

Can we foresee future maple invasions? A comparative study of performance-related traits and invasiveness of eight *Acer* species.

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Abstract

Determining traits correlated with invasiveness in order to identify potentially invasive species remains a priority in the field of invasion ecology. In trees, relative growth rate (RGR), specific leaf area (SLA) or plant height under optimal growing conditions have been identified as performance traits allowing pioneer exotic species to out-compete native species. However, few studies investigated the link between these traits and invasiveness on a continuous scale. Here, we compare the RGR, SLA, height, shoot-root ratio and number of leaves of seedlings of eight maple species (*Acer spp.*) with their invasiveness at the global level. Seedlings were grown in non-limiting conditions indoor in Gembloux, Belgium, and harvested after 2, 4 or 8 weeks. Global invasiveness was quantified using a combination of the number of regions and countries invaded in the GBIF database, the number of citations in the Global Compendium of Weeds (GCW) and the risk score estimated in the GCW. RGR, SLA, height and number of leaves after 8 weeks were positively correlated with invasiveness. We conclude that invasive maple species could benefit from an acquisitive strategy and that high growth and light capture also favors invasiveness of shade-tolerant species. Finally, we recommend a close monitoring of *Acer rufinerve* in western Europe due to its high RGR and SLA, comparable to other highly invasive maple species.

Keywords

Non-native trees; functional traits; RGR; SLA; relative growth rate

Introduction

The increasing number and extent of invasive species is one of the main drivers of biodiversity loss (IPBES 2019) and their impacts and management represent a great cost to society (Cuthbert et al. 2021). Invasive trees have the potential to greatly modify the structure of ecosystems and alter biological diversity and ecosystem services (Brundu and Richardson 2017, Dyderski and Jagodziński 2021). A species must go through several abiotic and biotic barriers to become invasive in natural habitats, and this process can take decades (Richardson et al. 2000). The lag-phase between introduction and actual impact on native habitats has been estimated to last about 170 years for trees in Germany (Kowarik 1995). A key goal in invasion ecology is to identify which species will progress through this invasion continuum and become invasive. Knowing which functional traits are associated with invasiveness can increase the efficacy of risk assessments (Gallagher et al. 2014) and allow early management actions before the problematic species become widespread.

The risk of naturalization of exotic trees increases with residence time and propagule pressure (Von Holle et al. 2005, Pyšek et al. 2009b, Fanal et al. 2021). To reach the final stage of the invasion process, invasive species possess a combination of traits that allows them to invade a given environment by outcompeting native species (Divíšek et al. 2018, Moravcová et al. 2015). Several studies compared traits between native vs. invasive species, trying to identify which traits allow the latter to outcompete native species in an area (Pyšek et al. 2009b, Godoy et al. 2011, Funk 2013, Wang et al. 2018, Dyderski and Jagodziński 2019, Mazzolari et al. 2020, Kumar and Garkoti 2021). Fewer studies compared invasive vs. non-invasive exotic species to investigate what traits distinguish successful invaders from the other exotic species. In a meta-analysis of trait comparison, van Kleunen et al. (2010) attested that for comparison between invasive species and native species being invasive elsewhere, performance-related traits are not significantly different. This is why it is important to consider the invasiveness of species at a global scale and to differentiate between invasive and less-invasive or naturalized non-invasive species in order to bring the strategy of invasive species to light (Divíšek et al. 2018).

Compared to non-invasive exotic species, invasive species seem to be positioned further along the leaf economics spectrum, towards an acquisitive strategy with rapid growth (Grotkopp et al. 2002, Gallagher et al. 2014, Shouman et al. 2020). Species with leaf and other traits that allow faster growth should be more successful invaders when introduced into resource-rich environments (Leishman et al. 2007).

Relative growth rate (RGR) has often been cited as a key trait in explaining the success of invasive tree species. RGR in optimal conditions shortly after germination provides a good measure of growth potential (Turnbull et al. 2008). Several studies demonstrated that invasiveness is related to how fast species can grow in optimal conditions after germination (Grotkopp et al. 2002, 2010, Dawson et al. 2011, Gallagher et al. 2014, Erskine-Ogden et al. 2016). However, in other studies, invasive species did not have a higher RGR than non-invasive ones (Bellingham et al. 2004, Van Echelpoel et al. 2016).

