



# Mechanisms involved in alien maples (*Acer* sp.) invasion process in the Central Europe. Testing hypotheses associated with species fitness

Peter Ferus<sup>1</sup>

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## Abstract

Maples (*Acer* sp.) are trees/shrubs of extraordinary aesthetic value, what favours them for wide utilisation in urban greenery. However, some of the non-native species became invasive in the new range and represent a threat to natural ecosystems. Therefore, after the definition of their frequency and planting history in Slovak cities and reinvestigation of ecological status, based on analysis of growth, reproduction biology, fruit dispersal, phenotypic plasticity and allelopathic potential, invasion hypotheses related to the species fitness were tested in non-invasive alien species, in respect of invasive box elder (*A. negundo* L.). Parks and residential areas from the socialistic era were dominated by silver maple (*A. saccharinum* L.) and private gardens by palm maple (*A. palmatum* Thunb.) cultivars. A shift to ‘locally naturalised’ was confirmed in the former, and palm maple was taken into consideration in the alien flora list (as casual). The fastest growth was found in silver maple and box elder. The latter showed also extraordinary reproduction earliness, largest fruit production, flight range and seed viability. Specific leaf area mostly decreased in box elder towards summer, indicating its large phenotypic plasticity. However, the largest allelopathic effect was observed in silver maple. Hence, ‘limiting similarity hypothesis’, ‘ideal weed hypothesis’, ‘propagule pressure hypothesis’ and ‘phenotypic plasticity hypothesis’ were essential for box elder invasion success. On the other hand, ‘ideal weed hypothesis’ and ‘novel weapon hypothesis’ seem to be crucial for silver maple naturalisation. Palm maple failed in all studied aspects, indicating colonisation stage of the invasion process.

**Keywords** Non-native maples (*Acer* sp.) · Invasion process · Planting history · Growth · Reproduction · Seed dispersal · Phenotypic plasticity · Allelopathy

## Introduction

Colonisation of the new “world” after A.D. 1500 triggered an unprecedented reciprocal plant species exchange between continents (Mack and Lonsdale 2001). As soon as the demand for alimentary, medicinal and ornamental plant species has been met in human population, influx of plant species interesting for forestry initiated in Europe (Benčať 1982). However, only a part of introductions was successful.

In order to become naturalised, any non-native (alien) species needs to overcome environmental and reproduction barriers in the new range. When it succeeds in colonising of disturbed and/or natural habitats, it becomes invasive.

This is the well-known “naturalisation-invasion continuum” concept, proposed by Richardson et al. (2000).

Theoharides and Dukes (2007) summarised factors underlying successful passing through respective phases of this route. As they indicate, after the long-distance transport (the 1st phase) of the intentionally introduced species, it is the propagule pressure (number of planted individuals) and higher genetic variability, ensuring better adaptability to local environmental constraints and seed production, play the key role in the second, the colonisation phase. To establish a self-sustaining population (3rd phase – naturalisation), plant competitiveness for resources and allelochemical production, positive interactions with pollinators and soil biota, are very helpful. However, usually there is a more-or-less long lag phase before a species switches to the forth phase, the landscape spread – invasion. Low genetic variability, insufficient population size or lack of suitable habitat stand most probably behind the lag phase. After these limits has been overcome, species starts to spread. The more effective

✉ Peter Ferus  
peter.ferus@savba.sk

<sup>1</sup> Mlyňany Arboretum, Institute of Forest Ecology SAS,  
Vieska nad Žitavou 178, Slepčany 95152, Slovakia

propagule dispersal mode it has, the more disturbance events and landscape fragmentation occurs, and the better bio-corridor connection is ensured, the faster the species spreads.

According to Drenovsky et al. (2012), functional traits are responsible for making a plant species invasive. Phenotypic plasticity was considered as decisive for their success. Van Kleunen et al. (2010) focussed on identification of invasiveness determinants by means of comparing 125 invasive and 196 non-invasive plant species and found that invasive species outperformed the non-invasive ones in all six trait categories (physiology, leaf area allocation, shoot allocation, growth rate, size and fitness). Ren and Zhang (2009) categorised eight invasion mechanisms into three classes, according to the ecological processes determining the invasion: 1. physical environment mechanisms, 2. resource use mechanisms and 3. enemy release mechanisms. A review of Daneshgar and Jose (2009) listed all to-date known plant invasion hypotheses with their overlaps. MacDougall et al. (2009) tried to unify them on the basis of general species fitness / niche differences approach. Furthermore, Dai et al. (2020) related distinct plant invasion hypotheses with respective phases of the invasion process, resulting in a compendious diagram.

Nevertheless, data from the field show that intentionally introduced species naturalise easier and it is more probable that they will become invasive than those introduced as contaminants or stowaways (Pyšek et al. 2011). The most infested regions in the world are Australia, southern Africa, northern America and Pacific islands, and species introduced for horticultural use (62%) predominate there (Richardson and Rejmánek 2011). Historical data on woody plant species introduced to Brandenburg, Germany during 400 years (1500–1900) show growing percentage of invasiveness in the course of the last 200 years – up to 9.6% (Kowarik and von der Lippe 2007). Out of 127 woody plant species escaping from culture in the Czech Republic, 17 are considered as invasive (Křivánek and Pyšek 2008). According to the last alien species inventory, there were 126 neophytic phanerophytes identified in the Slovak flora, but only 4 of them have the invasive character (Medvecká et al. 2012).

Maples (*Acer* sp.) are trees or shrubs of the northern hemisphere with high aesthetic value. Attractive habitus, often decorative bark structure and exotic leaf and inflorescence morphology predetermine them for wide utilisation in parks, urban greenery and private ornamental gardens (van Gelderen et al. 2010). However, nowadays there are more maple species with the invasive ranking in the world. Besides European Norway maple (*A. platanoides* L.) invading North-American forests (e.g. Martin 1999; Wangen and Webster 2006; Morrison and Mauck 2007) or Sycamore maple (*A. pseudoplatanus* L.) widely spreading in New Zealand (Shouman et al. 2017, 2020), North-American box elder (*Acer negundo* L.) represents one of the worst aliens on the

European continent (GBIF – Global Biodiversity Information Facility).

Native maple species in the Slovak cities have been accompanied by box elder and silver maple (*A. saccharinum* L.) for decades not only for their ornamental qualities, simple access to reproductive material but also because of their relatively high frost hardiness and resistance to urban environment (Supuka et al. 1991). However, the maple market supply has been transformed almost exclusively to the palm maple (*A. palmatum* Thunb.) cultivars in the past twenty years (Ferus 2018). Nowadays, the box elder has been ranked as invasive, the silver maple as casual and the palm maple has not been included in the latest inventory yet (Medvecká et al. 2012).

