

Differential growth patterns and fitness may explain contrasted performances of the invasive *Prunus serotina* in its exotic range

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Abstract This research investigates why the invasive American black cherry tends to dominate the forest canopy on well-drained, nutrient-poor soils, but usually hardly establishes on both waterlogged and calcareous soils in its exotic range. *Prunus serotina* was sampled from four soil types and two light conditions, to measure (1) radial growth; (2) height growth compared to the main native competitor, *Fagus sylvatica*; (3) leaf traits; (4) seed production; and (5) rate of fungal attack. We found that *P. serotina* invested a significant amount of energy in height growth and seed production on well-drained, nutrient-poor soils. These characteristics enabled it to rapidly capture canopy gaps and subsequently exert a mass effect on neighbouring stands. On moist soils, we found irregular growth patterns and high rates of fungal attack, while on calcareous soils, leaf traits suggested a low nitrogen assimilation rate, limiting the production of N-containing compounds. We conclude that *P. serotina* fails on waterlogged and calcareous soils because it is unable to allocate sufficient energy to fruiting and/or height growth. Conversely, it succeeds on well-drained, nutrient-poor soils because of high fitness which increases its invasiveness.

Keywords Height growth · Leaf traits · Plant fitness · *Prunus serotina* · Tree ring analysis

Introduction

A leading idea in invasion ecology is that exotic invasions result from a complex interaction between species invasiveness (i.e. the characteristics of non-native species that enable them to efficiently invade an ecosystem) and ecosystem invasibility (i.e. the properties of the new recipient ecosystems that make them susceptible to invasion) (Lonsdale 1999; Alpert et al. 2000). Most studies have investigated traits that predispose a non-native species to become a successful invader, i.e. to increase in abundance over native species (Williamson and Fitter 1996; Pyšek et al. 2009). Some morphological, demographic and life-history traits are now universally associated with invasiveness in vascular plants, such as, tall stature, vigorous vegetative spread, extended flowering period and a high fecundity (Rejmánek and Richardson 1996; Crawley et al. 1997; Kolar and Lodge 2001; Pyšek and Richardson 2007). However, recent studies have suggested that the role of individual traits, which to a large extent is stage- and habitat-specific (Kolar and Lodge 2001; Pyšek and Richardson 2007), is overestimated due to residence time (Bucharova and van Kleunen 2009; Pyšek et al. 2009), stage of the invasion process (Pyšek et al. 2009) and the effect of trait combinations. Surprisingly, ecophysiological

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traits have been poorly explored (Pattison et al. 1998; Durand and Goldstein 2001; Milbau et al. 2003). Most studies have compared the growth of invasive species in their native and exotic range (Zou et al. 2007) or the growth of invasive and native co-occurring species (Durand and Goldstein 2001; Pyšek and Richardson 2007), without looking at how growth varies among habitats in the exotic range. The first goal of this study is to analyze a set of ecophysiological traits of an exotic tree species in contrasted habitats.

Typically, successful invasive species associate fast growth to high fecundity which allows them, following a disturbance, to pre-empt space before natives can re-establish and subsequently to rapidly reach maturity to produce a mass of offspring (Hayes and Barry 2008). This strategy is associated with a better ability to capture space and resources (Harrington et al. 1989) and/or to a lower investment of energy to construct biomass (Dukes and Mooney 1999; Nagel and Griffin 2001) compared to natives. Moreover, many authors have suggested that greater phenotypic plasticity and in particular, a highly plastic response to light, is likely to confer greater invasiveness (Rejmánek and Richardson 1996; Yamashita et al. 2000; Durand and Goldstein 2001; Valladares et al. 2007), allowing invaders to take advantage of a variety of habitats (Dong and de Kroon 1994; Richards et al. 2006). The ability of plants to capture and utilize light is indeed an important determinant of species recruitment, growth potential and fitness, which is of utmost importance for alien species invading forest ecosystems (Standish et al. 2001). Rapid height growth is a well-known trait of successful gap invaders, such as *Ailanthus altissima* (Knapp and Canham 2000) and *Prunus serotina* (Closset-Kopp et al. 2007), and seems to be achieved primarily through greater photosynthetic capacity (Pattison et al. 1998). If an invasive species is to be successful in a fluctuating environment such as a chronically disturbed habitat, it has to be more 'plastic' in its response to different light levels than natives (Pattison et al. 1998) or, at least, to exhibit a higher fitness homeostasis (Hulme 2008). An advantage of studying trees when tackling this issue, which has been rarely considered until now in invasion ecology (but see Vanhellefont et al. 2010), is that age-specific size and growth can be measured retrospectively over long time spans. Here we took advantage of these properties to investigate growth patterns of an alien tree species across different gradients of resources.

Optimal partitioning models and life history theories suggest that plants located in various environments show differences in the partitioning of biomass among plant organs, which optimizes the capture of nutrients, light, water, and carbon dioxide in a manner that maximizes plant growth rate (Dewar 1993; Bazzaz 1996; McConnaughay and Coleman 1999). No species can maximize growth, maintenance, storage and reproduction across all environments. Greater allocation to one function results in a cost to other functions, potentially explaining why the success of invasive species is habitat-dependent and may change during a plant's lifetime (Funk and Vitousek 2007). However, it has been repeatedly suggested that invasive species are less constrained than natives by these ecological trade-offs (Sanford et al. 2003; Closset-Kopp et al. 2007). For example, the 'enemy release hypothesis' predicts that if an invasive species is released from a constraint present in its native range (e.g. diseases or specialized herbivores), it will increase fitness by several mechanisms, among which is a reallocation of resources from defence to growth (Crawley et al. 1997; Keane and Crawley 2002). Here, we compared the patterns of resource allocation to different functions across contrasted environments.

