

Article

A Comparison of Invasive *Acer platanoides* and Native *A. saccharum* First-Year Seedlings: Growth, Biomass Distribution and the Influence of Ecological Factors in a Forest Understory

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Abstract: Invasive shade tolerant species can have profound and long-lasting detrimental effects even on previously undisturbed forests. In North American forests, the invasive *Acer platanoides* is capable of dominating the understory where it could displace the native *Acer saccharum*. To understand the relative importance of various ecological factors in a forest understory on their establishment, we transplanted *A. platanoides* and *A. saccharum* seedlings in an urban sugar maple forest understory and their growth and survival were compared over a growing season. Seedlings did not differ in height, but biomass growth and assimilation rates were twice as high for the invasive species. Ecological variables accounted for only 23–24% of variation in growth. Seedlings of *A. platanoides* appeared to capture light more efficiently, with over 150% greater foliage biomass and surface area. *A. saccharum* seedlings were more negatively affected by herbivory. The more robust *A. platanoides* seedlings presented characteristics that could allow them to better grow and survive in shaded understories than their native congeners.

Keywords: biological invasion; *Acer platanoides*; *Acer saccharum*; urban forest; herbivory; light

1. Introduction

Invasive plant species can generate profound changes in the composition of native plant communities and ecosystem processes [1,2]. Although a minority of invasive species are woody plants, a small proportion of these are tolerant to shade, which allows them to invade undisturbed, closed-canopy forests [3,4]. Shade-tolerant trees can endure periods of suppressed growth before reaching the canopy when gaps are created [5]. This low growth rate, in combination with the long generation time of trees, results in lag phases that slow the invasion process, making it difficult to perceive as it unfolds, and hence, difficult to manage in its early stages [4,6–8]. However, these long-lived, competitive species, which may become dominant over time through succession, have the potential to deeply modify forest ecosystems and cause severe and pervasive impacts on plant communities [4,6,7].

A well-studied example is the invasion of North American forests by *Acer platanoides* L. (Norway maple), the most widespread species of maple in its native Europe [9]. Its attractive shape, vigorous growth, tolerance of harsh urban conditions, and ease of propagation make *A. platanoides* a prized landscape tree [10]. It has been widely planted, in part, to replace *Ulmus americana* L. (American elm) decimated by Dutch elm disease [10]. While perturbations, such as the creation of edges, roads or disturbed soils, may favour *A. platanoides* establishment [11–16], its shade tolerance, abundant production of wind-dispersed seeds, and ability to establish very dense seedling banks allow this species to invade even relatively undisturbed, closed-canopy forests [15,17–21].

Acer platanoides trees have deleterious effects on species richness and tree regeneration in the understory [17,18,22–24]. Moreover, *A. platanoides* densities in the regeneration layer are much greater than those of seedlings and saplings of its congener *Acer saccharum* Marsh. (sugar maple), in some cases, even under *A. saccharum* canopies [22,23,25]. *Acer saccharum* is the dominant native tree at the end of successional processes in cool mesic forests of eastern North America; it is shade-tolerant and forms seedling banks [5,26,27]. Thus, *A. saccharum* is ecologically very similar to *A. platanoides*. Because *A. platanoides* can not only dominate the understory, but also reaches the canopy at least a decade before *A. saccharum* [14], there are concerns that the invader may be displacing its native congener [14,17,19,23].

Understanding seedling dynamics is crucial in predicting succession and, in this case, *A. platanoides* invasion in *A. saccharum* forests [28]. A key phase in forest succession is the establishment of seedlings (see [29] and [20]). Moreover, closely related species are more likely to compete against each other because of their shared characteristics. Thus, comparing very similar native and exotic congeners *in situ* is recommended for identifying which traits promote invasiveness [30]. In consequence, our goal was to compare the performance of *A. platanoides* and *A. saccharum* first-year seedlings in the understory and determine the relative influence and possible interactions of several ecological factors. Specifically, in this experimental field comparison, we addressed the following questions: (1) How do *A. platanoides* and *A. saccharum* differ in terms of growth, biomass distribution and survival? (2) How is the growth of the two species affected by the following ecological factors: leaf herbivory levels, light availability, soil pH and moisture, and canopy species? To answer these questions, we planted first-year seedlings under exotic and native canopies in an urban maple forest. We compared the species before transplantation and after a growing season.

2. Methods

2.1. Field-Site Description

Mount Royal (45°30'N, 73°35'W) is a 190 ha urban forest that forms part of the Mont-Royal Natural and Historical Borough in the City of Montreal, Quebec, Canada [31]. The mountain itself (elevation 232 m) is one of the Monteregian Hills, a linear chain of isolated hills that extends eastward across the St. Lawrence River valley from Montreal into the Monteregie region of southern Quebec [32]. Average annual temperature is 6.2 °C, average annual precipitation is 978.9 mm (22.2% as snow), and the growing season lasts for about 195 days, from mid-April to mid-September (Environment Canada, climate normals 1971–2000).

