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Functional shift of sycamore maple (*Acer pseudoplatanus*) towards greater plasticity and shade tolerance in its invasive range

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ABSTRACT

What makes an alien plant species a successful invader remains a challenging question in invasion ecology. Although comparing functional traits of exotic species between their native and invasive ranges represents a sensible step when studying invaders, this approach is rarely applied and always disconnected from demographic attributes. In this study, we implemented a cross-continental comparison between native and invasive populations of sycamore maple (*Acer pseudoplatanus*), a tree native to central Europe and invasive in New Zealand. We analysed individual growth and population structure in addition to physiological, biochemical and metabolic leaf-traits of *A. pseudoplatanus* in both native (Northern France) and invaded (South Island of New Zealand) ranges under two light regimes (sun *vs.* shade). We found greater individual growth and shade tolerance in the invasive range. For a given sapling age, both basal stem diameter and height were more than twofold greater in New Zealand compared to France, irrespective of light conditions. At the leaf level, photosynthetic rates were higher along with higher leaf nitrogen content, leaf carbon content and leaf construction costs in New Zealand. However, French populations had significantly greater dark respiration and specific leaf area. Leaves of native trees contained more non-structural carbohydrates and chlorophyll but less soluble proteins than those of invasive trees. Our results indicate faster growth of *A. pseudoplatanus* in its invasive range compared to the native, which is at least partly due to greater shade-tolerance (i.e. more efficient photosynthesis at reduced costs under shade conditions) and plausibly to greater phenotypic plasticity to light. Functional shifts between the native and the invaded range allow the species to escape the growth-survival trade-off and exhibit greater growth in the invaded range. These shifts may be caused by differences in climatic conditions, biotic environment and/or in genotypes.

1. Introduction

Invasive alien plants are widely acknowledged as a major environmental problem, altering natural ecosystems worldwide and causing serious economical and social effects. What allows some alien plant species to become successful invaders remains a challenging question in invasion ecology (Van Kleunen et al., 2010). Most of the recent research effort has been devoted to identifying functional traits associated with invasion success (Godoy et al., 2011; Pyšek and Richardson, 2007) mostly by comparing invaders to co-occurring natives or to non-invasive aliens in the introduced range (e.g. Van Kleunen et al., 2010). But surprisingly, the relationships between functional traits and demographic patterns have received little attention so far, and whether these relationships differ between the native and the invaded ranges remains an unanswered question. To fill this knowledge gap, we used an intraspecific cross-continental assessment to compare the ecophysiology and the population structure of a tree species between its native and invaded ranges.

Invasion success has been linked to traits associated with fast growth such as high values for maximum photosynthetic capacity ($A_{\max}$), specific leaf area (SLA), leaf nitrogen content (LNC), and reduced dark respiration rate (R_d) (Baruch and Goldstein, 1999). However, whether these trait combinations reflect a more efficient carbon-capture strategy in invasives than in co-occurring natives, and hence a

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lower investment of energy to construct biomass (Nagel and Griffin, 2001), remains controversial (DeWalt et al., 2004). Another body of studies compared traits related to fitness and demographic processes, such as growth rate, fecundity and seed dispersal, concluding that tall stature, vigorous vegetative spread, high fecundity, and extended flowering period are associated with invasion success (Pyšek and Richardson, 2007; Rejmánek and Richardson,1996). Another important trait linked to invasiveness is phenotypic plasticity and in particular, a high plastic response to light levels (Yamashita et al., 2000). The ability of plants to capture and utilize light is an important determinant of species growth, recruitment, and fitness, which is of utmost importance for alien species invading forest ecosystems (Standish et al., 2001).

In contrast, few studies implemented intraspecific comparisons between invasive and native ranges of alien plant species (Bossdorf et al., 2005; Heberling et al., 2015; Hierro et al., 2005; Leishman et al., 2014). Even fewer addressed changes in functional strategies (Blossey and Notzold, 1995; Heberling et al., 2015; Lamarque et al., 2015; Zou et al., 2007), and none related functional changes to actual individual and population growth. Intraspecific comparisons revealed that a successful invader often exhibits more efficient resource-use strategies in its invasive range than in its native range. This has been primarily attributed to release from natural enemies (Liu and Stiling, 2006) and/or higher competitiveness (Davis et al., 2000) in the novel environment, which would allow the invader to allocate more resources towards growth according to the hypothesis of Evolution of Increased Competitive Ability (EICA) (Blossey and Notzold, 1995; Zou et al., 2007). Such a shift could also reflect post-introduction evolution, such as local adaptation (Whitney and Gabler, 2008), and/or phenotypic plasticity (Valladares et al., 2000). In addition, a successful invader may possess 'pre-adapted' traits that confer invasiveness in the introduced range and which are fine-tuned by adaptation to the new environment (Henery et al., 2010).

