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Invasion Ecology of *Acer platanoides* in an Old-Growth Urban Forest.

By

Justin Paul Rogers

**A thesis submitted to the Department of Environmental Science and Biology of
The College at Brockport State University of New York in partial fulfillment of
the requirements for the degree of
Master of Science in Environmental Science and Biology**

April 23, 2013

Invasion Ecology of *Acer platanoides* in an Old-Growth Urban Forest

By Justin Paul Rogers

APPROVED BY:

Advisor

Date

Reader

Date

Reader

Date

Chair, Graduate Committee

Date

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Comprehensive Abstract

Acer platanoides (Norway maple) is an exotic tree species with invasive potential that has been described as a prolific seed producer, shade tolerant, and a strong competitor for limiting resources. It has invaded many forests in the northeastern United States and Canada, including the Washington Grove, a 10 ha forest in Cobbs Hill Park in Rochester, NY. To quantify the extent of the invasion at the Grove, I surveyed the forest canopy, subcanopy, seedlings, saplings, shrub cover, herbaceous cover, seed rain, and seed bank. In a primarily *Quercus* (oak) canopy, *A. platanoides* was relatively sparse at 31 individuals/ha, but was the most abundant tree species in the forest subcanopy with 215 individuals/ha. Two other key findings include the prevalence of other invasive species in the understory (e.g. *Alianthus altissima* [tree of heaven]), and a lack *Quercus* regeneration. I suspected that superior competitive ability of *A. platanoides* was key to its invasiveness and wanted to test this at the seedling stage. Two native species (*Acer saccharum* [sugar maple], and *Quercus rubra* [red oak]) and the invasive were used in nine different competition arrangements grown under low shade, medium shade, and high shade (85%, 91%, and 97% shading, respectively). I measured photosynthesis rate, stem height, and stem diameter in control, intraspecific, and interspecific competition arrangements. Height growth and photosynthetic rate both decreased significantly with increased shade. *Q. rubra* had the highest overall photosynthesis rate (mean = $1.98 \pm 0.10 \mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$) and *A. saccharum* had the greatest change in height (mean change = $23.7 \pm 2.67\%$). In contrast to my expectations, I did not find any conclusive evidence

suggesting that the invasive *A. platanoides* was the superior competitor at the seedling stage.

In conclusion, the Washington Grove is heavily populated by the invasive *A. platanoides* and if left unmanaged, the area will further progress to resemble a nonnative stand. However, this pattern does not appear to be due to competition at the seedling level. To limit the further spread of the established trees I recommend felling all of the established invasive trees and removing any emerging seedlings. A long term management plan of invasive removal and creating conditions to promote *Quercus* recruitment will help promote a native forest.

Chapter 1

Old-Growth Forest Dynamics Following Establishment of Nonnative *Acer platanoides*

Abstract

The nonnative but commonly planted landscape tree *Acer platanoides* (Norway maple) is present in an old-growth forest in Rochester, NY. Previous research has found that this species can have a significant invasive impact on forest communities via its life history traits. In order to test the expectation that the forest is shifting to a nonnative community, the area was surveyed at random points along four parallel transects. At each point I identified and measured canopy and subcanopy trees, seedlings and saplings, herbaceous cover, and shrub cover. A soil seed bank study was performed to observe germination of seed in open canopy/greenhouse conditions. The current tree canopy was dominated by native species stems which included *Quercus rubra* (red oak), *Quercus alba* (white oak), *Quercus velutina* (black oak), *Prunus serotina* (black cherry), and *Acer saccharum* (sugar maple) (31.5%, 18.2%, 17.7%, 11.1%, 7.0%, respectively). However, *A. platanoides* was the most dominant species (31.3%) in the subcanopy of the forest as well as in the seedlings and saplings (41.4%). The seed bank analysis found successful germination of approximately 300 individuals of which the vast majority was native forbs. Relatively few woody species were encountered but did include another invasive tree species, *Ailanthus altissima* (Tree of Heaven). If the subcanopy compositional trajectory continues, the Washington Grove forest will be dominated by a nonnative, invasive

species, which may have additional ecological consequences beyond lost tree species diversity.

Introduction

The invasibility of communities and the impacts of threatening invasive species have important effects on a plant community's ecology and successional trajectory. Invasibility is generally linked to the removal of biotic or abiotic barriers that otherwise inhibit the establishment of various species; however, invasion potential appears dependent on the ecosystem of interest, spatial scale of study, and methodological approaches (Kennedy *et al.* 2002, Stohlgren *et al.* 2003, and Fridley *et al.* 2007). For instance, Kennedy *et al.* (2002) concluded that plant community diversity is negatively correlated to niche availability and susceptibility to invasion. In contrast, Stohlgren *et al.* (2003) found that at broader spatial scales, native plant diversity is positively correlated with exotic species diversity; however, Fridley *et al.* (2007) cautioned that despite this correlation, reduction of local species richness can further accelerate the spread of nonnative plants. In fact, it was often thought that undisturbed intact forests were resistant to invasion, but a recent study revealed that this assumption may not be accurate (Martin *et al.* 2009). Numerous additional factors (e.g. disturbance, dominance, increased nutrient supply) have been related to increased invasibility (Hobbs and Huenneke 1992, Davis *et al.* 2000, Mack *et al.* 2000, Smith *et al.* 2004, Gross *et al.* 2005, and Renne *et al.* 2006, Belote *et al.* 2008, Eschtruth and Battles 2009) but it appears that generalizations through which

invasion occurs remain elusive, and it seems likely that most any community is potentially susceptible to the establishment of nonnative species.

The impact of invasive plant species on ecosystems can be dramatic and potentially with cascading effects. Consequences of invasives include but are not limited to loss of native flora and fauna (Wilcove *et al.* 1998), shifts in ecosystem processes (e.g. productivity, decomposition, hydrology, and soil nutrient dynamics; Vitousek *et al.* 1997, Corbin and D'Antonio 2004), and habitat homogenization (Moles *et al.* 2008, Lososová *et al.* 2012). These varied ecological consequences of invasion may be linked to several generalizations regarding life history traits and behavior of nonnative species (Thompson and Davis 2011). First, some invasive plant species alter soil nutrient dynamics, which likely facilitates their own spread and competitive ability (Corbin and D'Antonio 2004). These effects, along with the alteration of the soil microbial community and enzymatic activity, may persist long after the removal of the invasive species (Elgersma *et al.* 2011). Second, invasive species are typically *r*-strategists with prolific reproduction (Rejmánek *et al.* 2005). Third, compared to non-invasive species, invasives generally have higher performance in physiology, leaf-area allocation, shoot allocation, growth rate, size, and fitness (van Kleunen *et al.* 2010). In addition to these traits, according to the enemy release hypothesis (ERH), nonnative species capitalize on the lack of natural herbivore presence and thereby gain a competitive advantage over native species (Keane and Crawley 2002). Thus, if a particular species has been documented to

have a plethora of “invasive type” life history traits; it can be considered a threat to any plant community.

The invasive *Acer platanoides* (Norway maple) possesses a suite of life history traits that make it a species of concern in the United States and eastern Canada. First introduced in 1756 in Philadelphia, this tree species is one of the most frequently planted and occurring street trees in many areas of the United States, often replacing *Ulmus americana* (American elm) trees lost to Dutch elm disease (Nowak and Rowntree 1990). *A. platanoides* was a logical choice for urban areas because of its ability to withstand poor soils, pollution, diseases, and pests (Nowak and Rowntree 1990) but Anderson (1999) found that forested communities near *A. platanoides* are at high risk for invasion. In the northeastern United States, the species has demonstrated the capacity to alter forests by changing the soil nutrient cycling rates (Gomez-Aparicio and Canham 2008), limiting growth of native trees (Galbraith-Kent and Handel 2008), and taking over in native forest canopies (Webb and Kaunzinger 1993, and Hunter and Mattice 2002). Furthermore, *A. platanoides* is very shade tolerant, allowing its seedlings to be highly competitive in the deep shade of the understory beneath its own canopy (Galbraith-Kent and Handel 2008). Webster *et al.* (2005) showed that *A. platanoides* can capitalize on increased light when compared to natives in the same area, suggesting that their seedlings have almost the equivalent of a decade’s head start to occupying the forest canopy. In extreme shade compared to areas of increased light, *A. platanoides* growth allocation favors enhanced root growth, evidence of phenotypic plasticity in its root: shoot trade-off, an evolutionary

adaptation to maximize survivability (Reinhart *et al.* 2006). Despite these *K*-strategist traits enabling this species to invade late-successional forests (Rejmánek *et al.* 2005, Martin and Marks 2006), *A. platanoides* has also been described as having *r*-strategist qualities (e.g., prolific seed production; Mitchell and Wilkinson 1982, fast growth; Kloeppel and Abrams 1995). Finally, soil invaded by *A. platanoides* reduces native species leaf growth and above- and belowground biomass (Galbraith-Kent and Handel 2012).

Cobbs Hill Park, an urban and frequently visited area in Rochester, NY, has many *A. platanoides* trees present in forested parts of the park. My initial observations also noted that native *Quercus* trees currently abundant in the canopy were not successfully regenerating. Given these observations, my study objective was to develop a projection of if and how invasive *A. platanoides* may change this mature, diverse forest. I characterized the species composition of the forest at multiple strata, from the seed bank to the canopy to ask if the forest at Cobbs Hill Park is shifting from a native-dominated stand to a nonnative stand. Using these data, I recommended management strategies to promote native stand development and diversity.

Methods

Site Characteristics

The study site was the Washington Grove forest of Cobbs Hill Park in Rochester, NY, USA (43°8'23"N, 77°33'51"W), which is owned and managed by the

city's Department of the Parks, Recreation and Human Services. As part of an urban park, Washington Grove is surrounded by a residential neighborhood, school, and the Cobbs Hill reservoir. The study area is approximately 10 ha of mixed-growth eastern temperate forest. In 2010, the annual mean temperature was 9.7°C and the mean annual precipitation was 952 mm, of which 429 mm fell in the growing season (Annual Climatological Summary, 2010). Total relief at the study site is 43 m and the microtopography can be described as pit-mound.

The forest canopy is fairly diverse but consists mostly of various *Quercus* species, *Prunus serotina* (black cherry), and *Acer saccharum* (sugar maple), which is typical for forest composition in this region. Numerous characteristics of the stand resemble those of an old growth forest, including the presence of several trees >90 cm DBH (diameter at breast height) with ages estimated (via increment boring) to be older than 150 years. The area is accessed daily by neighborhood residents, cyclists, and runners who use the 2.67 km of intermingling trails within the Grove. *A. platanoides* is not the only invasive species found within Washington Grove. I also discovered several other nonnative species at various levels of the forest stratum.

Forest Characterization

In the summer of 2009, forest composition was quantified within several different strata and functional groups, including the canopy, subcanopy, seedlings, saplings, shrubs, and herbaceous vegetation. Four parallel transects averaging 311 m in length were established in a roughly north-south direction across the Grove. They

were spaced evenly throughout the area, approximately 100 m apart, in order to capture the best representation of species present. A combined total of 59 random points were sampled using the point-quarter method. At each point, the canopy and subcanopy trees (defined as >10 m and 2-10 m in height, respectively) closest to the point in each of four equal quadrants were identified, and the diameter (DBH, diameter at breast height) and distance from the transect point measured. Randomized transect points were skipped if duplication of an individual tree occurred.

