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Genetic differentiation and phenotypic plasticity in life-history traits between native and introduced populations of invasive maple trees

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Abstract Genetically based phenotypic differentiation between native and invasive populations of exotic plants has been increasingly documented and commonly invoked to explain the success of some invasive species. Nonetheless, this basic information is lacking for invasive trees although they currently represent a major concern worldwide. Reciprocal common gardens were therefore set up in both native and introduced ranges of two exotic maple trees to assess the contribution of genetic differentiation and phenotypic plasticity to tree invasiveness. Almost 3,000 native and invasive seedlings of *Acer negundo* and *Acer platanoides* were planted in Canada and in France and their performances were compared in various life-history traits related to growth, leaf phenology and ecophysiology over 2 and 3 year periods. Invasive populations of *A. negundo* exhibited strong genetic differentiation in all the traits examined. Compared to their native conspecifics, they grew significantly larger in the introduced range and showed lower survival, reduced maximum assimilation rate and increased leaf area in the two gardens. They also expressed greater plasticity for growth and greater phenological sensitivity to temperature. Native and invasive populations of *A. platanoides* were plastic across environments but in contrast did not exhibit any genetic differentiation. This cross-continental comparison provides evidence that both genetic differentiation and phenotypic plasticity contribute synergistically to tree invasiveness. The influence of these respective processes depends on stage of invasion and the life-history strategy of each species. Plastic effects are likely more important during colonization and establishment whilst genetic effects may contribute more significantly during the spread of established populations.

Keywords *Acer negundo* · *Acer platanoides* · Tree invasion · Genetic differentiation · Phenotypic plasticity · Reciprocal common gardens

Introduction

A common line of investigations in invasion ecology has often been the search for specific functional traits promoting plant invasiveness (Hawkes 2007; Küster

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et al. 2008; van Kleunen et al. 2010). Numerous studies have shown that invasive species generally exhibit greater growth rate, higher maximum assimilation rate, higher leaf area allocation and higher phenological sensitivity to changing environments than native species of recipient communities (Grotkopp et al. 2002; Nagel and Griffin 2004; Godoy et al. 2009; Lamarque et al. 2011; Wolkovich and Cleland 2011). However, biological invasions also provide a tremendous opportunity to study evolutionary responses of species in response to spatio-temporal environmental changes (Maron et al. 2007; Urbanski et al. 2012). Because exotic species have to cope with new conditions before being able to spread throughout their introduced ranges (Allendorf and Lundquist 2003), adaptive genetic changes following genetic drift, hybridization between species or disparate source populations and novel selection pressures are expected to play a major role in plant invasions (Ellstrand and Schierenbeck 2000; Lee 2002). Selection can for example improve competitive ability in response to lower levels of abiotic stress and release from natural enemies (Alpert et al. 2000; Blossey and Nötzold 1995).

Any functional trait that is beneficial under novel environmental conditions is subjected to evolutionary processes (Bossdorf et al. 2005). Although this is not a general feature for all invaders (Franks et al. 2008a; Cripps et al. 2009; Andonian and Hierro 2011), many intraspecific comparisons have shown that, relative to their native conspecifics, invasive populations of exotic species exhibit genetic differentiation in a variety of traits related to flowering (Güsewell et al. 2006; Hodgins and Rieseberg 2011), reproduction (Ridley and Ellstrand 2009), dispersal ability (Cheptou et al. 2008), defense (Maron et al. 2004a; Rapo et al. 2010), growth (Blumenthal and Hufbauer 2007; Siemann and Rogers 2001; Hodgins and Rieseberg 2011) and ecophysiology (Buswell et al. 2011; Feng et al. 2011).

All the studies that have quantified genetically based phenotypic differences between native and invasive populations of exotic species have used the classical common garden approach (Connor and Hartl 2004; Vitasse et al. 2009a). Nonetheless, a challenge in analysing the results of these experiments is that most of them utilized only one common environment wherein genotype by environment interactions cannot be detected with this design. This leads to problems in interpretation when there are interactions between natural populations (Williams et al. 2008; Flory et al. 2011b). Quantitative genetic studies must be conducted across multiple common gardens. While this has been done within native or invasive ranges of exotic species to test for the latitudinal and altitudinal effects of climate (Rice and Mack 1991; Maron et al. 2007; Alexander 2010; Ebeling et al. 2011; Monty et al. 2013), reciprocal common garden experiments in both native and introduced ranges are still infrequent and have only been applied to herbaceous plants so far (Genton et al. 2005; Maron et al. 2004a, b, 2007; Williams et al. 2008; Hierro et al. 2013). This clearly slows down our understanding of the contribution of genetic changes to plant invasiveness.

The use of reciprocal common gardens also provides the capacity to estimate the magnitude of phenotypic plasticity, which is another mechanism often involved in plant invasions by allowing organisms to express advantageous phenotypes in wide range of environments (Richards et al. 2006). Several studies have shown that invasive species express greater phenotypic plasticity in various functional traits and also increased fitness relative to native species of the recipient plant communities (Sexton et al. 2002; Burns and Winn 2006; Zhao et al. 2010; Porté et al. 2011; but see Davidson et al. 2011). Intraspecific comparisons have however produced mixed results and there is no evidence to date that invasive populations evolve greater plasticity compared to their native conspecifics (Lamarque et al. 2013). A conclusion is even more difficult to draw for tree invasions because, with the exception of *Triadica sebifera* and *Melaleuca quinquenervia* (Kaufman and Smouse 2001; Zou et al. 2009), the genetic variation for plasticity between native and invasive tree populations has not been studied.