Specific leaf area (SLA) represents how fast a species can acquire resources through photosynthesis (Leishman et al. 2007). It encompasses both leaf construction costs (thickness and density) and leaf development. In Grotkopp et al. (2002), SLA was the main driver of differences in RGR between seedlings of invasive and non-invasive pine species. A seedling rapidly producing new leaves will have a higher SLA overall than a species producing the same leaves at a lower rate (Grotkopp et al. 2002). Gallagher et al. (2014) encourage the addition of SLA into screening procedures for invasive plants. However, differences in SLA between non-invasive and invasive plants is inconsistent (Grotkopp and Rejmanek 2007, Gallagher et al. 2011, Wang et al. 2018). The fast-growing strategy associated with a high SLA may only be advantageous in early-successional, resource-rich or highly disturbed environments (Leishman et al. 2007, Gallagher et al. 2014). Under water stress, a smaller SLA may lead to greater water use efficiency.

In 2011, van Kleunen et al. determined that herbaceous invasive species produced more biomass and had a higher shoot-root ratio than non-invasive congeneric species, notably in shaded conditions. In Porté et al. (2011), *Acer negundo* outperforms native species by allocating more

resources to the development of aerial structure over roots, leading to a higher shoot-root ratio. However, Wang et al. (2018) found that invasive plants might gain a competitive advantage in nutrient and water uptake by having a small shoot-root ratio. The importance of resources allocation to roots may be dependant on the receiving environment. In a mediterranean climate for example, increased root allocation may be critical for invasive species to survive summer droughts (Grotkopp and Rejmanek 2007, Erskine-Ogden et al. 2016).

Overall, the functional syndrome emerging from previous studies reflects that invasive species display an acquisitive strategy, with higher values for traits related to performance such as RGR, SLA, height and shoot allocation than non-invasive exotic species in resource-rich environments (Grotkopp and Rejmanek 2007, Herron et al. 2007, van Kleunen et al. 2010, Dawson et al. 2011, Lamarque et al. 2011, Gallagher et al. 2014, Mathakutha et al. 2019). Global change, especially nitrogen deposition, may amplify this syndrome.

To compare species with different levels of invasiveness, global databases are often used to retrieve traits. However, these traits have to be measured on species grown in the same environmental conditions to allow a fair comparison (van Kleunen et al. 2010). Most studies use pairs of congeneric species to test the difference between functional traits (Bellingham et al. 2004, Grotkopp et al. 2010, Dawson et al. 2011, Gallagher et al. 2014, Moravcová et al. 2015). Fewer studies compared a large number of congeneric species. Gallagher et al. (2011) found that invasive Acacias in Australia were taller than non-invasive ones. Invasive pine species also had higher RGR and SLA values (Grotkopp et al. 2002, Matzek 2012). Furthermore, examining the invasiveness along a gradient, instead of a “non-invasive” – “invasive” dichotomy, can allow an even better understanding of the relationship between invasiveness and functional traits.

Here, we focus on temperate deciduous tree species from the *Acer* genus. Maples are forest species that have been widely introduced around the world for centuries for their ornamental or silvicultural qualities. Their phylogeny has also been intensively studied (Li et al. 2019, Gao et al. 2020) and several maple species are highly invasive. These invasions have been widely

documented for decades, especially for *Acer negundo* in Europe or *A. pseudoplatanus* and *A. platanoides* in North America (Webb et al. 2000, Galbraith-Kent and Handel 2008, Sikorska et al. 2019).

Our aim is to test the functional syndrome of invasiveness promoted by performance traits (RGR, SLA, shoot-root ratio, plant height, number of leaves), by testing whether differences in functional traits of seedlings can be explained by the recorded global invasiveness of eight maple species. To allow a finer analysis of these relationships, we used a gradient of global invasiveness instead of the dichotomous “non-invasive” and “invasive” categorization often used in comparative studies.

Material and method

Species selection and quantification of invasiveness

Eight species were selected for this study, originating from three different continents (Europe, Asia and North America – see Table 1) and varying in observed global invasiveness. Four proxies of invasiveness were chosen, based on literature (Dawson et al. 2011, Erskine-Ogden et al. 2016): number of regions invaded in the Global Biodiversity Information Facility (GBIF 2022); number of countries invaded in GBIF; number of citations in the Global Compendium of Weeds (GCW, Randall 2017); and the “global risk score” used in the GCW. The regions are delimited as the 11 global regions presented in the GCW. The global risk score is a scoring system developed by Randall (2016) that quantifies a plant species invasive potential based on a combination of several characteristics: the types of human-mediated pathways of entry, the most significant dispersal mechanisms and the (potentially) significant impacts. To count the number of citations for each species in the GCW, we considered studies where the species is cited as “environmental weed”, “weed”, “invasive”, “agricultural weed” or “noxious weed” in the introduction range. As Erskine-Ogden et al. (2016) also stated, we understand that the GCW has uneven species coverage and sometimes redundant or lacking citations, but it is the most exhaustive source available on invasive species worldwide.

A Principal Component Analysis was performed on the four proxies of invasiveness with the “ade4” package (Dray and Dufour 2007) in R (R Core Team 2022). Number of citations was log-transformed. The coordinate of each species on the first PCA axis was defined as the global invasiveness score.

