# ORIGINAL PAPER

# Testing the enemy release hypothesis: a comparison of foliar insect herbivory of the exotic Norway maple (*Acer platanoides* L.) and the native sugar maple (*A. saccharum* L.)

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Abstract Norway maple (Acer platanoides) is a Eurasian introduced tree species which has invaded the North American range of its native congener, sugar maple (A. saccharum). One hypothesis used to explain the success of an invasive species is the enemy release hypothesis (ERH), which states that invasive species are often particularly successful in their new range because they lack the enemies of their native range. In this study, we hypothesized that Norway maple would have less insect damage than sugar maple due to such enemy release. Autumn 2005 and summer 2006 leaves of Norway and sugar maple were collected from six sites in New Jersey and Pennsylvania to compare percent leaf area loss, gall damage, fungal damage, and specific leaf area  $(cm^2/g)$ . Although both species had low overall mean levels of leaf damage (0.4-2.5%), in both years/seasons Norway maple had significantly less leaf damage than sugar maple. Insects were also collected to compare insect assemblies present on each tree species. The numbers of insect taxa and individuals found on each species were nearly equivalent. Overall, the results of this study are consistent with the enemy release hypothesis for Norway maple. In addition, sugar maples when surrounded by Norway maples tended to show reduced herbivory. This suggests that the spread of Norway maple in North America, by reducing amounts of insect herbivory, may have further ecosystem-wide impacts.

**Keywords** Acer platanoides · Enemy release hypothesis · ERH · North America · Herbivory

# Introduction

Biological invasion occurs when an organism from one location becomes established, generally through human interference, in another location containing organisms with which it has not shared an evolutionary history (Elton 1958). An invasive tree species in the United States that is receiving increasing attention is the Eurasian Norway maple (Acer platanoides). Norway maple became established in North American forests after being planted widely as a street tree to replace elm trees lost to Dutch elm disease (Nowak and Rowntree 1990). The naturalized distribution of Norway maple now covers much of the Northeastern United States and overlaps largely with the range of sugar maple (A. saccharum). Studies have shown that within its invasive range, Norway maple is capable of dominating forest stands and decreasing understory species richness (Webb and Kaunzinger 1993; Wychoff and Webb 1996; Martin 1999). These studies indicate that Norway maple successfully competes with sugar maple and will most likely

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increase its range and decrease that of the native sugar maple unless there is future intervention.

One major theory used to explain the success of invasive species in their introduced range is the enemy release hypothesis, or ERH (Jones and Lawton 1991; Keane and Crawley 2002). The ERH proposes that invasive species are able to succeed in their new range (achieving higher population densities and broader ecological ranges than in their native range) because they have been released from the pressures that kept their population in check in their native ranges, such as predation, herbivory, disease, and parasitism (Keane and Crawley 2002). In recent years a number of studies testing enemy release have been published, many providing support for this hypothesis (Wolfe 2002; Mitchell and Power 2003; Dietz et al. 2004; DeWalt et al. 2004; Reinhart and Callaway 2004; Liu et al. 2007), as well as some that provide evidence to the contrary (Agrawal and Kotanen 2003; Colautti et al. 2004). In one such study, Jongejans et al. (2006) used population transition matrix models to investigate the effects of specialist enemies in the native range of the invasive thistle Carduus nutans, and found that the removal of insect herbivores increased the population growth of this thistle by 166% on average. In 2005, Agrawal et al. examined the effects of various enemies on native and nonnative plant congeners, and found that although natives experienced greater levels of damage, variations among enemies and over time could cancel out or negate this effect. According to this study, variation in the net effect of enemies may create opportune times when invasive plants are able to temporarily gain ground in their introduced range Agrawal et al. (2005).

Norway maple has several characteristics which could contribute to its success as an invasive species, such as high shade tolerance as a sapling, the ability to cast deep shade, larger seeds than sugar maple, lower rates of seed predation than sugar maple, greater rates of carbon assimilation than sugar maple, and higher water use efficiency than sugar maple (Kloeppel and Abrams 1995; Lei and Lechowicz 1998; Webb et al. 2000; Meiners 2005). However, although the possibility that Norway maple experiences less insect herbivory as compared to native trees has been discussed, it has not been experimentally examined as a possible reason for the success of the species (Wychoff and Webb 1996; Webb et al. 2001).

