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# Seed and Seedling Ecology of Acer saccharum and Acer platanoides: A Contrast Between Native and Exotic Congeners

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# Seed and Seedling Ecology of
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**Abstract** - The exotic tree, *Acer platanoides*, is increasing in forests of northeastern North America, largely within the range of its native congener, *Acer saccharum*. A combination of field and controlled experiments was used on seeds and seedlings of these congeners to determine species characteristics that may be contributing to these floristic changes. *Acer platanoides* experienced lower rates of seed predation than *A. saccharum* in field experiments. Differences in the dispersal and allocation characteristics of the two species were small and not likely to explain the relative success of *A. platanoides*. Greenhouse-grown seedlings of *A. platanoides* were much larger than those of *A. saccharum* because of differences in seed size, not differences in growth rate. These data suggest that preferential seed predation and initial seed size differences may explain greater relative success in *Acer platanoides* seedlings.

## Introduction

Exotic species invasions are a problem of global concern due to huge costs for control and eradication (Pimentel et al. 2000) as well as potential impacts on natural ecosystems (Parker et al. 1999). For these reasons, factors that contribute to success of a species as an invader are of extreme importance in predicting potential invasions and in determining appropriate management strategies (Rejmánek 1999). Comparing native and exotic congeners provides a useful framework to determine characteristics contributing to invasiveness while accounting for similar evolutionary histories (Collins and Wein 1993, Schierenbeck et al. 1994, Van Clef and Stiles 2001). In this study, I compare the exotic *Acer platanoides* L. to the native *Acer saccharum* Marshall to better understand the spread and increase of *A. platanoides* in forests of northeastern North America.

*Acer platanoides*, a native of continental Europe, is commonly planted as a shade tree in North America because of its disease resistance, tolerance of poor soils, and overall attractiveness (Webb et. al 2000). From widespread horticultural plantings, this species has colonized natural areas throughout the eastern United States and now commonly occurs across a gradient of forest types from urban woodlots to

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relatively undisturbed old-growth forests (Anderson 1999, Martin 1999, Webb and Kaunzinger 1993, Webb et al. 2000). Invasion of forests by *A. platanoides* is associated with declines in understory species richness and in native tree regeneration (Martin 1999, Webb et al. 2001, Wyckoff and Webb 1996). The seedling pool of these forests is also dominated by *A. platanoides*, indicating that abundance of this species is likely to increase in the future (Webb et al. 2000, Wyckoff and Webb 1996).

Both *Acer saccharum* and *A. platanoides* are shade tolerant canopy trees characteristic of closed-canopy, often late successional, forests (Kloeppel and Abrams 1995, Lei and Lechowicz 1998, Webb et al. 2000). Both of these species primarily regenerate by forming seedling banks, remaining as seedlings in the understory for extended periods until a canopy opening occurs (Marks and Gardescu 1998, Webb et al. 2001). When these two congeners co-occur within forests, *A. saccharum* regeneration is inhibited (Martin 1999, Webb et al. 2001, Wyckoff and Webb 1996), presumably through competitive interactions. As the composition of the seedling bank determines which species will be available to recruit into a canopy opening, factors that determine the relative abundance of seedlings in the understory may regulate the composition of canopy recruitment.

As *A. platanoides* expands its range, interactions between these two congeners may become more widespread, increasing the prevalence of this invasions' influence on forest dynamics. I used a series of experiments to compare seed and seedling stages of *A. saccharum* and *A. platanoides* to determine the autecological mechanism(s) contributing to the contemporary shift in species composition occurring in North American forests. I examined seed dispersal, seed predation, germination, and seedling growth and biomass allocation.

## Methods

### Seed collection and storage

Seeds of *A. saccharum* were collected on 1 September 2000 from 5 trees on Rutgers Cook College campus (New Brunswick, NJ). *Acer platanoides* seeds were collected on 10 September 2000 from 12 individuals in a naturalized population on Rutgers Cook College campus. Seeds were sorted to remove damaged or unfilled fruits. Seeds were stored dry under refrigeration (5 ºC) until they were stratified following Young and Young (1992).

### Seed dispersal

To evaluate relative potential for dispersal by wind, the terminal velocity of samaras was calculated for each species. Slower terminal

velocities result in greater potential dispersal distance (Guries and Nordheim 1984). Undamaged samaras of both species (n = 120) were dropped in a laboratory from heights of 2, 3, 4, and 5 m, and the time of descent recorded. Seeds were released from the same orientation as on a maternal tree. Linear regression was used to determine the slope of the linear portion of the data, which represents the constant rate of descent once terminal velocity has been reached (Thompson 1993).