This study aimed at simultaneously assessing the influence of genetic differentiation and phenotypic plasticity on the success of invasive tree species. Although invasive trees have become a major concern around the world, processes contributing to their success are still relatively understudied (Delmas et al. 2011). Their long life cycles have for instance prevented scientists from easily identifying phenotypic trait differences between native and invasive populations through common garden experiments. Adaptive evolution processes that might have occurred among introduced populations of invasive trees have to date been studied only in *Triadica sebifera* L. (Siemann and Rogers 2001, 2003; Zou et al. 2007; Huang et al. 2010) and *Melaleuca quinquenervia* Cav (Blake) (Franks et al. 2008a, b; Franks et al. 2012). However, all of these experiments relied on a single common garden. The originality of our approach relied on the use of the reciprocal common garden methodology in the native and introduced ranges of exotic trees. It therefore provides novel insights to tree invasion biology by being the first to simultaneously assess the contribution of phenotypic plasticity and genetic differentiation to tree invasiveness. We specifically focused on *Acer negundo* and *Acer platanoides*, two aggressive invaders of deciduous forests in Europe and North America, respectively. We hypothesized that populations from native and introduced origins would be plastic across gardens, but more importantly, that they would express genetic differentiation in each garden. Relative to native conspecifics, invasive populations (1) would grow faster thanks to more advanced leaf phenology, higher photosynthetic rate and greater leaf area, and (2) would express greater plasticity for these traits across gardens. Genetic differences observed between population origins for each species would indicate that evolutionary changes could have favoured invasiveness of *A. negundo* and *A. platanoides* in their respective introduced range.

Methods

Study species

Acer negundo L. (Boxelder or Manitoba maple) is a deciduous early to mid-successionnal tree species native to North America, with a wide distribution extending from southern Alberta and central Manitoba to north-eastern Texas and New Jersey (Mędrzycki 2007). Mainly confined within flood-plains and riparian systems, it can also occur in dry coniferous forests, oak savannas and grasslands (Ward et al. 2002; DeWine and Cooper 2008). Fast growing but generally not exceeding 60 years of age (Maeglin and Ohmann 1973), the species is dioecious and protandrous with both wind dispersed pollen and seeds (Erfmeier et al. 2011). Intentionally introduced in Europe at the end of the seventeenth century (first known date is 1688 in England) to be later used as an ornamental tree species (Kowarik 2003), *A. negundo* is currently considered as invasive throughout southern, central and eastern Europe where it mostly occurs in riparian habitats characterized by high rate of flood disturbance and high soil nutrient level (Porté et al. 2011; Lamarque et al. 2012). However, it has also widely spread to form monospecific stands under drier conditions faraway from rivers, for instance along roadsides, industrial wastelands or dry ruderal sites (Erfmeier et al. 2011).

Acer platanoides L. (Norway maple) is the most widespread native maple in Europe, with a distribution range occurring from southern Scandinavia to northern Spain and northern Greece southward and to the Ural Mountains eastward and extending until Asia Minor and northern Iran (Santamour and McArdle 1982). The species is shade tolerant and generally found in mixed forests in lowlands, wide river valleys and low mountain areas (Nowak and Rowntree 1990). It is monoecious with insect pollination and wind dispersal of seeds (Rusanen et al. 2003; Renner et al. 2007). Introduced in the United States in 1756 and in Canada in 1778, it has commonly been planted during the latter half of the twentieth century as an ornamental shade tree (Nowak and Rowntree 1990; Wangen and Webster 2006). Tolerating a wide range of conditions (Lapointe and Brisson 2011), it has spread into urban woodlands and intact forests of northeastern North America as well as montane forests of the northern Rocky Mountains where it impacts under- and over-storey biodiversity and macro-invertebrate communities (Webb and Kaunzinger 1993; Bertin et al. 2005; Reinhart et al. 2005; Reinhart and VandeVoort 2006). Although *A. platanoides* has mean seed dispersal distances comparable to the native shade tolerant species suggesting that its proliferation in closed-canopied forests might be partially dispersal-limited, it exhibits greater fecundity and seed production and therefore can aggressively invade forest understories (Martin and Canham 2010). *A. platanoides* is currently considered as one of the most common exotic invasive tree species in North America (Fang 2005; Martin et al. 2010).