Mount Royal is part of the sugar maple-bitternut hickory domain [33]. The mountain is home to mature forests with various signs of human and natural disturbances. The main native canopy tree species are *A. saccharum*, *Fraxinus americana* L. (white ash), *Quercus rubra* L. (red oak) and *Betula papyrifera* Marsh. (paper birch). From 1960 to 1975, *A. platanoides* was planted for restoration purposes in some parts of the park, as its invasive status was little known at the time. However, *A. platanoides* also invaded the park via samaras that were wind-dispersed from nearby streets. Consequently, *A. platanoides* is now one of the major canopy species in the forest and is widely distributed. While *A. saccharum* is still the canopy dominant, with three times as many overstory trees as the invasive species, the reverse is true in the understory, where *A. platanoides* represents three times more juveniles [16].

2.2. Experimental Setting

Samaras of *A. platanoides* were collected in mid-September of 2006 in city parks and along streets next to Mount Royal. Samaras of *A. saccharum* were collected at the beginning of September of 2006 from two sites in the Monteregie region close to Montreal: Mont-Saint-Hilaire and Saint-Hyacinthe. The samaras were stratified for four months in sand and peat moss in a refrigerator maintained between 0 °C and 3 °C. In mid-February 2007, 300 emergent seedlings of each species were sown into 250 ml pots containing Pro-Mix (Premier Horticulture, Dorval, QC, Canada) and sand (50 kg of sand to 30 kg of Pro-Mix). The seedlings were maintained in a greenhouse at the Montreal Botanical Garden at a temperature of 12.0 ± 5.8 °C (mean $\pm$ SD). They were watered and fertilized (with 20:20:20 NPK) as needed.

In mid-May 2007, the seedlings were moved outside prior to transplantation. In mid-June 120 seedlings of each species were randomly selected and transplanted on Mount Royal. At the same time, we randomly selected an additional 24 *A. platanoides* and 27 *A. saccharum* seedlings to construct allometric equations for estimating the initial biomass of the transplanted seedlings. The roots were carefully cleaned before air-drying for over six months the seedlings and separately weighing the roots, shoots and leaves.

In the field, we randomly selected a total of 30 canopy trees ranging in diameter at breast height from 22 to 44 cm: 12 *A. platanoides* (31.6 ± 4.2 cm in diameter), 10 *A. saccharum* (32.2 ± 7.6 cm in diameter) and eight trees from four other locally abundant species (two *F. americana*, two *Picea glauca* (Moench) Voss, two *Pinus strobus* L., two *Q. rubra*; 31.8 ± 7.2 cm in diameter). The trees were

located in mesic sectors, representative of the dominant forest type found in the park, uncut in the past several decades, had a closed canopy, and comprised both *A. saccharum* and *A. platanoides* as canopy trees. The 240 seedlings were planted in groups of eight (four seedlings/species) around the adult trees without removing the understory vegetation. The seedlings were positioned 1.3 m from the trunk centre of each tree and at 45° to one another so that they were 1 m apart. The species were alternated so that one species would occupy the positions to the North, East, South and West of the tree, while the other species was in North-East, South-East, South-West and North-West positions. The positions occupied by each species were switched from one tree to the next.

In mid-September 2007, exactly three months after transplantation, we harvested half of the seedlings for biomass measurements (two of each species per tree, alternating cardinal directions, for a total of 55 *A. platanoides* and 56 *A. saccharum* because of losses incurred). Leaves were pressed flat for leaf area measurements (MK2 Area Meter, Delta-T Devices, Cambridge, UK). Both shoots and roots, the latter carefully cleaned of mineral soil, were air-dried for over six months prior to being weighed together with the leaves. The remaining seedlings were left in place until May 2008 to evaluate winter survival.

2.3. Descriptive Variables

Before transplantation and at harvest, we measured the diameter at the base of the stem, the height and number of leaves of all 240 seedlings. Before transplantation, we made the same measurements on the 24 *A. platanoides* and 27 *A. saccharum* seedlings that had been harvested to construct allometric equations. We subsequently predicted initial biomass of the transplanted seedlings from these allometric relationships (r^2 for leaves, stem, roots and total biomass, respectively; *A. platanoides*: 0.755, 0.798, 0.758, 0.861; *A. saccharum*: 0.626, 0.870, 0.747, 0.784). Total dry biomass (g), leaf dry mass (g), stem dry mass (g), root dry mass (g), foliar area (cm²) of the 55 *A. platanoides* and 56 *A. saccharum* seedlings harvested in autumn were used to calculate the parameters shown in Table 1. Survival was recorded at several times during the 2007 growing season and in the spring of 2008.

