



Reduced Herbivory on Exotic Buckthorn (*Rhamnus cathartica*)

Compared to Native Tree Species in an Illinois Woodland

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Woodland**

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TABLE OF CONTENTS

ACKNOWLEDGMENTS	iv
LIST OF FIGURES	vi
LIST OF TABLES	vi
ABSTRACT	1
KEY WORDS	1
INTRODUCTION	1
METHODS	1
RESULTS	3
DISCUSSION	3
LITERATURE CITED	6

LIST OF FIGURES

Figure 1.	Woodland in northeastern Illinois that has been invaded by <i>Rhamnus cathartica</i>	2
Figure 2.	Woodland in northeastern Illinois that is free of <i>Rhamnus cathartica</i>	2
Figure 3.	Leaves illustrating patterns of herbivory from the trees—A— <i>Quercus rubra</i> , B— <i>Tilia american</i> , and C— <i>Rhamnus cathartica</i> collected in northeastern Illinois	3
Figure 4.	Mean fraction of total leaves consumed by herbivores	4

LIST OF TABLES

Table 1.	Nonparametric test with a critical Q value of 3.653 among all species sampled from a northeastern Illinois woodland.....	4
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Abstract

European buckthorn (*Rhamnus cathartica*), an ornamental and fencerow shrub native to Eurasia, is a prolific invader throughout woodlands of the northeastern and midwestern United States and southern Canada. The spread of *R. cathartica* may result in the replacement of native species and the alteration of ecosystem processes. We present evidence of a potential mechanism underlying the success of *R. cathartica* release from herbivore pressures. We compared levels of foliar herbivory between *R. cathartica* and eight co-occurring native tree species in northeastern Illinois: sugar maple (*Acer saccharum*), shagbark hickory (*Carya ovata*), ironwood (*Ostrya virginiana*), black cherry (*Prunus serotina*), bur oak (*Quercus macrocarpa*), red oak (*Quercus rubrum*), basswood (*Tilia americana*) and witchhazel (*Hamamelis virginiana*). Herbivory on native species (ranging from 4.0% to 6.8% of leaf area consumed) was five to nine times higher than on *Rhamnus cathartica* (0.8%). These results, combined with studies documenting the evident herbivory in the native range of *R. cathartica*, suggest that exotic North American populations have experienced a release from herbivore pressure.

Keywords:

biological control, enemy release hypothesis, exotic species, herbivory, *Rhamnus cathartica*

Introduction

European buckthorn (*Rhamnus cathartica* L.), an ornamental and fencerow shrub from Eurasia, is a prolific invader throughout woodlands of the northeastern and midwestern United States and southern Canada (Kurylo et al. 2007; Fig. 1). The success of *R. cathartica* in replacing native species and altering ecosystem processes has been well documented (reviewed by Knight et al. 2007) and has prompted restoration/eradication efforts throughout its invasion range. Ecosystem processes and properties hypothesized to be altered by the invasion of *R. cathartica* include: faster decomposition rates; increased total soil nitrogen pools (Heneghan et al. 2002, Heneghan et al. 2004); and loss of diversity of understory flora (Leitner 1985), soil macrofauna (Heneghan et al. 2009), and other organisms (Knight et al. 2007). Phenological and morphological traits of *R. cathartica*, such as early leaf flush, late senescence (Harrington et al. 1989), and high seed production and growth rates (Archibold et al. 1997), may increase its invasive success. Through this broad suite of mechanisms, *R. cathartica* alters ecosystem processes and properties, and native communities, potentially expanding its niche and further allowing it to dominate woodlands in North America.

