Present and future population dynamics of *Prunus serotina* in forests in its introduced range

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to VMBA,
who went to New York before I did
and who would have loved this

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PRESENT AND FUTURE POPULATION DYNAMICS OF *PRUNUS SEROTINA* IN FORESTS IN ITS INTRODUCED RANGE

Thesis submitted in fulfillment of the requirements
for the degree of Doctor (PhD) in Applied Biological Sciences:
Land & Forest Management

Dutch translation of the title:

Huidige en toekomstige populatiedynamiek van *Prunus serotina* in bossen in het nieuwe verspreidingsgebied van de soort

Illustrations on the cover:

Front: Fruiting *Prunus serotina* in a pine forest in Lithuania
[photograph: Quinten Vanhellemont, September 2006]

Back: Resprouts of *P. serotina* in the Heidebos nature area in Belgium
[photograph: Karen Wuyts, September 2008]

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Woord vooraf

> *If you release a species outside its usual habitat, it might simply die. In some cases, however, the so-called invasive alien species thrive and destroy local flora and fauna. As you never know how things will turn out, reducing species invasions is crucial.* *(from: www.countdown2010.net)*

Dit is een van de 'Seven steps to save biodiversity' op de website van Countdown 2010. Het is eigenlijk wel gepast om 2010, het Internationaal Jaar van de Biodiversiteit, te beginnen met een doctoraat over de invasieve Amerikaanse vogelkers. Dit boekje is echter niet geheel en al mijn verdienste. Het zou immers niet zijn wat het is zonder de bijdrage van een boel mensen, die ik daar hier en nu dan ook voor wil bedanken.

In den beginne was er Martin, die me op het hart drukte dat een doctoraat geen 9-to-5 job is en dat je het écht moet willen. Kris stelde voor om onderzoek te doen naar Amerikaanse vogelkers ofte *Prunus serotina*. Geen onbekende boomsoort! In een ver verleden waren de kleine Vanhellemontjes immers gefascineerd door de 'lijm' die uit de vogelkersen in de tuin kwam en keken ze vol bewondering toe hoe papa Vanhellemont wijn maakte van de zwarte vogelkersjes. In een klap had ik twee promotoren én een onderwerp. Zonder Kris en Martin had ik de afgelopen vier jaar niet zo veel geleerd over invasieve soorten en vogelkers en had ik nooit kennis gemaakt met de teken in het Ossenbos, de bramen in Liedekerke en het verschijnsel verdwijnende proefvlakken in Vlaams Brabant en de Antwerpse Kempen. Kris kon als geen ander enthousiast zijn over variabele data en keurige abstracts en presentaties. Dankjewel!

Het Fonds voor Wetenschappelijk Onderzoek (FWO-Vlaanderen) en het Bijzonder Onderzoeksfonds van de Universiteit Gent maakten het onderzoek financieel mogelijk.

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Er bleken wel meer mensen geboeid door vogelkers.

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Contents

List of abbreviations and symbols

Abbreviations

ΔBA	change in basal area (m^2 ha^{-1})
BA	basal area (m^2 ha^{-1})
BAL	basal area of light-demanding tree species (m^2 ha^{-1})
BAS	basal area of shade-casting tree species (m^2 ha^{-1})
CI	competition index
dbh	diameter at breast height (cm)
df	degrees of freedom
diam10	diameter at 10 cm above the root collar (cm)
GLI	gap light index (%)
h	tree height (m)
N	stem density (ha^{-1})
NL	stem density of light-demanding tree species (ha^{-1})
NS	stem density of shade-casting tree species (ha^{-1})
sd	standard deviation
STR	Standardized Total Recruits: the number of seedlings produced by a tree with a dbh of 30 cm

Symbols

n	number of plots or samples
p	significance of statistical test
r	Pearson correlation coefficient
R^2	coefficient of determination

Definition of the seedling stages used in the thesis

Stage I	seedlings resulting from seeds germinated in the year of sampling
Stage II	seedlings smaller than 20 cm
Stage III	seedlings between 20 and 100 cm tall
Stage IIIa	seedlings between 20 and 120 cm tall
Stage IIIb	seedlings taller than 120 cm

Definition of some terms used in the thesis

barochory	the dispersal of plant seeds by gravity, i.e., seeds just drop from the parent plant
basal area	the sum of the cross-sectional areas, measured at breast height, of all the trees with a dbh > 5 cm that occur in a forested area of 1 ha
connectivity	a measure of the ease of movement between two patches based on the distance between the two patches and a patch characteristic, e.g., the probability of seed dispersal from a seed tree to a regeneration patch based on the distance between the patch and the seed tree and the size of the seed tree (cf. Eq. 5.1, p 73)
dyszoochory	the dispersal of plant seeds by animals that forage on seeds for food and lose the seeds during transport or forget about seed stocks they had hidden for the winter
zoochory	the dispersal of plant seeds by animals