Table 1. *Acer platanoides* and *A. saccharum* seedling growth and morphological parameters.

Parameter	Calculation
RMF (Root Mass Fraction)	Root mass/plant mass
SMF (Stem Mass Fraction)	Stem mass/plant mass
LMF (Leaf Mass Fraction)	Foliage mass/plant mass
SLA (Specific Leaf Area)	Foliage area/foliage mass (cm ² /g)
LAR (Leaf Area Ratio)	Foliage area/total plant mass (cm ² leaf/g plant)
RGR (Relative Growth Rate)	(ln y_2 – ln y_1)/(t_2 – t_1), where y = diameter (RGR-D), length (RGR-H) or total biomass (RGR-B), t is in days
NAR (Net Assimilation Rate per foliar area)	RGR-B/LAR (g/cm ² × day)

2.4. Ecological Factors

2.4.1. Leaf Herbivory and Pathogens

After pressing the leaves, we evaluated the proportion of the surface area of each leaf that was affected by herbivory (%), as described in Adams *et al.* [34]. These values were then averaged per seedling. We used three categories of damage: chewing, skeletonization and leaf miner damage (including all internal leaf damage that did not pierce the leaf). We found no signs of browsing by vertebrates, nor were any galls present.

A fungus that originated from Europe, *Rhytisma acerinum* (Pers.) Fries., and which affects *A. platanoides*, was first spotted in Montreal in 2004. This observation was made two years before the first epidemic having significant negative consequences on the growth of *A. platanoides* saplings and trees [35]. *Rhytisma* spp. are host-specific pathogens; hence, the other maple species on the site (*A. saccharum*, *A. rubrum* and *A. saccharinum*) were not infected by *R. acerinum*. Apart from tar spot disease on *A. platanoides* seedlings, we did not note the presence of bacterial or viral diseases and other fungal infections, but evidence of these appeared to be negligible.

2.4.2. Light

The hemispherical sensor (BF2, Delta-T devices, Cambridge, UK) technique was used to measure available light in the forest understory [36]. On 30–31 July and 1 August 2007, one sensor was placed just above the crown of each seedling and another in a nearby open field. Simultaneous measurements were taken at the two locations to obtain the proportion of available light reaching the understory (% PAR).

2.4.3. Soil pH

On 7–8 May 2008, mineral soil samples (0–15 cm) were taken, as close as possible to the seedlings, after removing the ground litter. Samples were air-dried and sieved (<2 mm dia.), after which 10 g of soil were mixed with 20 mL distilled water. Soil pH was measured electrometrically on these suspensions.

2.4.4. Soil Moisture

Volumetric soil water content was measured on 25 July and 8 September 2007, using an impedance-based sensor (ThetaProbe, Delta-T Devices, Cambridge, UK). Three measurements were taken (to 6 cm depth) about 5 cm from each seedling, and were averaged for the analysis. Prior to the first date, 39.2 mm of rain had fallen on 19–20 July, for a total of 48.5 mm of precipitation over two weeks. For the second date, 3.2 mm of rain had fallen two days before the measurements were taken, with additional rainfall a week later, for a total of 24.4 mm over two weeks. The measurements taken on the two dates were averaged in the analysis.

2.5. Data Analysis

(1) We used analyses of variance (ANOVA) to compare seedlings of *A. platanoides* and *A. saccharum* (Species) for all of the aforementioned descriptive variables (y). For the randomized complete block design, the model was $y = \text{Tree} + \text{Species} + \text{Tree} \times \text{Species}$, where Tree represents the 30 canopy trees as the blocks, which were a random factor, together with the interaction term. When the conditions of normality and homogeneity of variance were not met, y were rank-transformed before performing ANOVA. In some cases we needed to use a non parametric Friedman test. These analyses were carried out using JMP 7 [37].

(2) Effects of the ecological variables (matrix X) on the descriptive variables (matrix Y) were analyzed using redundancy-based analysis (RDA). Both matrices were centred and standardized per variable prior to ordination since the variables in each matrix were not in the same units [38,39]. Separate analyses were conducted on *A. platanoides* and *A. saccharum*, and performed only on the harvested seedlings so that herbivory measurements could be included. We used the following descriptive variables: RGR-D, RGR-H, RGR-B and NAR. There were five explanatory variables: herbivory, canopy species (*A. platanoides*, *A. saccharum*, or “other native species”), light, soil moisture and pH. Results were presented as correlation biplots with the descriptors and explanatory variables. The forward selection method [39] was used to evaluate the relative importance of explanatory variables in the RDA model. Monte Carlo permutation tests (based on 999 permutations) were used to determine the level of significance of each explanatory variable. Analyses were carried on Canoco 4.5 for Windows and plotted with CanocoDraw for Windows 4.0 [39].