I used the tree data collected to calculate relative density (RDe, based on frequency), relative dominance (RDo, basal area at breast height), and importance value (IV, sum of relative density and relative dominance) of each species encountered within the Grove for each of the canopy and subcanopy strata. The same tree data were also used to calculate the Shannon-Wiener Index (H'), a diversity index that accounts for both species richness and evenness. The index ranges from 0 (low community complexity) to 4 (high community complexity and diversity).

Seedlings and saplings <2 m in height were also identified to species and measured for height in a 3x3 m subplot at each transect point. Shrubs present within this same grid were identified to species and cover percentage estimated using a modified Daubenmire classification [1: 0-5%, 2: 5-25%, 3: 25-50%, 4: 50-75%, 5: 75-95%, 6: 95-100% (Daubenmire 1959)]. For consistency purposes, these subplots were located in the southwestern quadrant used in the point quarter method.

Similarly, in a 1 m² quadrat in the southwestern quadrant, herbaceous cover was estimated using the same modified Daubenmire method, and species were identified.

Light availability (photosynthetically active radiation, or PAR) was measured using a LI-COR LI-191 1-m long line quantum sensor. PAR was measured at 1 m above the forest floor at each of the 59 transect points. These data were compared to the amount of PAR of full ambient light in a non-shaded adjacent field to determine the percentage of full sun at each transect point in the Grove. DBH and tree coring measurements were taken to develop age-size relationships for *A. platanoides* trees in the Grove. The tree cores were taken approximately 0.5 m from the forest floor with a manual increment borer. A linear regression analysis ($\alpha = 0.05$) was used to assess the significance of the relationship. In the summer of 2012, I did a species survey of all the street trees that bordered the Washington Grove in order to quantify the relative density of those trees.

Seed Bank

The seed bank of the Washington Grove is an essential part of the forest because it may help predict the potential establishment of species not occurring in the current community. The seed bank was characterized by collecting soil samples (10x15x10 cm) that were removed from 10 random points on each transect in May 2009 (n=40). An A horizon was not always present at each removal point, so for consistency purposes if it was present it was removed and not inspected for propagules. The soil samples were kept cool at 5°C until they could be processed

(<72 h). The samples were sieved (4 mm) to remove larger debris and seeds that were larger than sieve size returned to the original sample. Then they were refrigerated at 5°C until they were placed in pots (<48 h). Potting was done by placing approximately 2-3 cm of sample soil over a sterilized peat mixture (Promix Bx, 80% peat Moss with perlite) in a 9x9x7.5 cm pot. Pots were then placed in The College at Brockport greenhouse in Brockport, NY. Soils were given 12 h of full sun and were watered regularly to keep soil moist. Potting was completed on June 5, 2009 and all pots were monitored for germination and growth until November 2009. As seedlings became identifiable they were recorded and removed from the pots.

Seed Rain

Measurement of propagule pressure was assessed by randomly placing three seed traps along each of the four parallel transects. The traps were 0.5x0.5 m (0.25 m²) frames placed on the ground. A fine screen mesh was stapled to the top of the trap, approximately 15 cm off the ground, to capture seeds and allow for water to pass through easily. Collections were made weekly during heavy seed rain periods and monthly during non-peak times; no collections were made when the ground was snow-covered. Collections were conducted during an entire year, from July 2009 to June 2010. After seeds were collected, they were identified to species when possible and recorded.

In 2010 (n=257) and 2011 (n=250) *Quercus* seeds (acorns) were collected at random from the forest floor throughout the entire Grove. These were then planted in

the greenhouse and the number of germinating seeds was recorded against the number of seeds planted in order to tabulate relative germination success of the seeds. These acorns were only planted if they did not appear to have any visible damage and did not float when placed in water, which is indicative of lifelessness.

Results

Forest Characterization

The canopy composition (Figure 1-1), with the exception of *A. platanoides*, was consistent with many of the upland forests in western New York: northern hardwood and oak (Goodell and Faber-Langendoen 2007). There was a mix of shade intolerant species (*P. serotina*), somewhat shade tolerant species (*Quercus* spp.), and very shade tolerant species (*A. saccharum*). The majority of the species were native species with the only exception being *A. platanoides*, which was the fourth most abundant canopy species, representing 10.6% of the canopy (by frequency) at a density of 30.6 individuals/ha in the current canopy. The subcanopy exhibited a substantial shift in composition. *A. platanoides* was the most abundant species of this forest stratum (37% by frequency, Figure 1-1), with an estimated 215 individuals/ ha, where the importance value for *A. platanoides* has quadrupled compared to the canopy. I examined the relative dominance of *A. platanoides* and witnessed an almost 600% increase from canopy (4.56%) to subcanopy (31.33%, Figure 1-1). Additionally, I only found one *Quercus* tree in the forest subcanopy, which suggests that few if any oaks will be present in the forest canopy in the next generation. In the

canopy and subcanopy combined, *A. platanoides* individuals comprised 24.2% of all trees. Figure 1-2 displays that as the relative density (%) of *A. platanoides* increases across forest strata, the Shannon-Wiener Index (H') value decreases suggesting that the tree diversity may also decrease in the Washington Grove (Table 1-1).

Of the seedlings and saplings surveyed (Figure 1-3), the species that occurred most frequently were, in order of decreasing frequency: *A. platanoides*, *Fraxinus americana* (white ash), *Sassafras albidum* (sassafras), *P. serotina*, and *Prunus virginiana* (chokecherry), representing species with variable shade tolerance. Not a single individual of any *Quercus* species was found along any transect and only four *Quercus* seedlings/saplings were observed in the forest outside of study plots. Herbaceous plant cover and shrub cover in this forest was also minimal; the most frequently encountered cover ranking was 1 (0-5%) on a modified Daubenmire scale. Additionally, only five herbaceous and six shrub (of 59) transect points had >50% cover for herbaceous (8.5% of points sampled) and shrub cover (10.2% of points sampled); however, exotic forb and shrub species were prevalent within the Grove compared to native species of these functional groups and included: *Alliaria petiolata* (garlic mustard), *Elaeagnus umbellata* (autumn olive), *Euonymus alatus* (burningbush), *Euonymus europaeus* (European spindle tree), *Hedera helix* (English Ivy), *Lonicera tatarica* (Tatarian honeysuckle), *Rhamnus cathartica* (common buckthorn), and *Rosa multiflora* (multiflora rose). Of the 59 transect points surveyed, 20% had at least one of these exotic species present.

Finally, the average amount of available light in Washington Grove approximately 1m above the forest floor was reduced to 1.12% of average of ambient light (full sun), but ranged from 0.22% to 17.5%.

Seed Bank

Over the six month period of this study, 358 seeds germinated. *Rubus* species (raspberries and blackberries) were by far the most prolific in my seed bank analysis (51.1% of all stems, Figure 1-4). *Rubus* species included *R. occidentalis* (black raspberry), *R. idaeus* (American red raspberry), and *R. odoratus* (purple flowering raspberry), but there were a large number of *Rubus* individuals that I was not able to identify to species. *Oxalis* (woodsorrel) spp. also had prolific germination, comprising 18.4% of the germinating seeds. This species was also present in control (non-seed bank) soil, which may suggest a seed source within the greenhouse. *Epilobium glandulosum* (Northern willowherb) (7%) and *Artemisia vulgaris* (common wormwood) (5.6%) were also found in the seed bank. *Populus deltoides* (eastern cottonwood) (16 individuals) was the most frequent seed among the tree species, this represents a fairly high frequency for tree species, given a soil sample size of 40. The invasive *Ailanthus altissima* (tree of heaven) (14 individuals) was the next most abundant tree in the samples. Other trees included *Populus tremuloides* (quaking aspen), *Liriodendron tulipifera* (tulip tree), and *Acer rubrum* (red maple) (Figure 1-4). None of these species emerged in any of the control test pots.

Seed Rain

A total of 397 seeds were collected and identified over the course of a year (Figure 1-5). *Prunus* seeds were the most abundant (20.9%) followed by *Carya ovata* (shagbark hickory) (13.1%), *A. saccharum* (11.8%), *P. deltooides* (11.3%), and *A. platanoides* (9.8%). A total of 27 tree species were encountered in the entire study (canopy, subcanopy, understory, seed bank, and seed rain), but seeds of only 14 tree species were captured in seed rain, including four not identified in the canopy: *Fagus grandifolia* (American beech), *P. deltooides*, *Quercus macrocarpa* (bur oak), and *Ulmus americana* (American elm). An important finding was that I captured four different *Quercus* species in the seed traps, *Q. alba*, *Q. macrocarpa*, *Q. rubra*, and *Q. velutina* and all were present in the forest canopy with the exception of *Q. macrocarpa*. It is possible that I have underestimated *Quercus* and other seeds since it was possible for forest foragers to remove them from traps. Of the *Quercus* seeds that were collected separately and grown from seed, 80.2% germinated in 2010, and in the following year 62.8%.

DBH versus Age

The DBH versus age relationship allowed me to predict the age of an *A. platanoides* tree from its diameter. The relationship was statistically significant ($r^2 = 0.448$, $p=0.005$; Figure 1-6). Based on the largest *A. platanoides* encountered in my survey (DBH = 70.0 cm, approximately 69.7 years of age) the invasion likely began sometime in the late 1930's.

Discussion

Forest Characterization

The results of this study demonstrate that the currently diverse Washington Grove forest is following a trajectory toward domination by nonnative species. *A. platanoides* abundance at the subcanopy and seedling/sapling strata of the forest is indicative of what the forest will resemble as a new generation of individuals reaches maturity. The catalyst for invasion by *A. platanoides* and the shift in successional trajectory was presumably the planting of nonnative *A. platanoides* as a street tree and its production of a high number of seeds. The output of seeds is almost twice that of the native *A. saccharum* (Meiners 2005). *A. platanoides* currently comprises 42% of the relative density of trees bordering neighborhood streets adjacent to Washington Grove. I estimated that the invasion of this area has been ongoing for at least 70 years (Figure 1-6). Currently, individuals of this nonnative species dominate many life stages, ranging from seedling to mature tree, and clearly represent a successful invasion. The success of *A. platanoides* is likely due in part to relatively strong propagule pressure, first from neighborhood street trees, and now mature trees within the forest. In fact, a meta-analysis suggested that invasive species typically introduced themselves to an area by out-producing contrasting native species (Colautti *et al.* 2006). However, the collected seed rain in Washington Grove was only 10% *A. platanoides*. The structure of wind-dispersed seeds allowed for further dispersal than heavier, nut-like seeds when falling from above, and in-turn wind-

dispersed seeds are easily blown out of seed traps. I think that because of this, the amount of *A. platanoides* seeds may have been underrepresented.

It was determined that *F. grandifolia* was 47% of trees within the region of central and western New York forests prior to European settlement followed by 22% *A. saccharum*, 5% *Quercus alba* (white oak), and 4% *Tsuga canadensis* (Eastern hemlock) (Marks and Gardescu 1992). Wang (2007) determined a similar pre-settlement composition for western New York forests, consisting of mostly late successional species: 37% *F. grandifolia*, 21% *A. saccharum*, 8.3% *T. canadensis*, and 5.1% *Tilia americana* (American basswood). Abrams (2003) used canopy disturbance (harvests) and suppression of fires after 1900 to explain the emergence of *Quercus rubra* (red oak), *F. grandifolia*, *A. rubrum*, and *L. tulipifera*. Today, in much of western New York, there is a mix of shade intolerant and tolerant species, representing many of the already mentioned species. These species are consistent with what I discovered in the Washington Grove, with the exception of shade tolerant, late successional species *T. canadensis*, which was absent here. Furthermore, *F. grandifolia* was observed in the Grove; however, it was not recorded during the course of this study, indicative of its relatively low abundance.