Common garden experiment

Two common gardens were established in Canada (Koffler Scientific Reserve at Joker's Hill, King City, ON; 44.03′N, 79.29′W) and in France (INRA Pierroton research station, Cestas, Gironde; 44°44′N, 0°46′W) (see Table 1 for climate and soil characteristics). Each

Table 1 Climate and soil characteristics in common gardens established in Canada (King City, Ontario) and France (Cestas, Gironde)

	Canada	France
Mean annual rainfall (mm)	853.8	830.5
Mean annual temperature (°C)	8.1	12.7
Mean January high temperature (°C)	−1.8	10.5
Mean January low temperature (°C)	−10.3	2.0
Mean July high temperature (°C)	27.2	26.7
Mean July low temperature (°C)	15.5	13.2
Type of soil	Clay	Sandy
Soil nitrogen (%)	0.18 ± 0.03	0.08 ± 0.01
Soil carbon (%)	3.02 ± 0.49	2.13 ± 0.16
Soil carbon/nitrogen ratio	16.95 ± 0.68	25.57 ± 2.88
Soil pH	7.46 ± 0.09	4.22 ± 0.21

King City climate data from the Canada's National Climate Archive (climate normals 1996–2011 from Toronto Buttonville Airport station, ON); Cestas climate data from the French National Weather Service (climate averages 1996–2011 from the INRA research station, Gironde)

garden was located both in the native range of one maple tree species and in the introduced range of the other. Seeds were collected during the fall 2006 from ten native (Canada) and ten invasive (France) populations of *Acer negundo* and from ten native (France) populations of *Acer platanoides* whilst collection was possible in only six invasive (Canada) populations of *Acer platanoides* due to a low masting year for that species in that region (see "Appendix 1"). For each species, populations were haphazardly selected among a pool of 40 populations naturally occurring in France and Ontario, Canada. Seeds were harvested from 10 to 13 maternal trees in each source population for a total of 300 seeds per tree. Seeds from each maternal tree were placed into a string net with humid vermiculite in February 2007 and submitted to a cold treatment (14 weeks at 5 °C in a cold chamber) at the nursery of the INRA Pierroton research station, France. They were sown in spring 2007 into seedbeds with a 2/3:1/3 mix of compost and sand. A total of 25 seeds were sown per maternal tree, i.e. 250 seeds per source population. Seedlings were planted in the gardens in winter 2006. There was no difference in seed germination between populations but we selected seedlings of similar height to minimize the light effect at the seedbed edges by removing only the fast growing ones. Both common gardens had the same surface of 0.5 ha and the same design with 4 blocks of 6 rows. Seedlings were randomly assigned to one of the 4 blocks and represented 6–13 maternal trees per population. On average, a total of 40 seedlings were planted per population, leading to 365 individuals per block and 1,460 per garden (2 species × 2 continents × 6–10 populations × 40 seedlings). In each garden, seedlings were spaced 0.5 m apart with rows separated by 1 m. They were watered on the planting date in both gardens and received ambient rainfall hereafter.

Growth

In both gardens, height and stem collar diameter of each individual were measured every year from 2008 to 2010. Height measurements were carried out using a graduated pole to 0.01 m accuracy while stem collar diameters were measured using an electronic calliper to 0.01 mm accuracy. For all analyses, we used final height and stem diameter (2010) to minimize transplantation effect.

Leaf phenology

Timing of leaf unfolding (LU) was monitored in the two common gardens during two consecutive years (2009 and 2010). Each of the 1,460 seedlings was examined every week during a month (from mid-March and late-April in the France and Canada gardens, respectively) for bud development. We recorded the development stage of apical buds from bud dormancy to leaf unfolding using a four stage scale (Vitasse et al. 2009b). For each seedling, leaf unfolding was considered reached when one of the leaves was fully expanded (stage no. 4). Leaf unfolding date (day of the year, DOY) was then estimated by linear regression between two measurement campaigns. For each population, leaf unfolding date was calculated as the average of the estimated dates for each seedling (n = 25).

Ecophysiology

Gas exchanges

For both species, gas exchange and leaf morphology were measured in each garden on 6 native and 6 invasive populations with 7 individuals per population, leading to a total of 168 seedlings sampled per garden. Populations were randomly chosen in the France garden and the same were kept for measurements in Canada. Gas-exchange measurements were carried out using a portable steady-state, flow-through chamber [PLC6 (U) broad] connected to an infrared gas analyser (CIRAS-2, PP Systems, Hitchin, UK) equipped with CO_2, temperature, humidity and light control modules. Gas exchange was measured inside a sealed cuvette of 2.5 cm^2 with a CO_2 concentration of 380 ± 3 ppm, a temperature of 22 ± 0.5 °C and a relative humidity of 80 ± 10 %. All measurements were made at saturated light (PPFD = 1,500 $\mu mol\ m^{-2}\ s^{-1}$) in order to obtain a light-saturated assimilation rate per unit leaf area (A_{area}, $\mu mol\ CO_2\ m^{-2}\ s^{-1}$; maximum assimilation rate at ambient CO_2). Prior to each measurement campaign, the gas analyser was calibrated in the laboratory using 400 ppm standard gas, while full CO_2 and H_2O zero and differential calibrations were performed in the field after a set of six measurements. Photosynthesis rates were measured during summer 2009 for *A. negundo* and summer 2010 for *A. platanoides*. Both years, two to three consecutive weeks were required in each garden to complete the photosynthetic measurements due to the need of sunny days. In France and in Canada, measurements were always done between 8.00 and 11.00 solar time on fully expanded sunny leaves. Two to three measurements were carried out on each individual, and data were recorded when assimilation curves remained stable during more than 20 s (CIRAS-2 graphing screen).

