A TEST OF THE ENEMY RELEASE HYPOTHESIS: COMPARISON OF INSECT AND FUNGAL DAMAGE TO LEAVES OF YOUNG, EXOTIC NORWAY MAPLE AND NATIVE SUGAR MAPLE

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ABSTRACT

Norway maple (*Acer platanoides*), originally introduced to North America from Eurasia as an ornamental tree, is an invasive tree in North America where it threatens to displace native trees, including the sugar maple (*Acer saccharum*). One of many possible explanations for why invasive plants such as the Norway maple may have an advantage in exotic habitats is the enemy release hypothesis (ERH), the idea that an invasive species thrives in the absence of its native enemies. Our hypothesis was that leaf samples taken from saplings of both species would show that the Norway maple suffered less leaf damage from herbivory and fungal infection than the sugar maple. In July 2009, leaves were sampled from three transects of the Drew University Forest Preserve, a *Fagus grandifolia-Acer saccharum-Quercus* spp. forest. Samples were analyzed to determine leaf damage in each species. Our study found slightly lower mean leaf damage for the Norway maple, but the difference was determined to be statistically insignificant. In addition, the mean leaf damage of both species was low, <6%. The results showed that the ERH likely does not play a major role in the Norway maple's invasion during the sapling stage. It is possible that specific differences between the Norway maple and the sugar maple in their ability to use resources play a more important role in Norway maple's success, and further research should investigate those differences.

INTRODUCTION

Invasive plants are species that have escaped their native biogeographic bounds and proliferate in non-native environments[1]. As these invaders multiply, they reduce the amount of resources available for native organisms, thus eventually displacing native species in many areas. This displacement can have far ranging consequences for the entire ecosystem[2], as well as massive economic costs to society[3]. Ironically, in some cases invasive species were intentionally introduced into new regions by humans for personal or public benefit.

One invasive species, the Norway maple (*Acer platanoides*), is a problem for native forest communities in the eastern United States. The Norway maple was first imported and grown as a landscaping tree in 1756[4]. More recently, it has become increasingly popular as a decorative street tree in urban areas because it is better adapted to thrive in areas affected by urban pollution and acid rain than the sugar maple (*Acer saccharum*). However, the Norway maple escaped into native forests and is linked to a decrease in native plants[5].

The Norway maple is a shade-tolerant plant, able to establish young saplings even on the floors of mature forests[5]. When a canopy disturbance occurs, these saplings have a substantial advantage over the shade-impaired saplings of the native sugar maple[6]. Norway maples also generate more shade than the sugar maple, thus inhibiting the germination and growth of other plant species in the forest[7]. Better understanding of the mechanisms underlying the invasion of the Norway maple and other invasive plants is critical to developing forest management plans to control the spread of invasive species and to restore affected ecosystems.

It is uncertain exactly why non-native species might have an advantage over the native species in an area to which they are introduced. High reproductive rate and the ability to exploit available resources are some of the common characteristics of successful invading species[8]. However, it is likely that there are many other contributing factors; one hypothesis that has gathered considerable support in explaining part of their success is the enemy release hypothesis (ERH)[9]. This hypothesis states that the invasive organism, in the exotic habitat, gains an advantage from the absence of its natural enemies: predators, parasites, diseases, etc. These enemies would normally perform an important role in controlling the organism's growth and spread. In their absence, the invasive organism may be able to expand faster and achieve higher population densities, effectively outcompeting its native counterparts. Biological control, such as introducing host-specific insects from the invasive species' native range, provides justification for ERH[10].

Various studies have been conducted to evaluate the validity of ERH. A large portion of the research on this topic has supported it, but others have cast doubts on its validity or its significance[11]. One study examined ERH as it applied specifically to the Norway maple in comparison to the sugar maple in terms of leaf damage. The results were generally consistent with ERH[12]. However, the study also suggested that additional insight could be obtained from a study specifically examining younger trees, especially considering the potentially greater impacts of leaf damage on this more vulnerable age-class of trees.

