An opposite result (invaders have a lesser advantage in the presence of herbivores) would suggest that biotic resistance is important for these species.

Rates of herbivory and the capacity for compensatory growth may vary considerably between open and understory conditions, as well as among plant types. We compared the effects of herbivory on growth and survival of native and invasive non-native species in both open and understory conditions. While competitive success in open environments may be predicted by height growth, survival may be a more important indicator of success in the understory (Kobe et al., 1995). Among woody species, growth rate in open environments is often negatively correlated with survival in understory conditions (Kitajima, 1994; Kobe et al., 1995; Walters and Reich, 1999; Sanford et al., 2003). We predicted that herbivory would reduce both growth and survival more for natives than for invaders, such that invaders would exhibit both greater understory survival and greater open growth than natives when exposed to browse.

2. Methods

2.1. Study species

We selected three pairs of native and non-native woody species, representing a spectrum of life form and shade-tolerance classes. The native shrub *Cornus amomum* (silky dogwood) and the invasive shrub *Elaeagnus umbellata* (autumn olive) are both classified as shade-intolerant and are found primarily at forest edges, while the native shrub *Viburnum dentatum* (arrowwood) and the non-native *Frangula alnus* P. Mill. (= *Rhamnus frangula* L.) (glossy buckthorn) are both classified as shade-tolerant and may be found in forest understories (Gleason and Cronquist, 1991; Weatherbee et al., 1999). The native tree *Acer saccharum* (sugar maple) and its non-native congener *Acer platanoides* (Norway maple) are both highly shade-tolerant (Gleason and Cronquist, 1991; Weatherbee et al., 1999; Meiners, 2005). Each of the non-native species chosen has been identified as an invasive threat in the eastern United States (US Forest Service, 1998; Swearingen et al., 2002) and may be found growing in close proximity to its paired native species in fields or forests near our study area.

2.2. Study site and experimental design

In June and July 2000, we planted seedlings of each species in eight replicate blocks within Mount Toby Demonstration Forest, an upland hemlock-hardwoods forest in Sunderland, MA (42.502°N, 72.517°E). Each replicate block consisted of one open and one understory plot, each 8 m × 20 m, with a surrounding 5-m treatment buffer. Understory plots were located in 14-year-old closed-canopy stands dominated by *Betula* species and *Pinus pensylvanica*. Open plots were created for this study by chain-sawing and removing trees from adjacent sections of these stands. Twenty rows of seedlings, each containing all six species, were planted in each of the eight open and understory plots. *F. alnus* seedlings were transplanted from local Massachusetts populations; all other species were purchased bare-root from nurseries. Native and non-native species of similar life form and shade tolerance were of similar...
height at planting. This experimental design has been previously described by Sanford et al. (2003), who reported first-year growth and survival data for planted seedlings within exclosures only.

Preliminary visual assessments detected evident browsing of twigs or leaves in uncaged seedlings of all species, in both open and understory environments (Sanford, 2002). To assess the impact of such browsing, a cylindrical exclosure was constructed from 1.2 m × 1.2 m chicken wire around each individual seedling in nine randomly chosen rows in each plot prior to the 2001 growing season.

2.3. Measurements

At the end of the 2001 and 2002 growing seasons, we measured height (extension height of the tallest growing tip) and basal diameter (using calipers) of each surviving planted seedling. Plants that had no above-ground shoots or that appeared to lack live buds were classified as dead. Presence of fruit or flowers was noted as well. To avoid the spread of invasive species, we removed all fruit every few days until final harvest. A subsample of plants was removed at the end of the 2001 and 2002 seasons for measurement of above-ground biomass allocation, reported elsewhere (Sanford et al., 2003; Knapp, 2006).

We used height as our primary index of growth, because of its relevance to light competition. Differences in height among species may reflect differences in architecture as well as in its relevance to light competition. Differences in height among species may reflect differences in architecture as well as in the understory, regardless of exclosure treatment, and in some cases species suffered a net height loss in the understory.