Leaf morphology and biochemistry

After gas exchange measurements, three to five fully expanded leaves were collected per individual. Leaf area was determined using a planimeter (Light Box model, Gatehouse, Scientific Instruments LTD, Norfolk, UK). Leaves were then placed in an oven at 65 °C until constant dry weight and leaf dry mass was measured with an electronic weigh scale (Explorer Pro, EP 114 model, Ohaus Corporation, Pine Brook, NJ, USA). Leaf mass per area index (LMA, $g\ m^{-2}$) was calculated as the ratio of leaf weight by leaf area. Finally, leaf samples were also used to analyze leaf nitrogen content. Leaves were crushed to a powder with a ball mill (MM 200, Fisher Bioblock Scientific, France) and nitrogen content (N_{mass}, %) was analysed using an elemental analyser Eager 300 CHNOS (FlashEA 1112, ThermoElectron Corporation, Waltham, MA, USA). Nitrogen content per leaf area (N_{area}, $g\ N\ m^{-2}$) was calculated as the product of N_{mass} and LMA and the photosynthetic N-use efficiency (PNUE, $\mu mol\ CO_2\ g^{-1} N\ s^{-1}$) as the ratio of A_{area} by N_{area}.

Statistical analyses

Statistical analyses were conducted separately for each species. Probability of survival was compared between seedlings from native and invasive origins using a generalized linear model with binomial distribution and logit link function (procedure GENMOD in SAS, version 9.1, SAS Institute, Cary, NC, USA). Differences in seedling growth, phenology and ecophysiology were tested with a generalized linear mixed model (procedure MIXED, REML method in SAS, version 9.1, SAS Institute, Cary, NC, USA). We treated location of garden (France or Canada), population origin (native or introduced) and the location x origin interaction as fixed factors and block nested within location, population nested within origin and the location x population nested within origin interaction as random factors. Random effects were further assessed using a log likelihood ratio test from the full and reduced models (Littell et al. 2006). Differences in each trait were also analysed within each garden with origin as a fixed factor and block and population nested within origin as random factors. The effects of all factors were considered significant at $P < 0.05$ in the GLMMs. Genetic differentiation for a given trait between seedlings from native and invasive populations was indicated by a significant origin effect. Because each garden represented a distinct environment, phenotypic plasticity across gardens for a given trait was detectable when there was a significant location effect. Differences in the magnitude of plasticity between population origins were reported when location x origin interactions were significant. We also indicated the magnitude of plasticity for each origin as the percent increase in a given trait across gardens, which is the most immediate way of exploring plasticity (Valladares et al. 2006; Williams et al. 2008): $[(\text{trait}_{France} - \text{trait}_{Canada})/\text{trait}_{France}] * 100$. Lastly, phenological sensitivity to temperature of

Table 2 Mean values (± SE) of traits for seedlings from native and invasive populations of *Acer negundo* and *Acer platanoides* growing in two reciprocal common gardens

Traits	*Acer negundo*				*Acer platanoides*			
	Canada (native location)		France (invasive location)		Canada (invasive location)		France (native location)	
	Invasive	Native	Invasive	Native	Invasive	Native	Invasive	Native
Survival	73.2 ± 3.0	96.1 ± 1.0	63.0 ± 3.3	74.0 ± 2.4	51.2 ± 5.3	56.3 ± 3.2	70.1 ± 3.4	71.1 ± 3.5
Diameter	8.31 ± 0.10	8.36 ± 0.10	15.88 ± 0.50	12.78 ± 0.36	6.17 ± 0.15	6.22 ± 0.13	10.21 ± 0.37	10.29 ± 0.28
Height	43.53 ± 3.26	51.06 ± 1.10	79.35 ± 2.91	72.13 ± 2.50	16.61 ± 2.91	16.36 ± 1.93	44.05 ± 2.96	50.02 ± 2.58
LU 2009	125.62 ± 0.21	118.75 ± 0.24	86.51 ± 0.33	84.42 ± 0.33	125.76 ± 0.40	125.76 ± 0.34	89.98 ± 0.47	89.52 ± 0.40
LU 2010	118.00 ± 0.39	108.90 ± 0.29	88.72 ± 0.32	93.49 ± 0.28	120.51 ± 0.39	120.55 ± 0.37	102.47 ± 0.35	102.51 ± 0.34
A_{area}	4.19 ± 0.25	5.35 ± 0.34	7.16 ± 0.32	8.82 ± 0.31	6.15 ± 0.33	5.25 ± 0.25	6.97 ± 0.26	6.50 ± 0.26
N_{area}	0.90 ± 0.04	1.43 ± 0.06	1.24 ± 0.02	1.69 ± 0.05	0.94 ± 0.04	0.92 ± 0.04	1.65 ± 0.04	1.77 ± 0.05
PNUE	5.05 ± 0.44	4.06 ± 0.27	5.87 ± 0.24	5.44 ± 0.26	7.18 ± 0.56	5.91 ± 0.30	4.37 ± 0.19	3.79 ± 0.19
LMA	53.15 ± 1.72	70.19 ± 2.12	41.07 ± 0.85	52.68 ± 1.21	57.90 ± 0.95	61.18 ± 1.27	67.72 ± 1.05	72.03 ± 1.40

Traits were measured according to the following units: survival: %, diameter growth: mm, height growth: cm, LU (dates of leaf unfolding): day of the year, A_{area} (maximum assimilation rate per leaf area): μmol CO_2 m^{-2} s^{-1}, N_{area} (leaf N content per leaf area): gN m^{-2}, PNUE (photosynthetic N-use efficiency): μmol CO_2 $g^{-1}N$ s^{-1}, LMA (leaf mass per area index): g m^{-2}

native and invasive populations was further studied using a linear regression model between leaf unfolding dates and mean winter temperature values. In 2009 and 2010, mean winter temperatures were calculated from 1 January to leaf unfolding dates in both the Canadian and French gardens (Vitasse et al. 2009a). Slopes of linear regressions were used to test for shifts in leaf unfolding dates per degree increase in temperature (day degree^{-1}).