The intention of this study was to examine, quantify, and compare the amount of leaf damage to young (diameter at breast height, DBH, between 1 and 10 cm) Norway maple and sugar maple trees. We predicted that Norway maples would exhibit less leaf damage than sugar maples at the same location. Leaf damage should function as a reliable indicator of damage caused by insects and fungi on leaf tissue. Damage to leaves not only costs the plant the resources it has invested in the leaf tissue, but also reduces its ability to photosynthesize, inflicting a host of detrimental effects upon the plant. A lesser degree of leaf damage from predation in the Norway maple would point to a potential competitive edge over the native sugar maple, and would provide useful insights into why the Norway maple is a successful invader in North American forests.

MATERIALS AND METHODS

Study Area

Our study area was located in the Drew University Forest Preserve (Madison, New Jersey; 40°46'N; 74°26'W), an 18 ha beech-sugar maple-oak forest within the boundaries of the campus[7]. The forest hosts high densities of both mature and young Norway maples. The forest is young, despite the presence of a hundred-fifty year old oaks. Throughout the mid-1800s, the land was a pasture devoid of trees. Very little is known of the forest's history after 1867[13]. Currently, there exists a high density of deer, especially white-tailed deer (*Odocoileus virginianus*), that have decimated the forest's understory and ground cover. The excessive consumption of understory plants has hindered the renewal of the forest; few tree seedlings were observed[7]. Our study was conducted in an approximately 3 ha portion of the preserve.

Sample Collection

Three transects were mapped out, varying from 65 to 100 meters in length. We kept 20 meters between our sampling area and the forest-edge. The maple saplings within 10 meters perpendicular to the transects were sampled. Three separate twigs within arm's reach were gathered from each tree; each twig contained three to nine leaves. Of the collected sample, 260 leaves of each species were randomly selected for analysis.

Damage Assessment

We assessed the percent of leaf area damaged on each leaf, using a leaf card index (Appendix) as a guide. The leaf cards aided estimation of the relative area of damage and the percentage damage corresponding to that area on the leaf[14]. We took into account any fungal and predatory damage, including, but not limited to: holes, tears, and brown spots. The type of damage (fungal vs. insect) was not recorded nor analyzed as part of the data. Spots of minor discoloration (eg. areas lacking chlorophyll) were not taken into account, because this type of damage could have resulted from causes other than predation.

Statistical Data Analysis

Statistical Package for the Social Sciences 17.0 (SPSS)[15] was used for statistical analysis. An independent, 2-sample t-test was used to compare the mean percentage leaf damage between Norway and sugar maples. The program also allowed us to analyze whether the difference was statistically significant. The data were first transformed to meet the assumptions of normality and equal variance inherent in the t-test.

RESULTS

Nearly all of the leaves of both Norway and sugar maple exhibited some degree of damage. Of those with damage, 63% of all Norway maple leaves and 51% of all sugar maple leaves had greater than 1% percent damage. The remainder of the leaves sampled had less than 1% leaf area damaged. Norway maple leaves had a mean of 5.079% (± .3694 S.E.) damage while sugar maple leaves had a mean of 5.492% ± (.6003 S.E.) damage.

When comparing the percent damage range of both species, sugar maple showed a far greater damage range than that of Norway maple. Sugar maple leaves showed a range of 70.0% damage, while its invasive counterpart, the Norway maple, showed a much smaller range of only 36.9% damage. The extreme damage values for each species also supported sugar maple's greater variability of damage (Figure 1). The highest recorded percentage damage for Norway maple reached 37%, while the highest for sugar maple was 70.0%, with a total of 8 leaves with damage higher than 40% (Figure 2, A and B).