In order to identify key traits/mechanisms which make a plant species invasive, a plenty of pair-wise experiments in invasive-native or invasive-non-invasive species pairs were conducted (e.g. Graebner et al. 2012; Minden and Gorschlüter 2016; Slate et al. 2020). However, only few works compare the performance of invasive, non-invasive and native congeners (Bohl 2013) and no one evaluates reactions of all the most frequent alien and native species. Therefore, through investigation of planting history and propagule pressure in Slovak cities along with the ecological status actualisation, as well as the experimental evaluation of growth, reproduction biology, fruit dispersal, phenotypic plasticity and allelopathic potential parameters in non-invasive alien maple species, invasion hypotheses related to the species fitness (namely ‘ideal weed hypothesis’ associated with the ‘nitrogen allocation hypothesis’, ‘limiting similarity hypothesis’, ‘novel weapon hypothesis’, ‘phenotypic plasticity hypothesis’ and ‘propagule pressure hypothesis’) were tested in respect of the box elder invasion success in this work. I suppose that due to different ecological status of the non-native species, a failure in several number of mechanisms/hypotheses can be expected.

## Material and methods

### Planting history, propagule pressure and present ecological status of non-invasive alien maple species

Field research on non-native maple species (except for the invasive box elder) in city parks, residential areas and private gardens was conducted in Bratislava, Nitra and Zlaté Moravce (2018) as well as Banská Bystrica, Galanta and Poprad (2019) – cities of a different administrative position and climatic characteristics located across Slovakia. Most of the residential areas with blocks of flats were established in the seventies and eighties of the past century (socialistic era). In Bratislava, Nitra and Zlaté Moravce, I surveyed those, which were recently built (Slnečnice (2011-present),

Martinák (1993–2018) and Ďateliniská (2012–present), respectively). Number of planted individuals of a species as well as those escaped from culture, were defined on hectare/garden number basis and tree age estimated (based on the growth parameters with consideration of species vigour). Adjacent bio-corridors were investigated for escapes using the same approach. A 30-year normal (1961–1990) of the average annual temperatures and the annual precipitation sums for respective cities were provided by the Slovak Hydrometeorological Institute. The nearest meteorological station to Zlaté Moravce was that in the Mlyňany Arboretum (approx. 10 km distant), for Banská Bystrica that at the Sliach airport (approx. 10 km distant) and for Galanta that in Kráľová pri Senci (approx. 20 km distant). These data enabled to outline the non-invasive alien species structure, planting history and propagule pressure as well as present ecological status of the most frequent species. In parallel, field and lab experiments were conducted in the most common alien and all four native maple species in the Mlyňany Arboretum IFE SAS.

### Climatic and soil characteristics of the experimental base

Mlyňany Arboretum is located in the western Slovakia, at the northern edge of the Danubian Lowland in a valley of Žitava river and southern margin of Tribeč and Pohronský Inovec hills. Its terrain undulates in the range of 160–204 m a. s. l. (Tábor and Pavlačka 1992). The area belongs to the warmest and driest region of Slovakia (Hořka and Barta 2012) with the average annual temperature of 9.5 °C and average annual rainfall of 574 mm (long-term average of 1970–1990). Detailed survey of Polláková (2018) revealed the following soil types beneath the respective maple tree groups and in the experimental field: field maple, Sycamore maple, palm maple and silver maple – stagnic cutanic luvisol, Norway maple, Tatarian maple and the experimental field – luvic chernozem, box elder – cutanic luvisol.

### Plant material

The collection of studied maple species comprised of four native (field maple – *Acer campestre* L., Norway maple – *A. platanoides* L., Sycamore maple – *A. pseudoplatanus* L. and Tatarian maple – *A. tataricum* L.) and three non-native maple species (box elder – *A. negundo* L. and silver maple – *A. saccharinum* L. of North-American origin, introduced to the area of present Slovakia in 1794 and 1820, respectively, and palm maple – *A. palmatum* Thunb. of south-east Asian origin, introduced after 1900), which have been widely planted in Slovakia. Groups of decades old trees with southern exposition growing in the Mlyňany Arboretum IFE SAS (except for box elder from the adjacent invaded riparian stand) were not only sources of the seed material for field

experiment and leaves for allelopathic potential analysis but also objects of phenological observations.

### Tree growth

Seedlings of the native and non-native maple species grown from fruits collected in the Mlyňany Arboretum (as described above) were transplanted to an open-space experimental field in the spring of 2014. Plantlets were planted into rows with 3 × 3 m spacing following order based on the final tree height described in literature (6 replicates of each species), so that eventual soil substrate variability could be avoided. When branching appeared, formation of tree crown from 1.5 m height started. Young trees were being watered regularly during the summer dry periods (July–August) in the first three years (5–10 L every 2–3 days). To regulate weeds, the area between trees was mowed four times a year. In the fourth year, grass was sown there. The tree height was measured using measure tape and from 2017 using height meter Suunto PM-5/1520 (Suunto, Finland) in early spring of each experimental year (2014–2019). From 2017 also trunk perimeter at 1.0 m height (because of slow growth of the palm maple) was measured with a measure tape and then recalculated onto trunk diameter.

### Reproduction

Phenological stages (flowering – BBCH 60–69, and fruit ripening – BBCH 81–89) dating was carried out in 2018 in adult plants from the arboretum (experimental seedlings of some species had not still fruited, year of the first fruiting was recorded). However, when fruiting, fruit number per tree and seed viability were defined.

Seed viability percentage was determined in a representative fruit sample (of at least 100 fruits per tree), which was stratified in wet gravel ( $\leq 4$  mm) stored in a cold room (3–5 °C), from period and as long as respective species required (Walter 2011). In the spring, fruit wings were removed, seeds cut longitudinally across embryos and each of them has been put into Eppendorf tube with 1 mL 1% (w/v) TTC (triphenyl-tetrazolium chloride) for 24 h in the dark. Seeds with reddish embryos (from established formazan) were taken as viable.

### Fruit morphology and aerodynamics

Fully developed fruits from every studied maple species were analysed for area, weight, fruit load (weight/area ratio), thickness and flight range. After harvesting from the adult trees growing in the Mlyňany Arboretum in autumn 2018, they were stored in a cold room till early spring 2019 (fruit humidity stabilised at approx. 15%). Silver maple fruits were collected in May 2019 and submitted to the analyses in fresh

state (fruit humidity of 42%). Fruit area was defined using a scanner and the Image J software. Thickness of the fruits was measured using a calliper rule, and the flight range was determined in the Wind tunnel of the Slovak Technical University in Bratislava. Individual fruits (20 per each maple species), held in hand in position copying the tree, 8 cm from the top and 80 cm from the side of the rectangular (2.6 × 1.6 m) wind tunnel (26.35 m long), were released into a homogenous air flux of approx. 3.8 m.s<sup>-1</sup> speed and distance to the fall point was determined by a measure tape.

## Phenotypic plasticity

Species phenotypic plasticity was assessed by means of specific leaf area (SLA) dynamics during the sixth year of cultivation (2018) in the experimental field. Top expanded leaves (6 replicates for each species) were collected in late spring (11th May), at the beginning (3rd July) and end of summer (23rd August) at 1300 h and SLA was analysed, as follows:

$$SLA = A_L / W_L (\text{dm}^2 \cdot \text{g}^{-1})$$

where  $A_L$  – leaf area defined by a scanner and Image J software,  $W_L$  – leaf dry weight.