In temperate Europe, the American black cherry (*Prunus serotina* Ehrh.) is currently considered as one of the most aggressive exotic tree species in forests, threatening both biodiversity and wood production (Verheyen et al. 2007). It thrives on well-drained, nutrient-poor soils, where it often forms pure stands, but fails to invade on waterlogged and calcareous soils (Starfinger 1997; Godefroid et al. 2006; Chabrerie et al. 2007; Verheyen et al. 2007). Unanswered questions are why the invader performs differently among soil types and most aggressive exotic tree species in forests why it is not successfully outcompeted by the common beech (*Fagus sylvatica* L.). Indeed, the latter grows on the same soil types, where it is widely recognized as the best competitor in European forests, due to its high shade-tolerance and late-successional status (Ellenberg 1996).

In this study, our second goal is to compare performances of *Prunus serotina* among contrasted habitats, by analyzing radial and height growth, leaf traits, seed production, and pathogen fungus attacks among four soil types and two light conditions (understory vs. opening). We also compared height

growth patterns between *Prunus serotina* and its main native competitor in the study area, the common beech (*Fagus sylvatica*). Our research hypothesis was that the greater invasion success of *Prunus serotina* under certain soil conditions results from a fast height growth and high seed production in response to canopy opening, which enables it to pre-empt space before natives.

Materials and methods

Study species

The American black cherry (*Prunus serotina* Ehrh.) is a gap-dependent tree species native to North America, which was introduced in many European forests for ornamental, timber production, and soil amelioration purposes (Starfinger 1997). For several decades it has spread throughout the temperate forests of Western and Central Europe, particularly on well-drained, nutrient-poor soils (Starfinger 1997; Chabrierie et al. 2007; Verheyen et al. 2007; Chabrierie et al. 2008). As seeds, *Prunus* is able to enter closed-canopy forests to form a long-living sapling bank known as ‘Oskar syndrome’, a strategy missing in native tree species. When a canopy gap occurs, saplings are released from suppression and grow rapidly to reach the canopy and fill the gap (Closset-Kopp et al. 2007). In clearcuts, large gaps and sparse tree plantations, *Prunus* often forms a low, closed carpet of small trees, which impedes natural regeneration of native tree species (Chabrierie et al. 2007). In light conditions, individuals become fertile at an average age of 8 years and produce thousands of seeds dispersed by gravity (ca. 95%), birds and mammals (ca. 5%) (Pairon et al. 2006; Closset-Kopp et al. 2007). *Fagus sylvatica* L. seems to be the only native tree species able to compete with *Prunus* under certain soil conditions (Chabrierie et al. 2007). In its native range, *Prunus* colonizes openings in mixed temperate forests and may transiently dominate stands during secondary succession (Auclair and Cottam 1971). It can grow in a wide range of edaphic conditions, except on very swamp and very dry soils (Marquis 1990; Starfinger 1997). However, it rarely achieves good quality trunks, except on meso-hydric, nutrient-rich soils (Hough 1965; Starfinger 1997), especially on the Allegheny plateau (USA) where the

European founder populations originate (Pairon et al. 2010, Petitpierre 2008).

Study site

This study was conducted in the temperate, mixed forest of Compiègne, located in northern France (49°22′N, 2°54′E, 32–148 m altitude, 14,417 ha area). This is one of the largest forests in France and the most heavily invaded by *Prunus*. The climate is of oceanic type, with a mean temperature and annual rainfall of 10.3°C and 677 mm year⁻¹, respectively. The geological substrate mainly consists of Palaeogenous sand (ca. 60% of total area) and Cretaceous chalk (ca. 20%), locally covered by Quaternary loess and alluvial deposits. The forest of Compiègne is characterized by a high diversity of soil conditions from acidic, nutrient-poor soils (podzols, alisols) to basic (rendzinic leptosols) and hydromorphic (gleysols) soils, through luvisols and cambisols (FAO-UNESCO world reference nomenclature).

The forest is managed as a high forest system dominated by even-aged plantations of common beech (*Fagus sylvatica*) (44% of the forest area), sessile (*Quercus petraea* Liebl.) and pedunculate oak (*Quercus robur* L.) (25%) and scots pine (*Pinus sylvestris* L.) (7%). Forest management represents the main disturbance regime, through periodic large-scale clearcuts (return interval of 110 and 180 years for beech and oak, respectively) and thinnings (every 4–10 years). Natural disturbances mainly consist of storm-induced treefalls with the last severe episodes occurring in 1982, 1983, 1984–1985, 1987, 1988, 1990–1991, 1993 and 1999.

Prunus is thought to have been introduced to the forest in the mid-eighteenth century, but was only reported as an invasive species in 1970. It has now spread to approximately 80% of the total forest area. While it massively invades podzols and luvisols, it usually fails to invade moist or calcareous soils. Local fungi may also influence the species’ invasiveness. The infection of roots by ectomycorrhizal fungi is the rule, and fungal diseases are quite common, especially on moist soils (pers. obs.). Two pathogen species have been identified in the study area: an almond powdery mildew (*Podosphaera tridactyla* (Wallr.) de Bary 1870; Ascomycota: Erysiphales; anamorph: *Oidium passerinii* G. Bertol.) and a cherry leaf spot (*Guignardia* sp.; Ascomycota: Botryosphaeriales; anamorph.: *Phyllosticta* sp.).

A recent genetic analysis revealed that all *Prunus* populations of Compiègne were genetically similar and originated from the same source population (Pairon et al. 2010).

Material collection and laboratory measurements

Where possible, we followed a factorial sampling design incorporating two factors: soil type and light condition. Four soil types were included; the first three corresponded to well-drained soils arranged along an increasing soil nutrient/pH gradient: haplic podzols (pH range = 4–4.5), luvisols (4.5–5.5), rendzinic leptosols (7–8), while the fourth corresponded to temporarily waterlogged soils i.e. gleysols (4.5–7). Two light conditions were studied. In the full light condition, the sampled trees were not overtopped by other trees. In the shade conditions, the sampled individuals were growing beneath the closed canopy of other deciduous tree species. We included stands in which the dominant canopy tree species were beech and oaks. To avoid potential biases related to spatial autocorrelation, we sampled different stands per soil type and per light condition, which were distributed over the entire Compiègne forest area. For each of the following studies we collected a specific set of *Prunus* individuals.

