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

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Sabrina Shouman[a], Norman Mason[b], Thomas Kichey[a], Déborah Closset-Kopp[a],
J. Mason Heberling[c], Ahmad Kobeissi[d], Guillaume Decocq[a],*

[a] *Unité Ecologie et Dynamique des Systèmes Anthropisés (EDYSAN, FRE 3498 CNRS-UPJV), Université de Picardie Jules Verne, 1 rue des Louvels, F-80037 Amiens Cedex, France*
[b] *Landcare Research, Private Bag 3127, Hamilton 3240, New Zealand*
[c] *Carnegie Museum of Natural History, Pittsburgh, PA, USA*
[d] *Department of Biology, Lebanese University, Hadat, Lebanon*

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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

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 $Wm^{-2}.yr^{-1}$ 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

2013 in New Zealand, June 2014 in France). Each transect consisted of a 2 m-wide band extending from an isolated reproductively mature maple tree, towards a direction chosen so as it did not meet any other mature *A. pseudoplatanus*, neither within nor in a radius of 100 m around the transect band. The transect length ranged from 100 m (France) up to 200 m (NZ). These distances were defined to take into account the dispersal capacity of *A. pseudoplatanus*. Therefore, we assume the vast majority of seedlings were offspring of the selected mother tree. Each transect was divided into 1 m^2 plots. Light intensity was measured 50 cm aboveground at the centre of each plot containing *A. pseudoplatanus*, and immediately after in full light conditions outside the forest; all measures were completed within 10 min. Each plot was categorized as within a gap (sun conditions; > 12% of full-light conditions) or below a closed canopy (shade conditions; < 5%) (Appendix A in Supplementary material). By doing this, we standardized sun and shade conditions across study sites. All *A. pseudoplatanus* saplings with a height above 15 cm were collected and their height and stem diameter above the collar were immediately measured. A stem disc was taken for further tree ring counting. Whenever tall individuals (> 3 m) were too rare within the transect we collected additional samples outside the transects (to get at least 10 individuals), but in the same habitat in order to gain an adequate representation of the full size range.

2.4. Leaf gas exchange

For photosynthetic measurements, we sampled upper branches from ten individuals of *A. pseudoplatanus* trees of 1–4 m height per site, growing in sun (at the centre of a large gap, $n = 5$) and shade (beneath a closed canopy, $n = 5$). Gas exchange measurements were performed on cut branches, following the protocol of Niinemets et al. (2005). From each individual, one branch was cut in the field and immediately recut under water. To maintain xylem water potential and minimize transpiration, severed ends were wrapped with wet paper towel, put in a bucket of water, and foliage was covered with a plastic bag for transportation to the lab, typically within 4 h. Upon returning to lab, branches were recut and cut stems placed in water, loosely covered in transparent plastic daily, and stabilized at room temperature under low light for 1–3 days before recording gas exchange measurements.

Gas exchange measurements were conducted on fully expanded, recently mature leaves using a LI-6400XT portable photosynthesis system equipped with CO_2 and temperature control modules, 2×3 cm sample chamber and a red-blue LED light source (LI-COR Biosciences, Lincoln, Nebraska 68504, USA). Leaf temperature was maintained at 25 °C under ambient humidity throughout measurements with sample chamber CO_2 concentration at 380 μmol mol^{-1} and sample chamber flow rate of 500 μmol s^{-1}. Leaves were photoinduced at a moderate irradiance level (300 μmol photons $m^{-2} s^{-1}$) until equilibration. Light levels were then progressively increased until light saturation (800–1500 μmol/$m^2 s^{-1}$). All individuals were light saturated at the highest light levels, with no apparent signs of photoinhibition. Light-saturated net photosynthetic rate (A_{sat}) was recorded after equilibrating for at least two minutes at each PPFD and reaching defined stability parameters based on photosynthetic rate and stomatal conductance to water. Following light saturation, light levels were decreased incrementally to 200 μmol/$m^2 s^{-1}$ and assimilation rate (A_{200}) was recorded following equilibration (data not shown). Lastly, the light source was shut off to measure daytime dark respiration (R_d) (Kok, 1948).

2.5. Leaf structural and biochemical characteristics

Immediately after gas exchange measurements, five fully expanded leaves per branch were collected, scanned to determine leaf area, and oven-dried at 60 °C for 72 h and specific leaf area ($cm^2 g^{-1}$) was calculated. Ground leaf samples were ashed at 500 °C for 4 h, and leaf ash concentration was calculated as ash mass divided by sample mass. Leaf nitrogen and carbon contents were determined using an elemental

analyzer (Flash EA 1112, Thermo Electron).

Leaf construction cost (*CC*) quantifies the amount of glucose equivalents required to construct a leaf in terms of carbon skeletons, reductant, and ATP, excluding additional costs for maintenance and substrate transport (Williams et al., 1989). Leaf CC_{mass} (g glucose g^{-1} leaf mass) was determined using a biochemical approximation (Boyd et al., 2009; Vertregt and Penning De Vries, 1987):

$$CC_{mass} = (-1.041 + 5.077C_{mass})(1 - 0.67Ash) + 5.325N_{mass}$$

where C_{mass} is mass-based leaf carbon content, *Ash* is leaf ash concentration (proxy for mineral concentration; Vertregt and Penning De Vries, 1987), and N_{mass} is mass-based nitrogen. We assumed leaf NO_3^- was negligible compared to organic N forms, and nitrate was the dominant form of N.

Resource-use efficiency (*RUE*) is broadly defined as the amount of carbon assimilated per unit resource (Funk and Vitousek, 2007). Potential photosynthetic nitrogen-use efficiency (PNUE) and potential photosynthetic energy-use efficiency (PEUE) were calculated as $A_{max,mass}/N_{mass}$ and $A_{max,mass}/CC_{mass}$, respectively.

2.6. Metabolic measurements

Six spatially separated populations, four in New Zealand and two in France, of *A. pseudoplatanus* were sampled during spring (December in New Zealand, June in France) and fall (May in New Zealand, October in France) and up to five mature trees per population were sampled. From each individual, two small branches containing between six and ten fully expanded leaves were collected, one from the upper peripheral part of the tree crown and one from the bottom of the tree (i.e. shaded by other leaves), representing sun and shade leaves, respectively. All samples were then stored at −80 °C prior to grinding.