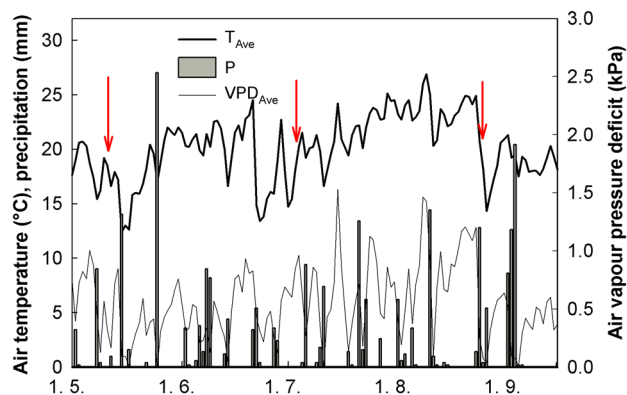
## Meteorological data

As a complementary information to the phenotypic plasticity experiment, daily average air temperature ( $T_{Ave}$ ), average air humidity ( $RH_{Ave}$ ) and precipitation sum ( $P_{sum}$ ) for period May–September 2018 were recorded by meteorological station of the Mlyňany Arboretum. From these data, daily average vapour pressure deficit ( $VPD_{Ave}$ ) of the air was calculated (Fig. 1):

$$VPD_{Ave} = (610.7 * 10^{(7.5 * T_{Ave} / (237.3 + T_{Ave}))} / 1000) * ((100 - RH_{Ave}) / 100) (\text{kPa})$$

## Allelopathic potential

Leaves from the southern part of mother (arboretum) tree crowns (whole maple species collection with addition of black walnut (*Juglans nigra* L.) as a reference) were collected in the summer of 2018. After having been air dried in a dark room, then oven dried for 1.5 h at 40 °C, they were stored in tightly closed plastic bags till the usage (November–December 2018). Before 1% (w/v) water extract preparation (24 h dark maceration at the lab temperature), leaves were crumbled into 0.5 cm particles. Macerates were paper-filtered and 100 ml of each were poured separately into a 25 cm Petri dish lined with 3 mm thick paper tissue and 3 replicates of 100 seeds of white



**Fig. 1** Dynamics of daily average air temperature ( $T_{Ave}$ ) and vapour pressure deficit ( $VPD_{Ave}$ ) as well as daily precipitation sum ( $P$ ) in the Mlyňany Arboretum from May to September 2018

mustard (*Sinapis alba* L. 'Maryna-C1'). Petri dishes were positioned into a cultivation chamber (Lovibond, Tintometer GmbH., Germany) and cultivated at 22 °C in the dark for 2 weeks. Thereafter, relative germination (RG) of white mustard seeds under leaf extracts was determined:

$$RG = (TG / CG) * 100(\%)$$

where: TG – germination (%) in treatment, CG – mean germination (%) in control.

This test was repeated twice.

## Physico-chemical parameters of the extracts

Leaf water extracts, applied in the allelopathic potential determination, were submitted to analysis of physico-chemical features – pH and electric conductivity (Jenway Enterprise 430, Jenway, UK), osmotic potential (refractometer PZO RR11, PZO, Poland) and concentrations of phenolic compounds (Table 1).

## Phenolics

Determination method of Nguyen and Niemeyer (2008) was applied. To 50  $\mu\text{L}$  aqueous extract, 450  $\mu\text{L}$  distilled water, 250  $\mu\text{L}$  Folin–Ciocalteu reagent and 1.25 ml 20% sodium carbonate were added and mixed together. The reaction mixture absorbance at 735 nm (Jasco-V630, Jasco Inc., Japan) was measured after 20 min lab incubation.

## Flavonoids

An aliquot of 0.4 mL water extract was added to 0.2 mL 10% (w/v) aluminium nitrate, 0.2 mL 1 M potassium acetate and 8 ml 80% ethanol. The absorbance of the reaction mixture at 415 nm (Jasco-V630 (Jasco Inc., Japan) was determined

**Table 1** Physico-chemical characteristics of 1% aqueous extracts (deionised water (control) pH of 6.79 and EC of  $0.70 \mu\text{S}\cdot\text{cm}^{-1}$ ) prepared from leaves of native and in Slovakia most frequent non-native maple (*Acer* sp.) species

Leaf extract	pH	EC ( $\text{mS}\cdot\text{cm}^{-1}$ )	OP (-MPa)	Phenolic acids ( $\text{mg GAE}\cdot\text{ml}^{-1}$ )	Flavonoids ( $\mu\text{g QE}\cdot\text{ml}^{-1}$ )	Tannins ( $\text{mg TAE}\cdot\text{ml}^{-1}$ )
<i>Native</i>						
CAM	5.27	4.7	0.018	0.83	34.7	0.37
PLA	5.29	47.4	0.007	0.74	66.9	0.45
PSE	5.59	49.8	0.015	1.12	110.7	0.51
TAT	4.64	32.8	0.022	1.44	71.8	0.96
<i>Non-native</i>						
NEG	4.18	61.9	0.015	0.36	64.6	0.07
PAL	4.20	6.9	0.015	0.21	51.2	0.06
SAC	4.60	3.6	0.029	2.29	86.3	1.56
<i>Reference</i>						
JUG	5.69	4.6	0.004	0.56	117.8	0.26

CAM field maple (*Acer campestre* L.), JUG black walnut (*Juglans nigra* L.), NEG box elder (*Acer negundo* L.), PAL palm maple (*Acer palmatum* Thunb.), PLA Norway maple (*Acer platanoides* L.), PSE sycamore maple (*Acer pseudoplatanus* L.), SAC silver maple (*Acer saccharinum* L.), TAT Tatarian maple (*Acer tataricum* L.), EC electric conductivity, OP osmotic potential, GAE gallic acid equivalent, QE quercetin equivalent, TAE tannic acid equivalent

after 40 min of incubation at the laboratory temperature (Park et al. 1997).

### Tannins

One millilitre of water extract was mixed with 5 mL of deionized water, 1 mL of 0.35% brown ammonium iron (III) citrate and 1 mL of 0.8% ammonia. Absorbance of the reaction mixture at 525 nm was measured (Jasco-V630 (Jasco Inc., Japan)) after 10 min of incubation at the laboratory temperature (ÚKZÚZ 2013).