Seeds collection and planting

Seeds were collected from mature individuals in 4 arboreta and parks in Southern and Central Belgium, in the localities of Seraing, Profondeville, Gembloux and Tervuren. At least 3 different parent trees were used for seed collection. Additional seeds of *Acer lobelii* were graciously furnished by Hugh Angus from The Maple Society, England. Supplementary seeds of *A. palmatum* and *A. saccharum* were purchased from a French supplier.

Seeds were washed with 1% sodium hypochlorite solution for three to five minutes, then rinsed with water. They were then put in wet, oven-sterilized river sand and stored in the fridge at 4°C for three months to break dormancy.

According to the number of available seeds, 4 to 8 seeds of each species were sown in 1-liter pots filled with seed-starting soil mix (DCM – ECOTERRA®) in late March. Pots were organized in 15 blocks, each block containing three randomly arranged pots for each species, one for each harvest – 2, 4 and 8 weeks after germination. These time intervals were chosen because it appears that relative growth rate within a few weeks after germination might be predictive of the overall growth potential and invasive risk (Grotkopp et al. 2002, Grotkopp and Rejmanek 2007, Dawson et al. 2011). The experiment took place in a heated laboratory with temperatures ranging from 18 to 25 °C. Pots were positioned in bright indirect sunlight, with light intensity varying from 3 000 to 30 000 lux at noon depending on the cloud cover. Seedlings were watered weekly, when the surface of the soil was dry, and additional seedlings were removed after one week to keep one seedling per pot. Each germination was dated so every seedling was the same age for each harvest time.

At harvest time, seedling height was measured as the height of the highest leaf tip, then pots were cut open and roots carefully washed in water. Leaves were spread out on white sheets of paper and scanned directly after harvest. The seedlings were separated into four parts – leaves, cotyledons, stems and roots – and dried in the oven at 60°C for 48h, then weighted to the nearest 10⁻⁴ g with an analytical balance (XA105 DualRange, Mettler Toledo®, Viroflay, France).

Growth Analysis

Relative growth rates (RGR) was measured for the intervals 2-4 weeks, 4-8 weeks and 2-8 weeks. We used the formula proposed by Hunt (1982), where W is the biomass at time t :

$$RGR = \frac{\ln(W_2) - \ln(W_1)}{t_2 - t_1}$$

Leaf areas were measured using the ImageJ software (Rasband n.d.). SLA at each harvest time was calculated as the ratio of leaf area (cm²) to leaf dry mass (g) (Cornelissen et al. 2003). Cotyledons were included in the calculation of the SLA as they are photosynthetic organs. Shoot-root ratio was calculated as the ratio of the above-ground biomass (leaves, stems and cotyledons) to the root biomass.

Statistical analyses

Closely related species tend to resemble each other, hence comparative studies generally investigate the phylogenetic signal between species to ensure a correlation between traits is not only due to the phylogeny (Freckleton et al. 2002, van Kleunen et al. 2010). In case of non-independence to phylogenetic structure, phylogenetically independent contrasts (PICs) are used to control the phylogenetic effect (Felsenstein 1985, Grotkopp et al. 2010, Dawson et al. 2011, Pyšek et al. 2014). We used a phylogenetic tree of 84 *Acer* species constructed with nuclear ITS and three cpDNA fragments by Gao et al. (2020) to identify the common ancestors and construct a sub-tree for our 8 studied species (Fig. 1).

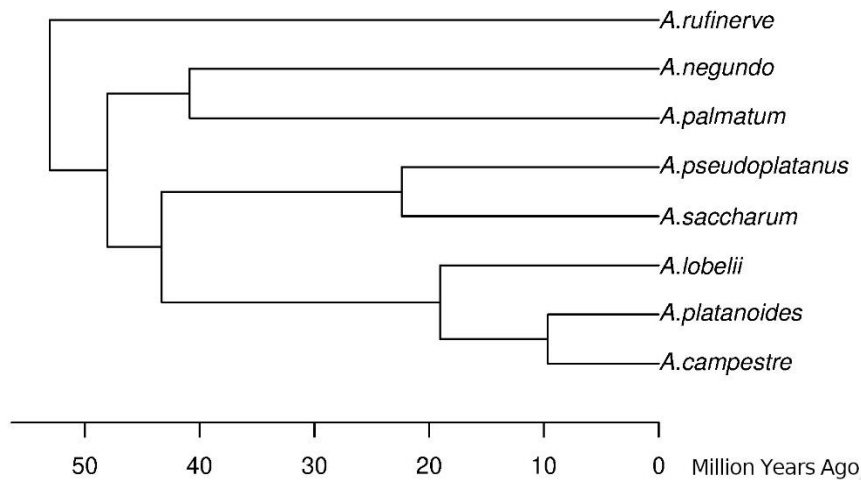


Figure 1: Chronogram showing the relationship between our 8 studied *Acer* species, based on the phylogenetic tree by Gao et al. (2020). X axis is in millions of years. The tree was coded in Newick format and drawn with the “ape” package.