Results

Survival and growth

The survival rate of *A. negundo* seedlings significantly differed between population origins ($\chi^2 = 75.23$, $P < 0.0001$; Table 2; Fig. 1a). Those from native populations survived better than their invasive conspecifics both in Canada (96 % vs. 73 %; $\chi^2 = 74.77$, $P < 0.0001$) and in France (74 % vs. 63 %; $\chi^2 = 11.21$, $P = 0.0008$). No significant differences in survival were found between native and invasive populations of *A. platanoides* ($\chi^2 = 1.14$, $P = 0.2851$; Table 2; Fig. 1c). Survival rates differed between the two common gardens for both species. Seedlings of *A. negundo* survived better in Canada than in France (85 % vs. 68 %; $\chi^2 = 64.65$, $P < 0.0001$) while seedlings of *A. platanoides* survived better in France than in Canada (71 % vs. 54 %; $\chi^2 = 33.06$, $P < 0.0001$).

There was a significant difference in diameter growth between population origins of *A. negundo* (significant origins effect; Table 3a). Seedlings from invasive populations grew significantly larger than those from native ones in France while no difference was observed in Canada (Table 2; Fig. 1b; see “Appendix 2” for analyses within garden). No significant differences were observed in height growth between population origins of this species (Tables 2, 3a). Invasive *A. negundo* seedlings grew taller than native ones in the French garden but the difference was not significant due to high variation for this trait (CV > 58 %). Seedlings of *A. platanoides* from native and invasive populations exhibited similar diameters and heights in both gardens (Tables 2, 3b; Fig. 1d). Moreover, there were significant differences in growth across gardens with larger and taller native and invasive seedlings of both species in France relative

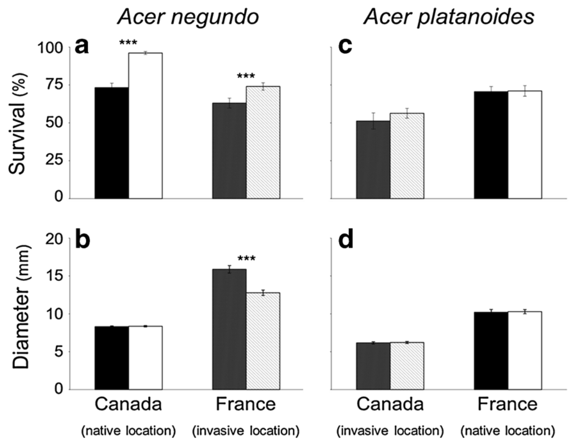

Fig. 1 Survival and diameter growth of seedlings from native (*white bars*) and invasive (*black bars*) populations of *A. negundo* (**a**, **b**) and *A. platanoides* (**c**, **d**) growing in reciprocal common gardens (Canada vs. France). The invasive origin of each species is represented with hatchings. Values represent mean ± SE for native and invasive population origins. ***$P < 0.001$

to Canada (significant location effects; Table 3). We found a difference in the magnitude of plasticity for diameter growth between population origins of *A. negundo* with native and invasive seedlings showing respectively a 35 versus 48 % increase in diameter between the Canadian and the French garden (significant location x origin effect; Table 3a; Fig. 2a). Native and invasive *A. negundo* populations had a 29 versus. 45 % increase in height between Canada and France but the location x origin interaction was not significant for that trait (Table 3a). Native and invasive seedlings of *A. platanoides* showed the same magnitude of plasticity for growth with a 40 and 65 % increase in diameter and height between Canada and France (Table 3b; Fig. 2d).

Leaf phenology

Leaf unfolding differed significantly between native and invasive *A. negundo* populations in the two locations (origin effect; Tables 2, 3a). Native seedlings unfolded significantly earlier in Canada while in France invasive seedlings unfolded significantly later in 2009 but earlier in 2010 (Fig. 3a, b). Seedlings of *A. platanoides* from native and invasive populations always unfolded at the same time in the two gardens (Tables 2, 3b; Fig. 3f, g). In addition, there were differences in dates of leaf unfolding between gardens for both species with mean leaf unfolding respectively occurring 40 and 27 days earlier in France than in Canada for *A. negundo* and *A. platanoides* seedlings (location effects; Tables 2, 3). The phenological plasticity varied significantly between *A. negundo* population origins (location x origin effects; Table 3a; Fig. 2b, c) and the magnitude of phenological sensitivity to temperature was slightly higher for invasive seedlings relative to their native conspecifics (3.24 ± 0.12 vs. 2.41 ± 0.45 days degree^{-1}; Table 4). Native and invasive *A. platanoides* seedlings did not differ in phenological plasticity and leaf unfolding advanced by 2.6 ± 0.5 days degree^{-1} for seedlings from both origins (Tables 3, 4; Fig. 2e, f).