Release from foliar insect herbivory may be part of the explanation for the success of Norway maple in North America, as insect herbivory can significantly impact plant success and survival. The removal of leaf tissue not only decreases the amount of photosynthetic surface available to the plant, but can impact the plant in various ways. Herbivory affects plants by reducing growth rate, decreasing nutrient mobility, increasing the rate of water loss, lowering photosynthetic rates in leaf tissue, reducing seed output, reducing the emergence of seedlings, and increasing the probability of tree dieback in grown trees (Aldea et al. 2005; Nykanen and Koricheva 2004; Zangerl et al. 2002; Bentley et al. 1980; Meiners et al. 2000; Lowman and Heatwole 1992). The absence of severe insect damage to Norway maple is one reason that this species remains a popular choice for a street tree, and may play a role in the invasion of Norway maple in North American forests. Our hypothesis is that Norway maple has less insect damage than sugar maple due to enemy release and that this difference in insect damage could contribute to the success of Norway maple in its nonnative range (although the latter part of this hypothesis was not tested here). This study sets out to quantify and compare the amount of herbivory suffered by the two species when they coexist in forest stands.

# Methods

#### Site criteria

In order to compare levels of herbivory for Norway and sugar maple, leaves were collected from six sites where the two species co-occurred (Table 1). Each site consisted of an area of contiguous forest greater than two hectares and containing a threshold of ten individuals of both Norway and sugar maple with a dbh > 5 cm within a 1 ha circular plot. Sites were a minimum of 5 km apart from one another. Sites 1, 4, and 5 had sugar maple densities which were equal to or higher than Norway maple densities, and sites 2, 3, and 6 had sugar maple densities. Leaves were collected three times from each site: in winter 2005, May 2006, and July 2006.

# Collection of autumn leaves

At each of the six sites, leaves were collected from a 1 ha circular plot (r = 56.42 m) which met the above criteria and was set at least 20 m away from the edge of the forest stand to prevent edge effects. Leaves were collected in December 2005 and January 2006 after leaf fall occurred. In each plot, four transects equal to the length of the diameter of the plot were placed through the center of the plot to achieve maximum coverage of the plot. A handful of leaves was collected every five meters (22 collections per transect) along each transect. Leaves were taken from the top layer of leaf litter and placed in separate bags for each half transect.

Twelve leaves, or the maximum number of leaves available if less than 12, of each species of tree were taken from each bag at random. In situations where the total number of leaves of one species was such that this method resulted in an N < 50 leaves, all leaves collected for the species were used for herbivory quantification. Using SigmaScan Pro 4.0, leaves were scanned to determine percentage area lost to herbivory. A general linear model in an analysis of variance (ANOVA) was used to compare mean percent area loss values for Norway and sugar maple (SPSS 11.5). Three factors were included in this model: site, species, and leaf. Because percentage values were used, the data were arcsine-root transformed.

# Collection of summer leaves

In May and July of 2006, live leaves were collected directly from individuals of Norway and sugar maple in order to compare insect damage. At each site, five individuals (>5 cm dbh) of each species were selected and two branches (one from the north side and one from the south side) were removed using a pole pruner. Branches were taken approximately 4.5 m from the ground. The 15 youngest leaves from each branch were removed and scanned using SigmaScan Pro 4.0. Area loss was separated into three categories: chewed, skeletonized, and leaf miner damage. Leaf gall damage and fungal damage were also quantified. The total area  $(cm^2)$  of each leaf used in the analysis of leaf damage was determined in order to compare leaf area of Norway maple and sugar maple. Specific leaf area (SLA, cm<sup>2</sup>/g) of Norway and sugar maple was compared by obtaining the dry mass of 10 leaves of each species with no herbivore damage from the sample of leaves collected in July in addition to measuring total leaf area.

A general linear model in an analysis of variance (ANOVA) was used to compare mean percent area loss values for A. platanoides and A. saccharum (SPSS 11.5). Five factors were included in this model: time, site, species, tree, and branch. Because percentage values were used, the arcsine-root transformation was used to account for the proportions.