Radial growth

Wood cores were taken in summer 2005 at a height of 1.30 m from a first set of 81 *Prunus* canopy trees (i.e., trees from the top-layer) for subsequent dendrochronological analyses. Due to the rarity of the species on certain soil types we had to use an unbalanced sampling design: 31, 24, 8, and 18 individuals were sampled on podzols, luvisols, leptosols, and gleysols, respectively. Wood cores were scanned with a flatbed scanner and analyzed using WinDENDRO[®] v. 2008 software (Regent Instrument Inc., Québec, Canada): tree rings were counted and measured for width (0.01 mm). The resulting ring-width series were visually inspected and cross-dated (Stokes and Smiley 1968). Pointer years showing an abrupt change in ring width were characterized (Schweingruber et al. 1990). Ring widths were converted into basal area increment (BAI; mm² year⁻¹) to clarify environmental change-induced growth rate variations (Duchesne et al. 2003). BAI is considered as the best

measure to detect changes in tree growth (Johnson and Abrams 2009).

Height growth

Plants with rhythmic growth, like temperate trees, typically develop an annual shoot, consisting in one or more structural units. Such “growth units” (GU; Caraglio and Barthelemy 1997) result from an uninterrupted event of primary growth. Eight new individuals of *Prunus* and eight nearby, naturally regenerated individuals of *Fagus*, ca. 2 m high, were randomly uprooted for each factor combination (2 species × 4 soil types × 2 light conditions × 8 replicates; $N = 128$) in spring 2006. By combining tree ring counting to GU measurement, we found no evidence of polycyclic growth under closed canopies, nor in full light; hence, each GU corresponded to an annual height increment. The age of the sampled trees ranged from 11 to 23 years, irrespectively of species. The length of the 10 most recent GUs was measured to the nearest cm. The cumulated height of GU over the 1996–2006 period was then calculated.

Leaf traits

As the efficiency by which a species converts light, water and nutrient into biomass is mainly determined by foliar characteristics, we related the growth characteristics mentioned above to leaf trait measurements. Eight reproducing *Prunus* trees were randomly selected for each factor combination ($N = 64$). From each plant, 20 green leaves were randomly sampled during late spring 2005. Just before collection, we measured their Chlorophyll Concentration Index (CCI) using a portable chlorophyll meter (Opti-Science, Tyngsboro, MA model CCM-200). Fresh leaves were cold-stored, rehydrated by saturation (Wilson et al. 1999), weighed, and scanned with a flatbed scanner to measure the one-sided projected leaf area (LA), using Winfolia[®] v. 2004 software (Regent instrument Inc, Québec, Canada). The leaves were then dried in an oven at 60°C for 72 h and weighed again to determine their dry mass (DM). Water saturated specific leaf area (SLA), leaf dry matter content (LDMC) and leaf water content (LWC) were determined using standardized procedures (Cornelissen et al. 2003). For

each parameter, the values of the 20 samples per tree were averaged. Dry leaves were then mixed ($N = 20$) and grounded, and their organic carbon (C; Anne method) and total nitrogen (N; Kjeldahl procedure) content were subsequently determined. Leaf carbon content (LCC), leaf nitrogen content (LNC) and C:N ratio were calculated.

Sexual reproduction

As *Prunus* was almost always sterile under shaded conditions, as well as on gleysols irrespective of light conditions, it was impossible to follow the same factorial design as above. Eight fruit-bearing individuals of *Prunus* were randomly selected on each of the three well-drained soil types, in full light conditions for sexual reproduction assessment ($N = 24$). Six racemes from the crown periphery were randomly sampled from each individual. They were covered in a bag in June 2005, to avoid predation, and harvested in early September 2005, after fruit maturation for seed counting. From each individual tree, 20 seeds were randomly collected to assess their germination capacity. The endocarp and seed coat were removed to break external dormancy and facilitate water imbibition before incubation. Seeds without embryo were counted but removed from further study. The remaining seeds were treated using gibberellin growth hormone (400 mg l^{-1}) and sown in 5.5 cm Petri dishes on filter paper, which was kept moist with distilled water. All Petri dishes were placed on a table in a growth room, with a thermoperiod at 20°C day and 16°C night and a 12 h photoperiod. Seeds were considered to have germinated at radicle emergence. The assay was maintained for 40 weeks.

Fungal diseases

We randomly selected 551 invaded forest stands over the entire forest to check for the presence/absence of almond powdery mildew and cherry leaf spot symptoms on *Prunus* leaves. Of those 551 stands, 212, 210, 56, and 73 were located on podzols, luvisols, leptosols, and gleysols, respectively. In each stand, we visually inspected the leaves of each individual between late spring and early summer 2005. Once an individual was found to bear species-specific fungal damages on its leaves, the population was considered

as contaminated. A stand was considered as safe when no sign of disease was found despite a careful inspection of the leaves of all individuals.

Data analysis

As BAI values did not comply with parametric assumptions, we examined the effect of soil type on BAI using a Kruskal–Wallis test, followed by cross comparisons of mean ranks with the non parametric variant of the Tukey test (Zar 1984). A relationship between BAI and GU length in full light conditions was searched using Spearman rank correlations.

GU and cumulated height values were log transformed to meet the assumptions of parametric analysis. ANOVA with post-hoc Tukey tests were used to test the respective and combined influences of soil type, light condition, and species on the GU length (three-way ANOVA) and cumulated height (repeated measure ANOVA). A trend analysis was further performed on cumulated height curves (CHCs) to characterize height growth patterns of both species. Linear and non-linear models (quadratic, cubic, logarithmic and exponential) were statistically tested for curve-fitting; we retained the model which had the best fit (highest R^2), and the linear model when it shared the best fit with competing models.

A two-way ANOVA was used to test the respective and combined effects of soil type and light condition on leaf traits. Leaf trait values were preliminary log transformed to meet the assumptions of parametric analysis; however, SLA could not be adequately transformed and Kruskal–Wallis and Mann and Whitney tests were used instead of ANOVA. Inter-traits correlations were assessed using Spearman rank correlations.

As the seed number per raceme and germination data did not meet the assumptions of normality, we examined the effect of soil type on sexual reproduction using a Kruskal–Wallis test, followed by the non-parametric variant of the Tukey test.