From the ground samples, mass-based leaf nitrogen and carbon contents were determined using an elemental analyzer (Flash EA 1112, Thermo Electron). Approximately 20 mg of dried powder sampled were then extracted in 1 ml 80% ethanol for 2 h at 4 °C while continuously agitated, then centrifuged for 5 min at 10 000*g*. The supernatant was collected and the pellet subjected to extraction in 60% ethanol and finally in water. All supernatants were combined to form the hydro-alcoholic extract from which soluble sugars (glucose, fructose and sucrose) were measured enzymatically using a commercially available kit (R Biopharm, Mannheim, Germany) after speed-vac evaporation. The centrifuged pellets were resuspended in distilled water and treated with α-amylase (SIGMA-ALDRICH, St Louis, USA) and α-amyloglucosidase from *Aspergillus niger* (ROCHE, Meylan, France) as described by Smith and Zeeman (2006) for starch hydrolysis. After incubation the tubes were then centrifuged at 12 000*g* for 5 min at room temperature. The supernatant containing soluble sugars, derived from starch degradation, were measured using the same commercial kit as above.

From 20 mg of leaf powder, total chlorophyll was extracted with 80% acetone, then absorbance at 645 nm and 663 nm was measured to estimate chlorophyll *a* and chlorophyll *b* respectively (Arnon, 1949). Soluble protein content was determined using a commercially available kit (Coomassie Protein assay reagent; Bio-Rad, München, Germany), using bovine serum albumin (BSA) as a standard (Bradford, 1976). Amino acids were quantified using the Ninhydrin method (Rosen, 1957).

2.7. Data analysis

Whenever necessary, measurements were converted between area (*i.e.*, m^{-2} leaf) and mass-based estimates (*i.e.*, g^{-1} leaf) using their corresponding SLA. All statistical analyses were performed in R (R Development Core Team, 2015). We first analysed all modalities together (2 countries x 2 light conditions) using a non-parametric Kruskall-Wallis analysis of variance and, whenever significant ($P < 0.05$), post-hoc pairwise comparisons were done using Tukey and Kramer tests
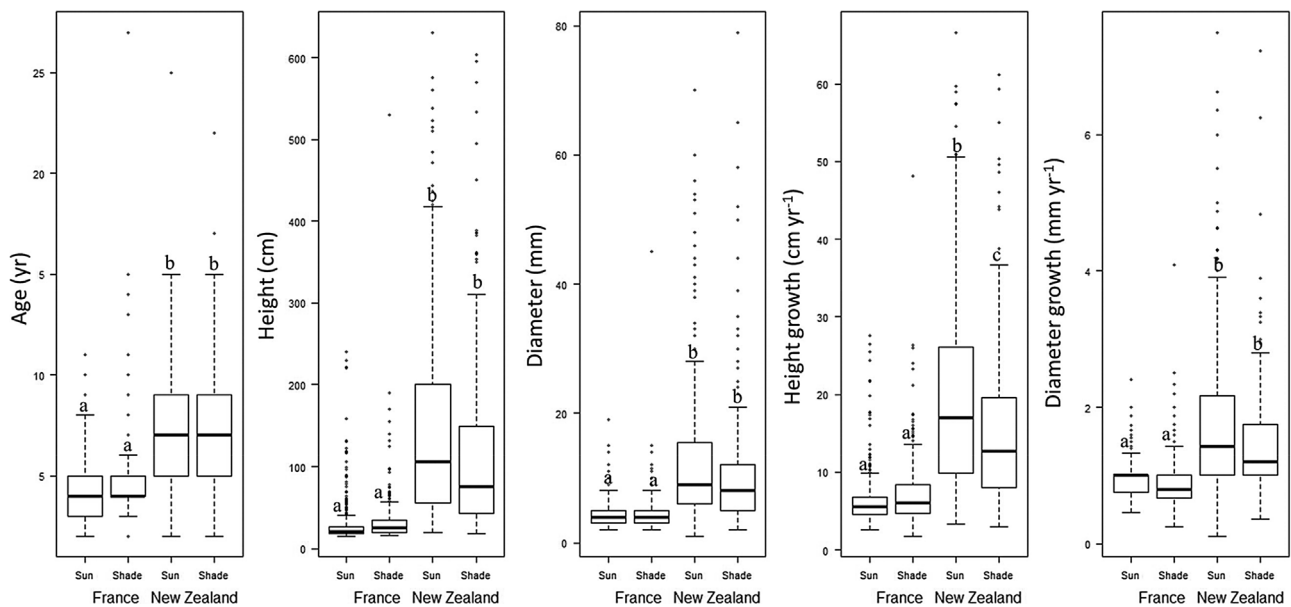
Fig. 1. Boxplots of age, height, diameter, height growth, and diameter growth of *A. pseudoplatanus* across native and invasive ranges at different light conditions. The upper and lower border of the box are the 75th and 25th percentiles, respectively. The black horizontal line within the box is the median and the error bars are the 10th and 90th percentiles. For each variable, boxplots with same letter were not significantly different ($P > 0.05$). Number of samples collected in France-Sun = 388; France-Shade = 562; New Zealand-Sun = 378; New Zealand-Shade = 212.

and *Kruskalmc, PMCMR* and *pgirmess* packages (Giraudoux, 2016). Since some of the parameters were highly variable in one modality compared to the others, we further compared these parameters between (i) shade and sun leaves within the two countries, and (ii) NZ and France within each light condition, using Mann-Whitney U tests. For comparison purposes, we modelled sapling performance in the native and invasive ranges under the two light conditions using curve fitting (linear and non-linear models) and *ggplot2* package (Wickham, 2011). We retained the model with the lowest AIC value.

