Research paper

Norway maple displays greater seasonal growth and phenotypic plasticity to light than native sugar maple

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Norway maple (*Acer platanoides* L), which is among the most invasive tree species in forests of eastern North America, is associated with reduced regeneration of the related native species, sugar maple (*Acer saccharum* Marsh) and other native flora. To identify traits conferring an advantage to Norway maple, we grew both species through an entire growing season under simulated light regimes mimicking a closed forest understorey vs. a canopy disturbance (gap). Dynamic shade-houses providing a succession of high-intensity direct-light events between longer periods of low, diffuse light were used to simulate the light regimes. We assessed seedling height growth three times in the season, as well as stem diameter, maximum photosynthetic capacity, biomass allocation above- and below-ground, seasonal phenology and phenotypic plasticity. Given the north European provenance of Norway maple, we also investigated the possibility that its growth in North America might be increased by delayed fall senescence. We found that Norway maple had significantly greater photosynthetic capacity in both light regimes and grew larger in stem diameter than sugar maple. The differences in below- and above-ground biomass, stem diameter, height and maximum photosynthesis were especially important in the simulated gap where Norway maple continued extension growth during the late fall. In the gap regime sugar maple had a significantly higher root : shoot ratio that could confer an advantage in the deepest shade of closed understorey and under water stress or browsing pressure. Norway maple is especially invasive following canopy disturbance where the opposite (low root : shoot ratio) could confer a competitive advantage. Considering the effects of global change in extending the potential growing season, we anticipate that the invasiveness of Norway maple will increase in the future.

Keywords: *Acer platanoides*, *Acer saccharum*, biomass allocation, forest canopy gap, invasive tree species, phenology, phenotypic plasticity, phenotypic variability, root : shoot ratio, seedling growth.

Introduction

In contrast to earlier views, forests may not be resistant to invasion by exotic tree species (Martin et al. 2009, Godoy et al. 2011a). In eastern and central North America, Norway maple (*Acer platanoides* L.) has become invasive in some deciduous forest understoreys where sugar maple (*Acer saccharum* Marsh) and associated species normally dominate forest regeneration (Webb et al. 2001, Reinhart et al. 2005, Webster et al. 2005, Martin and Marks 2006, Fang and Wang 2011). Norway maple, originally introduced as a street tree (Santamour Jr and McArdle 1982, Nowak and Rowntree 1990), is now invading natural areas in many urban and peri-urban

settings (Kloeppel and Abrams 1995, Bertin et al. 2005, Lapointe and Brisson 2011) where it is associated with the reduced regeneration and displacement of sugar maple and native flora (Wyckoff and Webb 1996, Martin 1999). Norway maple is not considered invasive outside its extensive natural range in Eurasia, although the species is expanding its range in Catalonia and the Basque country of Spain (Fernández-López et al. 1989, Sanz Elorza et al. 2004, Campos and Herrera 2009) and in other locations throughout Europe (see status reports on DAISIE; www.europe-aliens.org).

Longstanding explanations for the coexistence of ecologically similar forest species suggest that fine-scale differentiation in light requirements for establishment of seedlings can account for the ability of Norway maple to invade North American forests. Although both Norway maple and sugar maple are highly shade tolerant (Niinemets and Valladares 2006), subtle differences in the traits underpinning their shade tolerance or in the plasticity of these traits (Martin et al. 2010) may give Norway maple seedlings an advantage (Callaway et al. 2003, Valladares and Niinemets 2008). In particular, exploitation of temporal variation in light intensity caused by canopy gaps can be important in explaining the success of maple species in forests (Canham 1988, Lei and Lechowicz 1997, Paquette et al. 2010) as well as in managing forest regeneration in general (Paquette et al. 2006). Norway maple invasion increases following canopy disturbance (Martin and Marks 2006), which further suggests some role for ecological differentiation in response to forest light regime, among other disturbance-related factors, in explaining the invasion of Norway maple in eastern North American forests.

To investigate this possibility we compared the height, diameter and biomass growth, biomass allocation, physiology, seasonal phenology and phenotypic plasticity of Norway maple and sugar maple seedlings in a shade-house experiment. The trees were grown under light regimes simulating either a closed forest understorey or a canopy gap mimicking canopy disturbance such as single-tree mortality or removal, the conditions in which the species are most likely to compete for dominance. Following the well-established trade-off between high-light growth and low-light survivorship (Pacala et al. 1994), our primary hypothesis was that Norway maple would grow larger than sugar maple in the simulated canopy gap, but not in the simulated understorey light regime because sugar maple is reported to be somewhat more shade tolerant (Niinemets and Valladares 2006). Additionally, we wanted to test the possibility that the invasiveness of Norway maple may have less to do with differences in allocation, physiology or trait plasticity than with later senescence and exploitation of opportunities for growth near the end of the growing season (Kloeppel and Abrams 1995, Wolkovich and Cleland 2011). Indeed, the most likely northern European provenances of Norway maple brought as cultivars to North America

(Santamour Jr and McArdle 1982, Nowak and Rowntree 1990) would be adapted to a relatively warm and extended fall compared with sugar maple. We reasoned that Norway maple could function more effectively toward the end of the growing season, thus attaining greater growth over the season as a whole.