### Statistical analysis

Results from the experimental field (parameters related to the growth intensity, fruit production and phenotypic plasticity) and lab experiment (allelopathic potential) are means  $\pm$  standard errors (SEs) of 6 replicates ( $n=6$ ) – individual trees or hundreds of maple species fruits and white mustard seeds. In the analysis of fruit morphological and aerodynamic traits, we applied 20 individual fruits as replicates. Data on the tree height, trunk diameter at 1 m height, number of fruits per tree, seed viability, fruit area, thickness, weight, load and flight range as well as specific leaf area and relative germination of white mustard seeds under maple leaf extracts were submitted to one-way ANOVA in the Statgraphics Plus v. 4.0 software environment. Comparison of means was performed using Duncan's multiple range test. The only one predictor was species. Different letters/asterisk indicate statistically significant difference between species at the confidence level of 95%, double asterisk – at the confidence level of 99% and triple asterisk – at the confidence level of 99.9%. Thereafter, Pearson's coefficients ( $r$ ), defining the linear

regression strength, were determined for the relationships between maple fruit flight range and other morphological traits of fruits and then between relative germination of the white mustard seeds and respective maple extracts traits. Here asterisk represents a strong relationship ( $0.5 \leq r < 0.7$ ), double asterisk – a very strong relationship ( $0.7 \leq r < 0.9$ ) and triple asterisk – an extremely strong relationship ( $0.9 \leq r < 1$ ).

### Results

Physical survey of non-invasive alien maple species in Slovak cities (Table 2) revealed plantations of *A. saccharinum* in most parks, in all residential areas from the socialistic era as well as some of those, which were recently built. Particularly *A. palmatum* individuals have been planted to many recent and older residential areas in the last decade. However, I saw almost exclusively this species in private gardens. Concentrations of individuals of these two species varied across cities without any relation to their climatic parameters and administrative importance – in *A. saccharinum* it ranged in interval  $0\text{--}3.215 \text{ ha}^{-1}$  for parks and  $0.130\text{--}1.569 \text{ ha}^{-1}$  for residential areas, in *A. palmatum*  $0\text{--}0.697 \text{ ha}^{-1}$  for residential areas and  $0.025\text{--}0.118$  individual per a private garden. Concerning the age composition, parks were dominated by 60–70 years old *A. saccharinum* individuals and residential areas by those of 30–50 years. However, this species appears in new plantations, as well. On the other hand, *A. palmatum* started to be massively planted only in the past decade, what completely reflects present market offer (Online Resource 3). In spite of greenery management, in cities with higher concentration of planted *A. saccharinum* individuals (Zlaté Moravce and Nitra), escaped trees were



**Table 2** Distribution of planted non-native non-invasive maple species in parks, residential areas and private gardens of Slovak cities, differing in the administrative importance and climatic characteristics (Bratislava, Nitra, Banská Bystrica, Galanta, Zlaté Moravce and Poprad), as well as those escaped from the culture

City	Locality	Analysed area/ private garden no.	Non-native non-invasive species	Planted plants per ha/garden with age estimation (yrs.)	Escaped plants per ha/ garden with age estimation (yrs.)
Bratislava CAPITAL $t_{ave} = 9.8\text{ }^{\circ}\text{C}$ $P_{sum} = 576\text{ mm}$	Janko Kráľ park	24.07 ha	SAC	0.166 (1-10, 60-70)	0
	RA - Petržalka	161.75 ha	SAC	0.130 (1-10, 30-40, 40-50)	0
			PAL	0.043 (1-10)	0
	RA - Slnčnice	9.47 ha	PAL	0.106 (1-10)	0
	PH - Kalvária	352	PAL	0.048 (1-10)	0
			SAC	0.003 (10-20)	0
Nitra REGIONAL CAPITAL $t_{ave} = 9.8\text{ }^{\circ}\text{C}$ $P_{sum} = 539\text{ mm}$	City park	20.80 ha	SAC	1.057 (60-70)	0
	RA - Klokočina	168.73 ha	SAC	0.676 (1-10, 10-20, 30-40, 40-50)	0.030 (1-10, 10-20)
			CIS	0.006 (10-20)	0
			GRO	0.006 (20-30)	0
			RUB	0.012 (1-10, 20-30)	0
	RA - Martinák	7.17 ha	SAC	0.697 (20-30)	0.139 (10-20)
		PAL	0.697 (20-30)	0	
PH - Čermáň	416	PAL	0.118 (1-10)	0	
Banská Bystrica REGIONAL CAPITAL $t_{ave} = 7.9\text{ }^{\circ}\text{C}$ $P_{sum} = 703\text{ mm}$	City park	8.20 ha	-	-	-
	RA - Fončorda		SAC	0.157 (30-40, 40-50)	0
		63.50 ha	PAL	0.016 (1-10)	0
PH - Radvaň	386	PAL	0.039 (1-10, 10-20)	0	
Galanta COUNTY TOWN $t_{ave} = 9.7\text{ }^{\circ}\text{C}$ $P_{sum} = 502\text{ mm}$	City park	4.44 ha	-	-	-
	RA	33.08 ha	SAC	0.242 (30-40)	0
	PH	436	PAL	0.037 (1-10, 20-30)	0
Zlaté Moravce COUNTY TOWN $t_{ave} = 9.5\text{ }^{\circ}\text{C}$ $P_{sum} = 574\text{ mm}$	City park	5.60 ha	SAC	3.215 (60-70)	0.842 (1-10)
	RA	33.77 ha	SAC	1.569 (30-40, 40-50)	0.030 (1-10)
	RA - Ďateliniská	0.79 ha	-	-	-
	PH	328	PAL	0.058 (1-10)	0
Poprad COUNTY TOWN $t_{ave} = 5.8\text{ }^{\circ}\text{C}$ $P_{sum} = 579\text{ mm}$	City park	1.94 ha	-	-	-
	RA – Juh 1	44.15 ha	SAC	0.612 (30-40, 40-50)	0
	PH - Veľká	512	PAL	0.025 (1-10)	0
			GIN	0.002 (10-20)	0

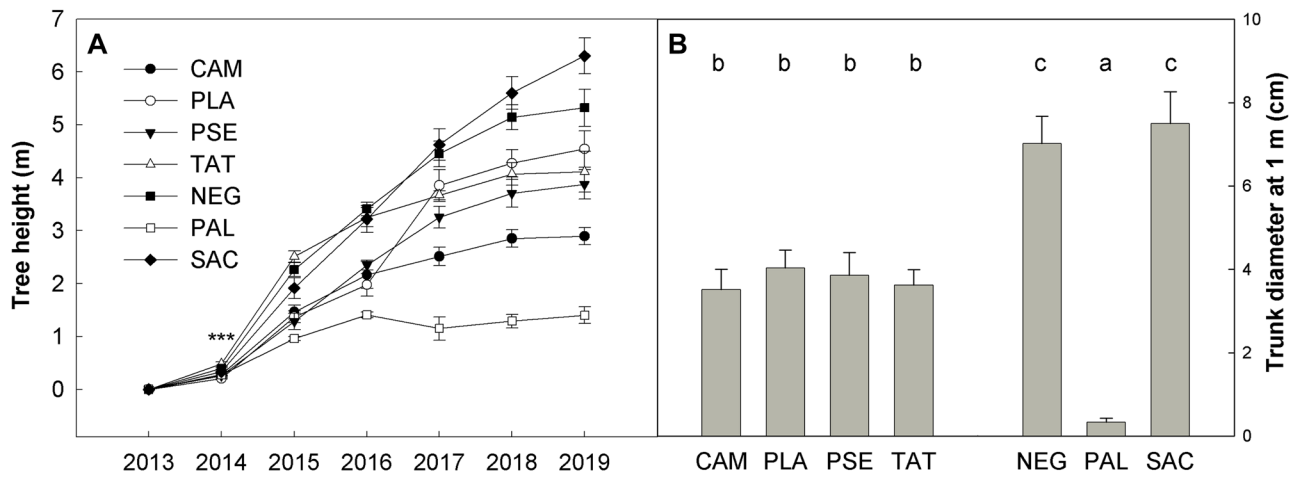
CIS vineleaf maple (*Acer cissifolium* Siebold et Zucc.), GRO Grosser's maple (*Acer davidii* var. *grosseri* Pax.), PAL palm maple (*Acer palmatum* Thunb.), RUB red maple (*Acer rubrum* L.), SAC silver maple (*Acer saccharinum* L.), PH private houses area, RA residential area