**Seed predation**

Three forest stands within 0.6 km of each other were selected within the Hutcheson Memorial Forest (East Millstone, NJ; 40°30'N, 74°34'W). All stands were approximately 45 years old and did not contain either *Acer* species at the time of the experiment, although both species were found within adjacent areas of the forest. This site selection would therefore assess seed predation in newly invaded habitats and would also prevent contamination of the experiment from external seed sources. The three stands varied in structure and composition and included: 1) a dense *Juniperus virginiana* L. stand with little understory; 2) a *J. virginiana* woodland with scattered *Malus* sp. and *Rosa multiflora* Thunb.; and 3) a mixed stand dominated by *Fraxinus americana* L., *Quercus palustris* Muenchh. and *Acer rubrum*. L. Two of these sites had a closed canopy, while the *J. virginiana* woodland had a few canopy gaps. Based on capture data at the site, the numerically dominant predators of woody plant seeds are white-footed mice, *Peromyscus leucopus* Rafinesque (Manson and Stiles 1998, Pearson 1959), which are abundant in both old fields and forests of northeastern North America.

Forty seed dishes were placed at 1-m intervals along a transect within each stand. Open-topped dishes (14 x 14 x 1 cm) made of black aluminum screening were anchored to the soil with a galvanized nail. Within each dish, 10 seeds (the entire samara) of either *Acer saccharum* or *Acer platanoides* were placed on 9 October 2000. Species were assigned randomly to each dish resulting in 20 dishes of each species along each transect. Seed removal was censused for all dishes on days 5, 10, 15, 20, and 30. At each census, a radius of 30 cm around each dish was searched for missing seeds and predator-removed hulls. Most intact seeds dislodged from these dishes are found immediately next to the dish, while hulls tend to move greater distances (S.J. Meiners, pers. observ.). Any seed not located within 30 cm of the dish or located as depredated remains was assumed to have been removed by a predator that cache seeds in the fall.

To further understand predation differences between species, seed removal data were separated into seed encounter and seed exploitation

components (Hulme 1994, Meiners and LoGiudice 2003), representing separate steps in the predation process (Hulme 1993). Encounter was defined as the time until the first seed was removed from a dish while exploitation was defined as the rate at which seeds were removed from dishes following encounter. It should be noted that encounter rates are conservative estimates, as dishes located by predators that did not remove any seeds would not be documented. Seed removal (overall seed survivorship), encounter, and exploitation data were analyzed with survival analyses (Cox regressions, Proc PHREG; SAS Institute Inc. 1989) to determine differences between species. These analyses integrate the number of events occurring (e.g., seed removal) with the time for that event to occur to generate a relative risk (Fox 2001, Meiners and LoGiudice 2003). In all analyses, data were stratified by site to remove inter-site variation in removal rates and thereby focus on differences between species.

**Greenhouse experiment**

A greenhouse experiment was conducted to compare potential emergence, growth, and allocation patterns. On 26 January 2001, fifteen stratified seeds of either *A. saccharum* or *A. platanoides* were planted in 15-cm standard pots filled with Pro-mix (Premier Horticulture Ltd., Dorval, QP) sterile growing medium. A total of 24 pots of each species were planted and placed randomly on a bench in the greenhouse of Eastern Illinois University. Pots were watered to saturation as necessary and placed under supplemental lighting to extend the photoperiod to 12 h. This lighting regime delivered a total PAR of approximately 9.0 mol/$m^2$/day, roughly equivalent to the total light reaching the forest floor in eastern deciduous forests (Bazzaz 1996). To determine the impacts of seed mass on growth rates, a sample of 110 seeds of each species was removed from their samaras, dried, and weighed.

Emergence was assessed after 28 days, at which time seedlings were thinned to a maximum of five per pot (resulting in an average of 3.8 seedling per pot at harvest). Differences between species in the number of seedlings emerging per pot were analyzed with a Wilcoxon rank-sums test. After 63 days the surviving seedlings were harvested and all soil rinsed from their roots. Total leaf area was measured with a LI-3100 area meter (LICOR Inc., Lincoln, NE). Seedlings were dried at 70 °C for 3 days, divided into root, stem, and leaf portions, and weighed. From these data, leaf area ratio (leaf area/total seedling biomass) and root:shoot ratio were calculated. Mean seed mass of each species was used to calculate relative growth rates with the formula: [ln (seedling mass) - ln (seed mass)]/ 9 weeks. Pot means were analyzed with ANOVA to determine the significance of species differences in growth and biomass allocation patterns.