(3) Finally, we evaluated the influence of canopy species on the other ecological variables—Light, soil moisture, soil pH and herbivory. We used ANOVA to compare canopies of *A. platanoides* with *A. saccharum*, or with all native species. The model was: $y = \text{Tree}[\text{Canopy}](\text{random}) + \text{Canopy}$, where Tree represents each of the 30 canopy trees and Canopy, the category of canopy type. In cases where normality and homogeneity of variance were rejected, y were rank-transformed before performing ANOVA. In some cases we needed to use a non-parametric test, the Wilcoxon (Mann-Whitney) test. We used a Chi-square test to compare the frequency of tar spot disease on *A. platanoides* seedlings, according to canopy type. These analyses were carried out using JMP 7 [37]. All results were considered statistically significant at $p < 0.05$.

3. Results

3.1. Comparison of *A. Platanoides* and *A. Saccharum* Seedlings

Survival was high for both *A. platanoides* and *A. saccharum* seedlings: of the 120 seedlings transplanted per species, each maple lost seven seedlings during the summer and *A. saccharum* lost three more seedlings over the winter (data not shown).

All other descriptive variables measured, including herbivory, together with results of ANOVAs which compared the two species, are presented in Table 2. Height did not differ between species, either prior to transplantation or at the end of the experiment. However, *A. platanoides* had greater total biomass than *A. saccharum*, both before transplantation and at harvest; this result was also consistent for all biomass components (*i.e.*, leaves, stem and roots) considered separately. For example,

A. platanoides was initially 19% heavier than *A. saccharum*, and this difference increased to 34% at harvest. Consequently, RGR-B was nearly twice as large for *A. platanoides* as for *A. saccharum*. *Acer platanoides* had a greater number of leaves than *A. saccharum*. Moreover, LAR and SLA estimates indicated, respectively, that *A. platanoides* had more foliage area per plant mass and more leaf surface per leaf mass than *A. saccharum*.

Table 2. *Acer platanoides* and *A. saccharum* seedling descriptive parameters before transplantation and at harvest. Mean values ($\pm$ SD) are given for each variable, together with test-statistics (*P*-values) for the species comparisons. Values in bold are significantly higher for a given species.

Parameters	Before transplantation			At harvest		
	<i>A. platanoides</i>	<i>A. saccharum</i>	F- or Q-test	<i>A. platanoides</i>	<i>A. saccharum</i>	F- or Q-test
	<i>n</i> = 120	<i>n</i> = 120	<i>n</i> = 240	<i>n</i> = 120	<i>n</i> = 117	<i>n</i> = 237
Diameter (mm)	3.60 (0.41)	3.40 (0.44)	11.15**	5.02 (0.78)	4.26 (0.57)	48.73***
Height (cm)	19.2 (5.5)	20.0 (5.1)	1.52 ¹	22.1 (6.4)	21.9 (5.2)	0.02 ²
Number of leaves	13.7 (4.0)	11.5 (2.3)	23.91***	11.1 (4.6)	9.6 (3.8)	11.23**
RGR-D ($\times 10^{-3}$ mm/mm $\times$ day)	—	—	—	3.5 (1.6)	2.4 (1.3)	31.74***
RGR-H ($\times 10^{-3}$ cm/cm $\times$ day)	—	—	—	1.4 (1.5)	1.0 (0.8)	2.25 ¹
Biomass	<i>n</i> = 55	<i>n</i> = 56	<i>n</i> = 111	<i>n</i> = 55	<i>n</i> = 56	<i>n</i> = 111
Total (g)	1.93 (0.44)	1.56 (0.34)	19.95***	3.22 (1.12)	2.12 (0.76)	45.16***
Roots (g)	0.44 (0.14)	0.28 (0.08)	40.36***	1.04 (0.42)	0.74 (0.29)	22.30***
Shoot (g)	0.44 (0.12)	0.35 (0.10)	13.13***	0.99 (0.38)	0.66 (0.22)	33.05***
Leaves (g)	1.06 (0.22)	0.93 (0.17)	10.50**	1.19 (0.46)	0.72 (0.33)	62.02*** ¹
Foliar area (cm ²)	—	—	—	298.9 (108.1)	172.6 (77.6)	89.45*** ¹
Biomass fractions	—	—	—	—	—	—
RMF	0.22 (0.04)	0.178 (0.03)	37.10***	0.32 (0.07)	0.36 (0.05)	7.75**
SMF	0.22 (0.01)	0.221 (0.03)	0.09 ²	0.31 (0.05)	0.32 (0.07)	0.53
LMF	0.55 (0.05)	0.602 (0.04)	39.23*** ²	0.37 (0.07)	0.33 (0.08)	9.27** ¹
SLA (cm ² /g)	—	—	—	259 (46)	243 (33)	14.14*** ¹
LAR (cm ² /g)	—	—	—	94.7 (22.2)	78.9 (21.0)	14.82***
RGR-B ($\times 10^{-3}$ g/g $\times$ day)	—	—	—	5.1 (2.8)	2.8 (3.1)	22.22***
NAR ($\times 10^{-1}$ g/m ² $\times$ day)	—	—	—	5.65 (3.95)	2.81 (7.05)	14.38*** ¹
Herbivory (%)	—	—	—	11.2 (10.2)	13.9 (14.0)	0.85 ¹

¹ Rank transformation, ² Friedman test, * *p* < 0.05, ** *p* < 0.01, *** *p* < 0.001.