observed in abandoned areas and locations with limited access in/near the parks and residential areas (concentration of 0.030–0.842 ha<sup>-1</sup> and age of 1–20 years). Much more maple species have been cultivated in the collections of Slovak botanical gardens and arboreta as compared to city greeneries (Online Resource 1). However, only few *A. saccharinum* trees were found in some historical/spa gardens (Online Resource 2).

Maple species started to diverge in seedling height (Fig. 2A) just after first the cultivation year ( $P=0.000$ ). Comparison of initial phases of the sigmoidal growth dynamics (after six years of cultivation) in four native and

three most frequent non-native species in Slovakia revealed the fastest height growth in North-American *A. saccharinum* and *A. negundo*, exceeding 5–6 m in 2019 and a little slower for the native species with around 3–4.5 m. The slowest growth was registered in south-east Asian *A. palmatum* with the height of ca. 1 m. Much smaller statistical differences between species in these groups were observed for tree trunk diameter at 1 m (Fig. 2B). The North American maples showed diameters of ca. 7.5 cm, native species ca. 4 cm and the Asian one only ca. 0.5 cm.

Concerning the reproduction biology (Table 3), flowering stage of most of the studied species was dated to different



**Fig. 2** Growth parameters (tree height (A) and trunk diameter at 1.0 m height after sixth year of cultivation (B)) of native and in Slovakia most frequent non-native maple (*Acer* sp.) species, as recorder during the field experiment conducted in the Mlyňany Arboretum. Triple asterisk indicate statistical difference between species at the confidence level  $P \leq 0.001$  and different letters at the confidence level

$P \leq 0.05$ . CAM field maple (*Acer campestre* L.), NEG box elder (*Acer negundo* L.), PAL palm maple (*Acer palmatum* Thunb.), PLA Norway maple (*Acer platanoides* L.), PSE sycamore maple (*Acer pseudoplatanus* L.), SAC silver maple (*Acer saccharinum* L.), TAT Tatarian maple (*Acer tataricum* L.)

decades of April in 2018, only silver maple flowered earlier – in the half of March. Fruits of this species were ripe as soon as in early May. In the rest species, fruits ripened in following order: *A. tataricum* – from the end of July, other native species from the late August, *A. negundo* from the beginning of September and *A. palmatum* from the half of October. First fruiting in the *A. tataricum* and *A. negundo* seedlings was observed in the fourth year of cultivation and in those of *A. campestre*, *A. pseudoplatanus* and *A. saccharinum* in the sixth year after sowing. However, the remaining two species still did not switch from juvenile to adult phase of the life cycle. Despite of an extreme inter- and intraspecific variability of fruit production per tree (especially in

the firstly-fruiting species), statistical analysis derived only one group of results. Nevertheless, seed viability showed significant difference only between *A. campestre* with 18.9% in average and *A. negundo* with 64.4% in average.

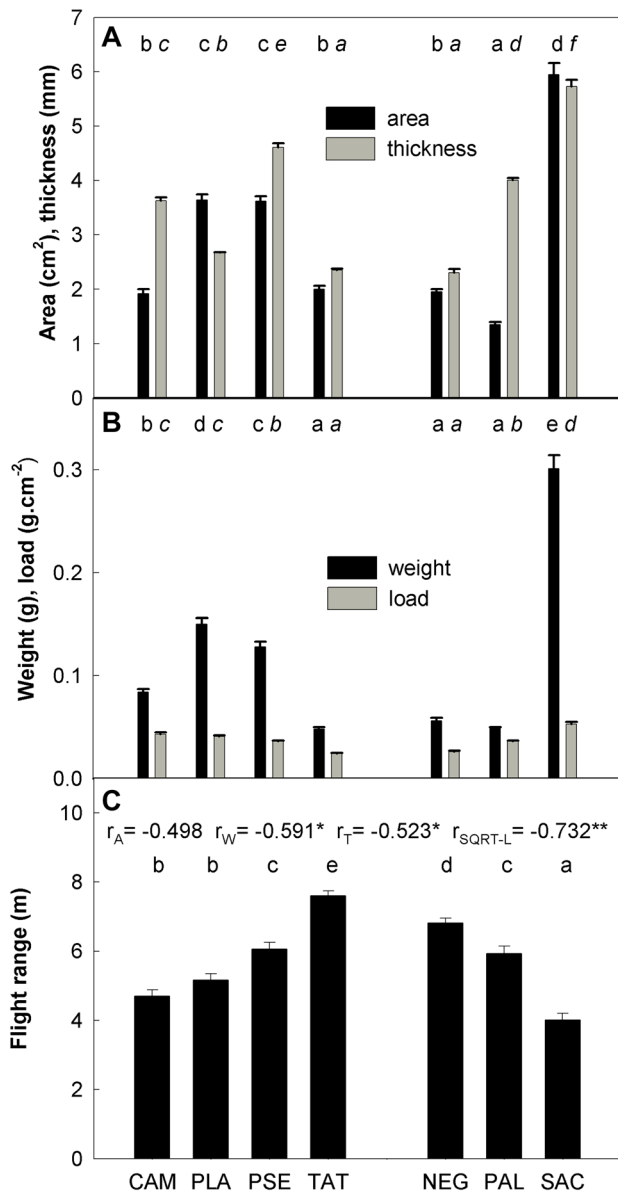
*Acer palmatum* fruits had the smallest area (near 1.5 cm<sup>2</sup>, Fig. 3A). Significantly higher one (approx. 2 cm<sup>2</sup>) was found in *A. campestre*, *A. tataricum* and *A. negundo*. Almost double area showed *A. platanoides* and *A. pseudoplatanus* fruits and those of *A. saccharinum* approached 6 cm<sup>2</sup>. Fruits of the latter species were the thickest (approx. 6 mm), as well. Significantly lower thickness was observed in *A. pseudoplatanus* fruits (almost 5 mm), then in *A. campestre* and *A. palmatum* with around 4 mm and lower in *A. platanoides*, *A. tataricum*