Methods

Experimental set-up

The overall experiment (to be detailed below) was a replicated split-plot design of two fixed effects (light regime (two levels) and species (two)) and a random effect (four replicate blocks). Each block comprised two shade-houses (eight total), each containing eight seedlings of each species arranged at random on four rows, for a total sample size of 128 experimental seedlings. Shade-houses had roof openings calibrated to provide different daily and seasonal amounts of direct-beam insolation in the gap and understorey light regimes, respectively (Paquette et al. 2010).

Norway maple seeds were collected in fall 2008 from mature trees located within or just outside Mont-Royal Park, a large natural area in central Montreal (Quebec, Canada); seeds from such trees account for the ongoing invasion of forests in Mont-Royal Park (Lapointe and Brisson 2012). Initially seeds were kept air-dry at 15 °C in paper bags. Quebec's *Ministère des Ressources naturelles et de la Faune* provided sugar maple seeds collected in 2006 just east of Montreal that had been stored in cool conditions. Seeds of both species were transferred outdoors for stratification and germination in mid-November 2008 in boxes filled with layers of moist sand and minced leaf litter. The soil surface was covered with 2.5 cm of extruded polystyrene foam and a white plastic sheet for insulation and protection from rodents. Winter protection was removed in late March 2009 and in mid-April 400 seedlings (200 per species) were transferred to 320 ml multi-cell containers placed at random in their respective light regime (see below). On June 15 the seedlings were transferred to 6.8 l pots filled with a mix of 50% sand and three commercial growth media (which included slow-release fertilization): 22% Fafard '3/1 Plus Planting Mix' (Saint-Bonaventure, Quebec, Canada), 17% 'Pro-Mix HP' (Premier Tech, Rivière-du-Loup, Québec, Canada) and 11% Fafard 'Pine bark nuggets' to improve pot drainage. All 400 seedlings had survived to this point, so those with deformities or mechanical or insect damage were culled; the remaining seedlings within each treatment were sorted from shortest to tallest and the extremes at both ends removed until only the 128 seedlings for each treatment plus 32 seedlings used as buffers at each end of the rows inside the shade-houses remained. Seedlings were kept moist using drip lines until the experiment ended in mid-October 2009. Their health was monitored regularly and occasional problems such as

insects kept in check (mostly by removing herbivores such as caterpillars by hand). In general, we aimed at maintaining growing conditions other than light (water, nutrient and health) within optimal levels in order to highlight the effect of light.

Many pot experiments studying the physiological and morphological response of seedlings to available light are conducted using a homogeneous light regime that does not account for daily variations in light intensity experienced by natural seedlings and known to be important for growth, biomass allocation, physiology and morphology (Wayne and Bazzaz 1993, Robison and McCarthy 1999, Dalling et al. 2004). A previous pot experiment confirmed that such homogeneous conditions are not an ideal proxy for forest understories and led to overestimation of Norway maple seedling growth and carbon gain (Paquette et al. 2010).

In this experiment we therefore used shade-houses designed to provide a more realistic dynamic simulation of forest light regimes (Paquette et al. 2010). These wood-frame shade-houses were erected at the Montreal Botanical Garden (+45°33.7′; −073°34.3′) in a split-plot design comprised of four blocks and two relative light intensities (understorey and gap, see below), with each treatment assigned at random within its block. The shade-houses were oriented north–south, each ~6 m long by 2.5 m wide and 1.5 m high. The walls were covered with green Coroplast™ (Granby, Quebec, Canada) leaving a 30 cm gap covered with black window screen (~50% light transmission) at the bottom for aeration and to keep rodents out. Shade-houses within a block shared a common central wall; walls and roof parts facing outwards were painted white to minimize heat build-up.

Light regime treatments were started on 5 May 2009; to simulate the spring conditions of deciduous forests the shade-houses had no roof prior to that (~60% available light). Dynamic conditions mimicking canopy gaps were created using roofs with movable parts to make continuous linear gaps running north to south along the length of the shade enclosures, the size of which could be precisely adjusted. The openings in the roofs extended to the north and south walls of the shade-houses to simulate a continuous forest cover and minimize edge effects.

The treatments were calibrated using data loggers and quantum sensors over several days and data from 9 September 2009 (cloudless day) taken as representative to show the effect of the treatments on available light (Figure 1) (Paquette et al. 2007a). Light was averaged every minute (from 5-s measurements) from sunrise to sunset, and then summed up over the course of one day. Measured relative light intensities were simply the ratios of the total (sum) daily inputs measured inside a given shade-house to that measured by a reference sensor placed on top of one of the shade-houses. We thus obtained relative light intensities of 4.9% full sun in the simulated understorey and 21% in the simulated gap light regime treatments.
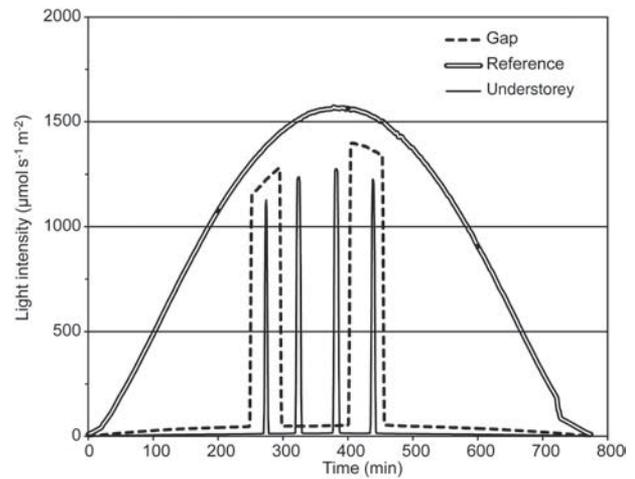

Figure 1. Light measurements inside the shade-houses during a sunny day (9 September 2009) used for characterization of both light regime treatments in the present study. Light was averaged every minute (from 5-s measurements) from sunrise to sunset, and then summed over the course of one day. Available light was computed as the ratio of the total daily inputs in both regimes to that of incident light reaching the shade-house roof (reference sensor). The highlight–gap treatment produced two high-light events per day, each lasting ~51 min (for a total of ~102 min per day), for an integrated global light intensity of 21% (with respect to incident light). The low light–understorey treatment produced four high-light events per day, each only lasting ~8 min (~33 min total), for a global light intensity of 4.9%.