Before transplantation, both species invested more in leaves than in other biomass components. At that time, although the LMF showed that *A. saccharum* invested a significantly higher proportion of its biomass in leaves, the leaves of *A. platanoides* were heavier. At harvest, biomass was more equally distributed among components for both species, but *A. saccharum* invested a slightly higher fraction of its biomass in roots, whereas *A. platanoides* invested in leaves. Thus, after their transplantation to the understory, both species shifted investment from leaves to roots and stem, although in the stem this

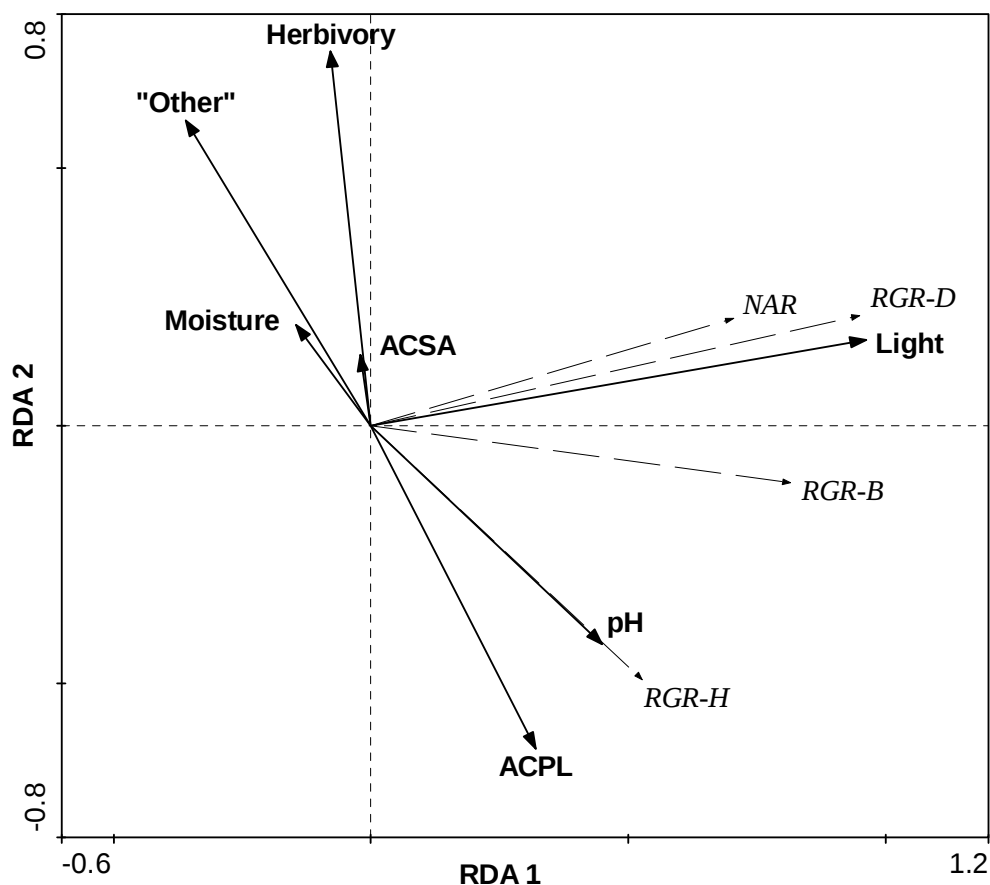
was in diameter rather than in height. Finally, the NAR of *A. platanoides* was twice as high as that of its congener.

Herbivory, measured as relative leaf area damage, did not differ significantly between species. With regard to the presence of tar spots on *A. platanoides* (data not shown), 45.5% of seedlings were infected and had, on average, 2.3 of their leaves presenting symptoms of the disease. Tar spots covered, on average, 8.6% of the surface of infected leaves. The inclusion of the disease increased total foliar damage by 6.4% ($11.88 \pm 10.14\%$).