**Table 3** Phenological (adult individuals) and reproduction parameters (seedlings in the 6th year of cultivation) of native and in Slovakia most frequent non-native maple (*Acer* sp.) species cultivated in the Mlyňany Arboretum

Species	Flowering (BBCH 60-69)	Fruit ripening (BBCH 81-89)	First fruiting (yrs.)	Fruit no.	Seed viability (%)
<i>Native</i>					
CAM	Apr 18-23	Aug 24-Sep 24	6	177±170 a	18.9±4.5 a
PLA	Apr 11-16	Aug 24-Oct 10	-	-	-
PSE	Apr 20-May 2	Aug 24-Sep 12	6	54±50 a	43.8±18.8 ab
TAT	Apr 25-May 9	Jul 27-Aug 8	4	3770±471 a	59.3±12.1 ab
<i>Non-native</i>					
NEG	Apr 9-13	Sep 3-Oct 5	4	19363±9425 a	64.4±6.3 b
PAL	Apr 20-25	Oct 15-19	-	-	-
SAC	Mar 12-19	May 4-9	6	22±1 a	33.3±17.9 ab

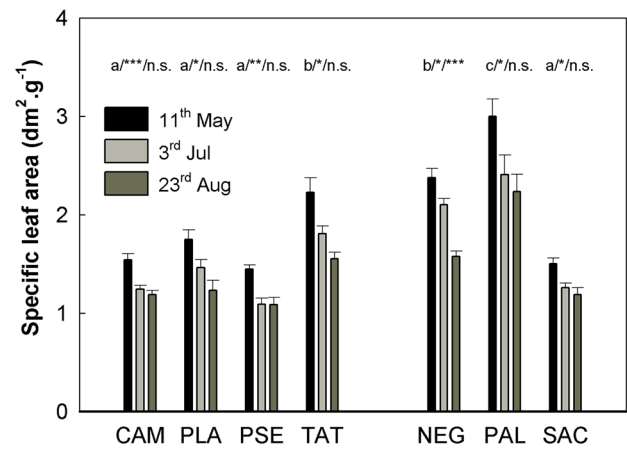
Letters indicate statistical difference between species at the confidence level  $P \leq 0.05$

CAM field maple (*Acer campestre* L.), NEG box elder (*Acer negundo* L.), PAL palm maple (*Acer palmatum* Thunb.), PLA Norway maple (*Acer platanoides* L.), PSE sycamore maple (*Acer pseudoplatanus* L.), SAC silver maple (*Acer saccharinum* L.), TAT Tatarian maple (*Acer tataricum* L.)



**Fig. 3** Morphological (area and thickness (A), weight and load (B)) and aerodynamic (flight range, C) features of fruits of native and in Slovakia most frequent non-native maple (*Acer* sp.) species with Pearson's coefficients of linear regressions (r) between flight range and respective morphological traits of fruits (indexed as follows: A – area, T – thickness, W – weight and SQRT-L – square root of the load). Letters indicate statistical difference between species at the confidence level  $P \leq 0.05$  (regular – first parameter, italic – second parameter), asterisk a strong ( $0.5 \leq r < 0.7$ ) and double asterisk a very strong ( $0.7 \leq r < 0.9$ ) linear relation. CAM field maple (*Acer campestre* L.), NEG box elder (*Acer negundo* L.), PAL palm maple (*Acer palmatum* Thunb.), PLA Norway maple (*Acer platanoides* L.), PSE sycamore maple (*Acer pseudoplatanus* L.), SAC silver maple (*Acer saccharinum* L.), TAT Tatarian maple (*Acer tataricum* L.)

and *A. negundo* with approx. 2.5 mm. The heaviest fruits were found again in *A. saccharinum* (around 0.3 g, Fig. 3B), half heavy ones in *A. platanoides* and slightly lower weights in *A.*



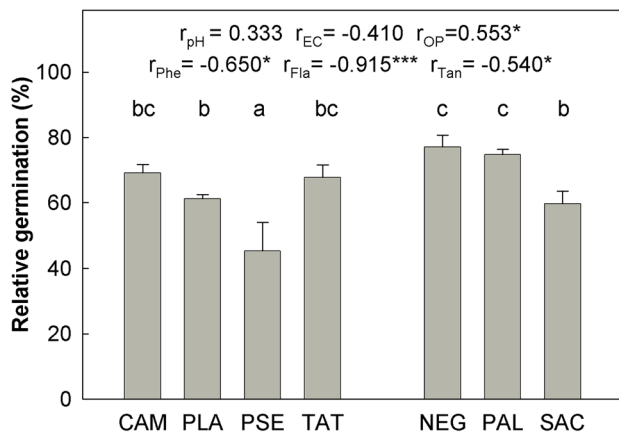
**Fig. 4** Phenotypic plasticity of four native and three most frequently planted non-native maple species as analysed by means of specific leaf area dynamics in the top expanded leaf during the sixth cultivation season in the field. Letters indicate statistical difference between species at the confidence level  $P \leq 0.05$ , asterisk – difference between measurement terms at the same confidence level, double asterisk – at the confidence level  $P \leq 0.01$  and triple asterisk – at the confidence level  $P \leq 0.001$ . CAM field maple (*Acer campestre* L.), NEG box elder (*Acer negundo* L.), PAL palm maple (*Acer palmatum* Thunb.), PLA Norway maple (*Acer platanoides* L.), PSE sycamore maple (*Acer pseudoplatanus* L.), SAC silver maple (*Acer saccharinum* L.), TAT Tatarian maple (*Acer tataricum* L.)

*pseudoplatanus*. Weight of *A. campestre* fruits neared to 0.1 g and the rest species had fruits of approx. 0.05 g. *Acer tataricum* and *A. negundo* showed the least loaded fruits (approx. 0.025 g.cm<sup>-2</sup>), in *A. pseudoplatanus* and *A. palmatum* the fruit load was 0.01 g.cm<sup>-2</sup>, in *A. campestre* and *A. platanoides* 0.017 g.cm<sup>-2</sup> and in *A. saccharinum* twice larger. However, flight range of *A. saccharinum* fruits was only 4 m (Fig. 3C) as compared to *A. campestre* and *A. platanoides* with values of around 5 m, *A. pseudoplatanus* and *A. palmatum* fruits of near 6 m, *A. negundo* ones of about 7 m and those of *A. tataricum* reaching 7.5 m. This parameter was most strongly correlated with square rooted fruit load ( $r = -0.732$ ). Moreover, an additional experiment in *A. saccharinum* seedlings revealed more than 40% establishment and 10% survival of the summer drought (Online Resource 4).