Ecophysiology

We found significant genetic differentiation between native and invasive *A. negundo* populations in all ecophysiological traits we measured (origin effects; Table 3a). Seedlings from native populations expressed higher A_{area} and $\mathrm{N}_{\mathrm{area}}$ and greater LMA in the two gardens (Table 2; Fig. 3c–e). In contrast, native and invasive *A. platanoides* seedlings exhibited weak genetic differentiation with significant origin effects for PNUE and LMA that were driven by differences in the French garden only (Tables 2, 3b; Fig. 2h–j; see "Appendix 2"). Seedlings of both species were highly plastic across gardens for these traits but we did not observe any differences in the magnitude of plasticity between population origins (Table 3). Seedlings of *A. negundo* from both native and invasive populations had 40 % higher A_{area}, 21 % higher $\mathrm{N}_{\mathrm{area}}$, 19 % higher PNUE and 24 % lower LMA in the French garden compared to the Canadian garden (Table 2). Seedlings of *A. platanoides* increased their A_{area} by 16 %, $\mathrm{N}_{\mathrm{area}}$ by 45 % and LMA by 15 % in France relative to Canada while showing 37 % higher PNUE in the Canada garden (Table 2).

Discussion

This study successfully contrasted the contribution of phenotypic plasticity and genetic differentiation to invasiveness of two tree species with native and invaded origins using reciprocal common gardens. First, we found a significant genetic differentiation between native and introduced populations for most of the traits studied in *Acer negundo* but not in *Acer*

Table 3 Generalized linear mixed models (GLMM) analyses of life-history traits for seedlings from native and invasive populations of a) *Acer negundo* and b) *Acer platanoides* growing in two reciprocal common gardens

Source of variation	*df*	Diameter *F* or LLR	Height *F* or LLR	LU 2009 *F* or LLR	LU 2010 *F* or LLR	*df*	A_{area} *F* or LLR	N_{area} *F* or LLR	PNUE *F* or LLR	LMA *F* or LLR
a) *Acer negundo*										
Fixed effects										
Location	1	328.76***	16.32***	12,148.90***	4,376.48***	1	110.49***	41.42***	11.24**	76.61***
Origin	1	16.91***	0.01	174.13***	32.00***	1	18.95**	96.19***	3.90†	51.55***
Location x origin	1	24.26***	1.07	55.15***	427.75***	1	1.18	0.50	0.72	1.35
Random effects										
Population (origin)	18	5.90*	1.50	1.10	1.50	10	0	0	0	0.50
Location x population (origin)	18	1.90	0.90	1.50	0	10	0	0	0	0
b) *Acer platanoides*										
Fixed effects										
Location	1	89.88***	31.97***	5,586.78***	1,505.49***	1	8.05*	269.80***	61.30***	70.97***
Origin	1	0.03	0.34	0.07	0.01	1	4.01†	3.00	9.42**	7.27*
Location x origin	1	0.01	0.23	0.22	0.19	1	0.08	3.18	0.55	0.81
Random effects										
Population (origin)	14	4.20	0.30	4.70	28.00	10	0	0.50	0	1.70
Location x population (origin)	14	3.50†	0	0	0.40	10	0	0.10	0	0

F values are given for fixed effects while log likelihood ratios (LLR) are given for random effect

LU, dates of leaf unfolding; A_{area}, maximum assimilation rate per leaf area; N_{area}, leaf N content per leaf area; PNUE, photosynthetic N-use efficiency; LMA, leaf mass per area index

† $P < 0.1$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

platanoides. Although populations of both species were plastic across gardens for all the traits under consideration, genetic variation for plasticity, i.e. potential for evolutionary changes, has been observed only in *A. negundo* with invasive populations expressing greater plasticity for growth and leaf phenology. These findings suggest that phenotypic plasticity and genetic differentiation act synergistically to provide introduced tree populations substantial potential for rapid adaptation to new environmental conditions. The contrasting patterns observed between the two species suggest that the relative importance of these two sources of phenotypic variation can depend on stage of invasion and the life-history strategy of the species.

Genetic differentiation

Whilst *A. platanoides* populations of native and introduced origins did not show notable genetic variation in the functional traits measured, there was a strong genetic differentiation between native and invasive populations of *A. negundo* in each garden. The genetic shifts were therefore independent of environmental conditions for this species. Invasive populations of *A. negundo* showed lower survival rate, greater diameter growth and increased LMA. In line with the results of a greenhouse experiment where invasive *A. negundo* genotypes showed higher trait values for growth and resource allocation to foliage than native ones (Lamarque et al. 2013), this study reveals that evolution towards faster growth at the expense of survivorship may have occurred in the introduced range of this species. The difference in the selection of competitive versus resistant genotypes between native and invasive populations of exotic species has also been documented in *Ambrosia artemisiifolia* (Hodgins and Rieseberg 2011) and *Rhododendron ponticum* (Erfmeier and Bruelheide 2010) while other studies found similar genetically based advantage in growth for invasive over native populations in exotic grasses (Bastlova and Kvet 2002; Leger and Rice 2003; Blumenthal and Hufbauer 2007; Flory et al. 2011a) and Chinese tallow tree (*Triadica sebifera*; Siemann and Rogers 2001; Huang et al. 2010). Interestingly, invasive *A. negundo* populations consistently showed lower maximum assimilation