The major replacement species of eastern US forests once dominated by *Quercus* species are *A. saccharum*, *A. rubrum*, *P. serotina*, *F. americana*, and *F. grandifolia* (Lorimer 1984, Smith and Vankat 1991, Abrams 1992). Of those species, *A. saccharum* is the most shade tolerant (Burns and Honkala 1990), and is one of the most important species in the current forest canopy of my study site (Figure 1-1).

Because *A. saccharum* and *A. platanooides* are congeners and have many of the same life history traits, they potentially could be occupying the same niche space along the successional trajectory of a northeastern US forest community. I believe that *A. platanooides* is out-competing *A. saccharum* on a community scale for available niche space because of the greater abundance of *A. platanooides* seedlings/saplings and subcanopy trees. In other studies which compared a variety of traits and characteristics of these species, *A. platanooides* was considered a superior competitor (Kloeppel and Abrams 1995, Meiners 2005, Morrison and Mauck 2007, Cincotta *et al.* 2009). Thus, because *A. saccharum* is a major replacement species of *Quercus* along a typical forest successional trajectory, *A. platanooides* appears to out-compete *A. saccharum*; this may be the fundamental reason why I have observed a composition shift from a *Quercus* dominated forest to a nonnative dominated stand.

Quercus recruitment failure in the subcanopy, sapling, and seedling layers is another reason why I expect further compositional shifts. With only one *Quercus* tree found in the forest subcanopy, I tested the viability of the acorns produced by the trees in the Grove. Based on *Quercus* germination rates, I concluded that the acorns in the Grove are viable, but conditions must not be favorable to promote their germination or survivability. I suspect that the amount of available light was too limiting for *Quercus* seeds to survive. Lorimer *et al.* (1994) found that tall subcanopy trees, like *Acer*, *Ostrya* (hophornbeam), and *Tilia* (basswood) within a primarily *Quercus* canopy inhibit the success of *Quercus* seedlings. They suggested that shade cast by the subcanopy is most limiting to the growth and survival of *Quercus*

seedlings, which may be likely in my study area as well. Reinhart *et al.* (2006) suggested that *A. platanoides* canopies can create deep shade, which limits the regeneration success of native species. Past research has shown that many *Quercus* forests in the Northeast are considered to be mid-successional, and not the climax communities they were once thought to be (Abrams and Downs 1990, Hix and Lorimer 1991, Abrams 1992). A dark canopy is the most likely reason for why there is a lack of herbaceous and shrub cover. Not only is it too dark for *Quercus* species to survive but also for many of the herbaceous and shrub species.

Rinkes and McCarthy (2007) determined that *Quercus* species also may experience recruitment failure because of disruption to the leaf layer. They found that removal of the leaf litter discourages recruitment success of *Quercus* species, and encourages recruitment of *A. rubrum*. *Q. rubra* seedlings emerge at a 50% greater rate when planted in deep (5 cm) leaf litter, as opposed to shallow (1-2 cm) litter (Kostel-Hughes *et al.* 2005). The leaf litter at my site is likely disturbed in some areas by heavy foot and paw traffic which also could be contributing to the lack of *Quercus* regeneration. It seems reasonable to conclude that *Quercus* regeneration is inhibited in the Washington Grove understory because it is too dark, and perhaps because of leaf litter disturbance. In fact, because *Acer* performs well in disturbed leaf litter (Kostel-Hughes *et al.* 2005), and has a greater shade tolerance than *Quercus*, I believe that with continued deep shade and regular recreational disturbance *Acer* encroachment will continue.

Seed Bank and Seed Rain

A. platanoides was largely absent from the seed bank and seed rain collections despite prevalence in the forest community. I believe that conditions in the greenhouse may have not been ideal for *Acer* germination. It is possible that relatively high temperatures limited *Acer* germination, as has been found for other species in similar seed bank studies, where a threshold ≥ 36 °C was too hot (Brändel and Schütz 2005); this temperature was occasionally exceeded in the greenhouse. The species that did emerge from the seed bank were all present in Washington Grove, but considered minor components of the community.

Of the trees that germinated in the seed bank study, all were native except for *A. altissima*. *A. altissima* is another invasive species in the United States and has many ecological concerns similar to that of *A. platanoides* (Gomez-Aparicio and Canham 2008). *A. altissima* is allelopathic (Heisey 1996); a producer of a large quantity of wind-borne seeds, which can have greater germination success in a shallow leaf litter (Kostel-Hughes *et al.* 2005); grows asexually through its root system (Hu 1979); and although described to be shade intolerant, has been found in the canopy of some old-growth forests in New York State (Knapp and Canham 2000). This species was not discovered during the forest characterization portion of my study, but several mature trees were located in the forest beyond my study transects. Of all the samples removed, *A. altissima* seeds germinated in samples from three of the four transects (27.5% of all total samples), suggesting that seeds of this species

are spread throughout the Grove and could potentially germinate if opportune conditions presented themselves (e.g., canopy gaps).

The composition of species captured during my seed rain study was relatively heterogeneous. I expected to find an overabundance of *A. platanoides* seeds in this portion of the study because of the large number of seedlings encountered, the number of mature trees in the forest, and presumed input from the neighborhood street trees; however, this was not the case (Figure 1-5). In contrast, *Prunus* seeds were most abundant. I did expect to see a large number of seeds produced from this species since it was the second-most important species in the canopy and subcanopy. Despite its intolerance to shade, it was the fourth densest species in the seedling and sapling observations. I expect to see a continued decline of *Prunus* germination and survivability in the forest development, given an expected increase of shade produced by an increase in *A. platanoides*.

Patterns of seed dispersal may also explain the lack of wind-dispersed *Acer* seeds collected. Matlack (1987) found that *A. platanoides* seeds will travel on average 50.3 m in a 10 km/hr breeze. It is possible; due to my seed trap design that the wind-dispersed seeds may have blown out of the seed traps during collection periods, which may have led to capturing such low number of wind-dispersed species. The heavier seeds (e.g. *Quercus*) would not have been as easily moved by wind, and I would consider their findings to be more accurate. However, the heavier seed rain likely does not reflect *Quercus* future potential in contributing to the canopy composition due to relative shade intolerance of these species.

Conclusion

The forest at the Washington Grove in Rochester, NY is changing from a native *Quercus*-dominated stand to a community dominated by invasive *Acer platanoides*. The current development of the forest subcanopy is a precursor of what this forest likely will resemble in the not-too-distant future. The relative density of seedlings and saplings, the next relative life cycle stage, is also discouraging. *A. platanoides* already is the most dominant species in these strata, and I expect that a change in the plant species composition to not be the only ecological consequence to this system (Wilcove *et al.* 1998). I expect this forest compositional change because *A. platanoides* is so successful in its nonnative range (Morrison and Mauck 2007, Cincotta *et al.* 2009), and can outcompete native tree species for resources (Kloeppel and Abrams 1995), and has favorable life history traits in order to thrive in the Washington Grove environment (Meiners 2005, Galbraith-Kent and Handel 2012). With the progressive increase of *A. platanoides*, there seems to be increased amount of shade, which I believe is the primary reason, perhaps in combination with litter disturbance on the forest floor, for the compositional shift from shade mid-tolerant or intolerant native species currently dominant in the canopy.

Management Recommendations

In order to restore this forest to what would be considered natural and native, I propose a two-step approach. The first step would be to remove all invasive species, beginning with the most abundant mature species. Since these studies concluded, the

Sierra Club of Rochester, NY has worked with city foresters to remove some of the larger *A. platanoides* trees from the area, along with other invasive species. I support the continuing removal of the nonnatives; however, this is not enough and must be done with care, so as to not encourage establishment of other invasive species (Webb *et al.* 2001). The creation of open canopy conditions by artificial and natural means has other ecological impacts to the community. For instance, gap creation via tree removal offers a window for invasion for other threatening invasive species like *A. altissima*. A restoration effort cannot be a one-time cutting event but must include a long-term commitment to invasive and nonnative species removal. Additionally, I would recommend reducing nonnative propagule pressure by also removing *A. platanoides* street trees, along with the *A. altissima* that are nearby the Grove. Those trees could then be replaced with stress-resistant native trees.

The second step of this management plan would be to encourage native species diversity and *Quercus* recruitment, in particular, in areas where canopy gaps are present. I recommend starting with the installation of physical barriers that inhibit disruption of the leaf layer. This may require the purchase of temporary fencing around key portions of the forest, which would surround the leaf litter and limit its disruption. This has been done to limit off-trail use at another urban park within the region, Delaware Olmstead Park in Buffalo, NY, (*personal observation*). If funding is limited, the continued use of fallen or cut trees to border the trails and limit off trail use/disturbance may be better than nothing. I also recommend adopting methodology prescribed by Březina and Dobrovolný (2011) to encourage *Quercus* recruitment, in

which regeneration areas no bigger than 0.3 ha are created with approximately 50% of full-sun in order to promote a medium regeneration rate. This medium regeneration rate would take up to 15-20 y to establish the seedlings, and would prescribe 8 y intervals of *Quercus* crops. If the management plan was successful in limiting invasive species success, and conditions were altered in order to favor *Quercus* germination, I believe this forest could be restored to maintain its current diverse native canopy.

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Tables

Table 1-1: Species Richness and Shannon-Wiener Index values for the three recorded forest strata in the Washington Grove.

Strata	Species Richness	Shannon-Wiener Index (H')
Canopy	14	2.19
Subcanopy	21	1.97
Seedlings/Saplings	11	1.77

Figures

Figure 1-1: Relative density (%), relative dominance (%), and importance value (0-200) of all tree species recorded in the forest canopy (> 10 m tall) (n=236) and subcanopy (2-10 m tall) (n=236), in order of decreasing importance value. Relative density was based on frequency; dominance was based on basal area at breast height, and both are expressed as a percentage. The sum of relative density and dominance gives the importance value for a particular species.