We calculated the K parameter from Blomberg et al. (2003), which indicates if there is a strong phylogenetic signal ($K > 1$) or a random pattern (K close to zero). We used the “picante” package in R for calculation of the phylogenetic signal and its significance (Kembel et al. 2010).

Differences between species for each trait 8 weeks after germination were first investigated with ANOVA’s and Tukey’s post-hoc tests. Species were used as fixed factor and block as random effect. Significance threshold was $p=0.05$. Assumption of normality was tested with Shapiro-Wilk tests and visual interpretation of normal probability plots. A correlation matrix was built with non-parametric Spearman’s rank correlation coefficients on the functional traits after 8 weeks. Linear mixed effect models were fitted to test the relationship between global invasiveness and RGR with harvest times as fixed effect (2-4 weeks, 4-8 weeks, 2-8 weeks), SLA with harvest times as fixed effect (4 and 8 weeks), and number of leaves, height and shoot-root ratio after 8 weeks, separately, with the “lme4” package (Bates et al. 2015). Each model was run with and without the random block effect, and we selected the model with the lowest AIC. Linear models were also fitted for each harvest time separately for RGR and SLA to allow a better comparison of the time intervals. The traits were treated as response variables and the invasiveness as fixed effect, so the variances of traits could be incorporated into the analyses. All the analyses were performed in R (R Core Team 2022).

Results

Quantification of invasiveness

To quantify the invasiveness of the eight maple species, a PCA was performed on the four proxies of invasiveness. The first component captured 81.1 % of the variance, and the second one 14.4 % (Fig. 2). All the proxies were highly correlated to the first axis, and each species' coordinate on this axis was assigned as its value of global invasiveness, which allows a quantitative analysis of invasiveness on a continuous scale (Table 1).

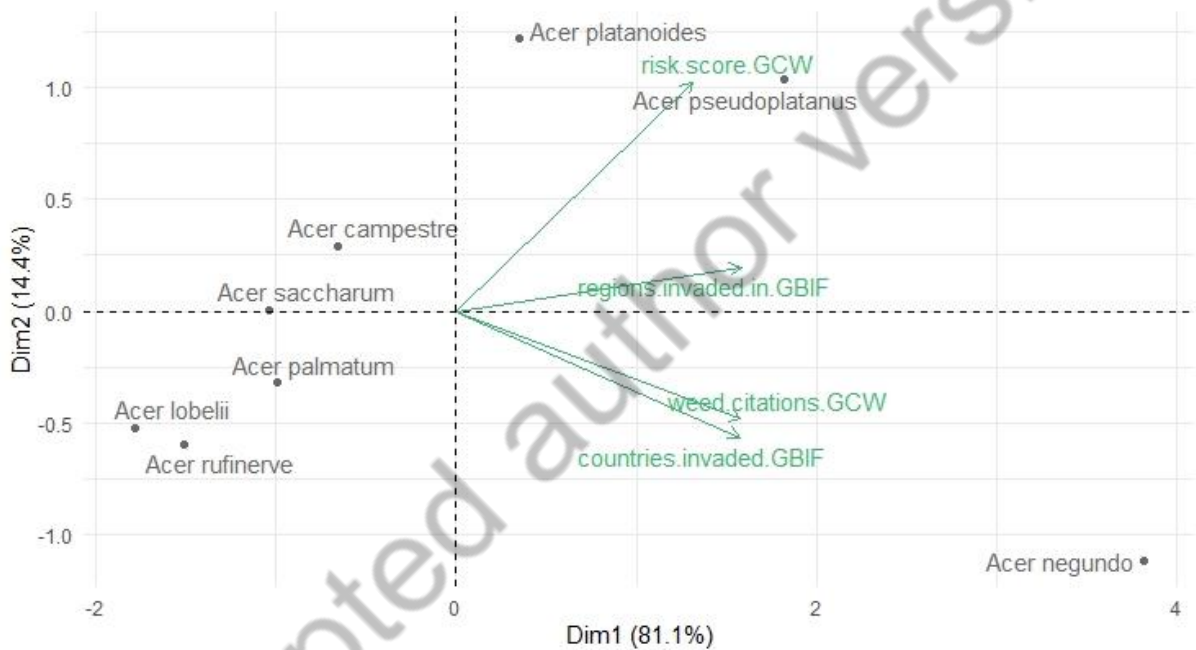


Figure 2: PCA on the 4 proxies of invasiveness for the eight studied maple species.