#### Insect collection

Concurrently with the collection of summer leaves, insects were collected at all six sites. Before removal of leaves from the tree branches in May and July, 2006, each branch was scanned thoroughly for insects. As the insects classified here represent only

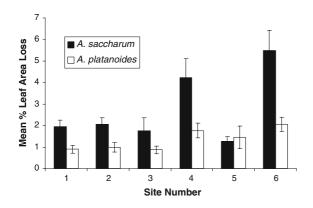
Table 1         Site location,           site coordinates, and         Image: Site location in the site coordinates in the site location in the site loc	Site number	Site location	Coordinates	Maple densities
comparative sugar maple and Norway maple	1	Madison, NJ	40°45′415″ 74°25′566″	Sugar maple densities = Norway maple densities
densities	2	Hillsborough, NJ	40°33'108"	Sugar maple densities < Norway maple densities
			74°38′360″	
	3	Morristown, NJ	40°47'709"	Sugar maple densities < Norway maple densities
			74°30′449″	
	4	West Orange, NJ	40°48'719"	Sugar maple densities > Norway maple densities
			74°14′481″	
	5	Ringwood, NJ	41°07′202″	Sugar maple densities > Norway maple densities
			74°14′127″	
	6	Swarthmore, PA	39°54′273″	Sugar maple densities < Norway maple densities
			75°21′650″	

those that were present on leaves collected for determining leaf area loss, this is a preliminary study and does not represent an extensive collection. All insects were removed and placed in vials for later observation. Vials were stored at 5°C. Insects were classified to the lowest identifiable taxon chiefly using Rose and Lindquist (1982) and Borror and White (1970). Many were classified to family; some were classified to genus and some only to order. Insects were also categorized as chewing, sucking, or predatory insects.

# Results

Autumn leaves, year 1

In an overall comparison of sugar maple and Norway maple based on fall leaves, sugar maple had a significantly higher amount of herbivory. The mean



**Fig. 1** Mean percent leaf area loss for *A. saccharum* and *A. platanoides* as determined using autumn 2005 leaves at each of the six sites. Bars represent one standard error of the mean. For sites see Table 1

percentage area lost by sugar maple  $(2.493 \pm 0.218$ , mean  $\pm$  SE) was nearly twice the mean percentage area lost by Norway maple  $(1.330 \pm 0.120$ , mean  $\pm$  SE) (Table 2, ANOVA details in Table 3). The mean area lost by sugar maple was significantly greater than that lost by Norway maple at sites 1, 2, 4, and 6, but not at the two remaining sites (Fig. 1). The mean percent area lost by Norway maple was similar across sites, and showed less variation than that of sugar maple. Of sugar maple leaves, 92.4% had some amount of leaf area lost due to insect herbivory, whereas 84.0% of Norway maple leaves had leaf area lost due to insect herbivory.

#### Summer leaves, year 2

In an overall comparison of Norway and sugar maple summer leaves, sugar maple had a higher mean percent leaf area loss than Norway maple. The mean percent leaf area loss of sugar maple (1.655  $\pm$  0.102, mean  $\pm$  SE) was about four times greater than the mean percent leaf area loss of Norway maple  $(0.401 \pm 0.052, \text{ mean} \pm \text{SE})$  (Table 2, ANOVA details in Table 3). Mean percent leaf area loss was higher in the July collection than in the May collection. Site differences accounted for significant variance in values of mean percent leaf area lost, yet the majority of sites showed that sugar maple had a significantly greater mean percent leaf area loss than Norway (Fig. 2). Of sugar maple leaves, 77.2% had some amount of leaf area lost due to insect herbivory, whereas only 47.8% of Norway maple leaves had leaf area lost due to insect herbivory (Fig. 3). The majority of leaves of both species which lost leaf area due to insect damage suffered chewing damage. Chewing insects damaged 76.0% of sugar maple leaves, and 44.8% of Norway maple leaves.

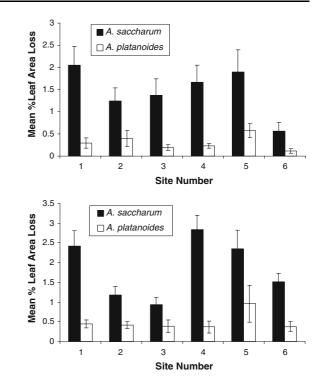
**Table 2** Overall means (across sites), standard errors, and *P* values of percent area lost, absolute area lost, percent fungal damage, leaf area, and specific leaf area from sugar maple and Norway maple leaves collected in the fall and the summer