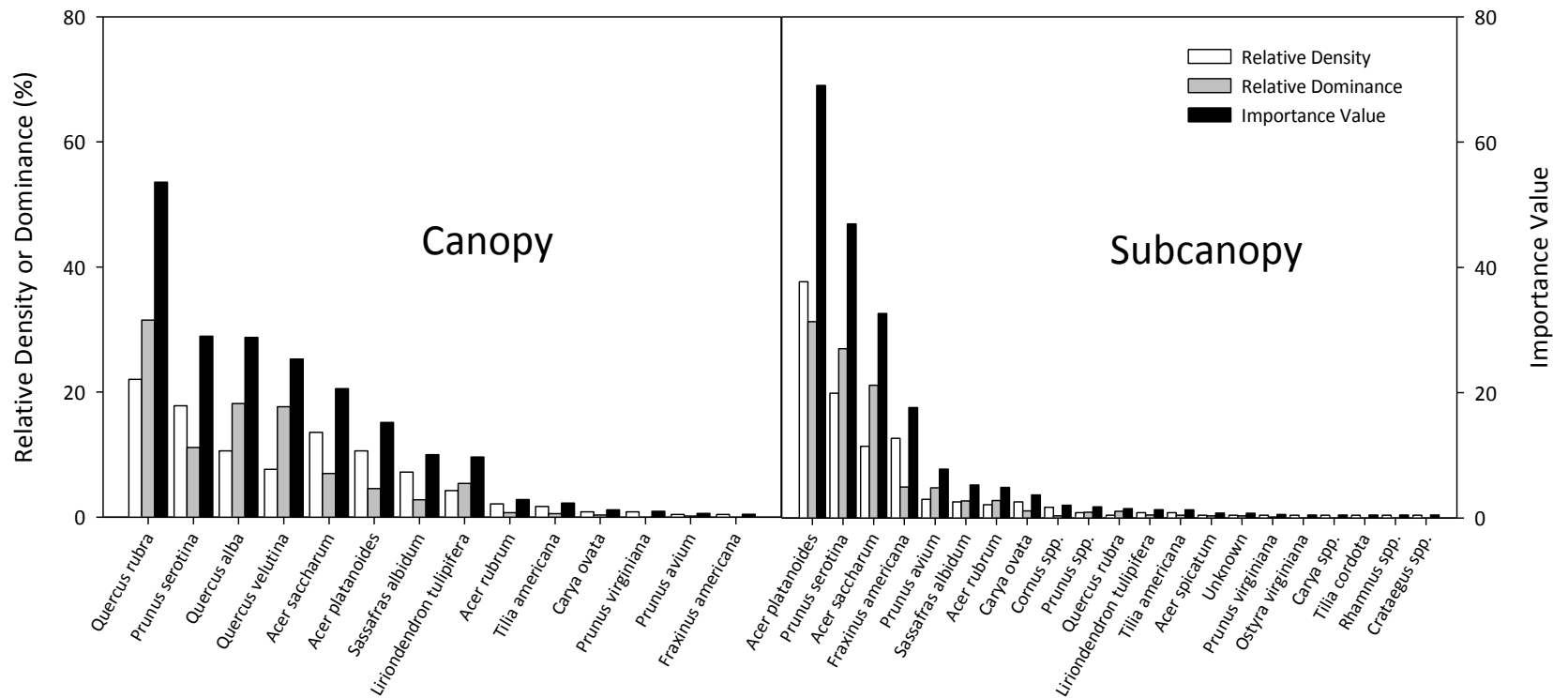


Figure 1-2: Relative density (%) of *A. platanoides* compared to the Shannon-Wiener Index (H') at the three levels of observed forest strata.

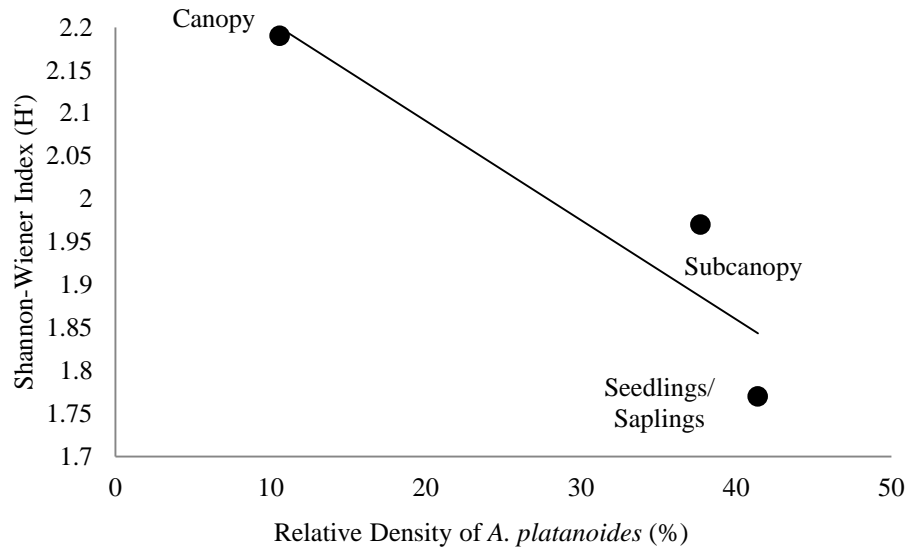


Figure 1-3: Relative density of all tree seedlings and saplings (<2 m height) recorded in Washington Grove (n=210).

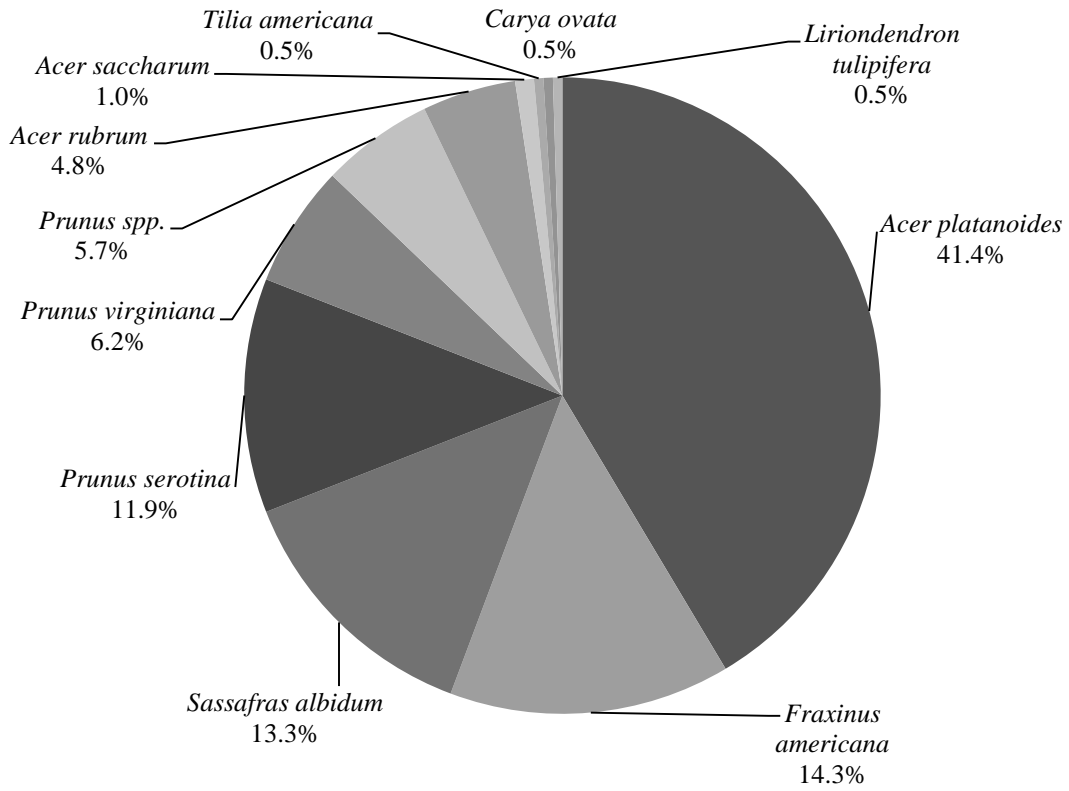


Figure 1-4: Relative density of all species present in the seed bank studies (n=358 seeds) (*=Tree species).

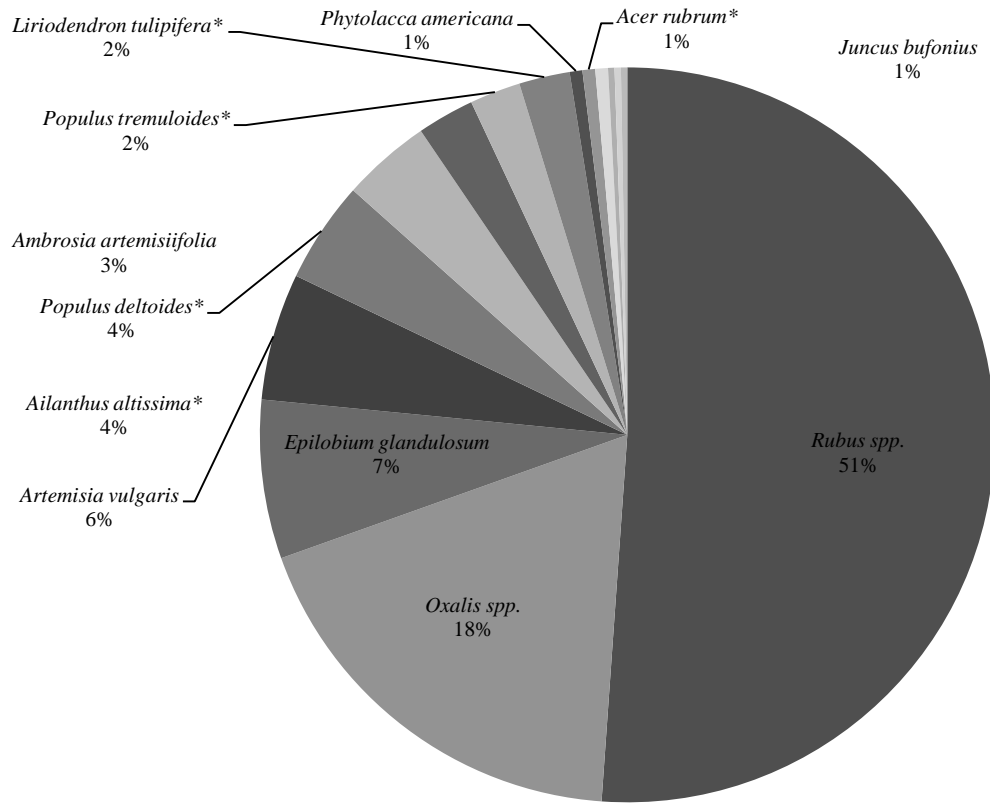


Figure 1-5: Relative density of all species collected in seed rain study (n=397 seeds)
 (*=Tree Species).