2.4. Calculations and statistical analyses

From data collected in September 2001 and 2002, we calculated annual absolute height and diameter growth rates (AGR_X = X_2002 − X_2001, where X = height or diameter) for each surviving planted seedling. We analyzed growth rates using mixed-model analyses of variance (SAS Institute Inc., 2002–2003), with canopy treatment (open versus understory), exclosure treatment (caged versus uncaged), species origin (native versus non-native), and species pair (i.e., shade tolerance/life form classification) as fixed effects, and with block as a random effect. We also performed the same analyses using relative growth rates (RGR_X = ln (X_2002) − ln (X_2001)). Trends for relative growth rates were essentially the same as those for absolute growth rates (Knapp, 2006); for purposes of brevity we present only the latter here.

We analyzed survival status by log-linear modeling, using the logit transformation with a binomial error distribution (SAS Institute Inc., 2002–2003), with canopy, exclosure, species pair, species origin, and block as categorical effects.

In each of the above analyses, we were primarily interested in whether the effects of exclosure differed between native and non-native species—i.e., in whether there were significant exclosure × species origin interactions. Where exclosure and origin effects varied among species pairs, we analyzed results separately within each species pair.

We used log-linear modeling, with plant height as a covariate, to determine the effect of exclosure on flowering status.

3. Results

Height and diameter growth rates were greater in caged than in uncaged seedlings, and greater in open plots than in understory plots overall. The effects of canopy and exclosure treatment interacted significantly, however. We present results separately for each canopy treatment.

In the open, height and diameter growth rates were greater in caged plants overall. The effects of exclosure on these variables varied among species pairs and were not consistently greater in natives than in non-natives (origin × exclosure × pair, F_{2,74} = 14.56, p < 0.0001 for height, F_{2,74} = 4.27, p = 0.02 for diameter).

Within the shade-intolerant shrub pair, the negative effect of browsing on each of these variables in the open was greater in the native C. amomum than in the invader E. umbellata (Table 1). Within exclosures, the two species had similar height and diameter growth rates, but when exposed to herbivory, the invader achieved greater height and diameter growth than the native. Within the shade-tolerant shrub pair, on the other hand, the effect of browsing on absolute height growth rate in the open was greater in the invader F. alnus than in the native V. dentatum (Table 1). F. alnus outgrew the native within exclosures, but when exposed to herbivory, the two species had similar height growth rates. Diameter growth in the open did not differ significantly between these two species, however, regardless of exclosure treatment.

Within the shade-tolerant tree pair, the effects of exclosure on 2001–2002 height and diameter growth rates did not differ significantly between the native A. saccharum and the invader A. platanoides (Table 1).

In the understory, by contrast, growth was generally negligible (Table 1). Annual height and diameter growth rates were not significantly greater than zero within any species in the understory, regardless of exclosure treatment, and in some cases species suffered a net height loss in the understory. Browsing in the understory significantly reduced 2001–2002 absolute height growth rate of native species as a group (F_{1,66} = 10.01, p = 0.002) but not of non-native species (F_{1,66} = 0.16, p = 0.69). Exclosure did not significantly affect diameter growth rates in the understory (main caging effect and all interactions, p > 0.2).

There was little overall effect of exclosure on survival (Table 2). In the open, exposure to browse did not significantly reduce 2-year survival rates (main caging effect and all interactions, p > 0.30). The invader A. platanoides had greater open-plot survival than the native A. saccharum regardless of caging, and neither of the invasive shrubs differed significantly from its native partner. In the understory, the effect of exclosure on survival depended on both species pair and species origin (origin × pair × caging interaction χ^2 = 9.25, df = 2, p = 0.01). Within the shade-tolerant shrubs, the invader F. alnus had greater survival than the native when unprotected but not when
Means (standard errors) of eight replicate plots; invasive species listed first in each pair. Within each pair, boldface indicates exclosure effect differs between native and invader (origin × exclosure effect $p < 0.05$ within species). Italics indicate survival differs between paired native and invader (origin effect $p < 0.05$ within pair × exclosure × canopy).
While our results for this species pair agree with the enemy release hypothesis, we also observed an example of biotic resistance, in that herbivory decreased growth of the non-native *F. alnus* in open plots more than its paired native *V. dentatum*. The degree of resistance encountered by *F. alnus* was insufficient to actually tilt the balance of performance in favor of the native species, however.