Finally, we used a χ^2 test to test whether the presence/absence of pathogen fungi was biased towards the soil type.

All statistical analyses were performed with STATISTICA[®] software v. 5.1 (StatSoft Inc. 1996). Results are expressed as means \pm 1 standard error (SE).

Results

Radial growth

Dendrochronological analyses revealed that in our sample, the age of *Prunus* individuals, which were all part of the canopy, ranged from 9 to 60 years (25 years on average). The oldest established in 1945 (Fig. 1). It is noteworthy that few of the sampled trees established before 1970, while the recruitment became massive and continuous since this date. This coincides with the date at which *Prunus* was reported as an invader in the forest of Compiègne for the first time.

Nine pointer years were identified from 1972 to 2004 (i.e. when the number of values is suitable for statistical analyses). Four of the years corresponded to a strong radial growth decrease (negative pointer

years): 1976, 1995, 1999, and 2004. Five other years were characterized by a strong radial growth increase (positive pointer years): 1977, 1984, 1987, 1993, and 2000 (Fig. 2).

BAI patterns were similar across soil types, except for the years 1988, 1989, 1996, and 1999, for which BAI was significantly lower on leptosols compared to the other soil types ($P < 0.05$). Visually, variations were more important before 1976, especially on gleysols, but the difference was not significant due to the low number of samples.

Height growth

In full light conditions, GU length correlated with BAI only for a limited number of years, namely 2001 ($\rho = -0.687$, $P < 0.001$), 1999 ($\rho = 0.577$, $P < 0.01$) and 1996 ($\rho = 0.516$; $P < 0.01$). Short GUs were

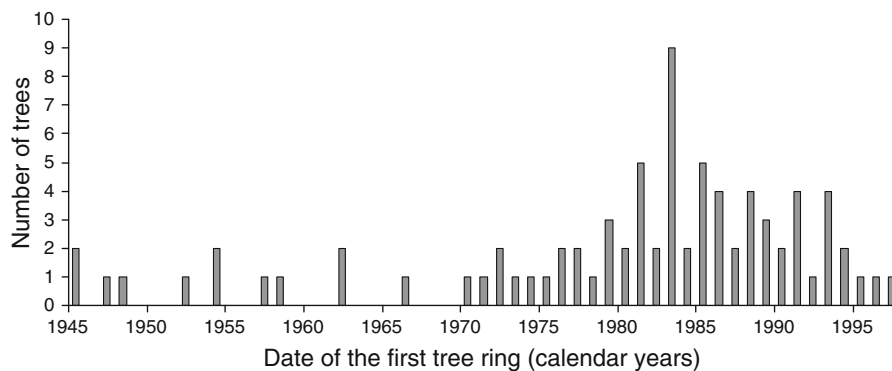


Fig. 1 The number of the sampled *Prunus serotina* canopy trees as reconstructed from dendrochronological analyses

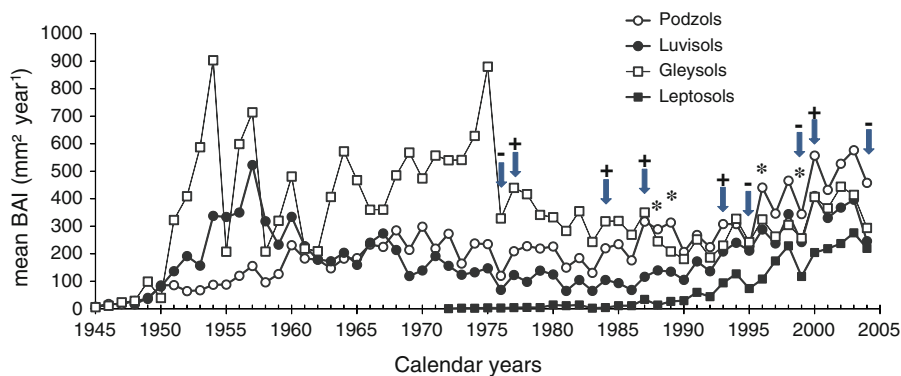


Fig. 2 Basal area increment (BAI) of *Prunus serotina* across different soil types. Values were averaged for each year and each soil type, and expressed in $\text{mm}^2 \text{year}^{-1}$. Results of a

Kruskal–Wallis test for the effect of soil type are shown with their level of significance: $*P < 0.05$. Arrows indicate the negative (–) and positive (+) pointer years

observed in 1997, 1999, 2001 and 2003, while long ones were recorded for 1998, 2000, and 2002.

Irrespective of light conditions, GUs were significantly longer for *Prunus* than for *Fagus* until the year 2000; after which point differences were not significant, except in 2005 (Table 1). The interaction with soil type was significant along the whole chronosequence, except in 2003, with *Fagus* performing better on luvisols and gleysols and *Prunus* on podzols, compared to the other soil types. Hence, the two species exhibited different height growth patterns with respect of soil type. Light availability significantly increased GU lengths only from 2000 onward, irrespective of the species and soil type.

The shape of the CHCs shows that height growth patterns of saplings strongly changed over the 10 years study period. For the two species, the slope of the CHC varies among the different environmental conditions (Table 2). *Prunus* exhibited a significantly higher cumulated height than *Fagus*, irrespective of soil and light conditions. The significance of the interactions between year and each of the three other factors (as well as their two-by-two combinations) indicates that year-to-year differences in cumulated height are context-specific, i.e. dependent on both species and environment. This is also reflected by the CHCs (Fig. 3). Trend analyses revealed that in shade conditions, irrespective of the soil type, a logarithmic model provided the best fit for *Prunus* CHC (Fig. 3a) while a linear model fitted the *Fagus* CHC the best (Fig. 3c). Conversely, in full light conditions, a linear

Table 2 Analyses of variance for cumulated height of *Fagus sylvatica* and *Prunus serotina* among the different soil types ($N = 4$), light conditions ($N = 2$), years ($N = 10$) and their interactions

Source of variations	Cumulated height	
	df	F value
Year	9	4.06***
Species	1	16.39***
Soil	3	1.29 NS
Light	1	0.12 NS
Year × species	9	13.40***
Year × light	9	15.90***
Year × soil	27	2.81***
Species × soil	3	0.46 NS
Species × light	1	0.43 NS
Soil × light	3	2.49 NS
Species × light × soil	3	4.72 **
Year × species × light	9	3.59 ***
Year × species × soil	27	3.52 ***
Year × light × soil	27	2.16 **
Year × species × light × soil	27	1.10 NS

F values and significance level from repeated measure ANOVA are presented: NS not significant, ** $P < 0.01$, *** $P < 0.001$

model provided the best fit for *Prunus*, irrespective of soil type (Fig. 3b). *Fagus* exhibited linear curves on gleysols and luvisols (Fig. 3d), with a steeper slope than for *Prunus* in the latter case (18.4 vs. 17.0) but exponential CHCs on leptosols and podzols.