Other measurements during the summer varied slightly according to cloud cover and season (sun angle), but the relative values were constant, with approximately four times as much light under the gap treatment as in the understorey. High-light events, occurring during the passage of the sun directly above the roof openings, were defined as sudden, marked increases in light intensity lasting ~51 min twice a day and ~8 min four times a day under the gap and understorey light regimes, respectively. These light regimes correspond to the conditions in which the two species are likely to compete, i.e., a natural non-disturbed forest understorey for the former, and a disturbed canopy following the mortality or removal of a single or few trees such as in a dense shelterwood (Paquette et al. 2006), for the latter.

Data collection and analysis

Seedling responses to the light regimes were evaluated for diameter, height and biomass growth, biomass allocation, physiology and trait plasticity. Total height from the ground (H; cm) was measured on 14 July and 24 August 2009, and final height and stem diameter just above the root collar (D_0; mm) on 24 September and 10 October, respectively.

The maximum photosynthetic capacity under saturating light (A_{max}) was measured using a LI-6400 portable photosynthesis system fitted with a red–blue light source and CO_2 injector (LiCor, Lincoln, NE, USA). Measurements were carried out on all seedlings on both periods; once from 28 July to 20 August,

and a second time from 15 September to 10 October 2009, under constant conditions of light (1500 µmol m^{-2} s^{-1}), CO$_2$ concentration (400 ppm) and leaf temperature (set at 20 °C), on the last mature leaf of each seedling during rainless mornings.

At harvest the seedlings were cut at ground level, the soil carefully sifted to collect the complete root systems, and the above- and below-ground tissues dried and weighed (g). Relative height growth rates (Kramer and Kozlowski 1979) were computed for three periods: germination to 14 July; 14 July to 24 August; and 24 August to 24 September using RGR = [ln (H_2)—ln (H_1)]/(t_2—t_1), where RGR is the relative height (H) growth rate of a seedling between time t_1 and t_2 (days).

Root : shoot ratios were computed as the ratio of root biomass to that of all above-ground components (including leaves). Other similar ratios were also computed (e.g., excluding leaves) but gave similar results. Statistical analyses were carried out using JMP 8 (SAS Institute Inc., Cary, NC, USA). Blocks and their interactions were assigned as random factors (R) in the following restricted maximum likelihood (REML) split-plot, third-order mixed model (Searle et al. 1992, Wolfinger et al. 1994, Littell et al. 2006): Block R (4); Light regime (2); Block × Light R; Species (2); Block × Species R; Light × Species; Block × Species × Light R. Tukey's honestly significant difference (HSD) tests were carried out where justified to investigate significant interactions ($P < 0.05$).

To examine and compare variability within species and between light regimes, we used the approach described in Niinemets et al (2003). First, we quantified the within-species total phenotypic variability of each response variable using coefficients of variation (CV = SD/mean) computed for all seedlings of a given species across blocks and light treatments. This CV provides a simple assessment of the natural variability of a given species. It is then possible to compare the variability (CV) of two populations (here the two species) using the asymptotic inference test for coefficients of variation described in Miller and Feltz (1997). Hence, we also computed a phenotypic plasticity index (PI) defined as the fraction of the total phenotypic variability unambiguously related to variability in the environment (here light regime) (Valladares et al. 2000, Godoy et al. 2011b):

$$PI = [\text{mean(gap)} - \text{mean(understorey)}] \\ / \text{Max}[\text{mean(gap)}, \text{mean(understorey)}]$$

where gap and understorey are the respective relative light intensity treatments. This perspective on phenotypic plasticity without concern for underlying genetic effects is commonly used in ecological studies where the genetic variance can be expected to be similar among the entities compared (cf. Gianoli and Valladares 2012).

To test differences among PIs we created a sample population from all possible permutations of individuals from a given species within a block, between those of the gap regime (8) and those of the understorey (8), for a total of 64 pairs per block and species (and an overall N of 512). For each of these pairs we computed a single PI for each of the five response variables, as well as their average. We then used the same REML model as above but with the light regime effect removed, to test for differences between species.

Results

All variables used to assess seedling responses to light regime varied significantly between species (Table 1). All variables also showed a strong effect of the different light regimes, either directly or in interaction with a species effect.

Close inspection of the interactions, however, revealed that under the simulated understorey (low relative light intensity), species differences were generally small and not significant, except for diameter growth and the rate of photosynthesis which were both to the advantage of Norway maple (although still relatively small in size) (Figure 2). Under the simulated gap (high relative light intensity), Norway maple exceeded sugar maple for all measured response variables except for root : shoot ratio, which was greater in sugar maple. These differences were significant and substantial in absolute terms (effect size). For example, Norway maple was on average 3× and 5× larger in height and above-ground biomass,

Table 1. Effect of light regime treatment and species on diameter growth (D), biomass (W) partitioning, physiological response (A_{max}) and relative growth rates (RGR), as assessed by REML analysis (P values for each effect and R^2 for the whole model are provided).

