

Patterns of *Prunus serotina* invasion in two contrasting forests

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Introduction

Prunus serotina Ehrh., a North-American tree species, is considered an invasive species in Western Europe. Most studies in its introduced range focused on areas heavily invaded by *P. serotina*. Nonetheless, the presence and abundance of *P. serotina* in these areas still reflects the massive plantings of the past (Starfinger et al. 2003). The large-scale plantings resulted in a high propagule pressure of *P. serotina*. Consequently, *P. serotina* exhibited a considerable invasion rate in these areas, which lead to problems in silviculture and nature conservation (Starfinger et al. 2003). Since actual rates of invasion appear to be largely determined by propagule pressure (Von Holle & Simberloff 2005), we wanted to study the spread of *P. serotina* in an area characterized by a far lower propagule pressure where the species has not been introduced deliberately. Would we still label *P. serotina* an aggressive invader in these circumstances? Besides, *P. serotina* has not yet fully occupied its potential range in Europe, and the spread of the species is thought to be limited by dispersal (Zerbe & Wirth 2006, Verheyen et al. 2007). To develop appropriate management strategies, we should gain insight into the factors that affect the colonization rate of *P. serotina* in new sites.

In this abstract, we compare the results of two studies on 70 years of forest development in areas with a low propagule pressure of *P. serotina*. The Liedekerke forest reserve (Belgium) and the Ossenbos forest reserve (the Netherlands) were particularly appropriate for our research because they have not been managed for over sixty years and *P. serotina* established spontaneously during the forest development. Based on the observed patterns of *P. serotina* colonization in these forests, we wanted to answer the following questions: which factors influenced the spread of *P. serotina*, and did *P. serotina* act as an invasive species in the studied forests?

Materials & Methods

A detailed description of the materials and methods can be found in Vanhellefont et al. (2009) and Vanhellefont et al. (in press) for the studies in the Liedekerke forest reserve and the Ossenbos forest reserve, respectively. Table 1 shows the main characteristics of the studied forest reserves. For the two forest reserves, we reconstructed the *P. serotina* invasion based on cadastral maps and aerial photographs, tree ring analysis, forest inventories and regeneration data.

Study area & data collection

Liedekerke: The Liedekerke forest reserve has been forested until 1926, when all the trees in the study area were cut. The subsequent management resulted in heathland and coppice. After WWII, management ceased, and the vegetation developed into a mixed deciduous forest with a herb layer dominated by *Rubus fruticosus* agg. In 1986, a 12.9 ha study area was defined and 65 circular plots (radius 15 m) were installed at the intersections of a 40 m x 50 m grid. These plots were used to study the changes in structure and species composition of the forest, based on ten-year interval data. The 65 plots were inventoried in 1986; 31 of the plots were sampled in 1996; and all the 65 plots were re-inventoried in 2006. Data were collected for the tree, shrub and herb layer. In addition, aerial photographs of the period 1944–1986 were used to gain insight into the vegetation development after WWII. The colonization of *P. serotina* within the study area was analyzed by (1) identifying and locating by GPS the initial points of colonization within the entire forest reserve, (2) setting up an age distribution for the *P. serotina* in the inventory plots, and (3) predicting the presence of *P. serotina* in the 65 plots based on the plot history, the connectivity to seed trees, the basal area, the percentage of basal area made up by shade-casting woody species, the change in basal area between 1986 and 2006, and the percentage of cover by *Rubus* spp. in the herb layer. For 54 subcanopy *P. serotina*, diameter growth and age were determined based on stem cross sections or tree cores.

Ossenbos: The Ossenbos forest reserve is situated in a landscape matrix with forest patches, heathlands, and bare sand. The forest developed on the heathlands and drift sands around a mound that had been planted with pine (*Pinus sylvestris* L.) and oak (*Quercus robur* L.) around 1832. The game densities are extremely high in the forest reserve: ca. 1 ha⁻¹ of red deer (*Cervus elaphus*), roe deer (*Capreolus capreolus*), and wild boar (*Sus scrofa*). Data were collected in 40 circular plots (radius 12.6 m) located randomly at the intersections of a 50 m x 50 m grid in the entire forest and in a 70 m x 140 m study area (the core area) in the eldest part of the forest reserve. Position, diameter, and height were measured for the living trees. The height and number of saplings were recorded in the circular plots. In the core area, regeneration was enumerated in four classes: seedlings-of-the-year, seedlings < 20 cm, 20 cm < seedlings < 120 cm, and seedlings > 120 cm. Besides, in the core area, the spatial position of the seed-bearing *P. serotina* trees was noted, and we counted seeds in litter samples. In addition, diameter growth was studied for *P. serotina* growing below *P. sylvestris* or *Q. robur* (13 samples), below *P. serotina* (11), or in a canopy gap (9) in the core area.