Where species differ in their abilities to resist or tolerate herbivory, the effect of browsing in a given forest can determine its successional pathway (Waller and Alverson, 1997). For example, under conditions of intense deer browse, regeneration of tree species in thinned forests may be indefinitely suppressed by dense growth of unpalatable hay-scented fern (*Dennstaedtia punctilobula*) (De la Cretaz and Kelty, 1999). Among woody species, successional status may be determined by a species’ position along a trade-off between growth in sun and survival in shade (Kitajima, 1994; Kobe et al., 1995; Walters and Reich, 1999). When grown within exclosures, the six species in our study occupied a common growth–survival trade-off curve, with the invader *A. platanoides* at the extreme shade-tolerant end of the spectrum. When exposed to herbivory, however, the invader *E. umbellata* appears as a noticeable outlier in the growth–survival pattern. The overabundance of deer in many North American forests (Waller and Alverson, 1997) may thus permit *E. umbellata* to dominate over a range of successional conditions.

The enemy release hypothesis posits an intrinsic advantage to being away from home, implying a common mechanism underlying the success of non-native invaders. It is possible, however, that individual species are invasive in individual ways (i.e., the ‘global competitor hypothesis’, Alpert, 2006). While group comparisons of natives versus non-native invaders seek to detect common features of invasive species, paired comparisons highlight factors of importance for individual invasive species. We matched each alien invader with an ecologically similar native in order to make both groupwise and pairwise comparisons. This design also allowed us to compare interspecific trade-offs among invasive and native species; this approach does not presume competition or similarity between any particular invader and any particular native, but still takes into account the spectrum of variation in the native community. In general, our data confirm the value of this experimental approach does not presume competition or similarity between any particular invader and any particular native, but still takes into account the spectrum of variation in the native community. In general, our data confirm the value of this experimental design, as variation in growth and survival among pairs was often greater than variation between native and invasive species within pairs.

We now consider results separately for each species pair.

4.1. *E. umbellata* and *C. amomum*

*E. umbellata*’s dominance in open habitats may be strongly facilitated by low susceptibility to local herbivores. Within exclosures, *E. umbellata*’s height growth in the open was similar to that of a native competitor, *C. amomum*, but without exclosures, the invader was over 90% taller on average by the end of the study. We paired *E. umbellata* with the native *C. amomum* because these two shade-intolerant shrubs are frequently found together at field edges near our study site. Evidence for possible herbivore facilitation of *E. umbellata* invasion extends beyond this pairwise comparison, however, as it was the only study species in which exposure to herbivory did not significantly reduce final height. Reproductive output of *E. umbellata* was also virtually unaffected by browsing. This lack of browsing impact is notable, as even introduced plant species are typically susceptible to attack by local generalist herbivores (Maron and Vila`, 2001; Keane and Crawley, 2002; Levine et al., 2004).

Lack of herbivore impact on growth can reflect either resistance or tolerance: either mammals are not browsing, or the plant is able to compensate for browsing through additional above-ground growth. During the 2001 growing season, Sanford (2002) visually assessed a subsample of plants within our study for evidence of browsing. In open environments, twig clipping was common in *C. amomum* (>50% of individuals affected) but rare in *E. umbellata* (<10% of individuals affected). Rates of twig clipping in the understory were similar for both species (approximately 30% of individuals affected).
These observations suggest that *E. umbellata* is resistant to browsing in open environments, but do not rule out compensatory growth as an additional factor contributing to the invader’s unreduced vigor in the presence of herbivores. *E. umbellata* produces short, sharp thorns, and although its scaly leaves are high in nitrogen (Knapp, 2006), they may provide poor nutrition due to low digestibility (Turner and Foster, 2000); these features may render the species unattractive to local generalists.