	D	RootW	Total AGW	Root : shoot	A_{max}	RGR1	RGR2
Light	<0.001	<0.001	0.002	0.345	0.007	<0.001	0.002
Species	0.004	0.001	0.001	0.004	0.001	0.009	0.003
L × sp.	<0.001	<0.001	<0.001	<0.001	<0.001	0.049	<0.001
R^2	0.93	0.86	0.91	0.54	0.40	0.69	0.88

Total sample size was 128. Height, above-ground (AG) biomass (W) from other compartments (e.g., wood or leaves only), and other ratios of below- to above-ground biomass produced results similar to diameter (D), total above-ground biomass (Total AGW) and the root : shoot ratio, respectively. RGR1 is the spring and early summer relative growth rate in height (germination to 14 July) while RGR2 is the pooled late summer and early fall relative growth rate (14 July to 24 September). Only fixed factors are shown (see Methods for details on the REML model).
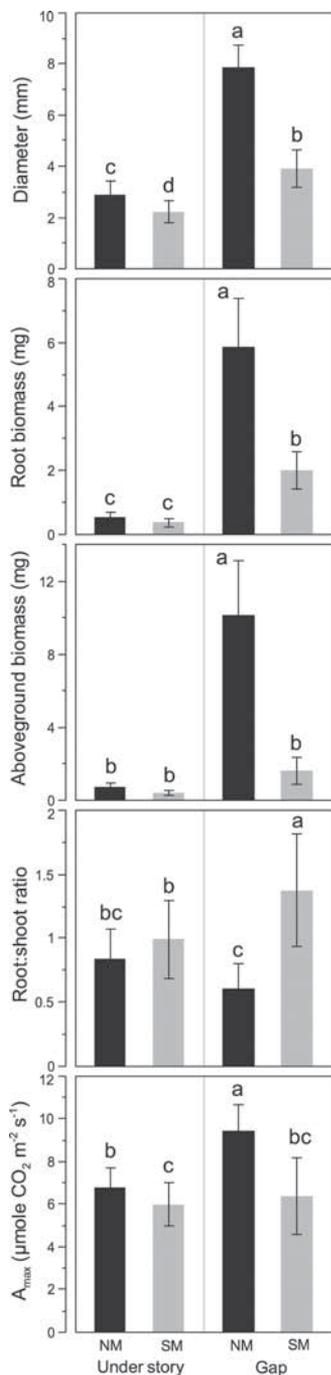
Figure 2. Mean responses of sugar (SM) and Norway (NM) maple seedlings to light regime treatments. Tukey's HSD tests are given where justified to investigate significant interactions; means not sharing a letter are significantly different. Error bars are one standard deviation. See Table 1 for details of REML analyses.
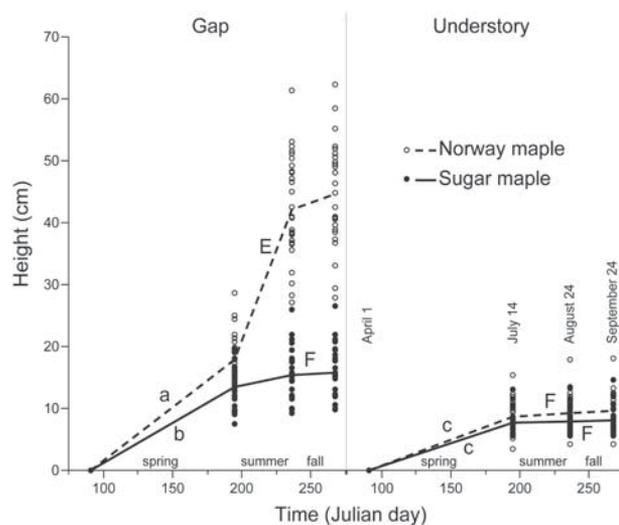

Figure 3. Height growth relative to time (Julian days—seasons and dates also provided for reference). Tukey's HSD tests are printed where justified to investigate significant interactions in the comparisons of relative growth rates (i.e., slopes). See Table 1 for details of REML analyses. RGR means not sharing a letter are significantly different: 'a–c' (lowercase) letters distinguish slopes during the first period (spring; germination to mid-summer); 'E, F' (uppercase) letters separate slopes during the pooled last two periods (summer/fall; midsummer to end of experiment). Full circles and lines: sugar maple; open circles and dotted lines: Norway maple.

late summer and fall measurement periods for the two species and light treatments (paired difference tests, not shown). For example, sugar maple showed only a slightly larger (not significant) decrease in A_{max} between the late summer and fall measurement periods than Norway maple (-0.33 vs. -0.28 μmol CO_2 m^{-2} s^{-1}). Similarly, seedlings of the high-light intensity treatment had a slightly larger decrease (-0.35) when compared with those of the low-light treatment (-0.27), also not significant. The results from both periods were therefore pooled and averaged for analysis, revealing a strong effect of the light regime treatment on Norway maple (increased photosynthesis under higher light), but no effect on sugar maple (Table 1; Figure 2). Although the difference between species was less important than in gaps (47%), maximum photosynthesis was also 13% higher for Norway maple under understorey low-light conditions than for sugar maple.