Collection time	Measurement	Sugar maple	Norway maple	P value
Autumn	Percent area lost	2.493 (0.218)	1.330 (0.120)	>0.001
Summer	Percent area lost	1.655 (0.102)	0.401 (0.052)	>0.001
Summer	Absolute area lost (cm <sup>2</sup> )	0.062 (0.012)	0.255 (0.030)	>0.001
Summer	Percent fungal damage	0.177 (0.017)	0.062 (0.012)	>0.001
Summer	Leaf area (cm <sup>2</sup> )	58.562 (0.763)	73.966 (1.285)	>0.001
Summer	Specific leaf area (cm <sup>2</sup> /g)	378.675 (4.068)	342.151 (8.115)	0.001

Standard errors are in parentheses. P values were calculated using a general linear model in an analysis of variance (ANOVA)

Species	% Area lost autumn leaves) <sup>a</sup>	ves) <sup>a</sup>	% Area lost (summer leaves)	mer leaves)	Absolute	Absolute area lost (cm <sup>2</sup> )		% Fungal damage <sup>a</sup>	Leaf area (cm <sup>2</sup> )	(cm <sup>2</sup> )
Sugar 2 Norway 1	2.493 (0.218) 1.330 (0.120)		1.655 (0.102) 0.401 (0.052)		0.841 (0.053) 0.255 (0.030)	)53) )30)	0.177 0.062	0.177 (0.017) 0.062 (0.012)	58.562 (0.763) 73.966 (1.285)	.763) .285)
Source (df)	Mean square	P value	Mean square	P value	Mean square	P value	Mean square	P value	Mean square	P value
Time (1)	NA		0.252	<0.001	41.179	<0.001	0.021	<0.001	3757.851	0.162
Site (5)	0.174	<0.001	0.080	<0.001	14.926	< 0.001	0.015	< 0.001	24836.616	<0.001
Species (1)	0.555	<0.001	2.613	<0.001	318.103	<0.001	0.023	< 0.001	206837.124	<0.001
Tree (4)	NA		0.007	0.367	8.175	0.037	0.001	0.575	10636.549	<0.001
Branch (1)	NA		0.010	0.206	0.0002	0.993	0.001	0.445	2390.680	0.265
Time*Species (1)	(1) NA		0.082	0.001	4.689	0.226	0.001	0.620	7037.101	0.056
Site*Species (5)	5) 0.025	0.007	0.061	<0.001	8.036	0.028	0.010	<0.001	12061.510	<0.001
Error	0.008		0.006		3.201		0.001		1921.0921	

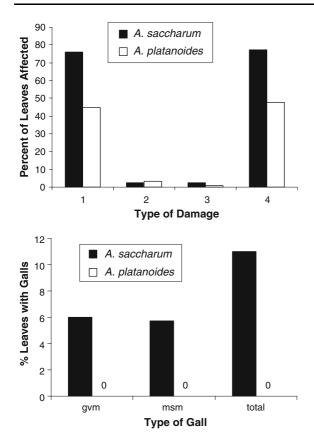
df for Error: 793 (area lost summer leaves), 995 (area lost fall leaves), 3509 (fungal damage), 3509 (all other parameters)



**Fig. 2** Mean percent leaf area loss for *A. saccharum* and *A. platanoides* as determined using live leaves at each of the six sites. The upper graph represents data from leaves collected in May 2006, and the lower graph represents data from leaves collected in July 2006. Bars represent standard error of the mean

In a comparison of sites including leaves from both summer collections, the three sites with the highest sugar maple densities had significantly higher mean percent sugar maple leaf area loss due to insect damage than sites with lower sugar maple densities. Sites with high sugar maple density had a mean percent sugar maple leaf area loss of  $2.212\% \pm 0.173$ (mean  $\pm$  SE), twice that of sites with low sugar maple density ( $1.116\% \pm 0.107$ , mean  $\pm$  SE). Mean percent Norway maple leaf area loss varied less between sites than that of sugar maple, and did not vary based on sugar or Norway maple density.