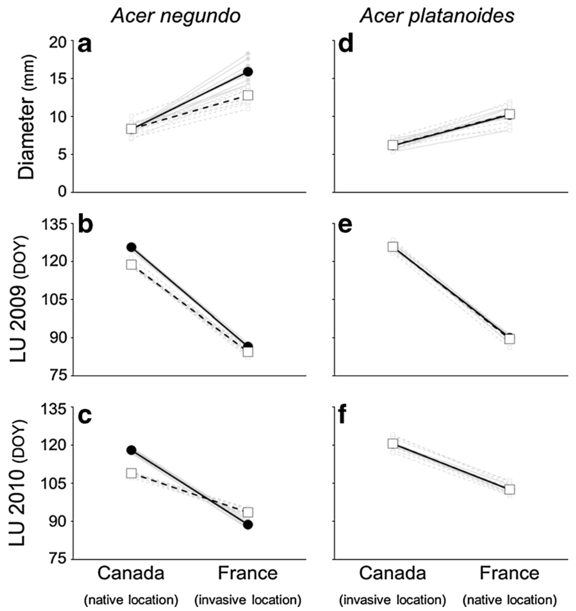

Fig. 2 Reaction norms for diameter growth and leaf unfolding (LU) of seedlings from native (*squares* and *dashed lines*) and invasive populations (*squares* and *solid lines*) of *A. negundo* and *A. platanoides*. Population means are shown in *grey* and the mean ± SE for native and invasive origins are shown in *white* and *black*, respectively

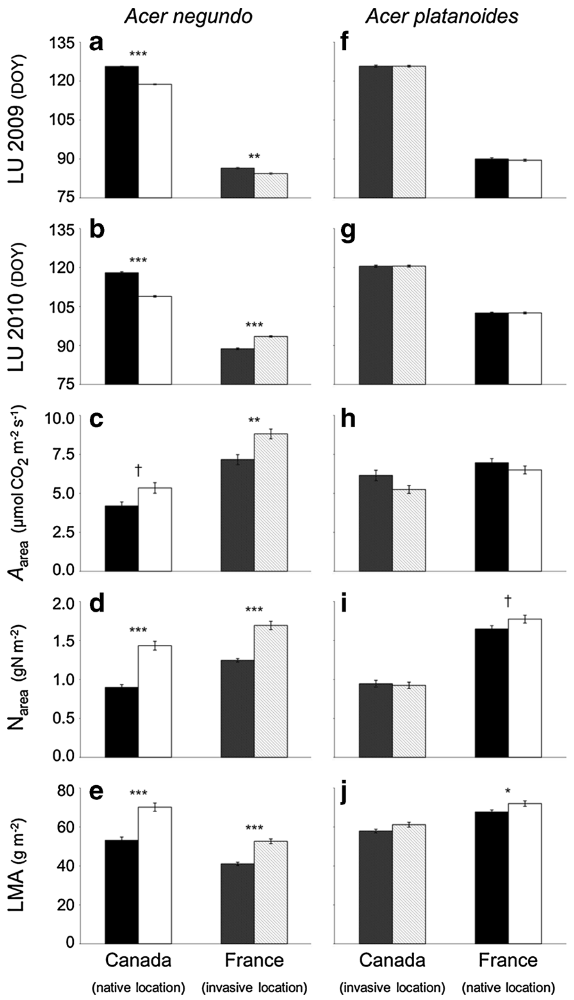

Fig. 3 Leaf unfolding (LU), assimilation rate per unit leaf area (A_{area}), nitrogen content per leaf area (N_{area}) and leaf mass per area index (LMA) of seedlings from native (*white bars*) and invasive (*black bars*) populations of *A. negundo* (**a**–**d**) and *A. platanoides* (**e**–**h**) growing in reciprocal common gardens (Canada vs. France). The invasive origin of each species is represented with hatchings. Values represent mean ± SE for native and invasive population origins. † $P < 0.06$, *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$

rates and lower leaf nitrogen contents in the two gardens compared to native conspecifics and therefore they did not have greater diameter growth in the introduced range through enhanced physiological capacities. This result suggests that physiological traits are not responsible for increasing the invasiveness of *A. negundo*. It also provides a new mechanistic insight for the commonly observed increase in growth among invasive populations because the literature has previously documented either no difference between native and invasive populations or physiological advantages for invasive populations in both exotic herbaceous and tree species (Bastlova and Kvet 2002; DeWalt et al. 2004; Zou et al. 2007; Mozdzer and Zieman 2010; Feng et al. 2011). Invasive populations of *A. negundo* exhibited lower LMA values, a characteristic positively associated with rapid production of biomass through greater photosynthetic surface area allowing greater light use efficiency and carbon assimilation (Pattison et al. 1998; Nagel and Griffin 2004). This indicates that morphological traits would play an important role in the success of this species within its invasive range. Given that faster turnover of plant parts in low-LMA genotypes allows a more flexible response to spatial patchiness of light and soil resources (Wright et al. 2004), the strategy for quick returns on investments of nutrients and dry mass in leaves may have been favoured in the highly competitive riparian habitats that *A. negundo* preferably invades in Europe. This would probably explain why this species outcompetes co-occurring native tree species under non-limiting resource conditions via greater resource allocation to foliage (Saccone et al. 2010; Porté et al. 2011).