Phenotypic PI was generally significantly larger for Norway than for sugar maple, with the exception of the root : shoot ratio (Table 2). Within-species total variability (CV; Table 2) was also generally larger for Norway maple, with the exception again of the root : shoot ratio and A_{max}. Yet those differences were not significant and thus the two species can be considered to have the same natural variability on those traits.

The RGR in height for the fall period (24 August 24 to 24 September) was often zero and showed a similar pattern

respectively, than sugar maple (Figures 2 and 3). Sugar maple allocated more biomass below-ground in gap compared with understorey regime.

Photosynthetic capacity was measured twice during the season; however, we found only very small (much below 1% decrease) and non-significant reductions in A_{max} between the

Table 2. Maple species mean total variability (CV) and phenotypic plasticity index between light regimes (gap vs. understorey), for each response variable.

	D	RootW	Total AGW	Root : shoot	A_{max}	Mean[1]
Total variability (CV, %)						
Norway maple	48	90	95	33	21	57
Sugar maple	34	77	80	36	23	50
Species effect (P)[2]	0.9619	0.9921	0.9911	0.9887	0.979	0.9886
Phenotypic plasticity index (PI)						
Norway maple	0.63	0.91	0.93	−0.27	0.28	0.60
Sugar maple	0.43	0.81	0.75	0.28	0.06	0.47
Species effect (P)[3]	0.0167	0.0172	0.0161	0.0588	0.0058	0.0116

Details as in Table 1.
[1]Mean PI were computed and tested on absolute (positive) values.
[2]Species effects for CV were computed using the Miller and Feltz (1997) asymptotic inference test.
[3]Species effects for PI were computed using all possible permutations of individuals within blocks and species and the same REML model as in Table 1 (less the light treatment effect).

among treatment and species to that of the summer period (14 July to 24 August), so those last two periods were pooled for analysis and compared against the spring period (1 April – 14 July). We noticed strong differences between spring and summer/fall relative growth rates, as expected. But more importantly, we also noticed that only Norway maple growing in the gap regime had any significant height growth in the summer and fall (Figure 3), whereas sugar maple in all light regimes, as well as Norway maples of the understorey regime, had stopped growing in height by mid-summer.

Discussion

In a modelling study, Martin et al. (2010) demonstrated that Norway maple in North America diverged from the often cited trade-off between high-light growth and low-light survivorship, presenting a greater than expected high-light growth with respect to its low-light survivorship, while sugar maple fell within or even slightly below expectation. All other species in that study, including many with which Norway maple is also competing as an invasive (e.g., *Acer rubrum* L., *Fagus grandifolia* Ehrh., *Betula alleghaniensis* Britt., *Prunus serotina* Ehrh., *Quercus rubra* L.), also followed the general pattern. The authors suggested that the departure of Norway maple from the growth–survival trade-off may result from its high level of physiological plasticity. This idea is consistent with two meta-analyses showing increased adaptability to changing conditions in invasive species compared with native congeners, especially when going from average to high resource availability (Daehler 2003, Davidson et al. 2011, but see Godoy et al. 2011*b*). However, others have not found such consistency (Palacio-López and Gianoli 2011, Godoy et al. 2011*b*); the former group of researchers more recently proposed that plasticity might be part of a more complex functional syndrome of invasive plants that also involve trait means and integration as key axes (Godoy et al. 2012). As for Palacio-López and Gianoli (2011), they argued that past meta-analyses did not account

for the phylogenetic relatedness of species (with unrelated species having a greater chance of differing, possibly due to multiple factors other than invasiveness).

Our experimental results support a role for both mean trait values and phenotypic plasticity in response to environment as a factor in the invasiveness of Norway maple. Norway maple grew much more than sugar maple under the simulated gap regime and in the understorey light regime had equal height growth and slightly larger stem diameter growth. We also observed a higher level of maximum photosynthesis in Norway than in sugar maple under both light regimes, which is consistent with other reports (Kloeppel and Abrams 1995, Reinhart et al. 2006). Thus, in contradiction to our main hypothesis, Norway maple actually outperforms or at least matches sugar maple growth and production potential under both understorey and gap light regimes.

It should be noted that our understorey light regime did not mimic the very lowest insolation that can occur in forest understories where maintenance and survival can become more important than growth, nor did we assay photosynthesis at low light levels that could contribute to maintenance and survival under very low insolation. It is possible that compared with Norway maple the functional ecology of sugar maple favours survival in deep shade over growth in response to gap formation. Morrison and Mauck (2007) and Sanford et al. (2003), however, both reported that mortality in shade did not differ much between these two maple species, with the former study even reporting a marginally significant advantage for Norway maple. Similarly, although maximum rates of photosynthesis do vary significantly between high- and low-light environments for sugar maple and Norway maple, quantum yields (i.e., the slope of the light response curve) do not (Beaudet et al. 2000, Paquette et al. 2010). Hence we should not expect a photosynthetic advantage for sugar maple under very low-light regimes.