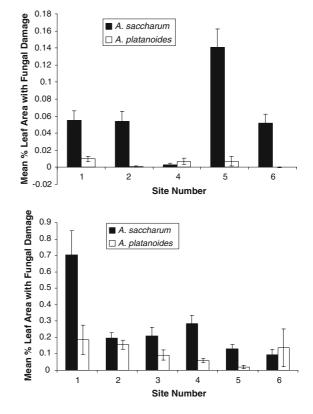
Of all leaves collected in both May and July, no Norway maple leaves contained gall damage, whereas 11% of sugar maple leaves contained gall damage. Two types of gall damage were present on sugar maple: galls from the gouty vein midge (*Dasineura communis*, Diptera) damaged 6% of sugar maple leaves, and galls from the maple spindlegall mite (*Vesates aceriscrumena*, Acari) damaged 5.7% of sugar maple leaves (Fig. 3). Sugar



**Fig. 3** Percentage of *A. saccharum* leaves and *A. platanoides* leaves with insect damage. The upper graph represents the percentage of leaves with different types of leaf damage. Chewing damage is labeled 1, skeletonizer damage is labeled 2, leaf miner damage is labeled 3, and general insect damage (including all categories) is labeled 4. The lower graph represents the percentage of leaves with galls from the gouty vein midge (gvm) and the maple spindlegall mite (msm)

maple also had significantly greater mean percent leaf area with fungal damage than Norway maple. Mean percent leaf area with fungal damage was significantly greater in July than in May. For the May collection, site 3 was removed from the analysis of fungal damage due to accidental fungal damage that occurred after collection. In a comparison of fungal damage for each site and collection time, the majority of sites had significantly greater fungal damage of sugar maple than of Norway maple (Fig. 4).

An overall comparison of sugar maple leaves and Norway maple leaves collected in May and July showed that Norway maple leaves had significantly greater surface area than sugar maple leaves (Table 2). Leaf area differed significantly between



**Fig. 4** Mean percent leaf area with fungal damage for *A. saccharum* and *A. platanoides* as determined using live leaves at each of the six sites. The upper graph represents data from leaves collected in May 2006, and the lower graph represents data from leaves collected in July 2006. Bars represent one standard error of the mean

sites, but leaf area did not change significantly between May and July. The mean specific leaf area of sugar maple (378 cm<sup>2</sup>/g  $\pm$  4, mean  $\pm$  SE) was significantly higher than the specific leaf area of Norway maple (342 cm<sup>2</sup>/g  $\pm$  8, mean  $\pm$  SE) in a comparison of the two species, although Norway maple showed greater variation than sugar maple (Table 2, n = 10).

# Associated insects

The number and type of insects collected in May differed from those collected in July. More insects were collected in May (69) than in July (29). In May, 33 insects from 7 insect orders were found on Norway maples, and 36 individuals from 5 insect orders were found on sugar maples (Table 4). In July, 13 insects from 5 orders were found on Norway

May 2006 collection				July 2006 collection			
Order	Туре	Ind. on Norway	Ind. on sugar	Order	Туре	Ind. on Norway	Ind. on sugar
Coleoptera	Chewing	2	3	Acarina	Sucking	1	0
Hemiptera	Sucking	10	19	Coleoptera	Chewing	2	6
Hemiptera	Predatory	2	0	Hemiptera	Sucking	5	0
Homoptera	Sucking	4	2	Homoptera	Sucking	3	1
Hymenoptera	Chewing	3	0	Lepidoptera	Chewing	0	1
Lepidoptera	Chewing	8	10	Orthoptera	Chewing	2	8
Orthoptera	Chewing	2	2				
Trichoptera	"Sponging"	1	0				
Unknown		1	0				
Total orders		7	5	Total orders		5	4
Total individuals		33	36	Total individuals		13	16

 Table 4 Distribution of insect orders on Norway maple trees and sugar maple trees from insects collected in May and July 2006 (total number leaves for each month)

maple, and 16 insects from 4 orders were found on sugar maple (Table 4). Overall, four taxa of chewing and three taxa of sucking insects were found on Norway maple, whereas three chewing taxa and two sucking taxa were found on sugar maple.

## Discussion

Analyses of both shed autumn leaves and live leaves showed the native sugar maple to have higher amounts of foliar insect damage than the invasive Norway maple. An analysis of summer leaves showed that gall damage was present on over 10% of sugar maple leaves, but entirely absent from Norway maple leaves. In addition, fungal damage on sugar maple summer leaves was greater than that on Norway maple summer leaves. Each of these findings is consistent with the enemy release hypothesis; however, there are several additional points concerning this data that should be considered.