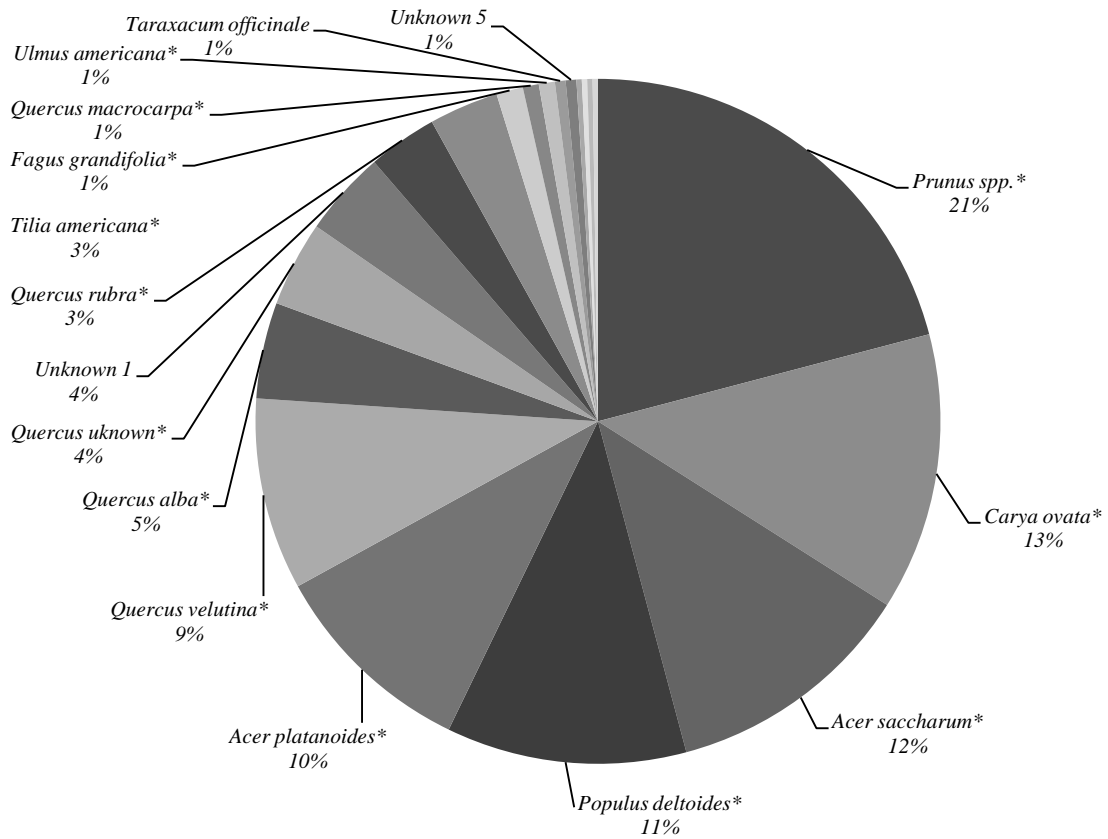
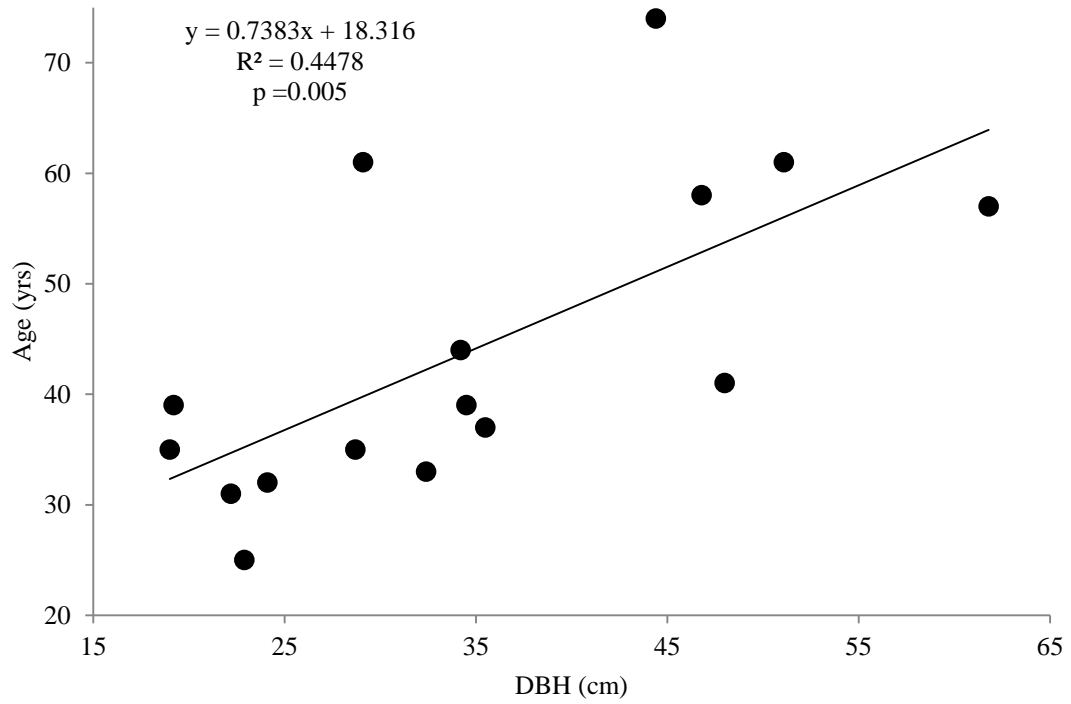


Figure 1-6: Relationship between diameter at breast height (DBH) and age for individual *A. platanoides* trees. Age of tree was determined with increment borer samples.



Chapter 2

Growth of Native and Nonnative Seedlings With Respect to Competition and Light Availability

Abstract

The invasive *Acer platanoides* (Norway maple) has been described to have superior life-history traits that allow it to be dominant in its nonnative range. These traits contribute to its ability to be a superior competitor in many northeastern forests. The Washington Grove at Cobbs Hill Park of Rochester, NY has seen a significant presence and continuing increase of this invasive species. I was interested in further understanding the differences at the seedling stage between this species and the native *Acer saccharum* (sugar maple) and *Quercus rubra* (red oak). In order to assess the differences, I planted transplants of these species in a greenhouse where seedlings were subjected to treatments of varying shade and intraspecific and interspecific competition. Photosynthetic rate, stem height, and stem diameter were measured repeatedly over a full growing season. In all shade treatments, *Q. rubra* had the greatest overall photosynthetic rate and *A. saccharum* had the greatest change in height. Growth in height and photosynthetic rate both decreased significantly with increased shade, as expected. In contrast to my expectations given observations of forest community dynamics here as well by others, I did not find any conclusive evidence to suggest that the invasive maple was the superior competitor at the seedling stage. Thus it appears that other factors are at play in the Washington Grove

that are limiting native species seedling growth and success and favoring *A. platanoides*.

Introduction

Plant species competition plays an integral role in shaping any plant community. A stronger competitor may have a better specific trait or a suite of traits (e.g. nitrogen fixation, shade tolerance, water use efficiency), have a trade-off mechanism (e.g. root versus shoot allocation) that is more beneficial for obtaining a limiting resource, or gained an advantage by escaping its native range and natural predators (Vitousek *et al.* 1987, Tilman 1999, Keane and Crawley 2002). These traits and behaviors are especially important in a community when nonnative invasive species are present. At one time, there were over 3,400 nonnative plant species in North America occupying over 40 million ha in the United States (Anon 1998, Qian and Ricklefs 2006). It is not certain how each one of these species will impact a plant community if given opportune conditions; however, understanding a plant's life history traits may help predict performance in specific plant communities (Thompson and Davis 2011).

Evidence in the literature suggests that some invasive species are likely to have competitive advantages over native species. A meta-analysis of plant traits suggested that invasive species compared to natives tend to have higher leaf area, lower tissue construction costs, greater phenotypic plasticity and are often found in areas of high resource availability, high physical disturbance, and deviation from the

natural disturbance regimes (Daehler 2003). A second meta-analysis generally concluded that invasive species when compared to non-invasives had overall greater photosynthetic rate, transpiration, tissue nitrogen content, water and nitrogen use efficiencies, leaf-area and shoot allocation, growth rate, size, and fitness (van Kleunen *et al.* 2010). Some invasives even display different traits in their introduced range, as compared to their native range. For instance, when grown in competition with native species in their nonnative range, *Centaurea solstitialis* (yellow star-thistle) displayed greater competitive resistance, larger seed size, larger seedling mass, and higher relative growth rate, as compared to congeneric native plants (Graebner *et al.* 2012). Invasive species can thus outcompete and eliminate native congeners from the ecosystem (Vitousek *et al.* 1996), through many of the mechanisms previously discussed.

One species that can capitalize on a disturbed habit, out-compete native species, and potentially limit native congeners is *Acer platanoides* (Norway maple). This species is an invasive species in many areas of the northeastern United States (Nowak and Rowntree 1990). Introduced in 1756 in Philadelphia, this tree species is possibly one of the most frequently planted street trees in the United States, often replacing *Ulmus americana* (American elm) trees lost to Dutch elm disease. It was a logical choice for urban areas because of its ability to withstand poor soils, pollution, diseases, and pests (Nowak and Rowntree 1990). However, natural areas near these plantings are susceptible to invasion given that many studies have documented that this species has invaded intact northeastern forests stands (Webb and Kaunzinger

1993, Hunter and Mattice 2002, Galbraith-Kent and Handel 2008, Gomez-Aparicio and Canham 2008). Invasion success can be attributed to the fact that *A. platanoides* is successful in full sun to deeply shaded habitats and may be prevalent in the soil seed bank of the areas that it invades (Webster *et al.* 2005). *A. platanoides* invasion success may also be due to the fact that it can limit native plant performance when native species are grown in *A. platanoides*-invaded soil (Galbraith-Kent and Handel 2012). Additionally, *A. platanoides* creates deep shade, yet its seedlings and saplings are competitive in the understory, which can further promote its invasion success (Galbraith-Kent and Handel 2008). Reinhart *et al.* (2006) found that it can also alter normal root: shoot growth to favor root growth in low light conditions, evidence of an evolutionary adaptation to maximize survivability. Finally, and not unique to this invasive, *A. platanoides* can increase rates of soil nutrient cycling, including net N mineralization, nitrification, Ca mineralization, and the availability of Ca, Mg, K, and N (Gomez-Aparicio and Canham 2008), which may give it a competitive advantage over native plants.

Several studies have compared *A. platanoides* and its native congener *Acer saccharum* (sugar maple) because they appear to fill the same niche. If species are occupying the same fundamental niche they are then in direct competition with one another. *A. platanoides* uses light, water, and nutrients more efficiently than *A. saccharum*, which most likely allows it to have a higher photosynthetic rate (Kloeppel and Abrams 1995). Also, when directly compared to *A. saccharum*, leaves of the nonnative *A. platanoides* also suffer less physical damage from herbivores,

consistent with the enemy release hypothesis (ERH) (Cincotta *et al.* 2009). The larger seed size and reduced grazing of *A. platanoides* seeds may also contribute to its invasion success (Meiners 2005). Early development studies also showed that *A. platanoides* produced more leaves, had greater root: shoot ratios, lower rates of winter die off, and earlier spring growth than its native congener, all of which may enhance success at an otherwise vulnerable life stage (Morrison and Mauck 2007). Finally, in a *Quercus* (oak)-dominated forest, *A. platanoides*' annual average height growth increments were nearly twice that of *A. saccharum* (Kloppel and Abrams 1995).

An area experiencing an overabundance of *A. platanoides* is the Washington Grove of Cobbs Hill Park in Rochester, NY. In this 10 ha forest, *A. platanoides* dominates the forest subcanopy, sapling, and seedling layers of a primarily native *Quercus* canopy (chapter 1). Disturbances or stronger competitive traits of *A. platanoides* may explain the forest community composition shift. Potential disturbances include recreation activity on and off trail, and biochemical stressors and pollutants associated with the urban setting (McDonnell *et al.* 1997). Stressors like these in disturbed areas have been associated with increasing plant diversity where the majority of the cover is often composed of invasive species (Sousa 1979, Crawford *et al.* 2001). I believe that disturbance and propagule pressure from nonnative *A. platanoides* street trees helped contribute to the invasion success.

The presence of *A. platanoides* coupled with the prospect of significant environmental changes is concerning. The *Acer* (maple) genus may limit *Quercus* species regeneration by casting deep shade beneath an *Acer* subcanopy (Lorimer *et al.*

1994). In the Washington Grove subcanopy, relative dominance of *Acer* species is 52.9% (31.3% *A. platanoides*, 21.2% *A. saccharum*, and 0.4% *Acer spicatum* [Mountain maple]). From personal observations, I have only encountered four *Quercus* seedlings in the entire 10 ha Washington Grove. I believe that with increased shade and direct competition among native and invasive species, photosynthetic and growth rates favor the invasive species and will continue to alter the already dynamic forest community composition. Therefore, the question addressed here is whether *A. platanoides* is more successful than *Q. rubra* or *A. saccharum* at the seedling stage under variable shade environments. In other words, is *A. platanoides* a stronger competitor in the forest understory?