Studies on plant invasions have been largely biased towards 'fast-invaders', i.e., those with early-successional life-history traits adapted to invade disturbed areas often with high resource availability (Rejmánek and Richardson, 1996), neglecting plant species most likely to invade relatively undisturbed communities, particularly forests (Martin et al., 2009). Shade tolerance in particular appears a crucial attribute of forest invaders, playing a key role in plant community dynamics (Valladares and Niinemets, 2008). But surprisingly, shade-tolerant species have often been far less studied, though they are likely to be highly persistent in native forest communities, increase in abundance during succession, and have long-term impacts on ecosystem functioning (Martin, 1999; Meyer and Florence, 1996); hence, their management, including prevention, early detection and control, is particularly challenging. This underappreciated role of shade-tolerance is the focus of the present study.

Here we implemented a cross-continental comparison between native and invasive populations of a tree species, the sycamore maple (*Acer pseudoplatanus* L., *Sapindaceae*), a widespread species throughout European forests, which is usually considered as a mid-successional, rather shade-intolerant species. It has been reported as an invasive species in other parts of Europe (e.g. Great Britain, Fennoscandia, Lithuania), in North America, Australia and New Zealand (Webb et al., 1988). In this latter case, it invades regenerating native beech forests (*Fuscospora*/*Lophozonia* spp.) and mixed conifer-broadleaved forests in the South Island, where it is considered a shade-tolerant invader (Williams, 2011). Our main goal was to determine whether individual growth and population structure of *A. pseudoplatanus* differ between native (North France) and invasive (South Island, New Zealand) ranges, and to what extent these differences can be shown by different resource use strategies. We hypothesize that *A. pseudoplatanus* (i) is more able to acclimatize to variation in light conditions, (ii) shows higher resource use efficiency, and (iii) as a result, exhibits greater individual growth in the invaded range than in the native range.

2. Materials and methods

2.1. Study species

Sycamore maple (*Acer pseudoplatanus* L., *Sapindaceae*) is a mid-successional, long-living (> 300 yrs) deciduous tree native to central Europe and south-west Asia (Jones, 1945). It is fast growing and relatively shade-intolerant. At the age of ca. 20 years, trees start flowering, with more than 800 inflorescences per adult tree and up to 30 wind-dispersed winged fruits per inflorescence. In closed-canopy forests, most fruits fall down in a radius of ca. 35 m around the mother tree, but occasional long distance dispersal may occur (Pandey et al., 2012). *A. pseudoplatanus* is considered a nitrophilous species, growing the best on fertile, moist soils, although it can tolerate a wide range of soil types. It also has a wide climatic tolerance but prefers cold, moist conditions. In Europe, *A. pseudoplatanus* is one of the most palatable species for browsing deer. It is also exposed to a number of fungal attacks, which can lead to premature defoliation and thus alter growth.

A. pseudoplatanus was originally introduced to New Zealand in 1880 as an ornamental, and reported as invasive in the late 1950s. Today, it is common in many modified habitats including abandoned gardens, roadsides, riverbanks in gullies, urban wasteland and secondary and regenerating forest stands, where it forms dense, deeply shading, monospecific stands (Hein et al., 2009). It is also able to invade short-stature native woody vegetation and appears to impede the expansion of the adjacent beech forest, although it does not invade beneath a closed beech canopy (Williams, 2011). In addition, native vegetation in New Zealand is almost exclusively evergreen, so the deciduous nature of *A. pseudoplatanus* may change conditions in ways that are detrimental to native vegetation, such as increasing leaf litter loads and changing rates of nutrient cycling (Vogt et al., 1986). No natural enemy of *A. pseudoplatanus* (including herbivores and parasites) has been reported yet in NZ.

2.2. Study sites

Two temperate forests in Europe (North France) and one in New Zealand (South Island), which share similar climatic and substrate conditions, were used. In particular, the three sites were similar with respect of solar radiation intensity (175 and 200 $\mathrm{W\,m^{-2}.yr^{-1}}$ at the ground level), annual hours of sunshine (1600–1750 h), air humidity (80%), and amplitude between minimal and maximal temperature throughout the year (8.5-9.6 °C) (see Appendix A in Supplementary material for an extended information on environmental conditions at the three study sites).

In France, the Hirson forest is located along the foothills of the Ardennes (49°57′N, 4°06′E, 215 m a.s.l.), and the Compiègne forest along the Oise and Aisne rivers (49°24′N, 2°53′E, 135 m a.s.l.). Mean temperature and annual precipitation (Hirson/Compiègne) are 9.1/10.0 °C and 1010/682 mm, respectively. The study stands consisted of pedunculate oak-dominated forest (*Quercus robur*) established on schist (Hirson) or sandy (Compiègne) alluvia. The main other canopy tree species are hornbeam (*Carpinus betulus*), ash (*Fraxinus excelsior*), beech (*Fagus sylvatica*) and lime (*Tilia cordata*).

In New Zealand, Peel forest is a remnant of podocarp forest in the foothills of the Southern Alps (−43°53′N, 171°16′E, 270 m a.s.l.). Mean temperature and annual precipitation are 10.5 °C and 1023 mm, respectively. The main canopy trees of the study site were the podocarps kahikatea (*Dacrycarpus dacrydioides*) and totara (*Podocarpus totara*) and the Malvaceae trees narrow-leaved lacebark (*Hoheria angustifolia*) and ribbonwood (*Plagianthus regius*).

2.3. Population structure and growth

Three random transects in Peel forest (NZ), two in Hirson (France) and one in Compiègne (France) were established in summer (December