In both years, the mean percentage of leaf area lost for Norway maple had very low site to site variation, whereas that of sugar maple varied greatly between sites. In year 1 (autumn leaves), the mean percentage of foliar insect damage of sugar maple varied strongly between sites (5.50% in Swarthmore, PA and 1.26% in Ringwood, NJ). An analysis of summer leaves in year 2 showed a similar pattern in both May and July collections. A recent study (Adams et al. 2008) comparing sites in Europe and North America has shown that in its native range, Norway maple likewise has strong site-to-site variation in herbivory (10–30%), but consistently low values in its introduced range in North America. In year 2 the site differences in the mean percentage of leaf area lost for sugar maple were found to be correlated to the relative densities of maple species at each site. Sites with higher sugar maple densities had nearly twice the mean percent sugar maple leaf area loss than that of sites with lower sugar maple densities. This pattern agrees with the resource concentration hypothesis put forth by Janzen (1970), which suggested that herbivores can find host plants more easily when the host plants occur at high density.

Although the differences in herbivory observed between sugar and Norway maple were consistent with the enemy release hypothesis, in both years the mean leaf area loss of both species was low. The area loss of sugar maple, though greater than that of Norway maple, is low enough to put in doubt the biological significance of this difference. However, studies have shown that low levels of insect herbivory can impact trees in multiple ways. Whittaker and Warrington (1985) studied the impacts of different levels of insect herbivory on sycamore maple (Acer platanoides) trees through experimental ant predation, in order to lower herbivore populations. Mean radial growth of these mature trees with 6-10% leaf area loss to herbivory, was 35% lower than sycamore trees with 1–1.6% leaf area loss to herbivory. Crawley (1983) found that oak trees with 12% leaf area defoliation

had a more than 50% reduction in acorn production compared to controls. It is plausible therefore that the difference in herbivory levels of sugar maple and Norway maple could over time result in differences in both tree growth and seed output, each of which would give the invasive Norway maple a competitive edge. Even relatively small amounts of damage may scale up to a large impact, as insect damage sites tend to decrease the function of neighboring leaf tissues as well (Zangerl et al. 2002).

Gall and fungal damage on sugar maple and Norway maple corresponded to the overall trend in herbivory observed. The complete absence of gall damage on the invasive Norway maple suggests that the two types of gall-causing insects responsible for this damage, the maple spindlegall mite and the gouty vein midge, are host selective. Gall-causing insects can have major impacts on trees: in cherry tree (Prunus) leaves and sumac (Rhus) leaves, leaf galls were found to reduce the photosynthetic rate of affected leaves by 24-52% compared to ungalled leaves (Larson 1998). In addition, certain leaf spot diseases can have major impacts on photosynthetic rates of infected leaves. Lopes and Berger (2001) examined the effects of rust disease and anthracnose disease on bean (Faba) leaves and found that although the effects of rust disease were minimal, anthracnose spots severely impaired the photosynthetic rate of infected leaves. Lopes and Berger (2001) also found that small fungal spots can have an area of effect which is much greater than the visible damage. Therefore, it is possible that the lack of gall damage and the lower level of fungal damage experienced by Norway maple trees could provide it with an advantage over sugar maple.

The larger average leaf size of Norway maple compared to sugar maple appears to be contrary to the trend of lower herbivore damage observed, as larger leaves are generally easier for insect herbivores to exploit than smaller leaves (Brown et al. 1991). However, the larger specific leaf area of sugar maple compared with that of Norway maple could account for the differences in leaf damage of the two species and provide an alternative explanation to enemy release. Thicker leaves may be tougher and more difficult to digest, and therefore smaller areas of leaves would be removed by herbivores. Also, thicker leaves could mean that smaller areas of leaf provide insects with a greater mass of leaf tissue. Interestingly, the results of the insect collection seem to contradict the findings of the analysis of leaf damage. For both collection periods, the number of insect taxa and the number of insect individuals found on sugar maple and Norway maple were nearly equivalent. Invasive trees are generally thought to harbor fewer insects, which in turn leads to fewer birds preying on the insects, but this does not seem to be the case for Norway maple. As the data obtained in this preliminary study contradict the idea that invasive trees are nearly insect-free, it suggests that more rigorous testing of this theory is needed.