3. Results

3.1. Population structure and individual growth

We recorded a total of 562/388 (shade/sun) and 212/378 individuals in France and NZ, respectively. Since *A. pseudoplatanus* does not seed bank and given our sampling design, we assumed that all of them were offsprings from the selected mother tree. Despite similar environmental conditions across sites (Appendix A in Supplementary material), invasive populations included older and taller saplings with larger stem diameter than native ones, irrespective of light conditions (Fig. 1). At the same age, basal diameter and height were more than twofold higher in New Zealand compared to France. The population structure was similar between shade and sun conditions in both ranges (Fig. 2). French populations were strongly skewed towards young individuals, with two thirds of the individuals aged less than 5 years irrespective of light conditions. In comparison, the invasive populations exhibited a bell-shape curve with a small peak at 4 (shade conditions) or 5 (sun conditions) year-old and a great kurtosis towards the right (i.e. older individuals). These data indicate that in the native range, mortality rates were high in early life stages (i.e. before the age of 6 years), irrespective of light conditions. In contrast, in the invasive range, saplings were less frequent in the first age classes (≤ 5 yrs) than in the native range, but much more frequent in subsequent classes (≥ 6 yrs), irrespective of light conditions.

The relationship between sapling height and diameter was similar in the two ranges (Fig. 3a), but at a given stem diameter, individuals tended to be taller in shade than in sun in France, indicating elongation, whilst no height difference was observed in NZ between shade and sun.

For a given age, invasive individuals were much taller with larger stem diameters than native ones, irrespective of light conditions (Fig. 3b, c). In sun conditions on average, height and radius' increments were 2 times higher in NZ than in France, while in shade they were 3.6 and 4.7 times higher, respectively. Individuals thus grew faster in the invasive than in the native range, irrespective of the light conditions.

3.2. Leaf gas exchange

A. pseudoplatanus had significantly greater area-based maximum photosynthetic rate ($A_{max,area}$) in the invasive than in the native range, particularly in plants from sun conditions (Fig. 4a). In contrast, leaf respiration rates ($R_{d,area}$, $R_{d,mass}$) were significantly lower in NZ than in France under shade conditions (Fig. 4c-d). Respiration efficiency (A_{max}/R_d) was greater in NZ than in France (Fig. 4e). Mann-Whitney U tests showed no differences between shade and sun leaves within each range for the functional traits, except for $A_{max,area}$ and $A_{max,mass}$, which were higher in shade conditions, in France and NZ, respectively (but see below: in NZ sun leaves had a lower SLA than shade leaves).

3.3. Leaf structural and biochemical characteristics

In the native range, leaves were biochemically (leaf N, leaf C, CC) and structurally (SLA) similar across sun and shade conditions (Fig. 5). In contrast, plants in the invaded range exhibited significantly lower SLA, N_{mass} and PEUE, but greater leaf N_{area}, C_{area}, and C_{mass} under high light (sun) compared to low light conditions (shade).

Compared to France, NZ individuals exhibited higher PEUE and CC_{mass} in the shade. Sun individuals in NZ had a lower SLA than those in comparable sun environments in France. Surprisingly, mean SLA did not differ between high and low light environments in France (Fig. 5g). Individuals in high light environments in NZ exhibited higher leaf N (N_{area}) and C (C_{area}, C_{mass}) investments than those in France leading to comparatively greater construction costs (CC_{mass}, CC_{area}). Photosynthetic nitrogen-use efficiencies (PNUE) were similar among ranges and light conditions (Fig. 5i). Leaf N concentration in spring and fall, as well as leaf C content in the fall, were higher in France than in NZ, irrespective of light conditions. Leaf C content in spring was higher in NZ than in France, but only in sun conditions, possibly due to a seasonal
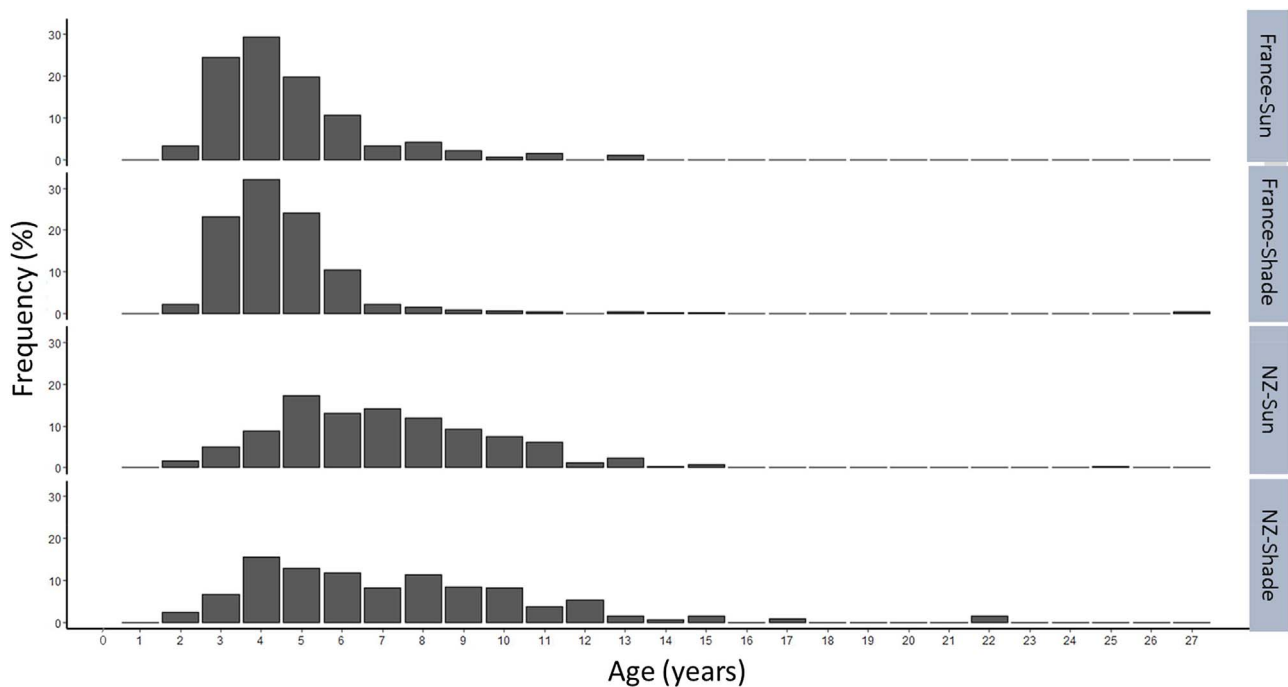
Fig. 2. Age (years) distribution of *A. pseudoplatanus* across native and invasive ranges at different light conditions. Number of samples collected in France-Sun = 388; France-Shade = 562; New Zealand-Sun = 378; New Zealand-Shade = 212.

growth delay (Table 1).