Table 1: Eight chosen maple species, origin, value of invasiveness proxies and global invasiveness determined as the coordinate on the axis 1 of the PCA. The global risk score and the number of citations are retrieved from the Global Compendium of Weeds, number of regions and countries invaded are retrieved from the GBIF database. Region names according to the GCW are EU: Europe, NA: North America, SA: South America, AF: Africa, EA: Eastern Asia, WA: Western Asia, CA: Central Asia, AU: Australasia.

Species	Origin	Global risk score	Number of citations	Regions invaded	Countries invaded	Global invasiveness
<i>A. negundo</i>	NA	34.56	165	7 (EU, AF, EA, WA, CA, AU, SA)	45	3.82
<i>A. pseudoplatanus</i>	EU	43.32	48	7 (NA, AU, CA, SA, AF, WA, EU)	18	1.82
<i>A. platanoides</i>	EU	43.2	43	3 (NA, AU, EU)	5	0.35
<i>A. campestre</i>	EU	21.6	13	2 (NA, EU)	7	-0.66
<i>A. palmatum</i>	EA	4.8	15	3 (NA, EU, WA)	3	-0.99
<i>A. saccharum</i>	NA	12.96	5	2 (EU, WA)	5	-1.04
<i>A. rufinerve</i>	EA	2.16	8	1 (EU)	5	-1.51
<i>A. lobelii</i>	EU	0	2	1 (EU)	1	-1.78

Analyses of traits

The number of seedlings harvested per species varied between 28 and 42, because of variation in germination and mortality rates. Nine to 14 RGR values were calculated per species for the 2-8 week interval, and 8 to 14 values per species for the 2-4 week and 4-8 week intervals. Mean values and standard errors of the traits for each species are available in tables 2 and 3, as well as pairwise significance from Tukey's test.

Table 2: mean values and standard errors of functional traits for each species after 8 weeks. N is the number of seedlings measures 8 weeks after germination. Significance letters obtained after Tukey's test are also given for each species and each trait.

Species	N	shoot/root	Height (cm)	SLA (cm ² /g)	Nb of leaves
<i>A. negundo</i>	14	5.56 ± 0.58 bc	20.38 ± 1.31 c	596.23 ± 40.91 c	8.5 ± 0.4 b
<i>A. pseudoplatanus</i>	13	2.90 ± 0.30 a	16.95 ± 1.00 c	353.84 ± 12.89 ab	6.8 ± 0.4 ab
<i>A. platanoides</i>	11	3.28 ± 1.12 ab	16.08 ± 1.58 bc	376.62 ± 12.29 ab	8.6 ± 0.9 b
<i>A. campestre</i>	9	2.42 ± 0.15 a	8.14 ± 1.02 a	346.39 ± 26.17 a	5.9 ± 0.5 a
<i>A. palmatum</i>	11	4.21 ± 0.31 ac	11.74 ± 1.08 ab	365.76 ± 21.68 ab	6.3 ± 0.7 ab
<i>A. saccharum</i>	13	3.12 ± 0.41 a	11.59 ± 0.77 ab	359.32 ± 18.98 ab	5.2 ± 0.5 a
<i>A. rufinerve</i>	10	6.06 ± 1.09 c	10.77 ± 0.43 a	432.63 ± 29.32 b	6.3 ± 0.3 ab
<i>A. lobelii</i>	13	3.45 ± 0.33 ab	9.81 ± 0.83 a	318.89 ± 16.53 a	6.5 ± 0.4 ab

Table 3: mean values of RGR (g.g-1.d-1), standard errors and significance letters for each time interval.

Species	RGR 2-8 weeks		RGR 2-4 weeks		RGR 4-8 weeks	
<i>A. negundo</i>	0.068 ± 0.006	b	0.099 ± 0.008	b	0.053 ± 0.006	a
<i>A. pseudoplatanus</i>	0.060 ± 0.003	ab	0.086 ± 0.011	ab	0.052 ± 0.005	a
<i>A. platanoides</i>	0.064 ± 0.005	ab	0.079 ± 0.012	ab	0.059 ± 0.014	a
<i>A. campestre</i>	0.046 ± 0.006	a	0.086 ± 0.010	ab	0.029 ± 0.008	a
<i>A. palmatum</i>	0.047 ± 0.005	a	0.072 ± 0.013	ab	0.034 ± 0.009	a
<i>A. saccharum</i>	0.045 ± 0.004	a	0.067 ± 0.008	ab	0.035 ± 0.005	a
<i>A. rufinerve</i>	0.052 ± 0.004	ab	0.071 ± 0.011	ab	0.040 ± 0.004	a
<i>A. lobelii</i>	0.048 ± 0.003	a	0.056 ± 0.016	a	0.044 ± 0.009	a

Relative growth rates between weeks 4 and 8 did not vary significantly between species (Table 3), but RGR between weeks 2 and 4 and between weeks 2 and 8 did ($p < 0.001$ for both), as well as SLA after 8 weeks ($p < 0.001$). *Acer Negundo* displayed the highest value of SLA after 8 weeks, followed by *Acer rufinerve* (Table 2). Overall, SLA values presented a great variation according to time and between species, but *A. negundo* had the greatest values during the whole experiment.