Table 1 Analyses of variance testing the effect of soil type ($N = 4$), light conditions ($N = 2$), and their interactions on the length of yearly growth units (GU) for *Fagus sylvatica* and *Prunus serotina*

Source of variations	df	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005
Species	1	38.97***	30.55***	14.22***	12.00***	5.96*	0.66 NS	0.04 NS	1.44 NS	0.00 NS	5.29*
Soil	3	1.62 NS	2.08 NS	4.91**	3.03*	2.13 NS	1.12 NS	2.44 NS	2.96*	0.18 NS	8.29***
Light	1	0.33 NS	0.83 NS	0.23 NS	0.04 NS	4.14*	12.57***	23.88***	46.72***	82.85***	159.15***
Species × soil	3	2.94*	4.74**	4.31**	4.84**	4.70**	4.60**	3.86*	0.82 NS	5.06**	4.85**
Species × light	1	0.05 NS	3.31 NS	0.02 NS	3.17 NS	0.95 NS	0.21 NS	1.95 NS	0.07 NS	0.66 NS	14.49***
Soil × light	3	3.39*	3.51*	1.85 NS	2.34 NS	0.51 NS	0.76 NS	0.15 NS	1.22 NS	1.28 NS	7.42***
Species × soil × light	3	2.15 NS	2.23 NS	0.58 NS	0.16 NS	3.40*	2.07 NS	4.49**	2.14 NS	4.54**	4.79**

F values and their level of significance from a three-way ANOVA are presented: NS not significant, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

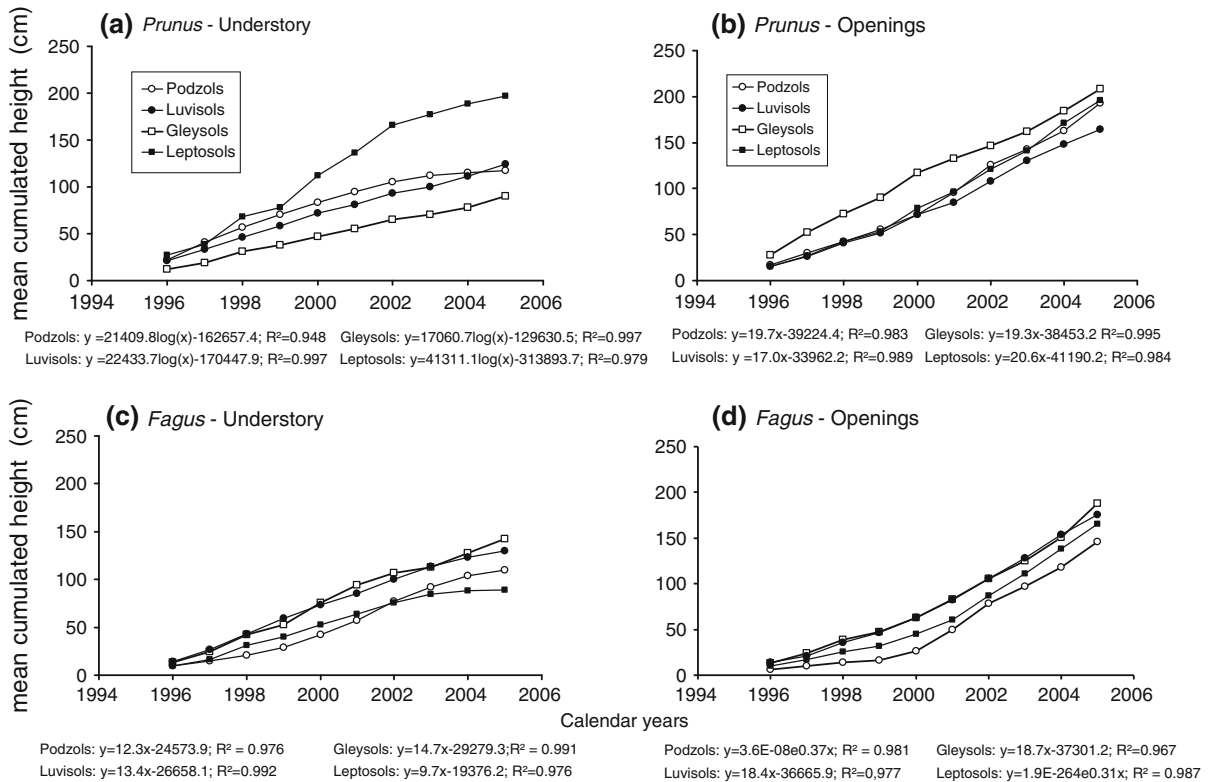


Fig. 3 Cumulated height (cm) of *Prunus serotina* (a, b) and *Fagus sylvatica* (c, d) trees growing on different soil types in forest understories (a, c) and in forest openings (b, c), as calculated from 1996 to 2005. Values are means from eight

sampled trees. The equations below each graph describe the curve having the best fit with measured data (highest R^2) according to trend analysis

Leaf traits

We found a statistically significant effect of light conditions for six of the nine leaf traits measured, with higher values produced in full light for DM, LDMC, LNC, LCC and C:N ratio, and lower values in full light for SLA (Table 3). Soil type had an effect on all leaf traits, except LA. In both understories and openings, leaves showed the highest values for LDMC, DM, LCC, LNC and C: N ratio on gleysols, but the lowest values of SLA and LWC. Among well-drained soils, no significant differences in leaf traits were found, with the notable exception of CCI, which was much higher on podzols than on the other soil types. The interaction between soil type and light was significant only for LWC and LA. Leaves from shade conditions showed higher values of LA than leaves collected in full light, except on leptosols where the

difference was not significant. The highest LWC values were recorded for sun leaves on luvisols.