Another potential mechanism underlying the success of *R. cathartica* is its release from co-evolved invertebrate herbivory subsequent to transplantation from Eurasia to a novel range in North America. Reduced herbivory in the invasive range compared to native range has been reported for many foreign plant invaders (Wolfe 2002, Colautti et al. 2004, DeWalt et al. 2004, Liu and Stiling 2006). This pattern has been termed the enemy release hypothesis (Crawley 1989, Keane and Crawley 2002). Results of field testing of this hypothesis are varied, with studies indicating that an exotic species does not always incur lower levels of herbivory in the introduced range (Agrawal et al. 2005, Chun et al. 2010), suggesting that conformance to the enemy release hypothesis depends

on the species under investigation. A second way to test for evidence of the enemy release hypothesis has been to compare herbivory levels between exotic and native species; exotic species would be expected to have lower herbivory than native species due to the absence of natural enemies in the introduced range. This has been shown for many exotic species, where levels of herbivory are lower compared to native species (Schierenbeck et al. 1994, Liu et al. 2007, Cappuccino and Carpenter 2005), assumedly resulting in increased invasive abilities of several exotic species (Wolfe et al. 2002, Stastny et al. 2005, Jogesh et al. 2008).

Despite the widespread range of *R. cathartica* in North America, comparisons of herbivory on *R. cathartica* to native species has not been well documented. A study conducted in the northeastern United States and Ontario, Canada, in which herbivory levels were compared between a group of exotic species (that included *R. cathartica*) and a group of native species, indicated that the native species experienced an average of 96% more herbivory (Cappuccino and Carpenter 2005); herbivory levels on individual species were not included. We tested the hypothesis that *R. cathartica* had lower herbivory levels than native species by comparing foliar herbivory on *R. cathartica* to eight native tree species: sugar maple (*Acer saccharum* Marsh.), hickory (*Carya ovata* Mill.), ironwood (*Ostrya virginiana* Mill.), black cherry (*Prunus serotina* Ehrh.), bur oak (*Quercus macrocarpa* Michx.), red oak (*Quercus rubra* L.), basswood (*Tilia americana* L.) and witchhazel (*Hamamelis virginiana* L.) in a northeastern Illinois woodland.

Methods

We conducted our research in a 40-ha woodland preserve at the Chicago Botanical Gardens in Lake County, Illinois, 64 km north of Chicago (Fig. 2). Soils are deep and fine-textured, consisting of silt and clay loams derived from loess or glacial till. Mean annual precipitation is



Figure 1. Photograph of a woodland in northeastern Illinois that has been invaded by *Rhamnus cathartica*.



Figure 2. Photograph of a woodland in northeastern Illinois that is free of *Rhamnus cathartica*.

approximately 93 cm and mean annual air temperature was approximately 9.4 °C between 1987 and 2002, according to a weather station within 5 km of the study site with an elevational range of 200 to 300 m.

We collected leaves in September of 2002, at peak leaf standing crop, after leaves had been exposed to a full season of herbivory (Fig. 3). The nine tree species selected were co-dominant in this woodland. We sampled five trees of each species separated by random distances of between 0.1 and 1.0 km. Prior to sampling, we visually estimated that herbivory was focused on low- to mid-canopy levels (< 6 m height). We sub-sampled each tree by clipping five stems from each side of the tree (north, south, east, west, and center) at random tree heights below 6 m. For *R. cathartica*, *P. serotina*, and *H. virginiana*, typically low-statured trees, this represented the entire height range of these trees. Each clipping contained a shoot from a terminal branch with an average of between 4 and 19 leaves per shoot for a total of 1,136 leaves across all species. The difference between the numbers of leaves scanned by species is a result of stems having varying numbers and sizes of leaves. We clipped the leaves from the shoots, removed stems, and then glued the leaves onto tabloid-sized herbarium paper.

We scanned each tabloid paper containing leaves with a Hewlett Packard scanner at a resolution of 300 dpi and then imported the resulting files into Adobe Photoshop. Images were converted to grayscale and shadows generated in the scanning process were erased. We outlined consumed areas to 1 pixel (85 μm), allowing us greater precision in measuring herbivory in skeltonized areas of the leaf that would not have been detectable with a leaf area meter. We estimated where the edge of the leaf existed prior to herbivory, based primarily on symmetry considerations and the general patterns of leaf morphology in individual species. Image analysis was performed using a plugin we wrote in Java for the open source program ImageJ from the National Institutes of Health (<http://rsb.info.nih.gov/ij/>) that calculated the total areal fraction of the leaf consumed by herbivores.