3.2. The Influence of Ecological Factors on Seedling Growth Parameters

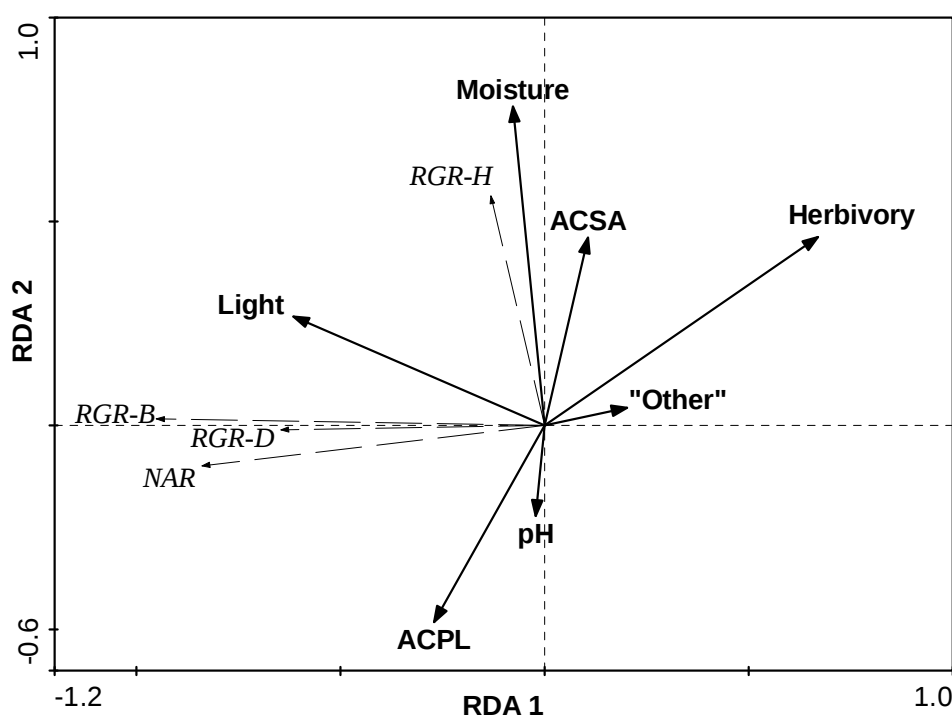
Figures 1 and 2 illustrate the results of redundancy analyses for *A. platanoides* and *A. saccharum* seedlings, respectively. Ecological factors explained 23.2% of the variation in *A. platanoides* seedling responses (Figure 1). Light was the only significant explanatory variable, contributing 18% of explained variance to the model. Light was positively correlated to all RGR estimates and NAR, more so for *A. platanoides* than for *A. saccharum* (Figure 2).

Figure 1. Redundancy-based analysis (RDA) correlation biplot representing growth parameters (dashed vectors) and ecological factors (solid vectors) of *A. platanoides* seedlings ($n = 55$). The first and second canonical axes explain respectively 19.6% and 2.9% of variation in the data. ACPL: *A. platanoides* canopy; ACSA: *A. saccharum* canopy; “Other”: other native canopy species.



Ecological variables explained 24% of the variation in seedling growth parameters for *A. saccharum*; herbivory explained 16%, mostly along the first axis, while light explained 7% along the second axis (Figure 2). Only herbivory and light contributed significantly to the model. Herbivory was negatively correlated with RGR-B, RGR-D and NAR, while light was positively correlated.

Figure 2. RDA correlation biplot representing growth parameters (dashed vectors) and ecological factors (solid vectors) of *A. saccharum* seedlings ($n = 56$). The first and second canonical axes explain respectively 19.4% and 3.1% of variation in the data. ACPL: *A. platanoides* canopy; ACSA: *A. saccharum* canopy; “Other”: other native canopy species.



When all 240 seedlings were analyzed together to compare the influence of canopy species on the other ecological variables (herbivory, light, soil moisture and pH), only light levels differed significantly between *A. platanoides* and *A. saccharum* canopies, and between *A. platanoides* and native species canopies (Table 3). Missing leaves were not considered to be the result of herbivory; however, this might well have been the case and consequently, herbivory values were almost certainly underestimated. Finally, there was no difference in the frequency of tar spot disease on *A. platanoides* seedlings in relation to canopy type ($\chi^2 = 0.87$, $p = 0.648$, $n = 25$).

Table 3. Ecological factors measured under *A. platanoides*, *A. saccharum* and other native species canopies. Mean values ($\pm$ SD) are given for each variable, together with test-statistics (p -values) for the canopy comparisons. Herbivory was tested on non-harvested seedlings only ($n < n$ total).