3.4. Metabolic measurements

We found very low concentrations of metabolites in fall leaves; we thus report values only from spring leaves, except for C and N (Table 1). Regarding non-structural carbohydrates (NSC), leaves in the native range contained much more glucose and fructose than those in the invaded range, irrespective of light conditions, but no difference was found for sucrose. Starch and soluble proteins were more abundant, and amino-acids less abundant, in NZ than in France, but only in shaded environments. Total chlorophyll, chlorophyll *a*, and chlorophyll *b* contents, as well as the chlorophyll:N ratio, were lower in the invasive than in the native range. No difference was observed between sun and shade leaves in the native range. In contrast, differences were strong in NZ, with leaves in shaded conditions containing more total chlorophyll, chlorophyll *a*, chlorophyll *b* and chlorophyll:N ratio but less sucrose, soluble proteins and chlorophyll a:b ratio than sun ones of the same tree.
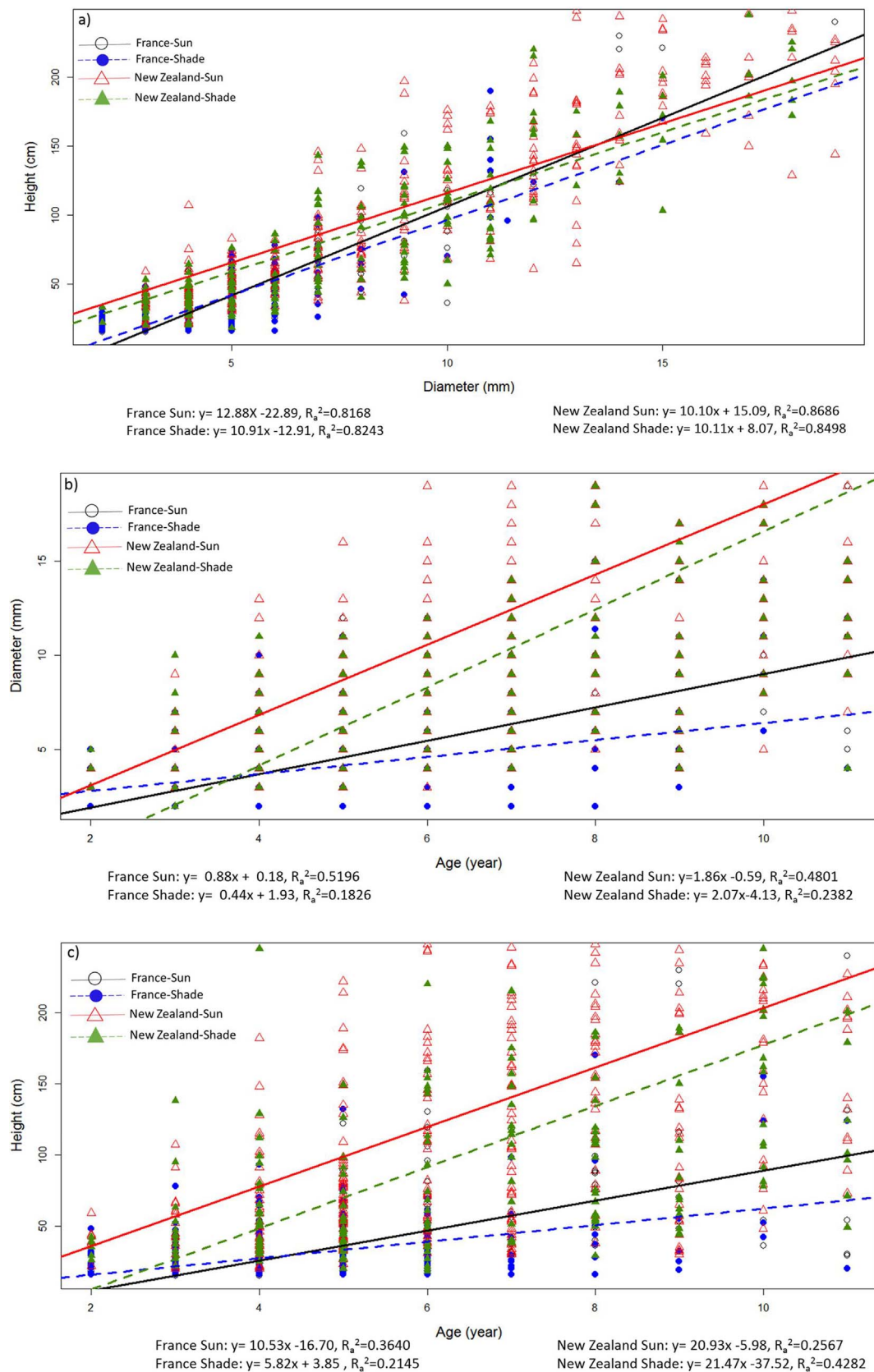
4. Discussion

In this study, we focused on *A. pseudoplatanus* as a remarkable example of an exotic tree species capable of invading closed-canopy evergreen forests regardless of their degree of disturbance. To our knowledge, this is the first study to link individual growth and population structure to physiological traits in a cross-continental comparison. Despite similar abiotic environments across regions, we found that in both shade and sun light conditions, invasive *A. pseudoplatanus* populations in New Zealand forests were composed of taller individuals with larger stem diameters and higher survival rates, compared to native French populations. While native individuals did not show physiological differences according to light availability, invasive populations strongly differed between sun and shade light in respiration efficiency and leaf traits such as SLA, construction cost, and N and C contents. Taken together, our results suggest that the greater performances of *A. pseudoplatanus* in the invaded range in terms of growth and survival may be due to the release from natural enemies or to

genotypic differences (e.g. incomplete sampling of the native gene pool). This, in turn, may explain the intraspecific shift towards higher shade tolerance (i.e. more efficient photosynthesis for reduced costs) and greater phenotypic plasticity to light, that may ultimately relax the species from the classic trade-off between growth in high light and survivorship in low light (Bazzaz, 1979; Pacala et al., 1996) in the invaded range.