The idea that the greater trait plasticity of Norway maple in response to environmental conditions could account for its

invasive ability (Martin et al. 2010, Davidson et al. 2011) is further supported by the patterns of phenotypic variability and plasticity observed in our experiment, which cannot be attributed to phylogenetic distance as proposed by Palacio-López and Gianoli (2011) to explain differences in plasticity between species. Although the natural phenotypic variability (CV) of the two maple species was not different, their plasticity (PI, variability due to changing environmental conditions) in response to light was (Table 2). For instance, Norway maple had a significantly higher PI in photosynthetic capacity than sugar maple (Table 2; Figure 2). Although Norway maple can adjust its photosynthesis to a changing light environment, this trait remains relatively constant (low CV) between plants within a given environment. Both species also had relatively low total phenotypic variability (CV) in root : shoot ratios, and showed little or no difference in phenotypic PI in response to light for that trait ($P = 0.0588$).

Lei and Lechowicz (1997) carried out a similar experiment where photosynthetic rates (and other physiological responses) were compared between two simulated light regimes (the edge and centre of gaps) for eight maple species, including sugar and Norway maple. Using the data provided in their Appendix ($n = 40$ per species and light regime), we computed a phenotypic PI for A_{max}. The results were surprisingly clear: Norway maple showed the highest plasticity in response to light regime of all eight maple species present, including sugar maple and co-occurring A. rubrum and A. pensylvanicum L. Sugar maple also had the lowest overall A_{max} of all maple species in that study for both light regimes. Interestingly, the only two species that came close to Norway maple in terms of plasticity, Acer ginnala Maxim. and A. palmatum Thunb., are also reported as potentially invasive to North America (see USDA Plants Database; plants.usda.gov).

The difference in mean relative allocation to roots between sugar and Norway maple is noteworthy. Sugar maple growing under the simulated gap light regime allocated about twice as much biomass to roots relative to above-ground biomass as compared with Norway maple. Furthermore, only sugar maple significantly changed its allocation pattern with light availability, with greater investment in roots under increased light. Canham et al. (1996) also reported increased root : shoot ratio in sugar maple with increasing light availability. This greater root : shoot ratio and associated below-ground storage of reserves is consistent with the species' longer persistence under very low light (Kobe 1997, Paz 2003, Myers and Kitajima 2007, Coll et al. 2008). This could be an advantage for sugar maple over the invasive Norway maple, especially in the deep shade of mature temperate stands. It could also be an advantage in water-limiting conditions, for example during extended droughts, or where deer browsing pressure is strong. Indeed, Morrison and Mauck (2007) do mention the lesser water use efficiency of Norway maple as a possible barrier to it invading drier forests (but see Kloeppel and Abrams 1995). It is

recognized that long-term survival in deep forest understorey does involve more than simply the capacity to tolerate low-light levels; success may also depend on the capacity to tolerate or avoid predation and pathogens, and store reserves (DeLucia et al. 1998, Paquette et al. 2007b), all things that sugar maple seems to be doing better than Norway maple (Godman et al. 1990, Lapointe and Brisson 2011). However, in any but the darkest or driest of conditions, a lower root : shoot ratio may actually be an advantage as investments in shoot are compounded and return more photosynthates over time. Thus, the lower root : shoot ratio in Norway maple would confer a productivity advantage consistent with its greater invasiveness following canopy disturbance. However, we could not test that hypothesis on first-year seedlings.

We also investigated whether Norway maple showed higher levels of functioning late in the growing season, thus attaining greater growth over the season as a whole. Indeed, the species is known for having a longer leaf lifespan and delayed leaf senescence with respect to sugar maple, which is hypothesized to be the result of the Northern European provenances cultivated in North America being adapted to a relatively warm and extended fall compared with eastern North America (Kloeppel and Abrams 1995, Munger 2003). This was indeed the case for height growth, which stopped near mid-summer in sugar maple under both light regimes, but was sustained into the fall by Norway maple growing under the gap regime. This growth advantage was not accompanied by any significant increase in maximum photosynthesis levels in the fall, nor in the longer maintenance of photosynthetic capacity through increased photoprotection (B. Duan, A. Paquette, P. Juneau, J. Brisson, B. Fontaine and F. Berninger, in preparation). Our data cannot preclude the possibility that sugar maple allocated photosynthates more to below-ground than above-ground growth after mid-summer (as suggested above to store reserves), but the timing of leaf coloring that we observed suggests that sugar maple production stops sooner than that of Norway maple at least in late fall.

A number of alternative hypotheses to explain invasiveness have been proposed, such as the release from natural enemies. The hypothesis was tested on the same pair of maple species with mixed results, Cincotta et al. (2009) confirming it, and Morrison and Mauck (2007) rejecting it. Lapointe and Brisson (2011), working on tar spot disease on Norway maple, found that natural enemies can also catch up to their evaded target species and may then help in controlling their invasiveness. Those ideas, as well as that of phylogenetic distance (above), cannot however explain the results found here where enemies of both maple species were controlled. Instead, the present experiment supports the idea of Norway maple being a superior competitor (to sugar maple) from having both better fitted and more plastic traits, as recently proposed by Godoy et al. (2012).

Furthermore, the capacity of Norway maple to take advantage of favourable conditions in fall, which may come at the

cost of increased early frost damage, as well as its superior plasticity in response to forest disturbance, may well increase the invasiveness of Norway maple as global change leads to increased growing season length and variability in climate (Schwartz et al. 2006, Cleland et al. 2007, Wolkovich and Cleland 2011).

References

Beaudet M, Messier C, Hilbert DW, Lo E, Wang ZM, Lechowicz MJ (2000) Leaf- and plant-level carbon gain in yellow birch, sugar maple, and beech seedlings from contrasting forest light environments. Can J For Res 30:390–404.