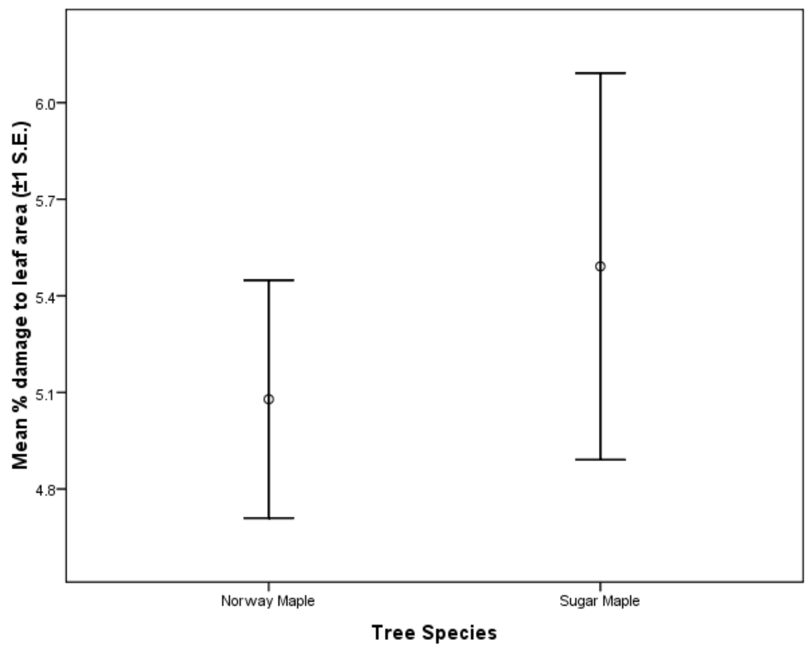

Figure 1 Untransformed mean percentage of leaf area damage for all specimens of each individual species. The error bars represent ±1 standard error of the mean value.

Prior to performing the t-test, the data were transformed using the square root in order to meet the assumptions of normality and equal variance. The square root transformation method was used instead of the arcsine transformation because the values were not based on count data. Rather, the data were established using the actual percentage measured, with the majority of data values falling in the range of 0 – 30%. Our null hypothesis was that both species were equally affected by insect and fungal damage, which we wish to disprove. The t-test and p-value measure the probability that we achieved significant results and can confidently reject the null hypothesis.