The Spearman correlation analysis performed on traits after 8 weeks shows that the RGR is highly correlated to height ($r_k = 0.7$). A higher shoot-root ratio is also correlated to higher SLA values ($r_k = 0.5$) (Fig. 2).



Figure 3: Correlation plot (Spearman coefficient) between traits. SLA at week 8, shoot-root ratio, number of leaves and height are measured 8 weeks after germination. RGR is measured between weeks 2 and 8.

The K parameter for phylogenetic signal was calculated for each trait; RGR 2-4 weeks: $K=0.609$ ($p=0.56$), RGR 4-8 weeks: $K=0.298$ ($p=0.99$), RGR 2-8 weeks: $K=0.422$ ($p=0.85$), SLA after 4 weeks: $K=0.298$ ($p=0.99$), SLA after 8 weeks: $K=1.115$ ($p=0.15$), height: $K=0.479$ ($p=0.77$), shoot-root: $K=1.43$ ($p=0.05$) and the number of leaves after 8 weeks: $K=0.484$ ($p=0.72$). As there was no phylogenetic signal detected, the phylogenetic structure was not accounted for in the following regression analyses.

Results from the linear regressions indicated that RGR was positively associated with the global invasiveness ($p<0.001$, t value=4.12, adj $r^2=0.26$; Fig. 4). Moreover, there was a significant effect of the time interval ($p<0.001$). Looking at the time intervals separately, we find a stronger effect of global invasiveness for RGR values measured between 2 and 8 weeks ($p<0.001$, t value=4.60) and between 2 and 4 weeks ($p=0.004$, t value=2.94) than for the 4 to 8 weeks interval ($p=0.028$, t value=2.23). Invasive species were significantly taller ($p<0.001$, t value=9.31, adj $r^2=0.48$) and grew more leaves ($p<0.001$, t value=3.95, adj $r^2=0.14$). A higher SLA was significantly associated with increased invasiveness ($p<0.001$, t value=9.74, marginal $r^2=0.47$, conditional $r^2=0.55$) after both 4 weeks ($p<0.001$, t value=10.44) and 8 weeks ($p<0.001$, t value=8.41). However, the relationship between the shoot-root ratio and invasiveness was not significant ($p=0.08$, adj $r^2=0.01$).