1 Introduction

Species have been transported to new areas, intentionally or unintentionally, ever since men started travelling and trading (McNeely 2001). However, the expansion in human mobility and trade has resulted in a sharp increase in the number of newly introduced species, mainly during the last 200 years (Mack *et al.* 2000, Lambdon *et al.* 2008). A small fraction of these introduced species has become or will become invasive in their introduced range. Those invasive species may disrupt ecosystem processes, oppress native species, and cause economic losses (Mack *et al.* 2000). Sala *et al.* (2000) showed that biological invasions are a major component of global environmental change, next to land use change, climate change, and high nitrogen deposition. As the adverse effects of invasive species have become more and more apparent, researchers all over the world have tried to gain insight into the ecology of invasions, and the number of studies focusing on invasive species has increased sharply during the last decades (Pyšek *et al.* 2006). Understanding the drivers and impacts of biological invasions may enable predicting future trends and identifying management priorities (Hulme *et al.* 2009). Biological invasions also represent ‘natural experiments’ that offer opportunities for studying the structure and dynamics of ecological communities. Investigating how ecosystems respond to the addition of new species may provide insights into ecosystem functioning (Sax *et al.* 2005).

In the following sections, we first briefly describe the invasion process and then focus on the three questions that are typically addressed in research on biological invasions: which species invade, which habitats are invaded, and how do invasive species affect the invaded ecosystem?

1.1 Invasive species

The basic definitions and concepts on biological invasions provided in this chapter are oriented towards invasive plant species although most of them may also apply to other taxonomic groups.

1.1.1 The invasion process: definitions and concepts

The terminology used to describe invasion processes and to refer to naturalized or invasive species varies widely, which has resulted in divergent interpretations and confusion on concepts and theories (Colautti & MacIsaac 2004). The definitions given below follow the standardized terminology for plant invasion ecology proposed by Richardson *et al.* (2000) and Pyšek *et al.* (2004).

Invasion is a process that requires a species to overcome a number of biotic and abiotic barriers (Richardson *et al.* 2000). These barriers, or filters, form the basis for the definition of the four stages that are generally recognized in the invasion process, i.e., introduction, acclimatization, establishment, and landscape spread (cf. Theoharides & Dukes 2007). Dependent on the barrier crossed and on the associated stage of the invasion process, a species is called alien, casual alien, naturalized, or invasive (Fig. 1.1).

Alien species are species that crossed a geographic barrier as a consequence of intentional or unintentional introductions that are the result of human activity (‘introduction’). Synonyms for alien are exotic, introduced, non-native, or nonindigenous.

Casual alien species are species that crossed an environmental barrier. They can grow and may even reproduce occasionally under the local environmental conditions (‘acclimatization’), but they are not able to form self-sustaining populations. They will only persist in areas where they are repeatedly introduced. Casual alien species are also called acclimatized, adventive, ephemeral, occasional escapes, subspontaneous, or transient.

Naturalized species overcame the reproductive barrier; they can reproduce and sustain populations over many life cycles (‘establishment’). Offspring is often found close to the adult plants.

Invasive species crossed the dispersal barrier. They generate reproductive offspring – often abundantly – at considerable distances from the parent plants, which enables the species to spread over large areas (‘landscape spread’). This definition of the term ‘invasive’ refers to the geographic and demographic status of a species, and does not include any reference to the possible environmental or economic impact of invasive species. Not all invaders are harmful species or **pests** (Richardson *et al.* 2000). The term '**transformer species**' is used to refer to the subset of invasive species that change the character, condition, form, or nature of natural ecosystems over a substantial area, relative to the extent of the ecosystem. Transformer species are sometimes also referred to as aggressive invaders.