Insect herbivory can impact ecosystem processes in multiple ways, as insects alter nutrient availability in the soil, remove plant biomass and sequester nutrients, and can impact the speed at which nutrient cycling occurs (Huntly 1991). Therefore the patterns observed in this study may have a meaningful impact on invaded ecosystems. Not only does Norway maple have significantly lower levels of herbivory than its native congener, but sugar maple trees had lower levels of herbivory when surrounded by more Norway maple than sugar maple. This may be an example of the concept of plant defense guilds put forth by Atsatt and O'Dowd (1976), which suggests that plants with strong anti-herbivore defenses may reduce herbivory of neighboring plants. Hjalten and Price (1997) tested this hypothesis using willow trees and stem-galling sawflies, and found that willows associated with neighbors of low palatability gained protection from sawflies. Therefore, although sugar maple populations suffer as a result of competition with Norway maple, sugar maple individuals surrounded by Norway maple individuals may benefit through reduced insect damage. As Norway maple tends to form monospecific stands in its introduced range, the results of this study suggest that these invaded ecosystems could have lower levels of insect herbivory overall. Ecosystem functions, such as production, consumption, decomposition, and nutrient cycling are impacted by insect herbivory. In such a situation, "ecosystem enemy release," in addition to population level enemy release, could be said to occur. As ecosystems dominated by an invasive species lacking "enemies" will be fundamentally changed in their nutrient cycling as well as their food chain composition, this "ecosystem enemy release hypothesis," or EERH, can and should be tested empirically.

Although the results of this study are consistent with the enemy release hypothesis, further testing would be necessary in order to determine if enemy release is a major factor contributing to the spread of Norway maple in its introduced range. Future studies should examine the impacts of low levels of herbivory on sugar maple and Norway maple. A comparison of insect herbivory of young Norway maple and sugar maple trees, as well as a comparison of root damage of these species, might reveal differences parallel to those observed in this study. Analysis of leaf chemistry of both maple species could be done as well. A more complete assessment of insect guilds found within Norway maple and sugar maple trees should be done. Lastly, the effects of reduced insect herbivory on forest stands containing high densities of Norway maple should be examined to gain a better understanding of the role of Norway maple in the ecosystems it invades.

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## References

- Adams JM, Fung W, Sullivan R, Cipollini D, TRAIN members (2008). Norway maple (*Acer platanoides* L.) has three times as much herbivory in its native range in Europe as in its introduced range in North America. Biol Invasions (in press)
- Agrawal AA, Kotanen PM (2003) Herbivores and the success of exotic plants: a phylogenetically controlled experiment. Ecol Lett 6:712–715
- Agrawal AA, Kotanen PM, Mitchell CE, Power AG, Godsoe W, Klironomos JN (2005) Enemy release? An experiment with congeneric plant pairs and diverse above- and belowground enemies. Ecology 86:2979–2989
- Aldea M, Hamilton JG, Resti JP, Zangerl AR, Berenbaum MR, DeLucia EH (2005) Indirect effects of insect herbivory on leaf gas exchange in soybean. Plant Cell Environ 28: 402–411
- Atsatt PR, O'Dowd DJ (1976) Plant defense guilds. Science 93:24–29
- Bentley S, Whittaker JB, Malloch AJC (1980) Field experiments on the effects of grazing by a Chrysomelid beetle (*Gastrophysa viridula*) on seed production and quality in *Rumex obtusifolius* and *Rumex crispus*. J Ecol 68:671–674