I had three species of interest: *A. platanoides*, *A. saccharum*, and *Quercus rubra* (red oak). *Q. rubra* was selected because it was the most important tree in the canopy (chapter 1), its seeds were readily available in the Grove, and it was thought to be a good representative of its genus. *A. saccharum* was selected because it has been identified as one of the successional replacement species in northeastern *Quercus*-dominated forests (Abrams and Downs 1990), and it is prevalent in both the current forest canopy and subcanopy at my study site. *A. platanoides* was selected because the successional trajectory of my study site suggests a future canopy dominated by this species, and I therefore hypothesized that this species is a better competitor than two common native tree species. I anticipate that *A. platanoides* is a stronger competitor because of the expectations outlined in the literature about invasives, and in particular for *A. platanoides* (Kloppel and Abrams 1995, Webb *et*

al. 2001, Bertin *et al.* 2005, Galbraith-Kent and Handel 2008, Cincotta *et al.* 2009, and Graebner *et al.* 2012). I expected that when *A. platanooides* is present, there will be significant reductions in seedling growth and photosynthetic rates in the native species versus when *A. platanooides* is absent and that these interspecific effects will be greater than those due to intraspecific competition.

Methods

Experimental Design

The experiment was performed in the greenhouse at The College at Brockport (Brockport, NY) in order to control environmental conditions. A total of 81 pots were planted to measure competitive interactions among the three species, with respect to different shade treatments. *Quercus* seeds were obtained from Washington Grove in the fall of 2010 and kept refrigerated (5°C). They were planted the following spring and grown for a period of four weeks before the seedlings could be transplanted into experimental pots. *A. platanooides* seedlings were obtained from the Washington Grove, and *A. saccharum* seedlings were obtained from The College at Brockport campus woodlot. The average height of the seedlings by species was: 10.64 ±0.30 cm – *A. platanooides*, 8.65 ±0.26 cm – *A. saccharum*, and 11.79 ±0.44 – *Q. rubra* at time of transplantation.

Nine different arrangements were used to assess intra- and interspecific competitive effects (Table 2-1). Seedlings were planted in different abundances and ratios in 8.36 L pots (22 cm diameter). Pots were filled to a depth of 17 cm of potting

medium, a commercially available sterilized peat mixture (Pro mix Bx, 80% Peat Moss, 15% Perlite). In the control arrangement for each species, one individual was planted in the center of the pot. For the intraspecific competition arrangements, four seedlings of the same species were planted in a square pattern, equidistant from each individual and the side of the pot. The interspecific competition arrangements were designed so the dominant species (three seedlings) were transplanted to surround the minority species (one individual) in a triangle pattern, equidistant from each individual and the side of the pot. Initial measurements were not performed until 7 d later to ensure that individuals survived transplantation. All three species were included in the control and intraspecific competition treatments. I was not interested in the effects of *Quercus* on either *Acer* species, only the interspecific effects of *A. platanoides* on both *A. saccharum* and *Q. rubra* and for comparison purposes *A. saccharum* on *Q. rubra* (Table 2-1).

These nine arrangements were replicated three times in each of three shade treatments: low shade (85% shading of full sun as measured with a LI-191 Line Quantum Sensor, LI-COR, Lincoln, NE), medium shade (91% shading of full sun), and high shade (97% shading of full sun). For comparison, the understory in Washington Grove at 1 m above the forest floor on average experiences shading that reduces full sun by 98.88%, a value similar to the high shade treatment. Shade treatments were created with shade cloth, and arranged in blocks that completely surrounded the pots from above and all sides, so that only the prescribed amount of light was available to the seedlings. Within each shade treatment, pots were arranged

approximately 10 cm apart from each other to reduce shading effects from other pots. Pots were rearranged regularly within their shade environment to reduce local area effects.

This study was conducted from July 10, 2011 to October 8, 2011; monthly measurements of plant height (soil to terminal bud), stem diameter (measured with calipers, 3cm above soil layer), and leaf counts were performed on representative seedlings. Pots were watered regularly to keep the soil moist (not limiting), and supplemental full spectrum lighting was maintained for a minimum of 12 h/d.

Photosynthesis

I used a LI-6400 Portable Photosynthesis System (LI-COR, Lincoln, NE) to measure photosynthetic rates ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) every four weeks for a total of four times over the duration of the experiment. One representative healthy leaf of one plant species was sampled from each of the 81 pots. In the intraspecific arrangement, one of the individual trees was sampled at random. In the interspecific arrangement, only the minority species subjected to competition was selected and measured. Measurements were conducted inside the shade treatments and always exposed to a consistent amount of prescribed light.

Allometric Equations

In order to determine the amount of dry biomass of individual plants of the three test species, destructive harvests were periodically performed on a subset of

individually grown plants (separate from the experimental plots described previously). For each of the three species, at least ten individual seedlings were harvested periodically throughout the growing season, representing as broad a size range as possible, to develop allometric equations. Plant height and stem diameter were measured in the same manner as described above and were recorded prior to harvest. Once these measurements were made, each seedling was separated into three parts: roots, stem, and leaves, to quantify below- and aboveground biomass. These parts were dried at 70 °C for 24 h and weighed. The dry weight measurements were weighed separately and summed in order to achieve a total overall dry biomass measurement. Then the dry biomass was plotted against both the height and diameter for that particular individual. An equation derived from a best fit line was developed to project biomass for all the species I measured during my study. From my calculations, stem diameter was the best measure of biomass for each species, and was used for this purpose for all three species.

In order to test the accuracy of the biomass equations, further destructive harvesting of the experimental seedlings was performed at the conclusion of the experiment. A total of 27 individuals were harvested: three of each species, or one per competition treatment. In the interspecific measurements it was always the minority species. The biomass from these experimental individuals fell within the 95% confidence interval of the allometric regressions, confirming the accuracy of the equations.

Statistical Analysis

For plant height, stem diameter, and the rates of photosynthesis, I was interested in understanding the complexities of interactions in my experimental design. A three-way ANOVA was used to examine the relationship of the three factors (species type, shade treatment, and competition arrangement) of my design ($\alpha = 0.05$). To avoid differences due to initial plant size, I analyzed stem diameter and plant height data by calculating percent change between the final and initial samplings (for relative height and diameter growth). Photosynthesis readings were taken monthly and results from each month were combined together by shade treatment for each competition arrangement because in general there was a pattern of consistency among variable times of the year. Combination of these data over time was done given consistent patterns with respect to treatments (species, competition, and shade) and because I was not interested in the temporal patterns, but was more interested in treatment effects and interactions. To satisfy normality assumptions of the statistical tests, a square root transformation was used for the photosynthesis measurements, and an arcsine transformation was used for the plant height measurements. In order to determine differences within treatment levels, a Tukey's post hoc test was used.

Results

Allometric Equations, Biomass, and Plant Height

I was able to develop equations predicting unknown biomasses for each species, based on measured stem diameters from a control arrangement (Table 2-2). Regressions for *A. platanoides* and *Q. rubra* explained 72.86% and 58.35%, respectively, of the variation in biomass. *A. saccharum* did not have a significant p-value but was still used to predict biomass.

The allometric equations were utilized to develop relative biomass relationships, and there were evident differences among individual species performance (Figure 2-1). Seedlings in the medium shade treatment (9% of full sun) gained the most biomass for all species. In fact, seedlings in the medium shade treatment had a significantly greater overall increase in biomass than did seedlings in the low ($p = 0.045$) and high ($p = 0.009$) shade treatments.

There were also significant among-species differences in plant height ($p \leq 0.001$, Figure 2-2). *A. saccharum* had significantly greater height growth than *A. platanoides* ($p = 0.001$) and *Q. rubra* ($p \leq 0.001$), which were not significantly different from each other. Across all three species, there were no statistical differences in percent change of plant height with respect to shade or competition arrangement. Also, there were no differences in the interactions among these comparisons; however, there were specific species differences as *A. saccharum* had a significantly greater change in plant height ($p = 0.003$ in both cases, Figure 2-3) than *Q. rubra* in both of the intraspecific and interspecific competition treatments.

Although not significantly different ($p = 0.272$), *Q. rubra* tended to have reduced height growth when planted in competition with *A. platanooides*, in comparison to its control and intraspecific arrangements (Figure 2-3).

Photosynthesis

Photosynthetic rates were significantly different between shade treatments ($p = 0.002$) across all species and competition treatments, and generally decreased with increased shade (Figure 2-4). Overall mean photosynthesis rates (averaged across all species and sampling dates) were low shade: $1.92 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ > medium shade: $1.44 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ > high shade: $1.17 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$. *Q. rubra* had a significantly higher rate than both *A. platanooides* and *A. saccharum* ($p \leq 0.001$ in both cases). There were no significant differences among the two *Acer* species when comparing all individuals among all treatments. The low and medium shade treatments did not have significantly different photosynthesis rates from one another but were both significantly higher than the high shade treatment ($p \leq 0.005$). Contrary to my expectation, the competition treatment did not statistically affect photosynthetic rates for any species ($p=0.071$, Figure 2-5) and thus photosynthesis rate results are presented as averages across competition treatments by species and shade treatment. A trend in the data, although not significant, is the mean photosynthesis rates of both native species which tended to increase slightly in the interspecific arrangement (Figure 2-5).

Photosynthetic rates varied between species and in different shade treatments. *Quercus* seedlings had significantly increased rates of photosynthesis with increasing light while *A. platanoides* had significantly higher rates only in low shade (highest light); however, *A. saccharum* showed no response to varying amounts of light availability ($p = 0.121$). Differences among species within each shade treatment also shed light on these species' ecophysiology. In the high shade (low light) treatment, there were no significant differences among species; however, as a general trend across all three treatments, *Q. rubra* had the greatest photosynthetic rates of the three species, and the difference between *Q. rubra* and both *Acer* species increased with increasing light. In the low shade (highest light) treatment, the photosynthetic performance of each species differed significantly, with *Q. rubra* > *A. platanoides* ($p = 0.012$) and *A. saccharum* ($p < 0.001$), and separately *A. platanoides* > *A. saccharum* ($p = 0.015$).

Discussion

The Washington Grove at Cobbs Hill Park is a dynamic urban forest that has been heavily invaded by the nonnative *A. platanoides*. Also of importance is that native *Quercus* species are not regenerating in the forest (chapter 1). Based on these data and evidence in the literature, I expected to find that *A. platanoides* was the overwhelmingly stronger competitor under experimental conditions (Kloepfel and Abrams 1995, Wyckoff and Webb 1996, Webb *et al.* 2001, Bertin *et al.* 2005, Meiners 2005, Martin and Marks 2006, Reinhart *et al.* 2006, Morrison and Mauck

2007, Galbraith-Kent and Handel 2008, Gomez-Aparicio and Canham 2008, and Galbraith-Kent and Handel 2012). Although I discovered differences in performance between species in my shade and competition treatments, there was no clear evidence suggesting that *A. platanoides* was a superior competitor at the young seedling stage of development.