Inter-trait correlations revealed few significant relationships, and most of the latter were expected (e.g. positive correlation between LWC and dry mass, C:N ratio and LCC, a negative correlation between C:N ratio and LNC). Remarkably, we found a positive correlation between CCI and LNC on leptosols under light conditions ($\rho = 0.809$, $P < 0.05$), as well as between CCI and both LWC and DM on podzols under shade conditions ($\rho = 0.762$ and $\rho = 0.786$, respectively; $P < 0.05$).

Sexual reproduction

Both the number of seeds per raceme and the number of seeds with an embryo were significantly higher on leptosols than on the other two well-drained soil types

Table 3 Analyses of variance for leaf traits measured on *Prunus serotina* leaves

Soil type		DM (g)	LA (cm ²)	SLA (mm ² mg ⁻¹)	LWC (g)	LDMC (mg g ⁻¹)	CCI	LCC (g)	LNC (g)	C:N ratio
Podzols	Shade	1.24 ± 0.25	20.4 ± 3.6	1.65 ± 0.12	3.09 ± 0.69	287.5 ± 12.9	16.1 ± 2.3	451.6 ± 34.4	20.4 ± 2.6	22.3 ± 2.9
	Light	2.10 ± 0.50	27.4 ± 5.1	1.31 ± 0.09	4.19 ± 0.68	333.2 ± 63.7	17.5 ± 3.2	577.2 ± 36.8	22.0 ± 3.1	26.6 ± 3.8
Luvisols	Shade	1.43 ± 0.33	22.7 ± 3.6	1.60 ± 0.12	3.82 ± 0.79	272.7 ± 7.5	14.7 ± 1.9	431.8 ± 67.0	20.4 ± 1.5	21.4 ± 4.1
	Light	2.38 ± 0.80	28.1 ± 3.3	1.25 ± 0.26	4.82 ± 1.18	326.8 ± 21.1	13.6 ± 2.2	523.4 ± 54.7	19.0 ± 3.4	28.8 ± 7.4
Gleysols	Shade	1.91 ± 0.62	24.3 ± 4.3	1.32 ± 0.20	3.69 ± 1.08	339.8 ± 24.2	17.5 ± 2.0	647.0 ± 58.1	22.0 ± 2.4	29.8 ± 4.7
	Light	2.33 ± 0.32	26.0 ± 3.1	1.12 ± 0.06	3.18 ± 1.09	433.7 ± 52.2	15.5 ± 2.6	819.9 ± 58.3	23.4 ± 2.7	35.2 ± 5.1
Leptosols	Shade	1.42 ± 0.26	22.1 ± 2.6	1.57 ± 0.13	3.37 ± 0.68	279.7 ± 15.8	15.4 ± 2.5	427.3 ± 47.6	19.7 ± 2.0	27.9 ± 9.0
	Light	1.69 ± 0.68	23.0 ± 5.2	1.44 ± 0.25	3.35 ± 1.33	334.0 ± 15.1	13.1 ± 1.7	552.9 ± 60.2	20.8 ± 4.0	21.8 ± 3.7
	<i>df</i>									
Soil	3	4.71**	1.62 NS	H = 14.79***	2.90*	29.23***	5.19**	58.41***	3.36*	8.32***
Light	1	26.66***	15.11***	U = 187.0***	0.83 NS	73.41***	0.01 NS	79.50***	0.37 NS	18.97***
Soil × light	3	2.19 NS	2.93*	-	3.54*	0.98 NS	2.73 NS	0.23 NS	1.05 NS	0.30 NS

For each of the 8 soil × light conditions, 20 leaves were collected on 8 randomly selected trees (N = 160 leaves per combination)

Leaves traits: DM dry mass, LA leaf area, SLA specific leaf area, LWC leaf water content, LDMC leaf dry matter content, CCI chlorophyll concentration index, LCC leaf carbon content, LNC leaf nitrogen content, C:N ratio

Values are means ± 1 SE. F values and their level of significance from ANOVA (except SLA: Kruskal–Wallis’ H and Mann and Whitney’ U test values) are given: NS not significant, * P < 0.05, ** P < 0.01, *** P < 0.001

Table 4 Seed production and germination capacity of *Prunus* among the three well-drained soil types in full light conditions

Soil type	Number of seeds per raceme	Empty seeds	Germination rate
Podzols	6.7 ^a ± 0.7	0.39 ^c ± 0.13	0.38 ± 0.11
Luvisols	6.3 ^a ± 0.5	0.12 ^b ± 0.04	0.56 ± 0.08
Leptosols	11.6 ^b ± 0.9	0.05 ^a ± 0.02	0.47 ± 0.09
	H = 13.8***	H = 7.7*	NS

Eight trees have been sampled per soil types. Seeds have been counted on six randomly taken racemes per tree. Seed viability has been assessed on 20 seeds randomly selected per tree

Number of seeds per raceme are means ± 1 SE, collected on eight trees

Empty seeds are the mean proportion ± 1 SE of seeds without an embryo, for twenty randomly taken seeds

Germination rate is the mean proportion ± 1 SE of embryo-containing seeds which have germinated

Statistical differences using Kruskal–Wallis tests are indicated by *NS* not significant; * $P < 0.05$; *** $P < 0.001$

(Table 4). The germination rate of viable seeds did not differ among soil types.