Bertin RI, Manner ME, Larrow BF, Cantwell TW, Berstene EM (2005) Norway maple (*Acer platanoides*) and other non-native trees in urban woodlands of central Massachusetts. J Torrey Bot Soc 132:225–235.

Callaway RM, Pennings SC, Richards CL (2003) Phenotypic plasticiy and interactions among plants. Ecology 84:1115–1128.

Campos JA, Herrera M (2009) Análisis de la flora alóctona de Bizkaia (País Vasco, España). Lazaroa 30:7–33.

Canham CD (1988) Growth and canopy architecture of shade-tolerant trees: response to canopy gaps. Ecology 69:786–795.

Canham CD, Berkowitz AR, Kelly VR, Lovett GM, Ollinger SV, Schnurr J (1996) Biomass allocation and multiple resource limitation in tree seedlings. Can J For Res 26:1521–1530.

Cincotta C, Adams J, Holzapfel C (2009) Testing the enemy release hypothesis: a comparison of foliar insect herbivory of the exotic Norway maple (*Acer platanoides* L.) and the native sugar maple (*A. saccharum* L.). Biol Invasions 11:379–388.

Cleland EE, Chuine I, Menzel A, Mooney HA, Schwartz MD (2007) Shifting plant phenology in response to global change. Trends Ecol Evol 22:357–365.

Coll L, Potvin C, Messier C, Delagrange S (2008) Root architecture and allocation patterns of eight native tropical species with different successional status used in open-grown mixed plantations in Panama. Trees Struct Funct 22:585–596.

Daehler CC (2003) Performance comparisons of co-occurring native and alien invasive plants: implications for conservation and restoration. Annu Rev Ecol Evol Syst 34:183–211.

Dalling JW, Winter K, Hubbell SP (2004) Variation in growth responses of neotropical pioneers to simulated forest gaps. Funct Ecol 18:725–736.

Davidson AM, Jennions M, Nicotra AB (2011) Do invasive species show higher phenotypic plasticity than native species and, if so, is it adaptive? A meta-analysis. Ecol Lett 14:419–431.

DeLucia EH, Sipe TW, Herrick J, Maherali H (1998) Sapling biomass allocation and growth in the understory of a deciduous hardwood forest. Am J Bot 85:955–963.

Fang W, Wang X (2011) Impact of invasion of *Acer platanoides* on canopy structure and understory seedling growth in a hardwood forest in North America. Trees Struct Funct 25:455–464.

Fernández-López C, López Pulido M, Amezcúa Ogayar C, Casado Ponce D. 1989. Catálogo bibliográfico de las plantas vasculares de Andalucía. Blancoana 7:3–68.

Gianoli E, Valladares F (2012) Studying phenotypic plasticity: the advantages of a broad approach. Biol J Linn Soc 105:1–7.

Godman RM, Yawney HW, Tubbs CH (1990) Sugar maple (*Acer saccharum* Marsh.). In: Burns RM, Honkala BH (eds) Silvics of North America; Volume 2: Hardwoods. USDA Forest Service, Washington, DC, pp 78–91.

Godoy O, Saldaña A, Fuentes N, Valladares F, Gianoli E (2011*a*) Forests are not immune to plant invasions: phenotypic plasticity and local adaptation allow *Prunella vulgaris* to colonize a temperate evergreen rainforest. Biol Invasions 13:1615–1625.

Godoy O, Valladares F, Castro-Díez P (2011*b*) Multispecies comparison reveals that invasive and native plants differ in their traits but not in their plasticity. Funct Ecol 25:1248–1259.

Godoy O, Valladares F, Castro-Díez P (2012) The relative importance for plant invasiveness of trait means, and their plasticity and integration in a multivariate framework. New Phytol 195:912–922.

Kloeppel BD, Abrams MD (1995) Ecophysiological attributes of the native *Acer saccharum* and the exotic *Acer platanoides* in urban oak forests in Pennsylvania, USA. Tree Physiol 15:739–746.

Kobe RK (1997) Carbohydrate allocation to storage as a basis of interspecific variation in sapling survivorship and growth. Oikos 80:226–233.

Kramer PJ, Kozlowski TT (1979) Physiology of woody plants. Academic Press, New York, pp 811.

Lapointe M, Brisson J (2011) Tar spot disease on Norway maple in North America: quantifying the impacts of a reunion between an invasive tree species and its adventive natural enemy in an urban forest. Ecoscience 18:63–69.

Lapointe M, Brisson J (2012) 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. Forests 3:190–206.

Lei TT, Lechowicz MJ (1997) The photosynthetic response of eight species of *Acer* to simulated light regimes from the centre and edges of gaps. Funct Ecol 11:16–23.

Littell R, Milliken G, Stroup W, Wolfinger R, Schabenberger O (2006) SAS system for mixed models, second edition. SAS Institute, Cary, NC.

Martin PH (1999) Norway maple (*Acer platanoides*) invasion of a natural forest stand: understory consequence and regeneration pattern. Biol Invasions 1:215–222.

Martin PH, Marks PL (2006) Intact forests provide only weak resistance to a shade-tolerant invasive Norway maple (*Acer platanoides* L.). J Ecol 94:1070–1079.

Martin PH, Canham CD, Marks PL (2009) Why forests appear resistant to exotic plant invasions: intentional introductions, stand dynamics, and the role of shade tolerance. Front Ecol Environ 7:142–149.