A test of the data for conformity with the requirements for a one-way analysis of variance (ANOVA) revealed that the data were neither normally distributed nor were the variances homogenous. Therefore, to detect differences among species in total areal fraction of the leaf consumed

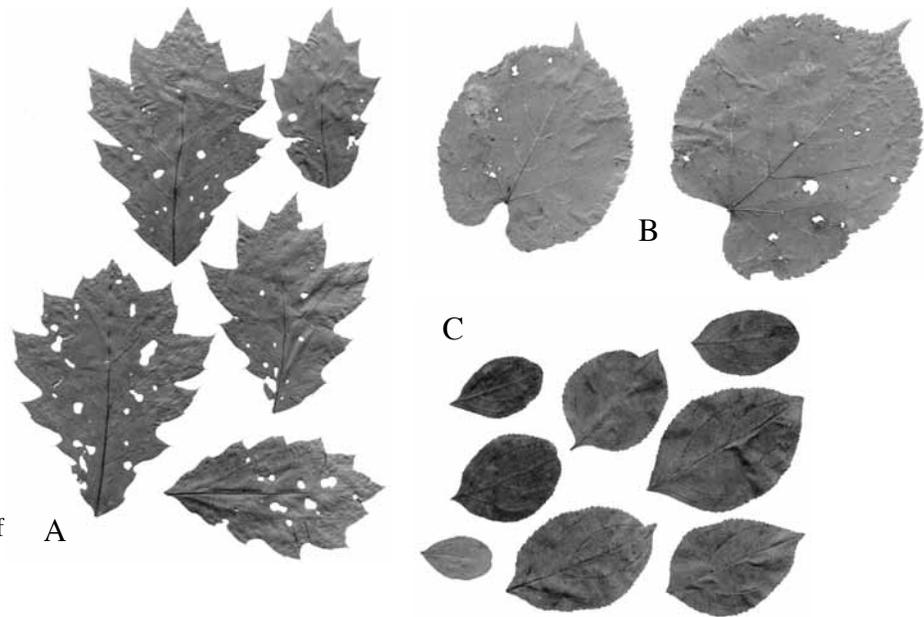


Figure 3. Leaves illustrating patterns of herbivory from the trees A—*Quercus rubra*, B—*Tilia americana*, and C—*Rhamnus cathartica*, collected in northeastern Illinois.

by herbivores, we used a nonparametric Kruskal-Wallis test and conducted nonparametric multiple comparisons using the tied-rank method of Dunn (1964). All tests were conducted using the alpha = 0.01 significance level.

Results

Consistent with our hypothesis, our results demonstrated that in this Illinois woodland, *R. cathartica* incurred lower herbivory compared to the eight native species with which it was compared (Table 1). The Kruskal-Wallis test rejected the hypothesis that herbivory was the same by species ($p < 0.0001$), whereas the multiple comparison test (critical statistic $Q_{0.01, 9} = 3.653$) indicated that herbivory was significantly lower on buckthorn compared to the native species (Table 1). The nonparametric multiple comparisons divided the nine species into three statistically distinct groups: the mean herbivory as a fraction of the total leaf area is the same for *A. saccharum*, *C. ovata*, *O. virginiana*, *Q. macrocarpa*, *Q. rubrum*, *T. americana*, and *H. virginiana*; *P. serotina* is its own group with a lower level of herbivory than the other native species; and *R. cathartica* having the the very lowest amount of herbivory (Table 1). The mean percent herbivory of *R. cathartica* was 0.8%, which was significantly lower than the mean of all native species that ranged from 4.0% to 6.8% (Fig. 4).