Factors	<i>A. platanoides</i> canopy	<i>A. saccharum</i> canopy	Other native spp. canopy	ACPL vs. ACSA F- or U-test	ACPL vs. all native spp. F or U-test
	$n = 96$	$n = 80$	$n = 64$	$n = 176$	$n = 240$
Light (%)	2.53 (1.34)	1.69 (0.87)	1.43 (0.64)	22.36*** ²	38.67*** ²
Soil moisture (%)	12.4 (3.2)	13.7 (4.8)	13.4 (2.8)	0.69 ¹	1.41 ¹
Soil pH	5.98 (0.55)	5.67 (0.40)	5.45 (0.62)	3.58	5.79* ¹
Herbivory (%)	9.5 (8.8), $n = 48$	15.2 (15.7), $n = 39$	14.4 (11.1), $n = 24$	2.44 ¹ , $n = 87$	3.71 ¹ , $n = 111$

¹ Rank transformation; ² Wilcoxon Test, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

4. Discussion

4.1. Growth, Biomass Distribution and Survival of *A. Platanoides* and *A. Saccharum* Seedlings

First-year *A. platanoides* seedlings transplanted in a low light forest environment were found to be superior to *A. saccharum* for all descriptive variables measured except height. For example, values of relative growth in biomass (RGR-B) and assimilation rate (NAR indicating biomass produced on a leaf area basis) were twice as large for the invasive as for the native species. Consequently, not only is *A. platanoides* initially bigger, possibly because of its bigger seed [40], but its growth during the course of our experiment was also greatly superior to that of *A. saccharum*. As saplings, *A. platanoides* also showed better carbon assimilation rates than *A. saccharum*, as derived from higher field photosynthetic net rates [41].

A superior height growth rate is a definite competitive advantage for faster canopy recruitment. However, we found no difference in height between *A. platanoides* and *A. saccharum*. It is possible that differences in height growth rates (RGR-H) could appear later in their development or after an episode of release, with *A. platanoides* being a more efficient colonizer of gap openings [19,42]. Indeed, as saplings, *A. platanoides* have higher height growth rates, in addition to higher high-light radial growths, than *A. saccharum* [21,35,41]. Also, the species exhibited similar patterns of biomass distribution, both in the greenhouse and at the end of the growing season in the forest. This pattern was also observed in seedlings of a previous study [43] and could indicate similar adaptations to the environment.

There were important differences in the leaves of the two congeners that may drive the difference in biomass growth (RGR-B). Leaves were more numerous for *A. platanoides* compared to *A. saccharum*; foliage biomass was 1.6 times higher, with a 1.7 times greater surface area. Our results agree with previous studies in that *A. platanoides* yearlings had more leaves than their congeners [29]. Both higher Specific leaf area (SLA, which indicates thinner leaves), and higher Leaf area ratio (LAR) for *A. platanoides* imply that biomass investment in leaves yielded greater light interception potential and

carbon gain than for *A. saccharum* [44]. Superior LAR is also related to higher growth in high and low light environments [45]. Furthermore, Kloeppel and Abrams [41] suggested that the thinner but denser (i.e., more mass per unit area) leaves of *A. platanooides* could explain its higher photosynthetic rate compared to *A. saccharum*. Leaf phenology could be a further advantage to *A. platanooides* because it bears leaves for a few days more in the Fall than *A. saccharum* [29,41,42]. Finally, *A. platanooides* has a root system with 1.4 times more biomass than *A. saccharum*, which could balance its resource-demanding foliage.

Survival in the low light conditions (less than 2% PAR, on average) of this experiment was high for both species, perhaps because seedlings emerged in a favourable environment or because the winter was warmer than usual and seedlings were insulated under a thick layer of snow for almost the entire cold season. Survival was similar for the two species during the growing season (94%). Over the winter, which is often the critical period for yearlings, *A. saccharum* incurred mortality (5%) while *A. platanooides* did not. Other studies also have found that survival after seedling transplantation in the understory did not differ between the two species in the first growing season, but that differences favouring *A. platanooides* emerged later on [29,43]. Also, a higher biomass growth rate (RGR-B) in field conditions can constitute an important advantage since it may be positively correlated with broadleaf seedling survival in deep shade [45]. Even small differences in growth can lead to large differences in survival rates since these differences in performance accumulate over time in long-lived species.

4.2. The Influence of Ecological Factors

The proportion of variation in growth parameters that was explained in the RDA by all ecological factors was somewhat low for the two species (23% for *A. platanooides* and 24% for *A. saccharum*). The most likely reason is that the study site did not present large gradients of either light or soil conditions because the seedlings were transplanted under closed canopies into sites where the species co-occurred in the canopy. However, the significance of two factors, light and herbivory levels, emerged from the analyses.

The present study did not find any significant effect of the canopy species on yearlings. Previous studies showed that *A. platanooides* canopy trees could hinder the regeneration of *A. saccharum* in some way while favouring their conspecifics [18,22–24]. Yet another study observed a strong positive effect of *A. platanooides*, even at low densities, on the growth of native seedlings, including *A. saccharum*; this positive effect was even more pronounced for conspecifics, with the exception of yearlings [46]. We also expected to find differences in soil pH between native and exotic canopies, as reported in the literature [47]. Considering the trees in the neighbourhood of seedlings in the present study, as did Gómez-Aparicio *et al.* [46], might have increased the explanatory power of the canopy species variable and its influence on the other ecological variables, especially in terms of herbivory and light levels. These authors showed that individual trees could influence the properties of the soil around them, but the effects decreased within a few meters away from the trunks.