Fungal diseases

Seventy-nine per cent of the *Prunus* populations established on gleysols ($N = 73$) were attacked by at least one fungus species, against 18% on well-drained soils ($N = 56$) ($\chi^2 = 198.9$, $P < 10^{-15}$). For the *Prunus* populations established on gleysols, 42 and 70% were attacked by *Podosphaera tridactyla* and *Guignardia* sp., respectively, against 8 and 16% on well-drained soils ($\chi^2 = 103.4$ and 166.9 , respectively; $P < 10^{-15}$). On the well-drained soils, the rate of attack significantly increased from leptosols ($N = 56$) (2 and 4%), through podzols ($N = 212$) (9 and 17%), to luvisols ($N = 210$) (13 and 23%) ($\chi^2 = 6.2$; $P < 0.05$ and $\chi^2 = 12.3$; $P < 0.01$).

Discussion

General trends

In this study, we used tree rings and growth units as retrospective dynamic indicators of invasive tree growth across contrasted soil and light conditions. This approach has rarely been undertaken in invasion ecology despite its potential for predicting the future role of an invasive tree in the development of invaded forest stands (but see Vanhellefont et al. 2010). Although this study was conducted in a managed forest, our results are likely to apply to unmanaged

forests as well since similar invasion patterns were observed in old-growth forest reserves (unpublished data). We found that light levels and soil properties interacted to affect *Prunus serotina* performance among habitats, a result already suggested by experimental studies for other species (Iason and Hester 1993; Marino et al. 1997). Consistent with the growth patterns described in its native range (Pan et al. 1997), the radial growth of *Prunus* responded well to major meteorological events (e.g. drought of 1976 and 2003—visible in 2004—, late spring frost in 1995; warm spring in 1987, wet favourable conditions in 1977 and 1993), irrespective of soil type (data from the Meteo France institute). Two radial growth sequences clearly emerged from our results: before *ca.* 1985–1990, the mean BAI tended to be constant, while it increased almost linearly afterwards. This suggests a sudden exposure of the *Prunus* understory individuals to full light conditions, probably as a result of several storm events that damaged the studied forest during the 1980–1990 decade, which relaxed competition for light. Indeed, species with high potential growth rates are known for responding markedly to increased irradiance (Vanhellefont et al. 2010) and being most sensitive to nutrient availability in low light conditions (Coomes and Grubb 2000). Hereafter, when referring to radial growth, rings corresponding to tree growth before and after 1990 will be assumed to have occurred in understory and full light conditions, respectively.

Regarding height growth patterns, while there were few significant relationships shown with soil as a single factor, there were significant two- and three-way interactions of soil with light and species.

Sapling growth of both *Prunus* and *Fagus* was significantly influenced by soil type in non-limiting light conditions, whereas this response was greatly reduced in low light environments, a result already reported in experimental conditions for beech (Minotta and Pinzauti 1996). The logarithmic shape of the CHCs found in shaded areas suggests that in the absence of light in the understory, there is an initial increase in the growth of *Prunus* saplings that is subsequently restricted, in accordance with the “sit-and-wait” strategy (Starfinger 1997). The comparison with *Fagus* revealed that, at least in the short term, the gap-dependent invader was able to develop a shade-tolerance strategy similar or even better than the native late-successional species. Conversely, in gap conditions the linear shape of the CHCs indicates that *Prunus* responds to light arrival better than *Fagus*, irrespective of soil type, by allocating a significant amount of energy to shoot development and GU elongation. Such patterns characterize a light-seeking strategy often observed for shade-intolerant species (Chaar et al. 1997), enabling them to quickly capture gaps. This contrasts with the shade-tolerant *Fagus*, which is less prone to acclimate to a sudden increase in light (Bazzaz 1996; Valladares et al. 2002). Remarkably, the GU length was more closely linked to the substrate than to the light level, a finding also reported by Margolis et al. (1988) for jack pine (*Pinus banksiana* Lamb.) and by Minotta and Pinzauti (1996) for common beech. A notable exception was found on gleysols (see below). Overall, these results are consistent with the thought that invasive species would be less constrained than natives by the classical trade-off between biomass and energy conservation traits, maximizing survival in the understory and rapid height growth in openings (Walters and Reich 2000; Sanford et al. 2003; Closset-Kopp et al. 2007). However as *Fagus* has a taller stature and a higher longevity than *Prunus* when adult, it should ultimately overtop and subsequently shade out the invader, as also suggested by the shape of the CHCs.

Although differences in height growth between light and shaded conditions were expected to be associated with differences in leaf traits (Poorter and Bongers 2006), this was confirmed only for a few traits in our study: LDMC, LA, C:N ratio and LCC were significantly higher in full light than in shaded conditions.

Invasion success on well-drained, nutrient-poor soils

Consistent with the general trends discussed above, *Prunus* exhibited very similar patterns of radial and height growth on luvisols and podzols. The higher values of BAI and GU length in openings compared to understories suggest a plastic growth response of the species to light. On podzols, overall, *Prunus* grew faster than *Fagus*. However, under shaded conditions, the CHC of *Prunus* was shaped logarithmically and growth was therefore restricted in the most recent years, whereas *Fagus* continued to grow linearly. Conversely, in openings, *Prunus* not only grew faster in the early years than *Fagus*, but performed better by maintaining linear growth. On luvisols, *Prunus* and *Fagus* exhibited very similar height growth patterns, indicating that they would be very similar in the race to form the canopy and therefore early establishment may play a larger role in determining which species may dominate on this soil type.

On both soil types, leaves exhibited significant differences in traits between sunny and shaded conditions. Although a high plasticity of leaves to light conditions does not always correlate with a high acclimation potential of existing leaves to a change of light level (Yamashita et al. 2000), our results are consistent with the typical sun-shade morphological response, including a decreased SLA with increased light levels (Sack and Grubb 2002). Sun leaves exhibited higher LA, LCC, and C:N ratio but similar CCI and LNC values, compared to shade leaves, suggesting an increased photosynthetic rate (Field and Mooney 1986; Evans 1989). However, as we did not compare *Prunus* leaf traits to those of co-occurring native species, we cannot confirm that the invader has higher SLA, photosynthetic capacity per unit leaf mass and LNC than natives as often reported (Pattison et al. 1998; Leishman et al. 2007).