Discussion

We demonstrated that herbivory on native co-dominant trees was five to nine times higher compared to the exotic *R. cathartica* (Fig. 4) in an Illinois woodland. These results are similar to several studies that found exotic species to have reduced herbivory compared to native species (Schierenbeck et al. 1994, Cappuccino and Carpenter

Table 1. Nonparametric test with a critical Q value of 3.653 among all species sampled from a northeastern Illinois woodland. Each species is compared with every other species to determine if there is a significant difference among species in percent herbivory. If $Q > 3.653$, a significance has been shown (bold). The table shows that buckthorn and cherry are distinct from each other and all other species, while the remaining species are indistinguishable from one another in terms of percent herbivory.

Species	<i>R. cathartica</i>	<i>A. saccharum</i>	<i>C. ovata</i>	<i>H. virginiana</i>	<i>O. virginiana</i>	<i>P. serotina</i>	<i>Q. macrocarpa</i>	<i>Q. rubrum</i>	<i>T. americana</i>
<i>R. cathartica</i>		11.74	11.37	14.75	12.93	8.76	12.50	12.14	11.81
<i>A. saccharum</i>			0.09	2.96	0.28	3.88	1.43	2.27	1.81
<i>C. ovata</i>				2.80	0.36	3.84	1.31	2.14	1.70
<i>H. virginiana</i>					3.47	7.00	1.41	0.35	0.83
<i>O. virginiana</i>						3.99	1.80	2.64	2.16
<i>P. serotina</i>							5.18	5.68	5.25
<i>Q. macrocarpa</i>								0.92	0.47
<i>Q. rubrum</i>									0.43
<i>T. americana</i>									

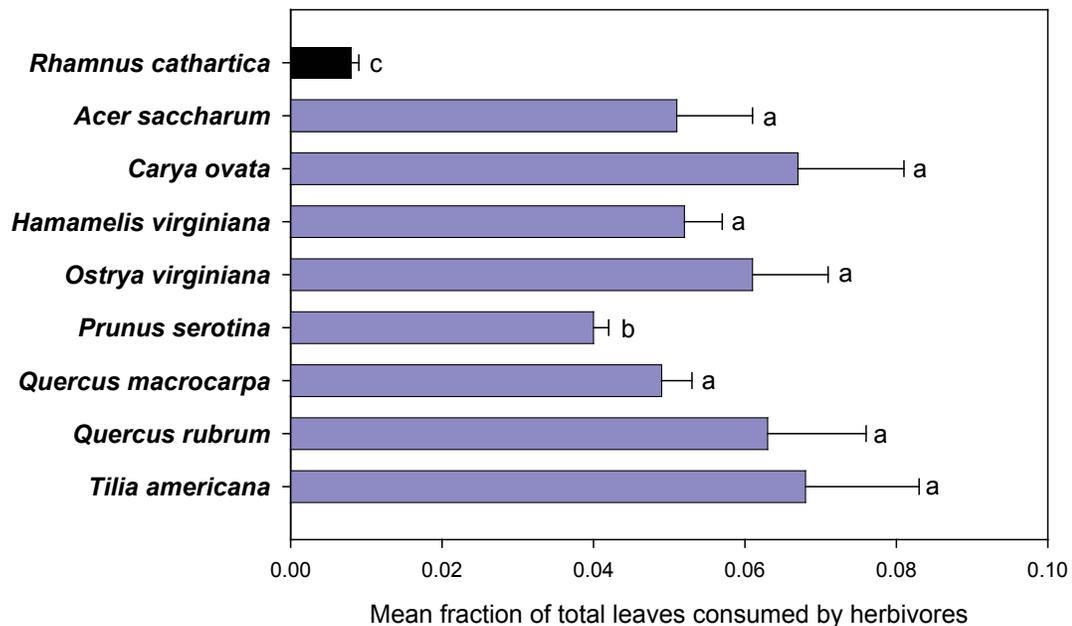


Figure 4. The mean fraction (and one standard error of the mean) of total leaves consumed by herbivores on exotic species (black bar) and native species (purple bars) in a woodland in northeastern Illinois. Statistical significance of differences between species was tested at the $\alpha = 0.01$ level of significance according to the method of Dunn using tied ranks.