4.1. Does A. pseudoplatanus shift towards greater shade-tolerance in its exotic range?

Shade tolerance is reflected by traits that improve the efficiency use of light, and thus increase carbon gain per unit leaf nitrogen (*carbon gain hypothesis*; Givnish, 1988). Main traits associated with shade tolerance are high photosynthetic rate in low light, low dark respiration rate, high SLA, high leaf nitrogen content per dry mass, high total chlorophyll content, low chlorophyll a:b ratio (Valladares and Niinemets, 2008). In our study, few of these traits differed significantly between the native and invasive populations growing under shaded conditions, with the notable exception of dark respiration rate ($R_{d.area}$) and maximum photosynthetic rate ($A_{max.area}$), which were 67% lower and 30% higher, respectively, in NZ compared to France. This indicates that in shaded conditions, invasive populations may exhibit increased carbon gains per unit respiration costs and thus increased photosynthetic benefits compared to native populations, as reflected by the increased A_{max}:R_d ratio and related increased height and diameter growth rates. Such a high respiration efficiency, which is related to a high growth rate, has been reported for several invasive species when compared to co-occurring natives (McDowell, 2002; Pattison et al., 1998), but also between ranges at the intraspecific level for several forest invaders such as Acacias (Atkin et al., 1998).

Leaves under shade light conditions contained more soluble proteins (which include Rubisco) and starch but less glucose, fructose and amino-acids in NZ compared to France. This difference suggests a greater allocation of nitrogen to CO_2 fixation and storage organs, which may explain the (non-significant) trend towards higher PNUE in NZ (Poorter and Evans, 1998). This shift in metabolite concentrations is consistent with the higher PEUE found for shade leaves of invasive

a)

France Sun: y= 12.88X -22.89, R_a^2=0.8168
France Shade: y= 10.91x -12.91, R_a^2=0.8243

New Zealand Sun: y= 10.10x + 15.09, R_a^2=0.8686
New Zealand Shade: y= 10.11x + 8.07, R_a^2=0.8498

b)

France Sun: y= 0.88x + 0.18, R_a^2=0.5196
France Shade: y= 0.44x + 1.93, R_a^2=0.1826

New Zealand Sun: y=1.86x -0.59, R_a^2=0.4801
New Zealand Shade: y= 2.07x-4.13, R_a^2=0.2382

c)

France Sun: y= 10.53x -16.70, R_a^2=0.3640
France Shade: y= 5.82x + 3.85 , R_a^2=0.2145

New Zealand Sun: y= 20.93x -5.98, R_a^2=0.2567
New Zealand Shade: y= 21.47x -37.52, R_a^2=0.4282

Fig. 3. Population structure of *A. pseudoplatanus* in native and invasive ranges at shade and sun light conditions represented by relationship between height and diameter (a), diameter and age (b), and height and age (c). The equations below each graph describe the lines having the best fit (lowest AIC) according to trend analysis with the adjusted R-squared.
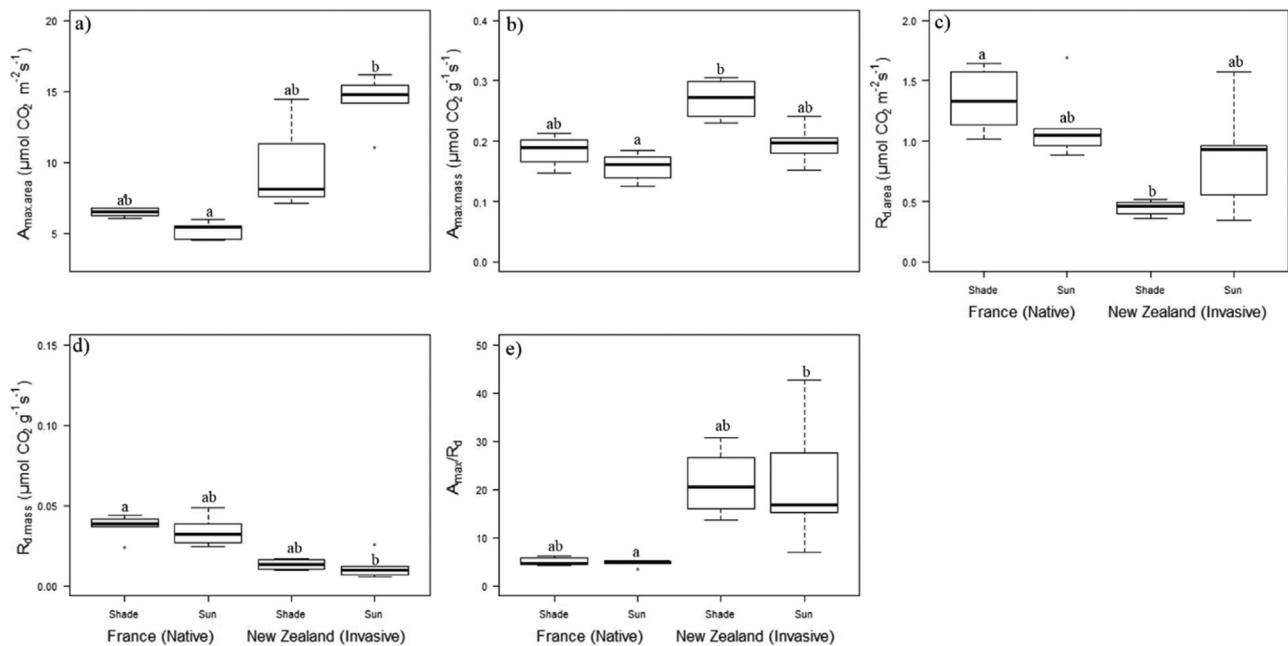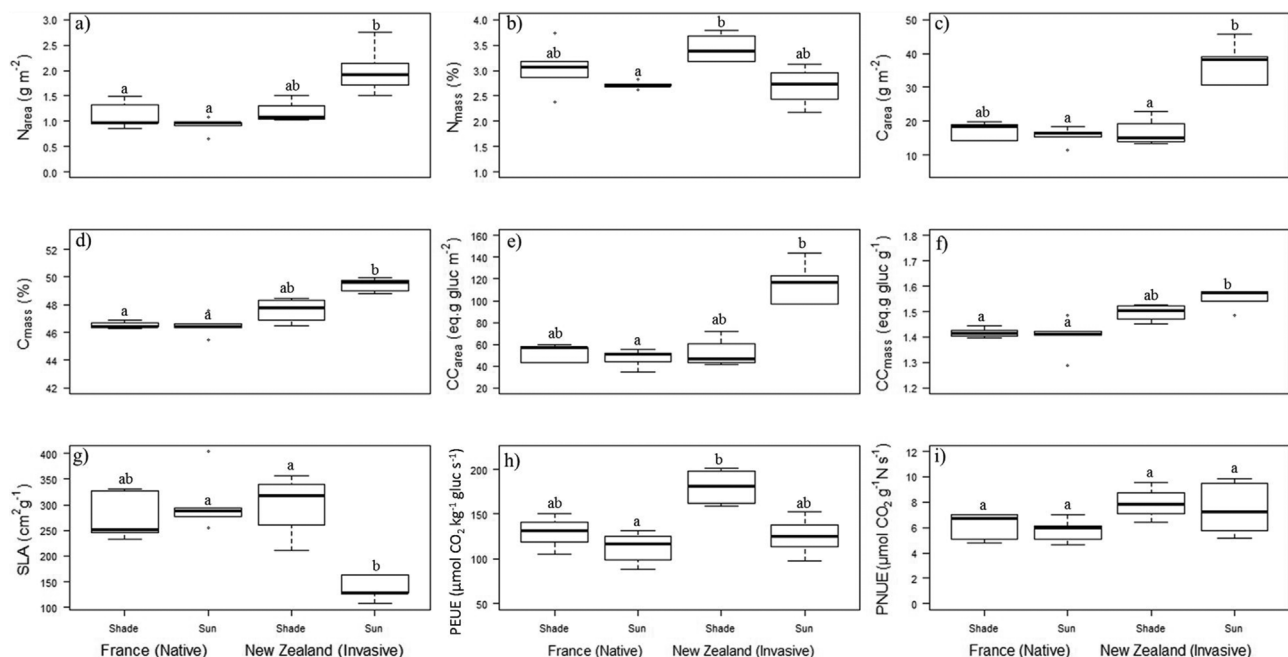
Fig. 4. Boxplots of leaf photosynthesis traits of *A. pseudoplatanus* across native and invasive ranges at different light conditions. The upper and lower border of the box are the 75th and 25th percentiles, respectively. The black horizontal line within the box is the median and the error bars are the 10th and 90th percentiles. For each variable, boxplots with same letter were not significantly different ($P > 0.05$). $A_{max,area}$, area-based maximum photosynthetic capacity; $A_{max,mass}$, mass-based maximum photosynthetic capacity; $R_{d.mass}$, mass-based dark respiration rate; $R_{d.area}$, area-based dark respiration rate; A_{max}/R_d, respiration efficiency.