- Borror DJ, White RE (1970) Peterson field guides: insects. Houghton Mifflin Company, New York
- Brown VK, Lawton JH, Grubb PJ (1991) Herbivory and the evolution of leaf size and shape [and discussion]. Philos Trans R Soc Lond Biol Sci 333(1267):265–272
- Colautti RI, Ricciardi A, Grigorovich IA, MacIsaac HJ (2004) Is invasion success explained by the enemy release hypothesis? Ecol Lett 7:721–733
- Crawley MJ (1983) Herbivory, the dynamics of animal-plant interactions. Blackwell, Oxford
- DeWalt SJ, Denslow JS, Ickes K (2004) Natural enemy release facilitates habitat expansion of the invasive tropical shrub *Clidemia hirta*. Ecology 85:471–483
- Dietz H, Wirth LR, Buschmann H (2004) Variation in herbivore damage to invasive and native woody plant species in open forest vegetation on Mahe, Seychelles. Biol Invasions 6:511–521
- Elton CS (1958) The ecology of invasions by animals and plants. Chapman and Hall, London, England
- Hjalten J, Price PW (1997) Can plants gain protection from herbivory by association with unpalatable neighbors? A field experiment in a willow-sawfly system. Oikos 78(2):317–322
- Huntly N (1991) Herbivores and the dynamics of communities and ecosystems. Ann Rev Ecol Syst 22:477–503
- Janzen DH (1970) Herbivores and the number of tree species in tropical forests. Am Nat 104:501–527
- Jones CG, Lawton JH (1991) Plant chemistry and insect species richness of British umbellifers. J Anim Ecol 60: 767–777
- Jongejans E, Sheppard AW, Shea K (2006) What controls the population dynamics of the invasive thistle Carduus nutans in its native range? J Appl Ecol 43(5):877–886
- Keane RM, Crawley MJ (2002) Exotic plant invasions and the enemy release hypothesis. Trends Ecol Evol 17:164–170
- Kloeppel BD, Abrams MD (1995) Ecophysiological attributes of the native Acer saccharum and the exotic Acer platanoides in urban oak forests in Pennsylvania, USA. Tree Physiol 15:739–746
- Larson CL (1998) The impact of two gall-forming arthropods on the photosynthetic rates of their hosts. Oecologia 115:161–166
- Lei TT, Lechowicz MJ (1998) Diverse responses of maple seedlings to forest light regimes. Ann Bot 82:9–19
- Liu H, Stiling P, Pemberton RW (2007) Does enemy release matter for invasive plants? Evidence from a comparison of insect herbivore damage among invasive, non-invasive and native congeners. Biol Invasions 9:773–781
- Lopes DB, Berger RD (2001) The effects of rust and anthracnose on the photosynthetic competence of diseased bean leaves. Phytopathology 91:212–220
- Lowman MD, Heatwole H (1992) Spatial and temporal variability in defoliation of Australian eucalypts. Ecology 73(1):129–142
- Martin PH (1999) Norway maple (*Acer platanoides*) invasion of a natural forest stand: understory consequence and regeneration pattern. Biol Invasions 1:215–222
- Meiners SJ (2005) Seed and seedling ecology of *Acer* saccharum and *Acer platanoides*: a contrast between native and exotic congeners. North East Nat 12:23–32

- Meiners SJ, Handel SN, Pickett STA (2000) Tree seedling establishment under insect herbivory: edge effects and interannual variation. Plant Ecol 151:161–170
- Mitchell CE, Power AG (2003) Release of invasive species and fungal and viral pathogens. Nature 421:625–627
- Nowak DJ, Rowntree RA (1990) History and range of Norway maple. J Arboriculture 16:291–296
- Nykanen H, Koricheva J (2004) Damage-induced changes in woody plants and their effects on insect herbivore performance: a meta-analysis. Oikos 104:247–268
- Reinhart KO, Callaway RM (2004) Soil biota facilitate exotic *Acer* invasions in Europe and North America. Ecol Appl 14:1737–1745
- Rose AH, Lindquist OH (1982) Insects of eastern hardwood trees. Canadian Government Publishing Centre, Hull, Quebec, Canada
- Webb SL, Kaunzinger CK (1993) Biological invasion of the Drew University (New Jersey) Forest Preserve by Norway maple (Acer platanoides L.). Bull Torey Bot Club 120:343–349

- Webb SL, Dwyer M, Kaunzinger CK, Wyckoff PH (2000) The myth of the resilient forest: case study of the invasive Norway maple (*Acer platanoides*). Rhodora 102:332–354
- Webb SL, Pendergast TH, Dwyer ME (2001) Response of native and exotic maple seedling banks to removal of the exotic, invasive Norway maple (*Acer platanoides*). J Torrey Bot Soc 128:141–149
- Whittaker JB, Warrington S (1985) An experimental field study of different levels of insect herbivory induced by *Formica rufa* predation on Sycamore (*Acer pseudoplatanus*) III. Effects on tree growth. J Appl Ecol 22:797–811
- Wolfe LM (2002) Why alien invaders succeed: support for the escape-from-enemy hypothesis. Am Nat 160:705–711
- Wychoff PH, Webb SL (1996) Understory influence of the invasive Norway maple (*Acer platanoides*). Bull Torrey Bot Soc 123:197–205
- Zangerl AR, Hamilton JG, Miller TJ, Crofts AR, Oxborough K, Berenbaum MR, de Lucia EH (2002) Impact of folivory on photosynthesis is greater than the sum of its holes. Proc Natl Acad Sci 99(2):1088–1091