## Results

### Seed dispersal

The mass of *A. platanoides* seeds was 65% greater than that of *A. saccharum* (Fig. 1a; ANOVA: $F_{1,218} = 115.83$; $P < 0.0001$). Time of descent for each species was linear between 3 and 5 m and was used to calculate terminal velocity. Despite greater seed mass,
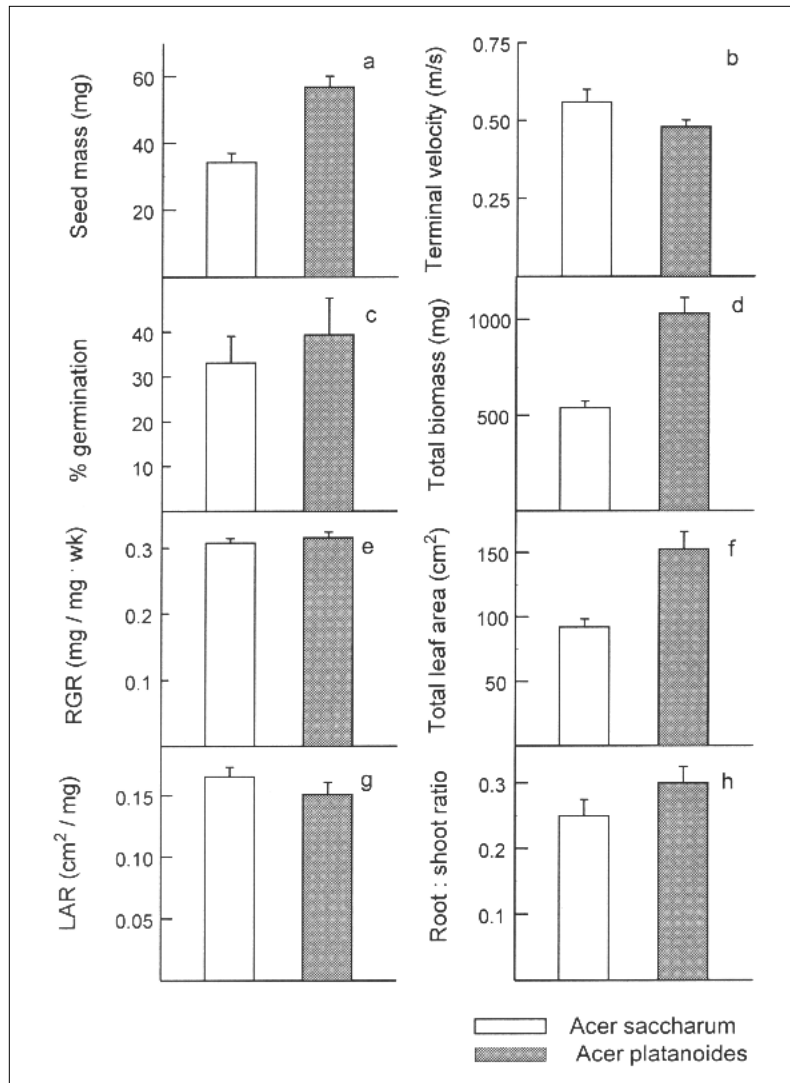


Figure 1. Comparison of the physical traits and allocation patterns of *A. saccharum* and *A. platanoides* seeds and seedlings. Values plotted are means for each species, with error bars representing 95% confidence intervals. Abbreviations in figure: RGR = relative growth rate; LAR = leaf area ratio.

*A. platanoides* had the slower terminal velocity when compared to *A. saccharum* (Fig. 1b; P < 0.0001).

## Seed predation

For both species combined, 79.2% of all seeds that were removed were found as discarded seed hulls, verifying predator activity in the three forest stands. Overall, *A. platanoides* experienced a slower rate of seed removal than *A. saccharum* (Fig. 2). Risk of predation for the native *A. saccharum* was 1.63 x (95% CI 1.43–1.86) that of the exotic *A. platanoides* (Wald $\chi^2 = 54.21$; df = 1; P < 0.0001). Species differences were also significant when separated into encounter and exploitation rates. Risk of encounter for dishes containing *A. saccharum* was 1.78 x (95% CI 1.17–2.70) that of dishes containing *A. platanoides* (Wald $\chi^2 = 7.28$; df = 1; P = 0.007). Similarly, seed exploitation following encounter was greater in *A. saccharum* with risk of removal 1.18 x (95% CI 1.03–1.35) that of *A. platanoides* (Wald $\chi^2 = 5.80$; df = 1; P = 0.016).