populations, which likely maximizes the whole-plant carbon gain. Surprisingly, the leaf chlorophyll concentrations (total chlorophyll, chlorophyll *a*, chlorophyll *b*) of shade individuals, as well as their chlorophyll:N ratio, were far lower in NZ than in France, whilst SLA did not significantly differ. This is apparently conflicting with the previously reported intraspecific trends in shade tolerance physiology (Givnish, 1988; Valladares and Niinemets, 2008), and suggests that *A. pseudoplatanus* invests less in light harvesting in its exotic range.

However, differences were strong within invasive NZ populations, with shaded individuals exhibiting much higher SLA and chlorophyll:N ratio than those in the sun, whilst no difference was observed in native populations. This suggests that only invasive populations are able to acclimate to various light conditions.

Leaves of *A. pseudoplatanus* under shade condition did not differ between the two ranges with respect to SLA, CC_{area} and C_{area}, suggesting that *A. pseudoplatanus* does not invest more in the protection

Fig. 5. Boxplots of biochemical leaf traits of *A. pseudoplatanus* across native and invasive ranges at different light conditions. The upper and lower border of the box are the 75th and 25th percentiles, respectively. The black horizontal line within the box is the median and the error bars are the 10th and 90th percentiles. For each variable, boxplots with same letter were not significantly different ($P > 0.05$). N_{area}, area-based leaf nitrogen concentration; N_{mass}, mass-based leaf nitrogen concentration; C_{area}, area-based leaf carbon concentration; C_{mass}, mass-based leaf carbon concentration; CC_{area}, area-based leaf construction costs; CC_{mass}, mass-based leaf construction costs; SLA, specific leaf area; PEUE, photosynthetic energy use efficiency; PNUE, photosynthetic nitrogen use efficiency.

Table 1
Mean values (± 1 SE) for metabolic traits of sun and shade leaves in the native and invasive ranges. Sun leaves were collected in the sun-exposed canopies and shade leaves were collected from lower shaded branches of the same trees. For all metabolic traits, only results for spring leaves are shown, except for leaf N and C (spring and fall leaves). Statistical differences between native and invasive populations and across light environments were tested using Kruskal-Wallis tests and multiple comparison post-hoc tests.