Table 1 Characteristics of the two studied forest reserves: area (ha), geographic location, soil type, minimum and maximum monthly mean temperature (T, °C), mean annual precipitation (Precip., mm), mean basal area (BA, m² ha⁻¹), and the main tree species

Site	Area (ha)	Location N	Location E	Soil type	T (°C)	Precip. (mm)	BA (m ² ha ⁻¹)	Tree species *
Liedekerke	21	50°52'	4°07'	sandy loam	2.5–17.2	821	31.1	<i>Betula</i> , <i>Quercus</i>
Ossenbos	54	52°08'	5°48'	sand	2–17	850	26.6	<i>Pinus</i>

* *Betula pendula* Roth & *Betula pubescens* Ehrh.; *Quercus petraea* (Matt.) Liebl., *Quercus robur* L. & *Quercus rubra* L.; *Pinus sylvestris* L.

Data analysis

For both forest reserves, we first reconstructed the invasion process. Next, we tried to identify factors affecting the establishment and growth of *P. serotina*.

Liedekerke: Forest development was analyzed based on the comparison of basal area and stem density for 1986–2006 (paired samples t-tests) and 1986–1996–2006 (repeated-measures GLM). We compared the characteristics of plots with and without *P. serotina* (t-tests) and predicted the presence/absence of *P. serotina* seedlings/saplings, shrubs, and trees in the plots (logistic regression). Apart from *P. serotina*, we also looked at *Sorbus aucuparia* L., a species that frequently co-occurs with *P. serotina* (Verheyen et al. 2007). In addition, diameter growth (multiple linear regressions) and allometric relationships between age and height or diameter at breast height (curve estimation procedure) were studied for *P. serotina*.

Ossenbos: We focused on the core area, located in the oldest part of the forest, and used the data on the circular plots to check whether the patterns observed in the core area held for the younger parts of the forest. First, we analyzed the spatial patterns of trees and shrubs in the core area to determine the past establishment of *P. serotina* (bivariate Ripley's L). Second, inverse modelling was used to calculate dispersal kernels for *P. serotina* seed and seedlings in the core area. Third, presence/absence of *P. serotina* was modelled with binary logistic regressions based on the plot characteristics such as basal area of the tree and shrub layers ($\text{m}^2 \text{ha}^{-1}$), stem density (ha^{-1}), and canopy openness (%). Fifth, to explain the abundance of the seedlings/saplings of a species, we performed a data reduction (PCA) on the plot characteristics, and calculated Pearson correlations between the seedling/sapling densities and the principal components. Last, we studied allometric relationships for *P. serotina* age (curve estimation procedure) and diameter growth (multiple linear regressions). Interactive effects between the canopy tree neighbourhood and the age of the studied *P. serotina* on the achieved diameter or height were investigated with ANCOVA analysis.

Results

For the two forest reserves, we present the results on *P. serotina* spread, on the factors affecting its presence/abundance, and on *P. serotina* growth.

Liedekerke: The first *P. serotina* established around 1970–1975 on sites with high light availability. Further *P. serotina* colonization started 10–15 years later, when these trees presumably started producing seeds. *Prunus serotina* has spread through the study area. Of the 65 plots, 14 were colonized in 1986, 33 in 2006. For *S. aucuparia*, the number of plots was 38 in 1986 and 60 in 2006. The largest increase in number of plots occupied occurred between 1986 and 1996. For the 30 plots which were inventoried thrice, *P. serotina* was present in 6 (1986), 15 (1996), and 17 (2006) plots and *S. aucuparia* in 17 (1986), 28 (1996), and 29 (2006) plots. In 2006, *P. serotina* seedlings and saplings (age < 12 yr) occurred in only 10 % of the plots.

Plots with *P. serotina* were characterized by a higher connectivity to seed trees, a higher overall basal area, and a higher basal area of shade-casting trees. Plots without *P. serotina* had a higher basal area of light-demanding trees and a high cover of *Rubus*. A plot was more likely to be colonized by *P. serotina* if its connectivity to the seed trees was high.