Concerning the specific leaf area (SLA), species acclimated to the rising air temperature and vapour pressure deficit (Fig. 1) to different extents. *Acer palmatum* showed the highest values on 11th May (3 dm<sup>2</sup>.g<sup>-1</sup>, Fig. 4). In *A. tataricum* and *A. negundo* we found ca. 0.7 dm<sup>2</sup>.g<sup>-1</sup> lower SLA and in the rest species it ranged from 1.5 to 1.75 dm<sup>2</sup>.g<sup>-1</sup>. Beginning July, species reduced SLA by approx. 20%, but 12% and 25% decrease was observed in *A. negundo* and *A. pseudoplatanus*, respectively. The only one species further reducing SLA (on 23rd August) was the *A. negundo*.

The largest allelopathic potential was observed in *A. pseudoplatanus*, extract from which lowered relative germination





**Fig. 5** Relative germination (RG) of white mustard (*Sinapis alba* L. Maryna-C1) seeds under 1% aqueous extracts from leaves of native and in Slovakia most frequent non-native maple (*Acer* sp.) species (distilled water represented control with RG of 100%, black walnut (*Juglans nigra* L.) leaf extract with average RG of 55.8% was the reference) with Pearson's coefficients of linear regressions ( $r$ ) between RG and respective physico-chemical features of extracts (indexed as follows: EC – electric conductivity, OP – osmotic potential, Phe – phenolics, Fla – flavonoids, Tan – tannins). Letters indicate statistical difference between species at the confidence level  $P \leq 0.05$ , asterisk – strong linear regression ( $0.5 \leq r < 0.7$ ), triple asterisk – extremely strong linear relation ( $0.9 \leq r < 1$ ). CAM field maple (*Acer campestre* L.), NEG box elder (*Acer negundo* L.), PAL palm maple (*Acer palmatum* Thunb.), PLA Norway maple (*Acer platanoides* L.), PSE sycamore maple (*Acer pseudoplatanus* L.), SAC silver maple (*Acer saccharinum* L.), TAT Tatarian maple (*Acer tataricum* L.)

(RG) of white mustard seeds by 55% (10% more than in reference black walnut, Fig. 5). Significantly lower effect showed extracts from *A. platanoides* and *A. saccharinum* (RG of ca. 60%) and the lowest one was recorded for extracts from *A. negundo* and *A. palmatum* (RG of ca. 75%). Their effect was extremely strongly related to the total flavonoids concentration ( $r = -0.915$ ) and strongly related to extract osmotic potential ( $r = 0.553$ ), concentrations of total phenolics ( $r = -0.650$ ) and tannins ( $r = -0.540$ ).

## Discussion

My field research carried out in Slovak cities points to the dominance of silver maple (*Acer saccharinum* L.) in city parks and residential areas from the socialistic era as well as in those from nineties of the past century (Table 2). Furthermore, as found in Bratislava and Nitra, silver maple has still been planted in parks and older residential areas. This is in accordance with defined principles of urban greenery formation from those times (Supuka et al. 1991; Reháčková and Pauditšová 2006). On the other hand, palm maple (*A. palmatum* Thunb.) was the most frequent maple species of private gardens. Nevertheless, in spite of common greenery

management, escaped seedlings only of silver maple were observed only in cities with warmer climate (in abandoned areas or those with restricted access), but no individual was found in neighbouring sub-urban or rural habitats. Since such a spreading is common for the non-analysed invasive box elder (*A. negundo* L.), my survey implied a movement towards the local naturalisation in silver maple and the need to take the palm maple into consideration (as casual) in the alien flora (for comparison see Medvecká et al. 2012). From the surrounding countries, silver maple has not been under consideration in Austria, Hungary and Romania recently (Walter et al. 2005; Borza et al. 2020, Sîrbu and Oprea 2011). It has been casual in the Czech Republic (Pyšek et al. 2012) and Ukraine (Burda and Koniakin 2019) and ranked as locally naturalised in Poland (Tokarska-Guzik et al. 2012). On the other hand, box elder is invasive in countries located more to the north (Austria, Czech Republic, Poland and Ukraine) and naturalised in Hungary and Romania, but palm maple has not been under consideration in any of these countries yet.

My field work brought also implications on species planting density/propagule pressure and age structure/planting history. Frequencies of silver maple individuals exceeding 1 tree per hectare were common in Slovak city parks and older residential areas, and age categories of 60–70 years and 40–50 years, respectively, predominated there. Furthermore, a palm maple tree was planted in every ninth to fortieth private garden and this planting boom might have started ten years ago. According to the recent work of Pyšek et al. (2009), probability of escape from culture among woody plant species increased with their residence time in the Czech Republic, whereas probability of naturalisation increased with their residence time in Europe. Frequency of escapes grew also with the planting density (propagule pressure) of a species, and naturalisation success depended on the species origin and fruit size (lower for Asian species and those with small fruits). Taking into account introduction to Europe and Slovakia (box elder – 1688 and 1794, silver maple – 1725 and 1820, palm maple – first half of the nineteenth century and beginning of the twentieth century; Benčať 1982), planting density and origin (North American box elder and silver maple, Asian palm maple) of the three most frequent non-native maple species, my results fit with these findings. Křivánek and Pyšek (2008), evaluating alien woody plant species in respect of their ecological status, calculated mean length of the lag phase (here time between first introduction and first record of escape from cultivation) for trees (116 years) and North-American woody plants (89 years). In the Slovak case, the lag period in silver maple was much longer.

Nevertheless, how does the invasive box elder differ from the other common non-invasive alien and native maple species in respect of growth, reproduction biology,

fruit dispersal, phenotypic plasticity and allelochemical potential? Concerning growth intensity, silver maple slightly exceeded box elder but palm maple was the slowest growing species from the maple collection (the native maple species were intermediate; Fig. 2). Marosz and Nowak (2008) referred to almost one half larger annual stem increment in two years old Norway maple (*A. platanoides* L.) seedlings compared to the box elder. Similar work of Marosz (2009) revealed following seedling heights in maple species at the end of another experiment: Sycamore maple (*A. pseudoplatanus* L.) – 5.16 cm, Norway maple – 6.97 cm, field maple – 8.38 cm and Amur maple (*A. tataricum* ssp. *ginnala* Maxim.) – 31.3 cm. Furthermore, box elder growing out of its native range (Caucasus foothills) vs. native field maple (*A. campestre* L.), as analysed for species biology, showed markedly larger increments (Ednich et al. 2015).

Compared to other species, phenology of silver maple was markedly forwarded (Table 3), providing almost one-month longer season. On the other hand, it switched to the reproductive phase 2 year later and produced two orders of magnitude less fruits with a half germination level in the fruitful year 2018 than the box elder. Moreover, low loaded fruits of box elder flew almost twofold farther than those of silver maple (Fig. 3). Silver maple seed predation was one order of magnitude larger in relatively quiet stand of the Mlyňany Arboretum as compared to the urban locations with much more frequent animal disturbance. Hence, less than half of them could establish seedlings, from which only a quarter survived the summer drought period (Online Resource 4). On the other hand, palm maple seedlings were still not fruitful (Table 3), and the best reproduction biology parameters from the native species were shown in Tatar maple (earliness, high fruit production and viability, flying range).