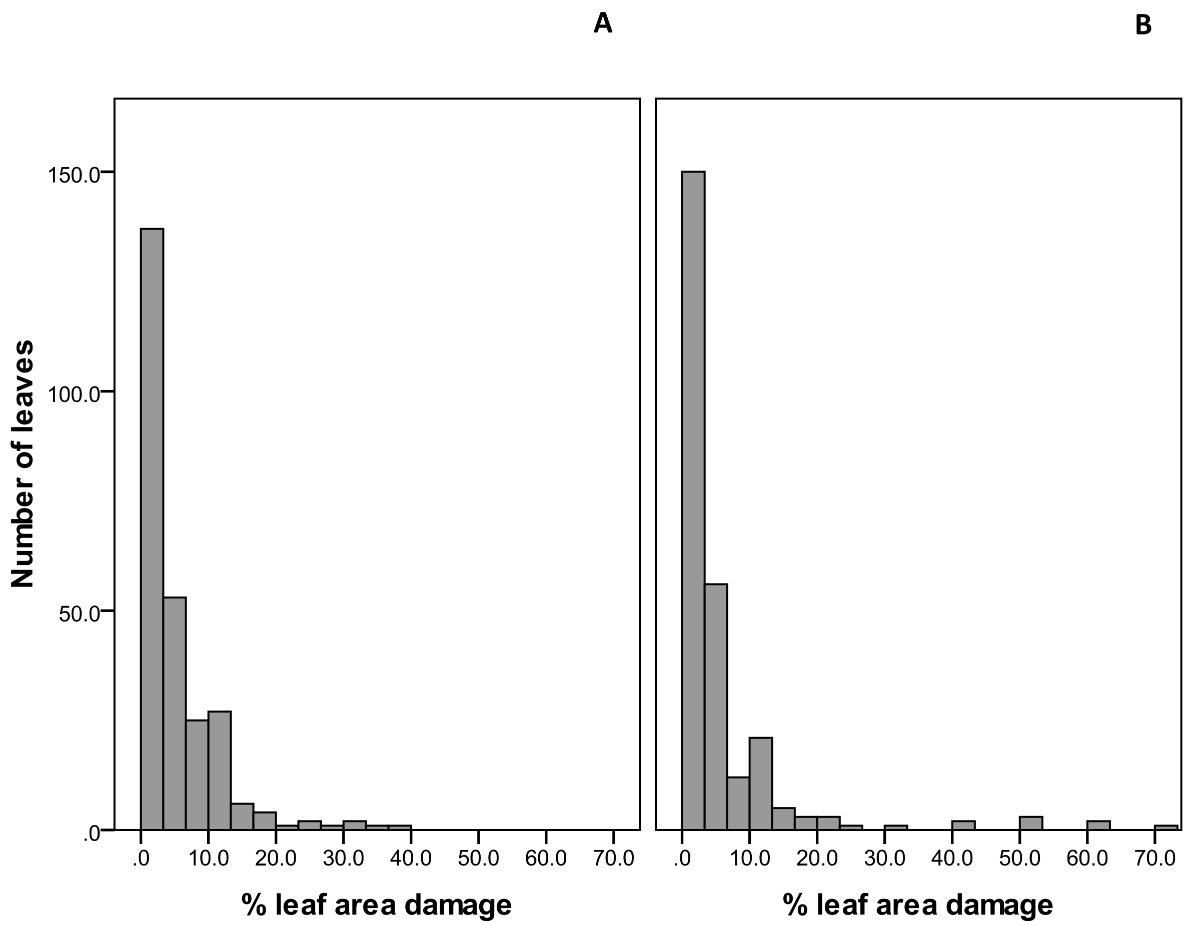

Figure 2, A and B Frequencies of damaged leaves of Norway maple (A) and sugar maple (B), displayed in 3.33% intervals. Sugar maple leaves were the only specimens to exhibit damage above 40 percent.

After the statistical analysis, it was shown that the means did not differ ($t=-.558$, $df=518$, $p=.558$).

DISCUSSION

Our original prediction stated that the Norway maple would suffer less leaf damage than the sugar maple due to the enemy release hypothesis[12]. However, this was not supported by our data. This is consistent with the findings of Morrison[16], who found that for both species, the damage due to fungal and herbivory damage were similar.

Our results did not agree with the findings of Cincotta et al[12]. Several factors could explain this. Since an area of only 3 ha in the Drew University Forest Preserve was sampled, we may have observed only local effects. This might mean that the samples obtained were subject to localized damage but this may not be what is happening over a wider geographic area. For example, insects and fungi might have had population densities unique to our study area. Also, instead of using technology to assess the amount of damage on each leaf, we used leaf area cards to estimate the percentages of damage. This visual approximation introduced potential observer error. Differences in damage assessment techniques between researchers may also have introduced error. In addition, we only sampled leaves from branches that were close to the ground and low enough to reach by hand. Since we did not sample leaves from all levels of the forest, it is possible that various levels of insect and fungal damage existed at different forest strata, which we did not take into consideration. Other studies, such as those conducted by Adams[14] and Cincotta[12], sampled leaves from all ages of trees, while our study focused specifically on saplings. For instance, in Adams's study, freshly fallen foliage was collected in autumn and assessed for damage, lumping all ages of trees together. Thus, it is plausible saplings do not show the same damage correlations found within mature trees.

Even though ERH did not apply to our study, there are other hypotheses that strive to explain why invasive species succeed in their non-native habitats. One example is the resource availability hypothesis (RAH), which states that certain exotic species tend to flourish when resource availability increases or when native plants competing for the same resources decrease in population size[9]. Other hypotheses still need to be explored. Further research should focus on traits that might allow the Norway maples to displace the sugar maple. For instance, Norway maples are more shade tolerant[7] and are capable of growing in dense groups[14]. Moreover, Norway maples have greater reproductive success than sugar maples because of their larger seed size and lower rates of seedling predation[16]. Norway maples also have thicker leaves than those of sugar maples, which suggests that it is harder for insects to digest the leaf tissue[12]. Therefore, the Norway maple trees may suffer less damage from predators in the new environment.