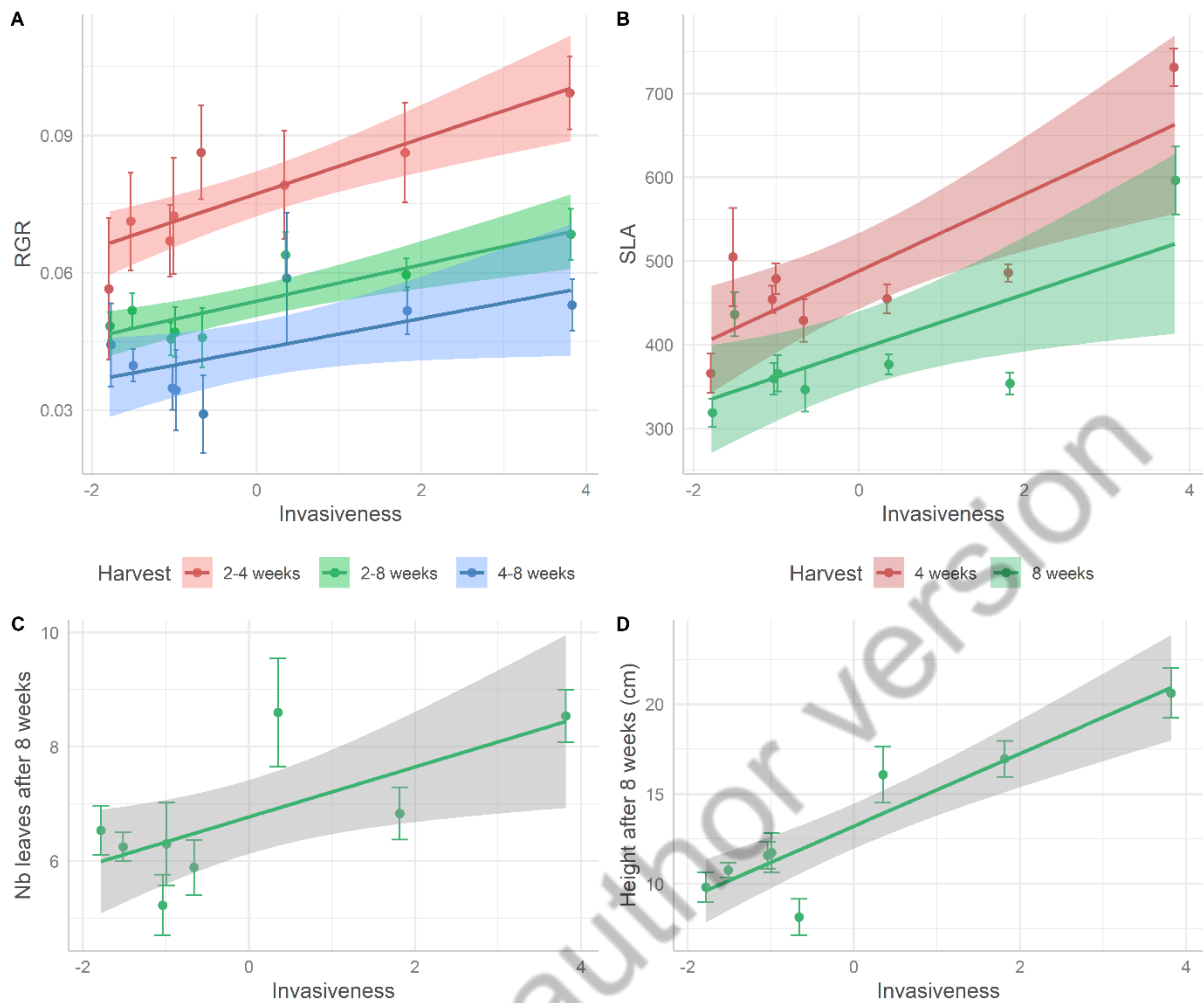


Figure 4: Predicted values for functional traits with significant relationship to global invasiveness. Mean values and standard errors are represented for each trait. Units are $\text{g}\cdot\text{g}^{-1}\cdot\text{d}^{-1}$ for RGR (A), $\text{cm}^2\cdot\text{g}^{-1}$ for SLA (B) and cm for height after 8 weeks (D).

Discussion

Because of their ornamental or wood production properties, maples have been widely introduced around the world for centuries in temperate forests, arboreta, parks and gardens. However, only a few species have become invasive in natural habitats. Predicting which tree species are more likely to become invasive is essential, and performance traits were correlated to invasiveness in studies performed on acacias and pines (Grotkopp et al. 2002, Gallagher et al. 2011, Matzek 2012). In this study, among the eight maple species we studied, we did find a positive relationship between relative growth rate at the seedling stage and the global invasiveness. Height was also highly correlated to RGR, which indicates that invasive species favor fast vertical growth. SLA and

number of leaves were also higher for invasive species, reflecting allocation of resources preferably to leaf construction and light capture. These results confirm a tendency towards an acquisitive trait syndrome for the most invasive species.

To ensure the phylogenetic independence of our traits, we calculated the K parameter of phylogenetic signal for each of the studied trait. We did not find any significant signal, and therefore we conducted the analyses without taking the phylogenetic structure into account. The use of phylogenetically independent contrasts is mostly needed when species from different genera are compared. In their study on pines, Grotkopp et al. (2002) analyzed the difference of traits between invasive and non-invasive species with and without phylogenetic control, and arrived at the same conclusions. Even when the traits are phylogenetically constrained, from a manager's point of view, the predictive value of traits contributing to invasiveness remains useful regardless of the underlying evolutionary process (Pyšek et al. 2014).

The timing of the harvests is important to highlight differences in trait values. Differentiation of RGR values between our species was most significant on the 2 to 8 and 2 to 4 weeks periods. However, RGR values between 4 and 8 weeks did not significantly differ between species. Most comparative studies that found a relationship between RGR, SLA and invasiveness used a 1 to 3 months time span. A longer period might blur the differences between species. In a study conducted in New Zealand on woody plants, Bellingham et al. (2004) found no relationship between RGR and observed invasiveness, but their growth period lasted for 5 to 11 months. However, other factors could explain their results, such as the invasiveness defined at a local scale and the stage of invasion considered.