The low rate of fungal attack found on well-drained soils indicates that *Prunus* did not have to invest energy in defending against pathogens on these soil types. Hence, it can increase allocation to other functions, such as reproduction, resource use efficiency, or growth, which could enhance its invasiveness (Durand and Goldstein 2001).

Although we found a lower number of seeds per raceme on luvisols and podzols, compared to leptosols, it should be noted that the number of racemes

per tree was much higher on luvisols and podzols than on leptosols (pers. obs.), consistent with the results of an earlier study (843, 361, and 165 racemes per tree on luvisols, podzols, and leptosols respectively in Closset-Kopp et al. 2007). Hence, the overall reproduction rate was highest on luvisols and, to a lesser degree, on podzols.

We conclude that *Prunus* was a successful invader on well-drained, nutrient-poor soils, as its growth strategy makes it less constrained by the classic trade-off between survivorship in the shade and rapid height growth in gaps, leading to a high fitness that allows it to produce large amounts of seeds, increasing propagule pressure on the surroundings.

Invasion failure on moist soils

Radial growth patterns, before 1990, were much more irregular for *Prunus* individuals growing on gleysols than on well-drained soils, especially between 1950 and 1977. This suggests that the understory individuals may be vulnerable to summer water stress, as also indicated by the low BAI recorded for years with an exceptional summer drought (e.g. 1976). Indeed, a tree growing on moist soil with its root system located at the level of the water table most of the year may not be able to acclimate to a sudden drought, compared to a tree of the same species that grows on a dry soil (such as the podzols in our study). Conversely, radial growth was much more regular after 1990 (i.e. when trees were probably exposed to more light), and also showed a slight decrease over time. Therefore, it is possible that the overstory trees were in decline, since BAI is expected to increase linearly with increasing tree age until senescence (Duchesne et al. 2003, but see Pan et al. 1997). Although *Fagus* was not the fastest-growing native species on gleysols (e.g. *Alnus glutinosa* or *Fraxinus excelsior* are known to have higher growth rates), the GU results show that it did grow faster than the invader in the understories, having the highest ranked CHC of all the soils, whereas the curve for *Prunus* on gleysols was the significantly lowest ranked. These growth patterns of *Prunus* were consistent with the set of leaf traits which was recorded on gleysols: higher LDMC, DM, LNC and LCC, but lower SLA and LWC values, compared to well-drained soils. These traits are typically associated with a strategy of efficient conservation of nutrients to the detriment of rapid biomass production (Poorter and de Jong 1999).

Overall, our results suggest that *Prunus* invested more in radial than in height growth under shade conditions ('shade-tolerance strategy'), but that the reverse trend occurred in openings ('canopy reaching strategy'). Yet, the lack of difference in leaf traits between shade and light, as well as the low values of LWC, indicated a low plasticity of the invader on this soil type.

Another factor contributing to the invasion failure on gleysols may be the very high rate of fungus attack, suggesting that *Prunus* is more exposed to attack on these soils, and may have to invest more energy in its defence against pathogens, compared to well-drained soils. The high LDMC and C:N ratio but low SLA values can be attributed to greater allocation to energetically expensive defensive chemicals, such as lignin and cell-wall components (Groeneveld et al. 1998; Nagel and Griffin 2001). The high energy requirements for leaf construction could constrain *Prunus* to invest less energy in other strategies, such as reproductive efforts, resource use efficiency or growth, and at the very least the pathogens will reduce resources available to these alternative allocations. As a result, *Prunus*' invasiveness is low on this soil type. Note that the fact that we found no reproducing trees on gleysols during field sampling tends to confirm that the invader cannot allocate energy to reproduction on this soil type, at least not every year.

Invasion failure on calcareous soils

Although BAI increased with time, the radial growth recorded on leptosols was very low compared to the other soil types, and even nearly null before 1986 (i.e. when individuals were probably growing in the understories). At least two of the four years for which BAI was significantly lower on leptosols than on the other soil types (1989 and 1996) coincided with exceptionally dry springs. In contrast, the cumulated height was the highest on leptosols under shade conditions, but similar to other well-drained soil types in openings. It is noteworthy that in its native area, *Prunus* growth was reported as the best on meso-hydric, nutrient-rich soils (Hough 1965; Starfinger 1997).

The lack of differences in traits between shade and light leaves on leptosols attested that *Prunus* has no plastic response to light arrival.

The shade leaves, which were collected in a year matching a short GU (2005), had the lowest

chlorophyll content among the well-drained soil types, suggesting lower light harvesting capacities; this was unexpected since the vegetation layers were often denser than on podzols and luvisols (pers. obs.). The positive correlation between LNC and CCI on the one hand, and the lack of correlation between LNC and the C:N ratio, on the other hand, suggest that photosynthetic rates may be limited by the nitrogen uptake capacities of the tree. The highest values of SLA for sun leaves were recorded on leptosols; now, it has been shown that species with high SLA might experience nitrogen depletion as they grow and absorb nitrogen at a lower rate than their potential (Osone et al. 2008). Several non-exclusive hypotheses would explain a less efficient nitrogen assimilation on leptosols compared to other well-drained soil types: the competition with the dense ground vegetation formed by clonal herbs and grasses (pers. obs.); a low development of the root system due to the proximity of the calcareous bedrock; a lower efficiency of the mycorrhizal symbiosis of *Prunus*, as reported in presence of lime for other tree species (Erland and Söderström 1991; Lehto 1994; Bakker et al. 2000). Limited availability of other nutrients may also contribute to the limited invasion success on calcareous soils. We conclude that on leptosols, *Prunus* did achieve a height growth similar to other well-drained soils, but failed to develop a significant “mass effect” to be a successful invader as it rarely reached the canopy on this soil type.

Overall, our results confirm that trait attributes favouring invasiveness (Küster et al. 2008) and the interaction between those traits vary among different habitats. Where *Prunus* exhibited a high fitness (well-drained, nutrient-poor soils), it was a successful invader because it was more competitive than its main native competitor, at least during the first decade following gap creation. Conversely, where it exhibited a low fitness, it hardly established because of low height growth performances (gleysols) and/or a low seed production (gleysols and leptosols).

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