Table 4 Phenological sensitivity to temperature[a] of native and invasive populations of *Acer negundo* and *Acer platanoides*

	Leaf unfolding/T° (day degree^{-1})		
	Slope	SE[b]	r^2
Acer negundo			
Native populations	−2.41*	0.45	0.93
Introduced populations	−3.25**	0.12	0.99
Acer platanoides			
Native populations	−2.64*	0.58	0.91
Introduced populations	−2.61*	0.55	0.92

[a] Mean temperature values were calculated from 1 January to 25 March for *A. negundo* and from 1 January to 30 March for *A. platanoides*

[b] SE of the linear regression slope

* $P < 0.05$, ** $P < 0.01$

Phenotypic plasticity

Seedlings from native and invasive populations of both species were highly plastic across gardens. This supports the interpretation that there is a high potential for future migration of these species to areas not yet colonized. We did not observe any difference in the magnitude of plasticity between native and invasive populations of *A. platanoides*. The higher levels of plasticity exhibited by this species compared to the native ones from deciduous North American forests (Kloeppel and Abrams 1995; Paquette et al. 2012) could thus be pre-adapted characteristics from its native origin. Populations of *A. negundo* originating from the introduced range contrastingly expressed increased phenotypic plasticity across gardens relative to their native conspecifics. This is in accordance with previous work that reported greater plasticity of traits in invasive over native populations of other exotic species in response to variation of abiotic conditions (Kaufman and Smouse 2001; Leger and Rice 2003; Chun et al. 2007; Zou et al. 2009; Qing et al. 2011). The significant population origin x environment interactions for growth and phenology suggest that increased plasticity could have played an important role in the invasion process of *A. negundo* by allowing the species to spread from wet to dry habitats (Erfmeier et al. 2011). The fact that invasive genotypes of *A. negundo* from France grew significantly better in the French garden but flushed significantly later in Canada even suggests that they might have evolved to be locally adapted to their new environment (Parker et al. 2003). In a previous study, invasive populations did not exhibit higher magnitudes of plasticity than native ones in response to nutrient availability (Lamarque et al. 2013), and therefore, other abiotic factors such as light or temperature may be important drivers of the adaptive response observed here in the introduced range. In addition, the difference in phenological sensitivity to temperature between native and invasive populations emphasizes the importance of climatic conditions and growing season length in controlling genetic differentiation in flowering phenology of invasive herbaceous species (Williams et al. 2008; Bastlova and Kvet 2002; Eriksen et al. 2012). The greater sensitivity to temperature of invasive *A. negundo* genotypes is likely to help them to keep colonizing new habitats in Europe because invasive species with flexible phenologies are expected to benefit from increased system variability and longer growing seasons (Wolkovich and Cleland 2011).

Different species, different patterns

Life-history traits were both environmentally and genetically determined among *A. negundo* populations but only environmentally controlled among those of *A. platanoides*, at least within the areas studied. The different outcomes observed for the two species matches the existing quantitative genetic literature with high inter-species variability (Bossdorf et al. 2005). One potential explanation could have been the distribution of the sampled populations, especially in the introduced ranges where the latitudinal variation among populations was greater for *A. negundo* than for *A. platanoides*. Patterns could have been explained by clinal variations in traits along a latitudinal gradient (Kremer et al. 2014), but this was not the case in our study (no clinal trend has been found, data not shown). A more plausible reason of the discrepancy between species is that the importance of phenotypic and genetic effects is specific to stages of invasion and life-history strategies of species (Dietz and Edwards 2006; Theoharides and Dukes 2007). *A. negundo* is a pioneer species in its invasive range and has capitalized on frequent disturbances of riparian communities to currently dominate these habitats across Europe whereas the late-successional and shade-tolerant *A. platanoides* is present but not yet dominant in deciduous forests of southern Ontario (Mędrzycki 2007; Porté et al. 2011; Lamarque et al. 2012). Contrary to the slow dynamic of *A. platanoides*, the very short generation time of *A. negundo* can stimulate rapid evolutionary changes among invasive populations favoring the more competitive genotypes. Phenotypic plasticity is likely the primary response when exotic species colonize and establish in their introduced range while adaptive genetic differentiation manifests later during the spread of species. *A. platanoides* has not reached yet these later stages in Canada (Lamarque et al. 2012).

Conclusions

Few attempts have been made to simultaneously address the importance of evolutionary processes in tree invasions. The reciprocal common garden based approach used here demonstrated that both phenotypic plasticity and genetic differentiation can act synergistically to promote the success of invasive plants. In this study, two tree species invasive in the other's native range did not behave identically in the two sets of processes examined. Hence, it is likely that stage of invasion and life-history strategies of species regulate the contribution of these processes to plant invasiveness. Our results finally suggest that exotic trees possess substantial genetic variation and plasticity to rapidly adapt to new environmental conditions, which would potentially lead to invasive range extensions. Evolutionary processes occurring amongst invasive populations should therefore be explicitly incorporated into management and risk assessment plans.

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