The Caucasian population of box elder was assigned to species with early vegetation commencement and completion (Ednich et al. 2015). As described in work of Matlack (1987), samara weight of box elder, palm maple as well as Norway maple and Sycamore maple from north-eastern USA were approximately of 34, 42, 134 and 89 mg, respectively – significantly lower than those from Mlyňany Arboretum (Fig. 3). However, diaspore area exceeded my observations only in the European species. As one of few authors, he also considered distance of the fruit lateral movement (flight) in a 10 km.h<sup>-1</sup> breeze. Estimated values for investigated maple species levelled at 41.1, 11.6, 50.3 and 60.1 m, respectively, thus showed completely different species order compared to my results. Average weight of six different silver maple fruit morpho-types levelled at 130.6 mg, fruit area was of 52 mm<sup>2</sup> and wing loading of 3.29 mg.mm<sup>2</sup> (Sipe and Linnerooth 1995) – again much lower values than I obtained. This knowledge corresponds with the results of Carón et al. (2014), showing larger seed mass and viability

in Norway maple and Sycamore maple from the latitudinal gradient in Europe, when identified as non-native to distinct locations. Square root of the wing loading is commonly related to fruit descent rate (Matlack 1987; Sipe and Linnerooth 1995) but in my maple species selection it was strongly correlated to the flight range (Fig. 3). Sound seeds of Japanese maple (*Acer palmatum* var. *matsumurae* Koidz.) dispersed to mean distance of 41.5 m in a conifer-hardwood mixed forest in Japan (Wada and Ribbens 1997).

Considering phenotypic plasticity, as defined by the specific leaf area (SLA) seasonal dynamics (Fig. 4), box elder, Tatar maple and Norway maple showed the largest differences (decrease) towards the summer period. Similar shift of SLA was observed in box elder populations secondary invading dry habitats in Halle region, Germany (Erfmeier et al. 2011). However, native populations of field maple as well as Norway maple and Sycamore maple was confirmed as also having large leaf morphological plasticity in respect of light supply gradient (Granata et al. 2020; Dyderski and Jagodziński 2019).

As presented in Fig. 5, native maple species had stronger negative allelopathic effect on mustard germination than the non-native ones, and silver maple was the best suppressor from the latter group. Just a few works deal with this aspect of the population establishment prerequisite in studied maple species. Yeryomenko (2014) analysed the dose-dependent suppressive effect of box elder leaf-litter extracts as well as rhizosphere elutes on cress and radish seed germination. Allelopathy of Norway maple in its new (North-American) range was studied by Rich (2004). In the paper of Fleshman (2015), palm maple was considered as not having a significant allelopathic effect on soybean and maize.

All the above described species characteristics refer to mechanisms associated with a concrete invasion hypothesis. Hence, we could directly evaluate validity of the ‘ideal weed hypothesis’ associated with the ‘nitrogen allocation hypothesis’, ‘limiting similarity hypothesis’, ‘novel weapon hypothesis’, ‘phenotypic plasticity hypothesis’ and ‘propagule pressure hypothesis’ (Dai et al. 2020). Rapid growth, phylogenetic distance from the native species (Li et al. 2019), large phenotypic plasticity and massive fecundity with effective propagule dispersal in the invasive box elder point to importance of all these hypotheses except for the ‘novel weapon one’ in its invasion success in the Central Europe. However, this hypothesis might play a specific role during the naturalisation process in silver maple (much lower fruit production and dispersal as well as phenotypic plasticity will probably hinder its proceeding to invasive behaviour). This knowledge is in line with a meta-analysis published by Lamarque et al. (2011) recognising several hypotheses simultaneously explaining tree invasions. Furthermore, my observations and recent literature sources revealed no regulatory pest of silver maple and palm maple in the Central

Europe but recorded a powdery mildew (*Sawadaea bicornis* (Wallr.) Homma) affecting performance of the invasive box elder (Mieslerová et al. 2020). Thus, from hypotheses related to species resistance to pests and diseases (‘biotic resistance hypothesis’, ‘enemy release hypothesis’, ‘evolution of increased competitive ability hypothesis’, ‘pathogen accumulation hypothesis’ and ‘shifting defense hypothesis’) the ‘pathogen accumulation hypothesis’ seems to be involved in the box elder invasion success.

Invasive box elder populations have usually been studied from the point of view of growth and phenotypic plasticity. As found out by Saccone et al. (2010ab), fast growth and large shade tolerance stood behind the box elder success in the European floodplain forests. Lamarque et al. (2012) showed, that introduced box elder population was denser than the native one, but those of Norway maple stayed similarly dense. Furthermore, in a study of Porté et al. (2011), besides the fast growth, box elder displayed comparable photosynthetic capacity and nitrogen allocation as co-occurring native species in riparian forests and they were conservative along the light, nutrition and disturbance gradient. However, in non-limiting light and nutrient conditions, total leaf area and SLA was substantially larger for box elder (advantageous plastic reaction).

As presented by Reinhart and Callaway (2004), invasion of box elder and Norway maple in their non-native ranges was enhanced not only by absenting natural enemies but also by soil biota associated with dominant native species, but its effect became more inhibitory as these maples had established. This supports the ‘enhanced mutualism hypothesis’ importance for their invasion success. Finally, no polyploidisation and/or hybridisation process has been reported to date in invasive maple species (‘new adaptation hypothesis’). On the other hand, Lamarque et al. (2015) identified lower genetic differentiation in an invasive box elder population located in France compared to a native Canadian one but it was not reduced in an invasive Norway maple population in Canada.

Urban environments provide important support for alien taxa establishment through repeated species introduction, reduction of natural competitors and resource supply (nutrition, water, pH), then through their long-distance spread along transport corridors (air/water fluxes) as well as fragmentation and diversification of habitats with distinct level of disturbance, which help them to spread farther (Potgieter and Cadotte 2020). As a result, non-indigenous floristic hotspots appear in large human agglomeration, like Durban in South Africa, where they were associated with level of disturbance, distance of informal settlements and soil moisture (Appalasyam et al. 2020). However, high level of disturbance can also act as a barrier for species establishment. This is also the case of managed urban areas, enabling establishment of trees only in abandoned areas/spots or those

with limited access for management, as was observed by me. Since most of plant invasions starts in human agglomerations with concentrated alien flora, the above mentioned ‘urban effect’ can partly overlap with the ‘invasion meltdown hypothesis’ and ‘species richness hypothesis’ (Dai et al. 2020). The rest of hypotheses concerning the ecosystem invasibility, namely ‘disturbance hypothesis’, ‘empty niche hypothesis’ and ‘fluctuating resource hypothesis’, needed to be also involved, when the box elder expanded from urban to rural areas and reached semi-natural and natural ecosystems (MacDougall et al. 2009). Saccone et al. (2010b) concluded that direct facilitation of the box elder colonisation of riparian habitats along Rhone, France was very likely the biotic process provided by native pioneer *Salix* and that indirect facilitation by adult conspecifics contributed to population establishment.

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## Declarations

**Competing interests** The author has no financial or non-financial interests to be disclosed.

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