In order to combat the spread of invasive species, biological control has become an increasingly popular method of eradicating exotic, invasive species. Our research did not provide support for using this method of control on the Norway maple. Also, Cincotta et al.[12] and Adams[14] admit that the difference in leaf predation between the Norway maple and the sugar maple was very small and may be biologically insignificant. In 2004, the high fungal damage found in Canadian Norway maples[14] could possibly lead to a dwindling of the Norway maple population. Future progression of this pathogen might impact the American Norway maple trees.

In conclusion, leaf damage sustained by Norway maple and sugar maple trees was similar. In our study, Norway maples had a slightly larger proportion of damaged leaves, but sugar maples had higher percentages of damage on individual leaves. Although our study findings did not coincide with ERH, it also did not disprove the hypothesis. Since this study concentrated on saplings only, other studies should be conducted focusing on various other age groups of trees and incorporate a variety of locations. Further research should take into account the effect of resource availability, such as chemical properties of the soil, access to nutrients, and environmental pollution. Overall, it is probable that there is more than one single factor that gives the Norway maple its successful invasive properties. A better understanding of the ecological traits of Norway maples in its non-native habitat will contribute to improved control of the species in northeastern forests. Improved control and protection will allow for more diverse forests where native species are able to flourish as well.

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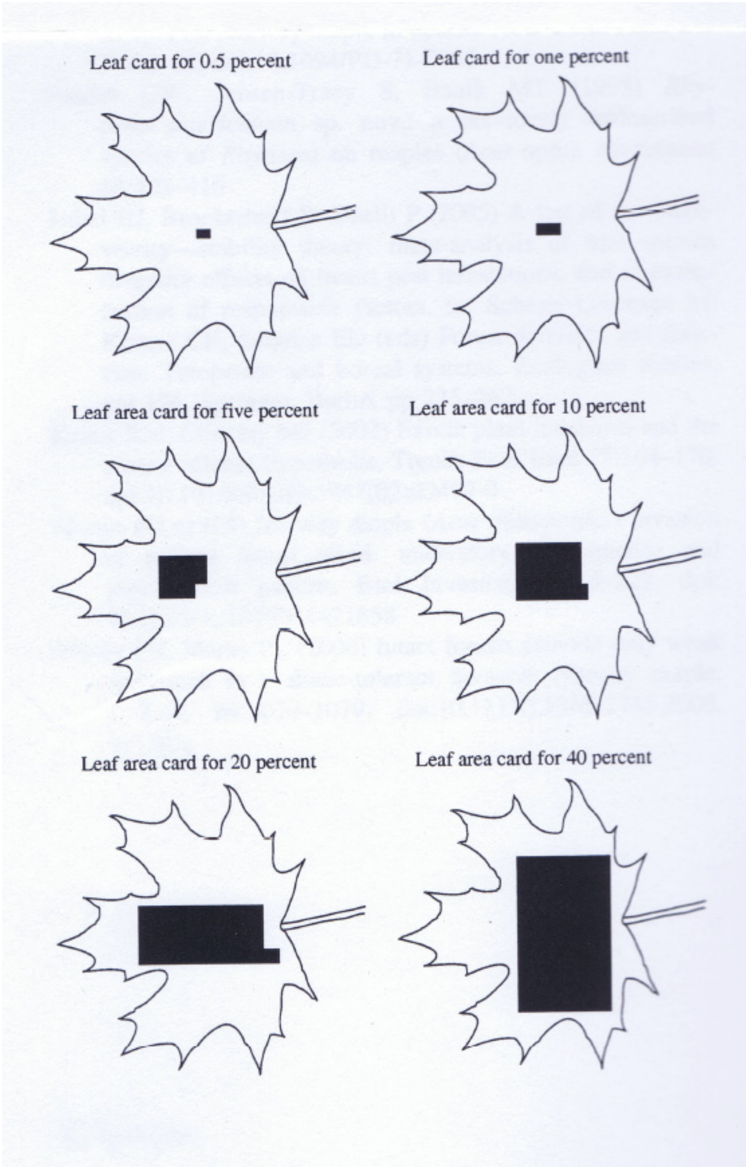
APPENDIX



Leaf card index showing the percent damage[14]. Used to visually estimate relative percent damage in our leaf samples.

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