## Greenhouse experiment

Germination of stratified seeds did not differ significantly between the two congeners (Fig. 1c; Wilcoxon rank sums test: $\chi^2 = 1.32$; df = 1; P = 0.25). Seedlings of *A. platanoides* were 98% larger (ANOVA: $F_{1,43} = 29.62$; P < 0.001; $R^2 = 0.41$) and had a greater total leaf area (ANOVA: $F_{1,43} = 18.16$; P < 0.001; $R^2 = 0.30$) than seedlings of *A. saccharum* (Fig. 1d–f). However, relative growth rate did not vary between species (ANOVA: $F_{1,43} = 0.542$; P = 0.46; $R^2 = 0.01$). Neither assessment of biomass allocation differed between the two species (Figs. 1g,h), with both root:shoot ratio (ANOVA: $F_{1,43} = 2.22$; P = 0.14; $R^2 = 0.05$) and leaf area ratio (ANOVA: $F_{1,43} = 1.34$; P = 0.25; $R^2 = 0.03$) having non-significant differences.
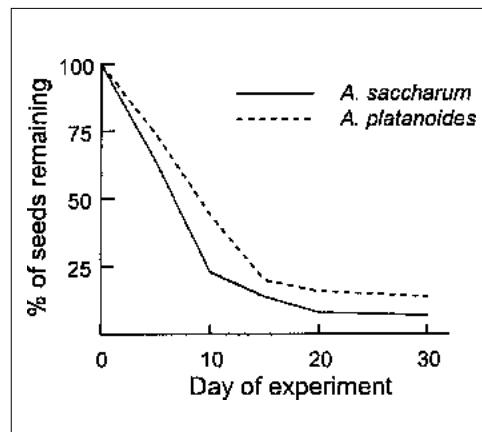


Figure 2. Seed removal of *A. platanoides* and *A. saccharum* subjected to seed predators. Data are pooled across all three experimental sites and incorporate both encounter and subsequent exploitation of seeds.

## Discussion

Differences in seed dispersal and allocation patterns appear insufficient to explain the current transition from native *A. saccharum* to exotic *A. platanoides* species in many northeastern forests. The slower terminal velocity for *A. platanoides* seeds would result in potential for a slightly greater dispersal distance in closed-canopy forests and may result in differential colonization of unoccupied sites (Guries and Nordheim 1984). However, both species develop persistent seedling banks (Webb et al. 2001), reducing dependence on yearly seed inputs for successful regeneration. Both species also appear to show marked annual fluctuations in seed production with large seed crops followed by one or more years of relatively small crops (S.J. Meiners, pers. observ.; USDA 1990).

Early seedling biomass allocation patterns were also very similar between the two species. Lei and Lechowicz (1998) found relatively small differences between *A. saccharum* and *A. platanoides* in photosynthetic traits and allocation patterns across a range of light levels (from 1.5 to 20% full sun), particularly compared to the variation found across the genus *Acer*. Studies of the physiological characteristics of co-occurring native *Acer* species find much larger differences among species, resulting in differential success in heterogeneous habitats (Sipe and Bazzaz 1995). The overall similarity in the physiology and allocation patterns of the two species in this study indicates adaptions for very similar environmental conditions.

At the end of the greenhouse experiment, *A. platanoides* seedlings were nearly twice the mass of *A. saccharum*. However, this size difference is not the result of differences in relative growth rates as they are nearly identical between the two species after accounting for differences in seed size (Fig. 1e). This suggests that initial size at the seed stage accounts for greater final biomass. Larger seeds can confer tree seedlings with an increased ability to establish under shaded conditions, withstand environmental stresses, and tolerate herbivory (Jurado and Westoby 1992, Saverimuttu and Westoby 1996). The larger seeds of *A. platanoides* may therefore allow the species to establish across a wider range of environmental conditions. Furthermore, resulting size differences in seedlings may allow *A. platanoides* to compete more effectively with other seedlings in the forest understory. *Acer platanoides* seedlings typically dominate the understories beneath both *A. saccharum* and *A. platanoides* canopy trees (Martin 1999, Webb et al. 2001, Wyckoff and Webb 1996)

This study finds clear evidence of differential seed predation that favors survival of the exotic congener. This effect appears to be a combination of differences in encounter rates and subsequent removal

of seeds of the two species. Differences in seed encounter rates suggest that the local seed predators may not have immediately recognized *A. platanoides* as a suitable food source or that they were not actively searching for seeds of this species. In contrast, predators located dishes of natives at faster rates. Differences between the congeners in removal following encounter were much smaller, but still significantly favored survivorship of the exotic species. Species preference may result from the milky latex associated with *A. platanoides* tissues (Webb et al. 2000), which may make seeds distasteful. Differential predation rates between these congeners indicate the potential for seed predation to determine future composition of canopy trees in these communities (Hulme 1996, Pyke 1990).

This study suggests that the larger size and reduced predation of *A. platanoides* seeds enables this species to differentially invade forests at early demographic stages. These findings, in combination with the apparent competitive ability (Martin 1999, Webb et al. 2001, Wyckoff and Webb 1996) and positive response to disturbance (Anderson 1999) of *A. platanoides*, help to provide mechanisms explaining this species' spread throughout northeastern North America.

## Acknowledgments

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