Trait (units)	Native (France)		Invasive (New Zealand)		
	Sun	Shade	Sun	Shade	*P-value*
Glucose (nmol/mg DW)	149.2 ± 18.2[a]	153.2 ± 18.0[a]	54.6 ± 9.2[b]	55.2 ± 3.9[b]	< 0.0001
Fructose (nmol/mg DW)	106.5 ± 13.1[a]	120.0 ± 13.1[a]	39.5 ± 5.9[b]	38.8 ± 1.7[b]	< 0.0001
Sucrose (nmol/mg DW)	135.3 ± 22.8	129.1 ± 16.4	135.2 ± 12.5	101.3 ± 13.3	0.17
Starch (nmol/mg DW)	187.1 ± 44.9	104.5 ± 15.5	173.4 ± 22.8	213.5 ± 36.7	0.20
Amino Acids (nmol/mg DW)	4.73 ± 0.99[ab]	8.49 ± 2.31[a]	3.37 ± 0.70[b]	3.58 ± 0.59[ab]	0.04
Soluble Proteins (µg/mg DW)	3.30 ± 1.08[ab]	1.51 ± 0.40[a]	6.49 ± 0.58[c]	4.69 ± 0.46[bc]	< 0.0001
Total Chlorophyll (µg/mg DW)	3.84 ± 0.44[ab]	4.47 ± 0.36[a]	0.96 ± 0.06[c]	1.44 ± 0.08[bc]	< 0.0001
Chlorophyll *a* (µg/mg DW)	2.85 ± 0.32[a]	3.30 ± 0.27[a]	0.76 ± 0.04[b]	1.08 ± 0.06[b]	< 0.0001
Chlorophyll *b* (µg/mg DW)	0.98 ± 0.12[ab]	1.17 ± 0.09[a]	0.20 ± 0.01[c]	0.36 ± 0.02[bc]	< 0.0001
Chlorophyll *a/b*	2.92 ± 0.07[ab]	2.80 ± 0.03[a]	3.72 ± 0.17[b]	3.09 ± 0.17[a]	0.001
Chlorophyll/N	1.17 ± 0.15[ab]	1.30 ± 0.12[a]	0.40 ± 0.02[c]	0.64 ± 0.03[b]	< 0.0001
N Spring (%)	3.36 ± 0.18[a]	3.5 ± 0.23[a]	2.47 ± 0.11[b]	2.25 ± 0.07[b]	< 0.0001
N Fall (%)	2.09 ± 0.11[ab]	2.34 ± 0.13[a]	1.49 ± 0.10[c]	1.68 ± 0.10[bc]	0.0001
C Spring (%)	46.9 ± 0.2[a]	47.0 ± 0.2[ab]	48.2 ± 0.3[b]	47.1 ± 0.3[ab]	0.006
C Fall (%)	46.5 ± 0.1[ab]	47.3 ± 0.3[a]	45.0 ± 0.4[bc]	43.8 ± 0.2[c]	< 0.0001

against herbivores in NZ compared to France. This is consistent with the very low concentration in glucose and fructose of shade leaves in NZ compared to France, which are sugars providing substrates for the synthesis of defence compounds (Hartmann and Trumbore, 2016), and with a number of studies which revealed the existence of a trade-off between C allocation to NSC and to growth in trees (e.g. Genet et al., 2010; Myers and Kitajima, 2007). A high SLA enables shade leaves to intercept more light per unit leaf dry mass, but at the same time increases plant mortality in shade since producing a large leaf area at reduced construction cost makes these leaves sensitive to mechanical stress and herbivory (Gamage, 2011). Although we were not able to directly assess herbivory in this study, NZ forests differ from French ones by the lack of wild ungulates. Moreover, no pest or parasite has been reported on *A. pseudoplatanus* in NZ (Landcare Research, unpublished data), whilst sapling predation by ungulates and fungal attacks are very common in France (see Appendix A in Supplementary material). The majority of the field studies that quantified some aspects of herbivore impact support the idea of an enemy release in introduced populations (Bossdorf et al., 2005), which allows plants to shift towards a faster growth strategy, to increase their population size, to facilitate their spread, thus contributing to their invasive success (Leishman et al., 2014). A cross-continental test of the Enemy release hypothesis with *Acer platanoides*, another maple species native to Europe and often co-occurring with *A. pseudoplatanus* in its native range, revealed that leaf herbivory was three times lower in North America than in Europe (Adams et al., 2009). We thus hypothesize that *A. pseudoplatanus* is released from its natural enemies in NZ, and thus that more energy is available for growth, especially in shade conditions, in accordance with the *Stress tolerance hypothesis*, which proposes that shade tolerance can be translated into maximization of the resistance to biotic and abiotic stresses in shade conditions (Kitajima, 1994). Moreover, shade tolerance and herbivory release may together increase tree growth by affecting difference resource-uptake functional traits (Salgado-Luarte and Gianoli, 2017).

Unexpectedly, invasive populations exhibited greater leaf CC_{mass} and C_{mass}, indicating higher leaf energy investments. A similar result has been reported for invasive populations of *Prunus serotina* in France compared to native populations in the USA, possibly associated to a greater leaf longevity (Heberling et al., 2015), allowing the plant to assimilate carbon over a longer period for the same initial investment in leaf construction (Funk, 2013). A greater allocation of energy to leaf survival over elongation and optimal photosynthesis can explain the greater shade tolerance (Gamage, 2011; Kitajima, 1994) and thus, the observed longer life span of *A. pseudoplatanus* saplings in shady

understories.

Taken together, these results indicate that *A. pseudoplatanus*, a relatively gap-dependent, light-demanding species in its native range, shifts to greater shade tolerance in its invasive range. Such a shift has been documented in the field for *Acacia dealbata* (Aguilera et al., 2015). Here we further demonstrate that this greater shade tolerance is not achieved by harvesting shade light more efficiently but by minimizing respiration costs and, plausibly, by investing less energy into protection against herbivores. This emerges as a common strategy among successful invaders in low-light conditions (Funk, 2013).

4.2. Does A. pseudoplatanus exhibit greater phenotypic plasticity in its exotic range?

A. pseudoplatanus showed larger diameter and height growth rates in the invaded than in the native range, irrespective of light conditions. Since sun and shade conditions did not fundamentally differed across study sites, this could be viewed as an indicator of high phenotypic plasticity (i.e. the property of a genotype to express different phenotypes in different environments; Aguilera et al., 2015; Funk, 2008; Godoy et al., 2011), which has often been invoked to explain invasion success (Godoy et al., 2011; Richards et al., 2006). In both sun and shade light conditions, invasive populations of *A. pseudoplatanus* displayed increased photosynthetic rates at the cost of high leaf nitrogen. It is noteworthy that while no significant differences in functional traits were found between sun and shade populations in the native range, there were important light-mediated trait differences in NZ (i.e. higher $A_{max,area}$, N_{mass}, SLA and PEUE, but lower N_{area}, C_{area}, C_{mass} and CC_{area} in shade than in sun). This demonstrates the emergence of functional differentiation of leaves in invasive populations.

Whilst the CC_{mass} values recorded in the native range are within the range of the values reported for European broadleaved species (1.23–1.53 eq. g gluc g^{-1}; Niinemets, 1999), those recorded in NZ were particularly high, especially in sun conditions, but still in the range given in the literature (1.2–1.8 eq. g gluc g^{-1}; Poorter et al., 2006). This high construction cost of sun leaves observed in NZ likely reflects a high content of lignin since C content was high while NSC were either the same as (sucrose and starch) or even less abundant (glucose and fructose) than in sun leaves in France. This finding was rather unexpected since a low CC has been invoked as a trait of potential invasiveness (Boyd et al., 2009; Nagel and Griffin, 2001) although some invaders may have higher CC than their native congeners (e.g. McDowell, 2002). While CC_{area}, C_{mass}, C_{area}, N_{area} were the same between sun and shade and within the range of values reported for the native range (Petritan

et al., 2010), they were higher in sun than in shade in the invasive range, again indicating a foliar functional differentiation between light conditions. Another indicator of higher phenotypic plasticity in the invasive range is the variability of the values recorded for the different functional traits, which were systematically greater in NZ than in France (see standard errors in Table 1 and Fig. 3).