The mean diameter growth of the subcanopy *P. serotina* in 2001–2006 was $2.8 \pm 0.2 \text{ mm yr}^{-1}$. Diameter growth (mm yr^{-1}) was determined by the diameter at breast height (dbh, in

cm) and age of the tree and competition with neighbouring trees (CI): diameter growth = $4.911 + 0.487\text{dbh} - 0.028\text{dbh}^2 - 0.077\text{age} - 0.071\text{CI}$ ($R^2 = 0.80$). The relationship between age (yr) and dbh (cm) was described most accurately by: $\text{age} = 7.254\text{dbh}^{0.402}$ ($R^2 = 0.79$).

Ossenbos: *Prunus serotina* first became established in the Ossenbos around 1940. Successful recruitment of *P. serotina* into the tree layer occurred mainly in gaps of the *P. sylvestris* - *Q. robur* canopy layer. *Prunus serotina* shrubs occurred more often below the light-demanding *P. sylvestris* and *Q. robur* than below the shade-casting *P. serotina*. In 2006, *P. serotina* was by far the most abundantly regenerating species and the only species with seedlings taller than 120 cm. *Prunus serotina* was found in all circular plots, and the high densities of seedlings smaller than 20 cm point towards the build-up of a persistent seedling bank.

The dispersal kernels showed that seeds and small seedlings of *P. serotina* mostly occurred close to a source tree while large seedlings showed the highest densities between 10–15 m from the source tree. Accordingly, the abundance of *P. serotina* regeneration was correlated significantly with seed density for small seedlings, and with basal area/canopy openness for larger seedlings. Ln-transformed abundances of *P. serotina* saplings were significantly correlated with the principal component that combined maximum tree height, basal area of tree and shrub layers, and stem density.

Radial growth of *P. serotina* was related to dbh: $\ln \text{growth} = 0.083 + 0.491\text{dbh}$ ($R^2 = 0.66$). *Prunus serotina* growing in gaps and below *P. serotina* showed a clear relationship between age and dbh ($R^2 = 0.96$ and 0.86) and between age and height ($R^2 = 0.94$ and 0.83). The increases of dbh and height with age were higher in gaps than below *P. serotina* (interaction: $p = 0.013$ and $p = 0.034$).

Conclusion

The initial *P. serotina* status was comparable in the two forest reserves: *P. serotina* had not been planted and the initial propagule pressure was low. Nonetheless, the outcome of the *P. serotina* invasion process contrasted sharply between the two studied forests: *P. serotina* was omnipresent and very abundant in the Ossenbos while the species did not act as an aggressive invader in the Liedekerke forest reserve. Consequently, it appears to be important to study an invasive species and the recipient ecosystem jointly and to gear the control measures to the characteristics of the recipient ecosystem.

Long-distance dispersal events and windows of opportunity triggered the invasion of *P. serotina*. Further colonization was directed by connectivity to seed sources and light availability. In the Liedekerke forest reserve, the presence of native shrub species, the quick canopy closure, and the recalcitrant herb layer seemed to hamper further *P. serotina* establishment. Conversely, in the Ossenbos forest reserve, the high herbivore pressure favoured *P. serotina* above native species, which resulted in *P. serotina* dominance.

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References

- Starfinger U., Kowarik I., Rode M. & Schepker H., 2003. From desirable ornamental plant to pest to accepted addition to the flora? - the perception of an alien tree species through the centuries. *Biological Invasions* 5:323–335.
- Vanhellemont M., Wauters L., Baeten L., Bijlsma R.-J., De Frenne P., Hermy M. & Verheyen K., in press. *Prunus serotina* unleashed: invader dominance after 70 years of forest development under high herbivore pressure. *Biological Invasions* DOI 10.1007/s10530-009-9529-x.
- Vanhellemont M., Verheyen K., De Keersmaecker L., Vandekerckhove K. & Hermy M., 2009. Does *Prunus serotina* act as an aggressive invader in areas with a low propagule pressure? *Biological Invasions* 11:1451–1462.
- Verheyen K., Vanhellemont M., Stock T. & Hermy M. 2007. Predicting patterns of invasion by black cherry (*Prunus serotina* Ehrh.) in Flanders (Belgium) and its impact on the forest understorey community. *Diversity and Distributions* 13:487–497.
- Von Holle B. & Simberloff D., 2005. Ecological resistance to biological invasion overwhelmed by propagule pressure. *Ecology* 86:3212–3218.
- Zerbe S. & Wirth P., 2006. Non-indigenous plant species and their ecological range in Central European pine (*Pinus sylvestris* L.) forests. *Annals of Forest Science* 63:189–203.