The enemy release hypothesis implies, first, that introduced species experience less herbivory than in their home ranges, and, second, that they experience less herbivory impact than co-occurring native species (Levine et al., 2004). Our results for *E. umbellata* are clearly consistent with the second prediction. It remains possible, however, that *E. umbellata* may be similarly exempt from large-mammal herbivory in its home range. Differences in herbivory impact, palatability to local herbivores, or investment in structural or chemical defenses between its home and away ranges would create additional support for enemy escape as an underlying cause of this invader’s success.

4.2. *F. alnus* and *V. dentatum*

*F. alnus*’ susceptibility to local herbivores differed between canopy treatments. Herbivore impact gave the invader a survival advantage over the native *V. dentatum* in the understory, but did not give the invader a growth advantage in open environments. Rather, browsing by local herbivores reduced height growth of *F. alnus* relative to native species and prevented early reproduction in uncaged *F. alnus*. Because early reproduction has been identified as a characteristic of ruderal and invasive species (Cornelissen et al., 1998; Rejmanek and Richardson, 1996), the ability of local herbivores to effectively delay reproduction in *F. alnus* suggests that biotic resistance may slow invasion by this species.

Maron and Vilà (2001) note that plants strongly affected by generalist herbivores in their native range may not escape them in their introduced range. *F. alnus* is an optimal deer forage (Gonzalez-Hernandez and Silvo-Pando, 1999) and a preferred food of roe deer (*Capreolus capreolus*) and red deer (*Cervus elephas*) within its European range (Bobek et al., 1997). In light of *F. alnus*’ dietary value, it is perhaps surprising that deer browsing did not reduce its growth in understory plots as well. Understory plants remained very small throughout the duration of the study, however, and generalist herbivory may be less severe for small plants (Levine et al., 2004).

4.3. *A. platanoides* and *A. saccharum*

We found that *A. platanoides* had greater seedling survival rates than *A. saccharum* in both open and understory plots, regardless of exclosure treatment. By contrast, Bertin et al. (2005) inferred tree seedling mortality in urban forests of central Massachusetts from a survey of standing dead and live stems, and concluded that mortality of *A. platanoides* was similar to that of shade-tolerant native species. Prior field studies have documented greater seedling abundance of *A. platanoides* than of *A. saccharum*. In a forest preserve in New Jersey, for example, the invader was nearly twice as abundant as the native in the canopy, but over five times as abundant as the native among small seedlings and saplings (Webb and Kaunzinger, 1993). Invasive seedlings were also more common than native seedlings in a suburban forest in New York; *A. platanoides* seedlings were common under both adults of both congeners, but *A. saccharum* seedlings were absent under *A. platanoides* (Martin, 1999). Our results suggest that the greater abundance of *A. platanoides* may partly reflect greater seedling survival, but that this greater seedling survival is not explained by differential impact of generalist herbivores. Differential herbivory may affect survival at an earlier stage, however; Meiners (2005) documented lower seed predation of *A. platanoides* than of *A. saccharum* in the field.

5. Conclusions

Although introduced plants may be vulnerable to herbivory by local generalists, such herbivory may still facilitate invasion if it has an even more negative effect on growth and survival of natives (Maron and Vilà, 2001; Vilà and Weiner, 2004). Colautti et al. (2004) reviewed 13 prior studies comparing presence or effect of enemies on co-occurring native and introduced plants, and found no general trend of greater enemy impact on natives. The search for a general explanation of invasiveness that will apply to most invaders may obscure factors that are important for individual species, however. Although we did observe that differential herbivory by generalists can favor non-native invaders, this pattern did not apply equally to each of the three invaders or to each measured index of plant performance. Our results are thus consistent with a Canadian field survey which found that non-native species had lower levels of herbivore damage than natives overall, but that there was much variance in damage within each group (Carpenter and Cappuccino, 2005). Although there remains controversy over the generality of enemy release as an underlying cause of invasiveness, our results clearly indicate that native large-mammal herbivory can facilitate individual non-native invaders such as *E. umbellata*.

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