As expected, photosynthesis measurements found a positive relationship between available light and rate of photosynthesis. This pattern did vary with species, suggesting that they had different physiological abilities to photosynthesize in low light conditions. My data suggest that for young seedlings, *Q. rubra* has the greatest tolerance for shade, despite its categorization as being less shade-tolerant than the two *Acer* species (Burns and Honkala 1990, Kloeppel and Abrams 1995). Of further interest is that *A. platanoides* had a significantly higher rate of photosynthesis than *A. saccharum* in the low shade (greatest light availability) environment. In terms of how this may impact Washington Grove, *A. saccharum* is very shade tolerant (Burns and Honkala 1990) and is often the replacement species (Abrams and Downs 1990) to dominate in this forest's natural successional trajectory in this region. Previous studies have shown however that when these two *Acer* species have been studied concurrently, *A. platanoides* has grown faster, produced more leaves, had lower rates of winter die off, and experienced earlier spring growth (Kloeppel and Abrams 1995, Morrison and Mauck 2007). Variation among photosynthesis rate and the amount of variable light, along with what has been uncovered in previously

mentioned research, may be contributing to the success of *A. platanoides* over *A. saccharum*.

Photosynthetic rates illustrate an incomplete story and do not lead to the same conclusions about competition as the growth results. The relative height growth for *A. saccharum* was greatest; specifically worth noting is that it was significantly greater than any other species in the high shade, lowest light environment. *A. platanoides* was most limited in darkest conditions and replication of these conditions could assist to maximize the relative success of *A. saccharum*. Martin and Marks (2006) found that intact, deeply shaded forests were best at slowing the rate of invasion by *A. platanoides*; thus a dark forest may encourage native *A. saccharum* and limit encroachment of *A. platanoides*. However, if a potential restoration goal for this area is to promote *Quercus* regeneration, a very dark setting is not the best to encourage survival of a medium-shade tolerant species such as *Quercus rubra* (Dai *et al.* 2002, Bertin *et al.* 2005).

A proposed mechanism by which *A. platanoides* has been successful is by possessing dominant competitive ecophysiological traits (Kloeppe and Abrams 1995, Meiners 2005, and Morrison and Mauck 2007). Anecdotally, this appears to be the case in Washington Grove where I have observed the composition of the subcanopy, sapling, and seedling layers. In contrast to this expectation, there was no experimental impact of *A. platanoides* on the photosynthetic rates of native species at the young seedling stages. Martin (1999) had suggested that an allelopathic inhibition by *A. platanoides* may be possible, but my results do not support the idea

of such an interaction because the interspecific arrangements showed a no effect. Furthermore, Rich (2004) discounted allelopathy as a competitive mechanism of *A. platanoides*. But, further evidence of non-observable competitive effects at certain life stages was discussed by Brudvig and Evans (2006). They argued that invasive plants may not be competitive at the seedling stage, finding that the invasive *Lonicera tatarica* (Tartarian honeysuckle) did not have a significant impact on native seedlings of *Q. alba* (white oak), despite dominance displayed at later growth stages. Intraspecific competition also did not hinder same species photosynthesis in my study but, these same species neighbors may have benefited the target seedling since rates were higher on average. Thus neighbors, regardless of species, do not impede photosynthesis rate at low light conditions. This is not what I expected, since Kloeppe and Abrams (1995) found that *A. platanoides* increased its annual height at a rate of twice that of *A. saccharum* in a *Quercus* forest. My analysis, which had a similar shade setting as Kloeppe and Abrams (1995), also considered relative plant height growth, but I found that *A. saccharum* had grown taller despite lower photosynthetic rates, regardless of shade or competition treatment.

Q. rubra height was not significantly inhibited by the presence of *A. platanoides* when compared against results from the control or intraspecific groups. This could be interpreted to mean that as more *A. platanoides* seedlings become established in Washington Grove, as is the current trend, *Quercus* seedlings/saplings may be inhibited, thus contributing to the lack of regeneration within the Grove. As time progresses and more invasive individuals reach maturity, *A. platanoides* will

continue to be taller than the *Quercus* seedlings, and I can expect it to limit the native species' success (Tanner *et al.* 2005). Furthermore, if *Quercus* species in this area share characteristics with another member of its genus, *Q. douglasii* (blue oak), there could be compounding competitive effects where recruitment success could be limited by both intraspecific and interspecific competition (Gordon and Rice 2000). However, that seems doubtful given current lack of *Quercus* seedlings and saplings.

It does remain somewhat of a puzzle that I did not see more of a significant dominance by *A. platanoides* at the seedling stage. I would anticipate because of previous findings from work with *A. platanoides* on a regional scale, that greater competitive differences may become more obvious in the Washington Grove in the future (Kloeppel and Abrams 1995, Bertin *et al.* 2005, Reinhart *et al.* 2006, Galbraith-Kent and Handel 2008, Gomez-Aparicio and Canham 2008). Similar to my results, Morrison and Mauck (2007) found that photosynthesis and die-off rates were very similar between the two *Acer* species, sampled during their first year of seedling life. Exploration of other characteristics, for instance, below-ground interactions, may be necessary in future research in order to determine what gives *A. platanoides* the competitive edge over *A. saccharum* when focusing on the seedling developmental stage.

Conclusion

A. platanoides in any treatment or arrangement did not have the highest rate of photosynthesis and did not have the highest percent change in height, nor did it

exhibit inhibitory competitive effects. I suspect that experimental evidence for dominance by *A. platanoides* may have been apparent if the time frame of my experiment had been extended beyond a few months. A study lasting for several years may have been more appropriate for examining competitive interactions between *A. platanoides* and native forest tree species. Additionally, Kloeppe and Abrams (1995) found higher photosynthetic rates in *A. platanoides* saplings (exact age not specified), where here I used seedlings. I would also anticipate a developing significant difference between control and interspecific competition for *Quercus* given that *Q. rubra* had a lower rate of height change when planted with *A. platanoides*, than when grown alone or in competition with members of its own species. In terms of photosynthesis rate, the native species seedlings were not impacted by the invasive species presence. However, with a longer time frame, significant differences may develop between *Q. rubra* change in height and an increase by *A. platanoides* because the invasive has been described as so fast growing (Kloeppe and Abrams 1995).

Management Recommendations

Knowing that a long term goal for the Washington Grove is to restore *Quercus* species and reduce *A. platanoides* recruitment, my recommendation would be to encourage greater light conditions in Washington Grove, along with a long-term physical removal of unwanted species. Cuttings of larger *A. platanoides* (which has already begun), which is necessary to limit their dispersal, also have a direct effect of

creating an increased light environment. I anticipate that this will increase *Quercus* germination, but it may also encourage increased growth of *A. platanoides* and other potentially invasive species located in Washington Grove [e.g. *Ailanthus altissima*, *Lonicera tatarica* (Tatarian honeysuckle), and *Rhamnus cathartica* (common buckthorn)]. I expect this because as more light becomes available to the forest floor, this could encourage germination from a suite of species seeds present in the Grove. Additionally, I would recommend off-site reduction of nonnative propagule pressure. Managers may want to consider removing *A. platanoides* street trees, along with other threatening invasives growing in proximity to Washington Grove. Those trees could then be replaced with stress-resistant native trees in order to fill the void. A management strategy to control *A. platanoides* must be long term and adaptive so as to anticipate initial unforeseen problems.

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Tables

Table 2-1: Competition study individual pot arrangements. Each arrangement was replicated three times in each of the three shade environments.

Species	Ratio (# of individuals)	Competition Type
<i>Acer platanoides</i>	1:0	Control
<i>Acer saccharum</i>	1:0	Control
<i>Quercus rubra</i>	1:0	Control
<i>Acer platanoides</i>	4:0	Intraspecific
<i>Acer saccharum</i>	4:0	Intraspecific
<i>Quercus rubra</i>	4:0	Intraspecific
<i>A. platanoides:Q. rubra</i>	3:1	Interspecific
<i>A. platanoides:A. saccharum</i>	3:1	Interspecific
<i>A. saccharum:Q. rubra</i>	3:1	Interspecific

Table 2-2: Allometric equations relating total dry biomass (g) to stem diameter (cm) for each species of interest (n=10).

Species Name	Allometric Equation	R ² Value	p-value	Diameter Range (cm)
<i>Acer platanoides</i>	biomass = 0.775(diameter) – 0.8928	0.7286	0.002	1.45-3.51
<i>Acer saccharum</i>	biomass = 0.1292(diameter) + 0.2374	0.0644	0.479	1.27-2.44
<i>Quercus rubra</i>	biomass = 3.2647(diameter) – 4.2182	0.5835	0.010	1.52-3.89

Figures

Figure 2-1: Mean initial to final percent change of plant biomass (g) (\pm SE) for three different test species in multiple shade treatments across all competition treatments. Biomass was determined using allometric equations (Table 2-2) based upon stem diameter (cm).

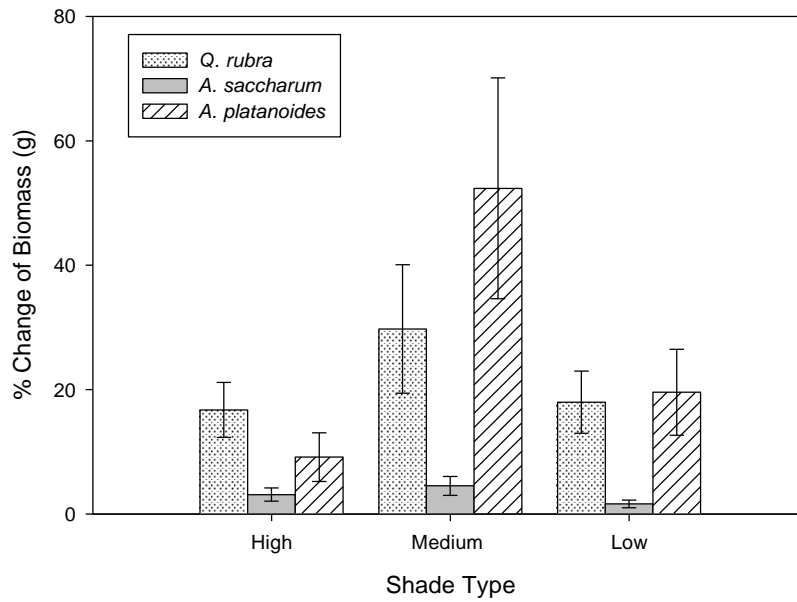


Figure 2-2: Initial to final percent change of plant height (cm) (mean \pm SE) for three species in three shade treatments averaged across all competition treatments.