4.2.1. Growth and Understory Light Levels

Higher light intensities favoured the growth of both species. It was the most influential factor for *A. platanoides* seedlings, explaining 18% of the variation in growth, compared to 7% for *A. saccharum* seedlings. The most likely explanation is that *A. platanoides* could respond better to even small increments in light intensity because, as we have shown, its foliage characteristics allow more efficient light capture. In consequence, when compared to *A. saccharum*, *A. platanoides* did not seem to face a trade-off between maintaining higher growth (e.g., through high LAR) and survival in low light. This finding was confirmed by an experimental study using simulated light regimes to compare yearlings of the two *Acer* species [42].

Interestingly, higher light levels in the understory were associated in this study with the presence of *A. platanoides* in the canopy. Previous studies had suggested that, on the contrary, *A. platanoides* casts deeper shade than native species [13,22,23,25]. Laboratory and field experiments in Montana have shown that the deleterious effects observed in the understory could be explained by lower light levels under *A. platanoides* canopies compared to native canopies [48,49]. However, unlike northeastern hardwood forests, no species with shade tolerance comparable to that of *A. platanoides* (e.g., *A. saccharum* and *Fagus grandifolia* Ehrh.) were found at the Montana site.

At any rate, the tar spot epidemic of the previous year, which affected only *A. platanoides*, might be a confounding factor in that crown damage was still apparent a year later [50]. In consequence, longer term studies are needed to clarify the relationship between *A. platanoides* and understory light levels to verify whether our observations represent simply a transient state resulting from the tar spot epidemic.

4.2.2. The influence of Leaf Herbivory on Seedling Growth

When we compared the herbivory levels observed in *A. platanoides* and *A. saccharum* seedlings (11% and 14%, respectively), the proportion of affected leaves did not significantly differ between species. Our results are comparable to those of Morrison and Mauck [29], who examined leaf herbivory in *A. platanoides* and *A. saccharum* yearlings (about 10% for insects or slugs in August), also without finding a significant difference between the two species. Findings of the present study and that of Morrison and Mauck [29] contrast strongly with the results of another study on leaf herbivory in older plants [51], which found greater herbivory for *A. saccharum* than for *A. platanoides*, although absolute herbivory levels of both species were lower in the latter study. This apparent contradiction illustrates that ontogenic stage must be considered when assessing herbivore damage to a plant because its development can affect its defences and tolerance, as well as herbivore preference (for a review, see [52]).

While herbivore damage on *A. platanoides* and *A. saccharum* was compared in previous studies, the resulting impacts on plant growth were not investigated [29,51]. Our results from RDA indicate that herbivory was more important for the growth of *A. saccharum* than that of *A. platanoides* seedlings, more so than light, and explained as much as 16% of the variation in *A. saccharum* growth. For *A. saccharum*, herbivory decreased RGR-B and NAR, and might explain the large variation measured in these parameters. It is possible that *A. platanoides* seedlings were less affected by similar herbivory

levels because they had more leaves, with a greater surface area, and hence, the same proportion of herbivory still left a higher leaf surface for photosynthesis.

Future studies could consider other types of interactions with natural enemies. For example, the soil biota has been shown to facilitate invasions by *A. platanoides* [53] and other plants [54–56]. In addition, it is necessary to monitor the influence of tar spot disease over the coming years, especially its effects on the regeneration of *A. platanoides*. We have shown previously that the disease can severely impact the growth of saplings and trees as well as sapling survival, but we did not measure its impact on seedlings [35]. In the current study, fungus damage was not important compared to that caused by invertebrate herbivores. However, the seedlings had been transplanted late in the spring, probably past the peak inoculation period for the fungus [57].

5. Conclusions

The present experimental study contributes to the body of knowledge on the invasive species *A. platanoides* by comparing a variety of growth and biomass distribution parameters with that of the native dominant, *A. saccharum*, in a forest understory during the crucial seedling establishment phase. Overall, environmental factors had only a slight influence on the two maple species. At any rate, the robust *A. platanoides* first-year seedlings demonstrated certain advantages over the native dominant *A. saccharum*. The higher growth estimated over the course of the experiment for *A. platanoides* in the shaded forest understory could result in a higher survival rate if this advantage were maintained in the future. On the other hand, *A. platanoides* seedlings could also benefit more readily from canopy openings in sugar maple forests than their native congener because of their advantageous foliar characteristics.

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Conflict of Interest

The authors declare no conflict of interest.

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