2005, Liu and Stiling 2006). On the other hand, several within-community comparisons indicate that introduced species do not consistently receive less damage from herbivores than native species, suggesting that the enemy release hypothesis may not be applicable to all invasive plants (reviewed by Colautti et al. 2004). Our results should be interpreted conservatively due to sampling in a relatively small area and in sampling restricted to low and mid-canopy levels. We confined our observation to replicated individuals of several species in the one area, making the reasonable assumption that this area hosted a representative population of leaf herbivores in the woodland. Confining this preliminary study to a single 40-ha woodland ensured enough individuals for adequate replication of the species, while maintaining a relatively homogeneous, spatially consistent herbivore community.

While our study is the first that we know of to directly quantify herbivory levels on both *R. cathartica* and native species, indirect, anecdotal evidence from other studies suggests that herbivory on *R. cathartica* is lower than on native species across a large portion of its non-native range. In Minnesota, repeated observations (that were not quantified) suggested a lack of herbivory on *R. cathartica* (Yoder et al. 2008). In addition, a study in northeastern United States and Ontario, Canada, (Cappuccino and Carpenter 2005) found lower herbivory on group of exotic species (including *R. cathartica*) compared to a group of native species. Taken together, these findings support the speculation that herbivory on *R. cathartica* is lower than on many native species throughout North America.

Although we did not explicitly test the enemy release hypothesis (i.e., by comparing *R. cathartica* herbivory in its native and introduced range), some evidence suggests that *R. cathartica* is released from herbivore pressure in its non-native range. It has been reported that herbivory is common in the native Eurasian range of *R. cathartica* (Gassman et al. 2008) with many species-specific plant-herbivore relationships (Bagnall 1930, Malicky et al. 1970, Gassman et al. 2008), including herbivory by insects (that would assumedly not occur in North America) that directly consume leaves (Gassman et al. 2008). If *R. cathartica* is exposed to more herbivory in its native range than in its invasive range, as this evidence would suggest, then it appears that *R. cathartica* conforms to the enemy release hypothesis.

While we did not measure the impacts of herbivory on photosynthetic or growth rates, several studies indicate that small differences in the amount of leaf area consumed by herbivores can have large effects on growth and photosynthesis. In our study, we found that herbivory was between approximately 3% to 7% less on *R. cathartica* compared to native species. A 5% increase in the total amount of leaf area removed by caterpillars on wild parsnip (*Pastinaca sativa*) resulted in a 25% decrease in total plant photosynthesis (Zangerl et al. 2002), while mechanical removal of 2% of leaf area on *P. sativa* resulted in a 9% reduction in above-ground biomass production

and a 14% reduction in below-ground biomass production (Zangerl et al. 1997). In another study, a 1% decrease in the total leaf area consumed by insect herbivores on the exotic Chinese tallow tree (*Sapium sebiferum*), resulted in a 100% increase in aboveground biomass production at a dry prairie site, while a 6% reduction had no effect on production in a more mesic environment. These studies illustrate the potential for small amounts of herbivory to have large consequences on growth, but they also indicate that the consequences of herbivory on growth vary by species and/or environment. Species and or environmental variation in growth response to herbivory are well documented, with reports of reduced growth, compensatory growth, and no effect (reviewed by Mitchell et al. 2006, Nability et al. 2009). While some research has shown that decreased herbivory on exotic plants compared to native plants may reduce productivity and competitive abilities of native plants (Crawley 1989), potentially increasing the susceptibility of native plant communities to invasion by unencumbered exotics (Jogesh et al. 2008), we do not have the data to support these contentions in our study system. Future research should address if herbivory on exotic *R. cathartica* compared to native species influences growth rates and competition.

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