Martin PH, Canham CD, Kobe RK (2010) Divergence from the growth–survival trade-off and extreme high growth rates drive patterns of exotic tree invasions in closed-canopy forests. J Ecol 98:778–789.

Miller GE, Feltz CJ (1997) Asymptotic inference for coefficients of variation. Commun Statist Theory Meth 26:715–726.

Morrison JA, Mauck K (2007) Experimental field comparison of native and non-native maple seedlings: natural enemies, ecophysiology, growth and survival. J Ecol 95:1036–1049.

Munger GT (2003) *Acer platanoides*. In: Fire effects information system http://www.fs.fed.us/database/feis/. US Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory.

Myers JA, Kitajima K (2007) Carbohydrate storage enhances seedling shade and stress tolerance in a neotropical forest. J Ecol 95:383–395.

Niinemets Ü, Valladares F (2006) Tolerance to shade, drought and waterlogging of temperate, northern hemisphere trees and shrubs. Ecol Monogr 76:521–547.

Niinemets Ü, Valladares F, Ceulemans R (2003) Leaf-level phenotypic variability and plasticity of invasive *Rhododendron ponticum* and non-invasive *Ilex aquifolium* co-occurring at two contrasting European sites. Plant Cell Environ 26:941–956.

Nowak DJ, Rowntree RA (1990) History and range of Norway maple. J Arboric 16:291–296.

Pacala SW, Canham CD, Silander JA Jr, Kobe RK (1994) Sapling growth as a function of resources in a north temperate forest. Can J For Res 24:2172–2183.

Palacio-López K, Gianoli E (2011) Invasive plants do not display greater phenotypic plasticity than their native or non-invasive counterparts: a meta-analysis. Oikos 120:1393–1401.

Paquette A, Bouchard A, Cogliastro A (2006) Survival and growth of under-planted trees: a meta-analysis across four biomes. Ecol Appl 16:1575–1589.

Paquette A, Bouchard A, Cogliastro A (2007a) A less restrictive technique for the estimation of understory light under variable weather conditions. For Ecol Manag 242:800–804.

Paquette A, Bouchard A, Cogliastro A (2007b) Morphological plasticity in seedlings of three deciduous species under shelterwood under-planting management does not correspond to shade tolerance ranks. For Ecol Manag 241:278–287.

Paquette A, Fontaine B, Messier C, Brisson J (2010) Homogeneous light regime in shade-house experiment overestimates carbon gains in Norway maple seedlings. J Hortic For 2:117–121.

Paz H (2003) Root/shoot allocation and root architecture in seedlings: variation among forest sites, microhabitats, and ecological groups. Biotropica 35:318–332.

Reinhart KO, Greene E, Callaway RM (2005) Effects of *Acer platanoides* invasion on understory plant communities and tree regeneration in the northern Rocky Mountains. Ecography 28:573–582.

Reinhart KO, Gurnee J, Tirado R, Callaway RM (2006) Invasion through quantitative effects: intense shade drives native decline and invasive success. Ecol Appl 16:1821–31.

Robison SA, McCarthy BC (1999) Growth responses of *Carya ovata* (Juglandaceae) seedlings to experimental sun patches. Am Midl Naturalist 141:69–84.

Sanford NL, Harrington RA, Fownes JH (2003) Survival and growth of native and alien woody seedlings in open and understory environments. For Ecol Manag 183:377–385.

Santamour FS Jr, McArdle AJ (1982) Checklist of cultivated maples. III. *Acer platanoides* L. J Arboric 8:241–246.

Sanz Elorza M, Sobrino Vesperinas E, Dana Sánchez ED (2004) Atlas de las plantas alóctonas invasoras en España. Organismo Autónomo Parques Nacionales, Madrid

Schwartz MD, Ahas R, Aasa A (2006) Onset of spring starting earlier across the Northern Hemisphere. Glob Change Biol 12:343–351.

Searle SR, Casella G, McCulloch CE (1992) Variance components. John Wiley and Sons, New York.

Valladares F, Niinemets Ü (2008) Shade tolerance, a key plant feature of complex nature and consequences. Annu Rev Ecol Evol Syst 39:237–57.

Valladares F, Wright SJ, Lasso E, Kitajima K, Pearcy RW (2000) Plastic phenotypic response to light of 16 congeneric shrubs from a Panamanian rainforest. Ecology 81:1925–1936.

Wayne PM, Bazzaz FA (1993) Birch seedling responses to daily time courses of light in experimental forest gaps and shadehouses. Ecology 74:1500–1515.

Webb SL, Pendergast TH IV, Dwyer ME (2001) Response of native and exotic maple seedling banks to removal of the exotic, invasive Norway maple (*Acer platanoides*). J Torrey Bot Soc 128:141–149.

Webster CR, Nelson K, Wangen SR (2005) Stand dynamics of an insular population of an invasive tree, *Acer platanoides*. For Ecol Manag 208:85–99.

Wolfinger R, Tobias R, Sall J (1994) Computing gaussian likelihoods and their derivatives for general linear mixed models. SIAM J Sci Comput 15:1294–1310.

Wolkovich EM, Cleland EE (2011) The phenology of plant invasions: a community ecology perspective. Front Ecol Environ 9:287–294.

Wyckoff PH, Webb SL (1996) Understory influence of the invasive norway maple (*Acer platanoides*). Bull Torrey Bot Club 123:197–205.