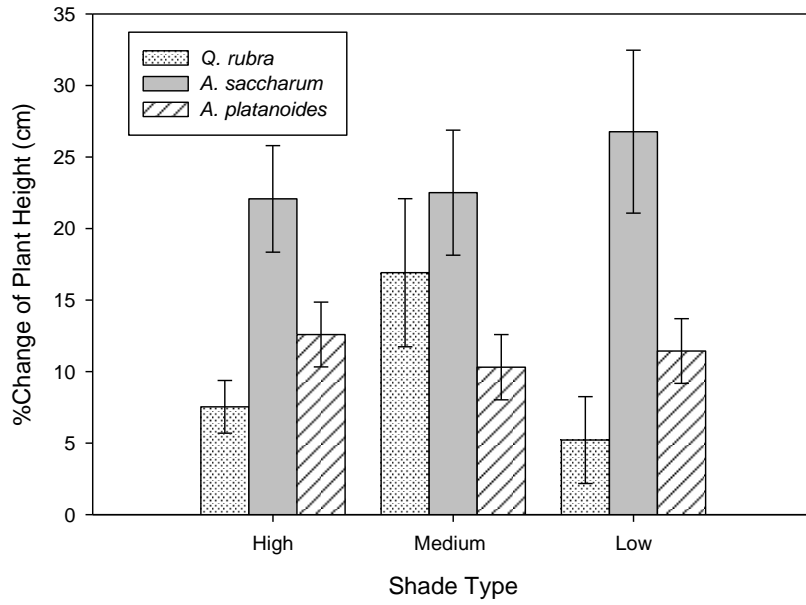


Figure 2-3: Percent change of plant height (cm) (mean \pm SE) of two native species in various competition treatments. The interspecific arrangement is planted with *A. platanoides*.

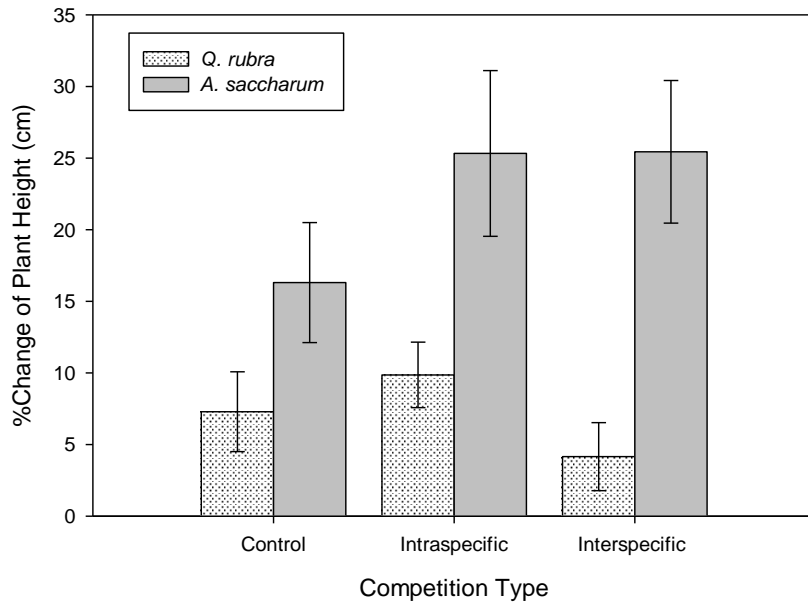


Figure 2-4: Mean (\pm SE) photosynthesis rates ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) for each species in varying shade treatments averaged across all competition arrangements.

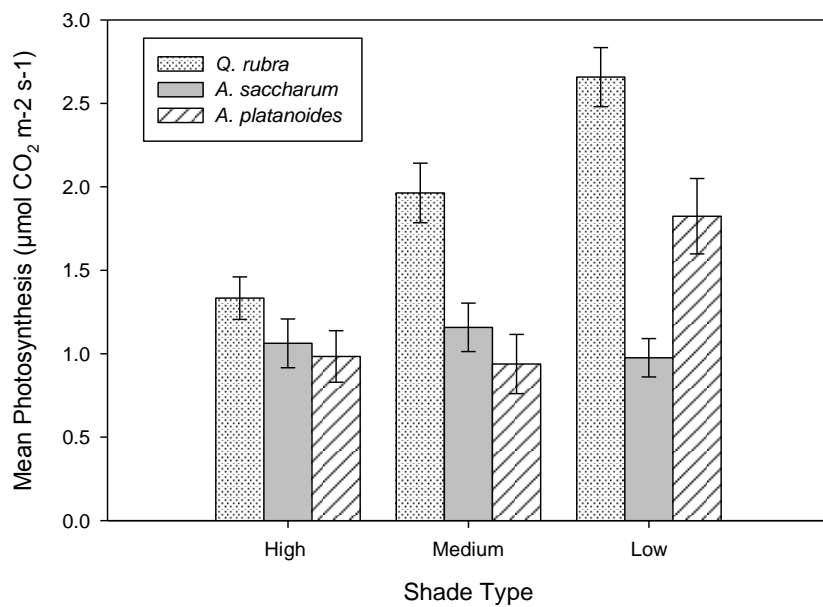
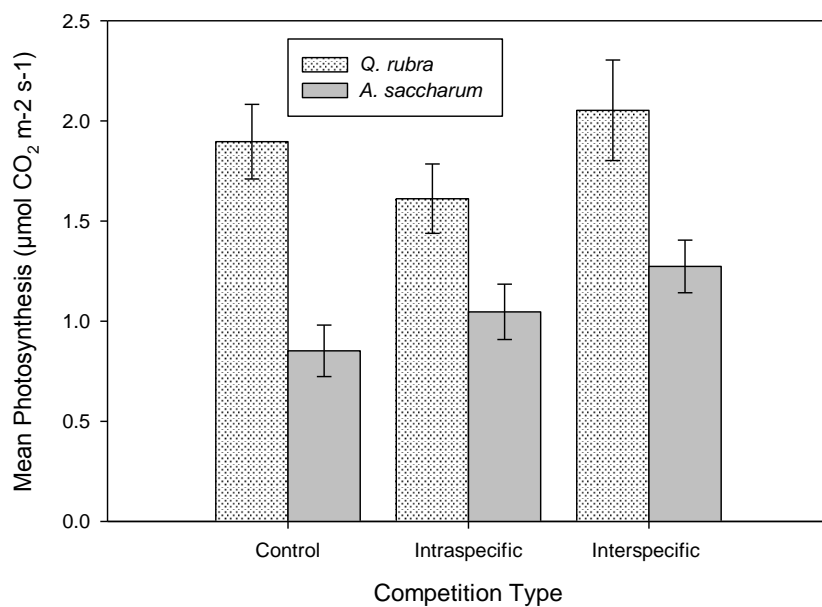


Figure 2-5: Mean (\pm SE) photosynthesis rates ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) of two native species in various competition treatments averaging all measurements over time. The interspecific arrangement is planted with *A. platanooides*.



Synthesis Chapter

Summary

All plant communities are potentially susceptible to nonnative species invasion (Hobbs and Huenneke 1992, Kennedy *et al.* 2002, Stohlgren *et al.* 2003, Fridley *et al.* 2007, and Martin *et al.* 2009) and a particular species that poses a threat in the region of Western New York is *Acer platanoides* (Norway maple) (Webb and Kaunzinger 1993, and Hunter and Mattice 2002). An example of the success of this species is the Washington Grove of Cobbs Hill Park in Rochester, NY. The forest tree community is fairly diverse and is primarily composed of *Quercus* species, *Acer saccharum* (sugar maple), *Prunus serotina* (black cherry), and other native trees. Initial observations of the forest uncovered an obvious presence of the nonnative *Acer platanoides* and a lack of native *Quercus* (oak) species recruitment. I surveyed the forest plant community (herbaceous understory to canopy trees), seed bank and seed rain. Knowing the relative composition of all of the forest strata I was able to describe current plant species composition and the likely successional trajectory. In a separate analysis, I wanted to further understand the competitive interactions between the invasive and two native species at the seedling level and with respect to varying light treatments.

My results indicate that the forest is shifting to a nonnative dominated community. Almost a quarter of the canopy and subcanopy trees was composed of the invasive *A. platanoides* and also appears to be on a trajectory of continued increase. In the forest canopy *A. platanoides* was 30.6 individuals/hectare (10.6% of

canopy trees) but at the subcanopy level a daunting 215 individuals/hectare (37.7% of subcanopy trees). A second important finding was the lack of the native *Quercus* recruitment. I encountered only one *Q. rubra* (red oak) tree in the forest subcanopy, and an absence of any in the seedling/sapling stages in my study plots despite canopy gaps that should presumably facilitate oak success. Furthermore, I also discovered the presence of the following invasive species also present in the Grove: *Alliaria petiolata* (garlic mustard), *Elaeagnus umbellata* (autumn olive), *Euonymus alatus* (burningbush), *Euonymus europaeus* (European spindle tree), *Hedera helix* (English Ivy), *Lonicera tatarica* (Tatarian honeysuckle), *Rhamnus cathartica* (common buckthorn), and *Rosa multiflora* (multiflora rose). The presence of other invasive species provides further evidence of the susceptibility to invasion of the area.

I was left to then explore why *A. platanoides* was so successful and what was contributing to recruitment problems for the *Quercus* species. The literature suggests that *A. platanoides* has several traits and behaviors that facilitate its invasiveness. Like many invasive plant species, it exhibits a number of *r*-selected traits including prolific seed production (Mitchell and Wilkinson 1982) and fast growth (Kloppel and Abrams 1995, Webster *et al.* 2005). In contrast to many nonnative species and the dogma that mature, intact forests are typically resistant to invasion (Rejmánek 1989), *A. platanoides* also has *K*-selected traits contributing to its invasion success. Traits that facilitate its success in intact forests include energy and nutrient efficiencies (Kloppel and Abrams 1995) and its shade tolerance (Gomez-Aparicio and Canham 2008) which corresponds with casting a dark canopy beneath established

individuals that limit native species success (Galbraith-Kent and Handel 2008). Thus, it seems reasonable to expect that *A. platanoides* is a superior competitor contributing to its success and the demise of native trees here.

I studied interspecific species interactions of the invasive and the native species at the seedling stage to test this assertion of superior competitiveness (including intra- versus interspecific interactions) in three different shade treatments. I measured stem height, stem diameter, biomass (via modeling and destructive harvesting), and photosynthesis rate. To my surprise, I did not discover any evidence that *A. platanoides* had a competitive advantage. In fact, *Q. rubra* had a greater rate of photosynthesis overall, and *Acer saccharum* had the greatest percent change in height despite the presence of *A. platanoides*.

It was puzzling that I did not encounter results indicating that *A. platanoides* was the stronger competitor. With this not being the case, I was left to conclude one of two scenarios. First, *A. platanoides* does not begin to display competitive superiority until later in its development (e.g. saplings). Second, I neglected to capture a plant function that is leading to invasive success at an early developmental stage. For instance, I may have discovered differences in plant functions if I had observed belowground root competition, or nutrient uptake and storage among species. The major scope of this project did focus on aboveground production, where I may have missed possible belowground inhibitory competitive effects on either roots or nutrient supply that could potentially be granting *A. platanoides* a competitive edge.

Even though *A. platanoides* is not competitively superior at the seedling level, it is obvious that the species success has and will continue to alter the forest community composition. As such, the Rochester Regional Group of the Sierra Club has taken an active role in managing the forest to maintain the existing diversity of trees. Since my study was conducted, this group along with the City of Rochester has taken steps toward limiting further encroachment by *A. platanoides*. Their work has thus far followed closely to management recommendations outlined in chapter 1. They have felled all established *A. platanoides* trees and removed most evidence of seedling and sapling establishment. They also used the felled trees to border the trails to limit off trail use which may facilitate *Quercus* seed germination. It is difficult now to find *A. platanoides* individuals present within the area. However, I believe work still needs to be done to eliminate the original source of invasion - the street trees. With the removal of those trees and other present exotics, along with an adaptive long-term management plan focused on invasive species removal, this forest can once again continue along a native successional trajectory.

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