Compared to pines and acacias, both light-demanding pioneer species, the studied maple species differ in their shade tolerance and intermediate position in forest succession (Lei and Lechowicz 1990, 1998, Wada and Ribbens 1997, Petit et al. 2017). All studied species can tolerate shade and usually exploit small gaps in the forest cover. Porté et al. (2011) and Lamarque et al. (2015) already highlighted *A. negundo's* ability to outperform native species and spread in temperate

resource-rich forests due to its high SLA. *Acer pseudoplatanus* invades native forests by means of its resource-use efficiency, especially its high photosynthetic rates in shady conditions (Shouman et al. 2020). *Acer platanoides* is also a forest species that combines high growth rates with moderate shade tolerance, a unique combination of traits that allows it to invade established North-American forests (Martin et al. 2010). Our study supports that rapid growth and fast light acquisition as early as on the seedling stage are important sources of invasiveness for invasive maples, even in shaded environments.

We found no pattern for the relationship between shoot-root ratio and invasiveness. *Acer negundo* and *A. rufinerve* both had the highest values, which indicates they invest more resources into their above-ground development, as it has already been observed for *A. negundo* in a study by Porté et al. (2011). However, other invasive species such as *A. pseudoplatanus* and *A. platanoides* did not show the same pattern.

In our study, *Acer rufinerve* was assigned a rather low global invasiveness value, because of the low number of regions invaded and low number of citations as invasive. However, it shares similar trait values to the very invasive *A. negundo*, particularly SLA and RGR values. The species has recently been added to the European and Mediterranean Plant Protection Organization (EPPO) list of invasive species because of its regeneration in three Belgian forests, where it outcompetes native plants and already represents an important management cost (EPPO 2022). It is described as an early-successional forest species that occupies small gaps and edges of oak-dominated forests (Branquart et al. 2011). In more shaded or semi-shaded areas, *A. rufinerve* is taller than *A. pseudoplatanus* at the same age, and their radial growth is comparable (De Ruyver 2021). If *A. rufinerve* has the capability to maintain populations under forest cover, its high SLA values in our experiment indicate that the species probably has the potential to display rapid growth when put to light by clearings or other perturbations. This maple species also presents prolific resprouting, and vegetative regeneration is an important driver of invasiveness, making the control and eradication extremely challenging (Nunez-Mir et al. 2019). We therefore suggest that *A. rufinerve* might not have completed the invasion process yet, which could explain its low invasiveness value

in our study. We recommend a close monitoring of the species in other temperate countries, to identify invasions of natural habitats at early stages.

A limitation of our study is the origin of the collected seeds. All seeds were collected in western Europe, which is the native range for some species and the introduced one for others. If genetic differentiation has been observed in the invaded area for *A. negundo*, it is not the case for *A. platanoides* (Lamarque et al. 2015). This could be due to the life-strategy or the stage of invasion – genetic differentiation appears in the latest stages, when the trees spread from established populations (Lamarque et al. 2015). A meta-analysis by Bossdorf et al. (2005) concluded that some sort of genetic drift was often observed in the introduction range of invasive plants, sometimes leading to enhanced growth. Choosing seeds exclusively from invaded ranges would therefore probably have only sharpened the distinction between less-invasive and highly invasive species. Also, we did not test the plasticity of the species for the studied functional traits. However, previous studies stated that species traits, not plasticity, most explain the variations in invasion success (Palacio-López and Gianoli 2011, Matzek 2012). High plasticity seems to be more important in the naturalization process (Pyšek et al. 2009a, Gallagher et al. 2011, Lamarque et al. 2015).

From our results, it appears that invasive maples favor fast growth, rapid leaf production and high SLA, promoting efficient light capture. As shown for pioneer species such as pines and acacias, this acquisitive trait syndrome also applies to shade-tolerant species such as maples. Because most introduced exotic tree species are pioneer species, traits relative to the invasion of shady established forests have long been neglected (Martin et al. 2009, 2010). Yet more conservative traits such as shade-tolerance may play an important role in the invasion of ecosystems with low disturbance regimes. Fridley et al. (2022) recently stated that a “fast-but-steady” functional syndrome, implying both fast growth capacity and persistence in the shaded understorey might promote invasion success in forests. A comparison of these traits on a larger sample of pioneer, intermediate and closed-canopy invasive tree species might help build a more comprehensive profile on the strategies of invasive trees.

Conclusion

Our study contributes evidence that performance-related traits such as RGR, SLA, leaf production and height of the seedlings can help predict which species are invasive, even for shade-tolerant species such as maples. Once naturalized, species that become invasive present an acquisitive trait syndrome characterized by fast growth, rapid leaves production and efficient light capture *via* high SLA. *Acer rufinerve*, an early-successional maple invasive in a few western European countries, displays trait values close to *A. negundo* and should be monitored carefully.

Accepted author version

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Statements & Declarations

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Competing interests

The authors have no relevant financial or non-financial interests to disclose.

Author contributions

All authors contributed to the study conception and design. Material preparation, data collection and analysis were performed by Aurore Fanal. The first draft of the manuscript was written by Aurore Fanal and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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