The degree to which these range-level differences are plastic or genetic remains unknown. Several studies have shown that invasive populations were more plastic than native populations (see Bossdorf et al., 2005) but whether these trait shifts result from environmental variation, pre-adaptation or post-introduction evolution remains unclear. We cannot fully exclude genotypic differences between the studied populations since the geographic origin of introduced populations in NZ is unknown and we obviously sampled only a limited part of the native genetic pool (Petit et al., 2003). However, a recent cross-continental common garden experiment investigating this issue with the closely related Norway maple, *A. platanoides,* revealed that populations of native and invasive origins were not genetically different (Lamarque et al., 2015). Given the long generation time of *A. pseudoplatanus* and its short residence time in New Zealand, it is also unlikely that post-introduction evolutionary changes has time to play out (De Kort et al., 2013).

Environmental variation between the two study regions may be important. Even if we selected sites so as to minimize differences in abiotic conditions (see Appendix A in Supplementary material), the two regions slightly differ by their macroclimatic (higher annual rainfall and trend towards milder winters in NZ than in N France) and microclimatic conditions (evergreen forest in NZ *vs.* deciduous forest in N France), which might extend leaf phenology and the growing season (Harris and Decourtye, 1991). While the 'sun' and 'shade' sites in the native and invaded ranges were carefully selected to be comparable in terms of light environment, it is possible that leaf-level light availabilities differed between NZ and France. Growth rates in mid- to late-successional species have been reported to saturate at surprisingly low light levels (e.g., 1% full sun to achieve half growth saturation in the related North American species *A. saccharum*; Pacala et al., 1994). In the current study, 'shade' sites were < 5% ambient light ('deep' to 'moderate' shade *sensu*, Pacala et al., 1996), whereas 'sun' sites were > 12% ('small gap' to high light *sensu,* Pacala et al., 1996). Therefore, the different responses to light between native and invasive *A. pseudoplatanus* populations may partly be due to fine-scale differences in the local light environments. However, given the discrete light level categories (sun *vs.* shade) for each population were assigned functionally from the forestry literature (Pacala et al., 1996) and several sites were sampled in each range to reduce the chance of any systematic range-level light level differences, it is highly unlikely that any range-level light level differences drive the trait patterns we report. Phenotypic plasticity is thus likely an important factor explaining the invasive success of *A. pseudoplatanus* in New Zealand.

4.3. Does A. pseudoplatanus escape the growth-survival trade-off in its exotic range?

The growth-survival trade-off hypothesis predicts that growth rates in high light and survival in low light are inversely correlated across species (Kobe et al., 1995; Valladares and Niinemets, 2008). *A. pseudoplatanus* appears far less constrained by this trade-off in NZ than France, as we observed greater height and radial growth in invasive populations, but also older saplings, irrespective of light conditions and despite similar light environments across regions. The difference of survivorship was particularly pronounced in the shade; while very few saplings were more than 6 years old in either light environment in the French populations, most saplings were substantially older in the understory of NZ forests, even in the shade. Since the species does not build a seed or seedling bank (Jones, 1945), we can discard any storage effect. In addition, shade conditions were maintained all the year in NZ

forests since they were dominated by evergreen broad-leaved species and podocarps. *A. pseudoplatanus* saplings were not suppressed in shade, as revealed by the relationship between age and height (steeper slopes in France than NZ; Fig. 3c). This apparent relaxation of expected growth constraints under low-light suggests that the invasive populations are capable of infiltrating and establishing in closed-canopy forests, where they can subsequently accumulate a growing sapling bank, which may confer it a competitive advantage on native species when a canopy gap is created (Closset-Kopp et al., 2007). This competitive advantage is reinforced by growth performance, since increments in NZ were much higher than those observed in France for both height and diameter growth, especially in shade conditions (respectively 3.6 and 4.7). Interestingly, the relationship between height and diameter was the same between sun and shade in NZ, whilst in France trees clearly showed an elongation response to light (see Fig. 3a). Stem elongation is a typical shade-avoidance trait, known for being suppressed in shade-tolerant species (Gommers et al., 2013). Due to its fast growth under different light regimes, *A. pseudoplatanus* may reach the canopy before natives, reproduce and disperse seeds around, contributing to its invasiveness in the exotic range.

Such a release from the growth-survival trade-off has previously been shown for the closely related *A. platanoides*, which displays both high survivorship in low light and high growth rates in high light conditions compared to the native species (Martin et al., 2010). A similar release has also been reported for other invasive species (Lei and Lechowicz, 1990; Pattison et al., 1998) and advocated as a common attribute of successful forest invaders (Closset-Kopp et al., 2007). However, the physiological mechanisms behind this hypothesis have largely been unexplored; our results support the idea of shift towards greater shade tolerance in NZ, but not at the expense of fast growth in high light conditions.

5. Conclusion

We established that *A. pseudoplatanus* adopts different growth performances, and physiological and metabolic strategies in its invaded and native ranges under different light regimes, as a plausible consequence of different environment conditions. Those likely include fine climatic variations over the year and release from natural enemies. These differences highlight the importance of considering range-level variation in functional trait with responses to light being a particularly important factor in forests. Our results provide an important step toward establishing and understanding how shade tolerant tree species shift their individual growth, population dynamics and photosynthetic function in the invaded range compared to the native range. However, home-and-away common garden experiments are needed to fully disentangle the respective role of phenotypic plasticity, environmental variation, pre-adaptation and post-introduction evolution in successful invasions. We encourage cross-continental comparisons across more regions and including more invasive plant species, to cover a range of climatic and biotic conditions and provide more robust tests of the influence of enemy release and extended leaf phenology on invasion success.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ppees.2017.11.001.

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