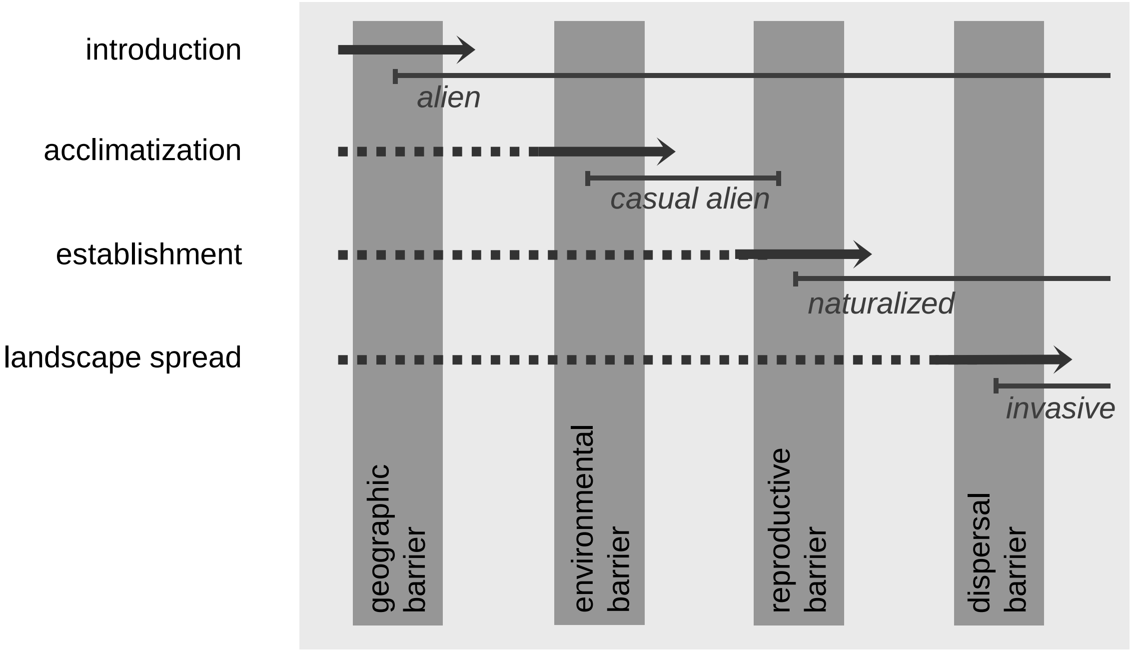


Fig. 1.1 The four stages of the invasion process, with the barriers that introduced species should overcome to become alien, casual alien, naturalized, or invasive (after Richardson *et al.* 2000)

Few introduced species proceed through the four stages and end up as an invasive species. The 'tens rule' (Williamson & Fitter 1996) suggests that around 10 % of the alien species become casual alien species, 10 % of the casuals becomes naturalized, and 10 % of the naturalized species becomes invasive. Thus, only 1 out of 1000 aliens might become invasive. The time needed to overcome the four barriers and become invasive will differ between species, and most species experience a lag phase, i.e., a delay, during the invasion process. Kowarik (1995) distinguished two consecutive lag phases: the time lag between initial introduction and establishment and the lag between establishment and subsequent spread (cf. Theoharides & Dukes 2007). The occurrence of these lag phases implies that the present invasion patterns mainly result from species' introductions and ecosystem conditions of up to a century ago (Hulme 2003). Many invasive species in Europe are indeed still expanding their ranges (Williamson *et al.* 2009).

1.1.2 Invasiveness and invasibility

Lonsdale (1999) showed that the number of invasive species in a region, i.e., the level of invasion (sensu Chytrý *et al.* 2005), is the result of the properties of the invasive species, the properties of the region, and the number of species introduced, i.e., the colonization pressure (sensu Lockwood *et al.* 2009). Understanding the dynamics of invasions requires insight into the characteristics of the invasive species, i.e., invasiveness, and the features of the invaded environment, i.e., invasibility (Richardson & Pyšek 2006). However, disentangling the effects of species invasiveness and community invasibility is difficult (Facon *et al.* 2006, Moles *et al.* 2008). Invasions are context-dependent, and species might only become invasive when certain environmental conditions are met. Moreover, some factors, e.g., propagule pressure, might affect both invasiveness and invasibility.

Invasiveness, or the invasion potential of an alien species, refers to its capacity to naturalize and spread in its introduced range. Both invasion history, e.g., residence time (the time since the first introduction) and propagule pressure, and intrinsic species traits have been found to affect species invasiveness (Richardson & Pyšek 2006, Milbau & Stout 2008b). Yet, identifying a key set of species traits that account for invasiveness has turned out to be an unrealistic aim (Williamson 1999). Nonetheless, some traits seem to be better correlated with invasiveness than others, and certain recurring combinations of traits, i.e., ecological strategies, have been found to facilitate invasion (Küster *et al.* 2008). Species traits that may positively affect the invasion potential of a species are a wide native range, high reproductive success, effective dispersal over long distances, high phenotypic plasticity, uniparental reproduction, rapid evolution, and high levels of genetic variability and polyploidy (Richards *et al.* 2006, Richardson & Pyšek 2006, Pairon 2007, Hanspach *et al.* 2008, Bucharova & Van Kleunen 2009).

Invasibility, i.e., the overall susceptibility of a region, community or habitat to invasion, cannot be inferred simply from the level of invasion. Some regions may have been subject to a larger number of introduced species, a more intense propagule pressure, or may have just encountered species with a higher invasiveness (Sol *et al.* 2008). The invasibility seems to be higher in areas or sites with a large impact of human activities, low intensities of competition, low levels of environmental stress, high resource availability, fluctuating nutrient availability, and altered disturbance regimes (Milbau *et al.* 2003, Richardson & Pyšek 2006, Hulme 2007, Chytrý *et al.* 2008, Waldner 2008). The spatial scale of the studied invasion patterns will determine which factors are important in explaining invasibility (Milbau *et al.* 2009): climate might be important on the scale of continents (Kriticos *et al.* 2003) or countries (Gassó *et al.* 2009) whereas biotic interactions will become important on the scale of a single site (Silvertown *et al.* 1994).

Propagule pressure has been identified as a major component of species invasiveness (Bucharova & Van Kleunen 2009) as well as a determinant of habitat invasibility (Von Holle & Simberloff 2005). Both components of propagule pressure, i.e., the number of individuals involved in any one introduction event (propagule size) and the number of discrete introduction events (propagule number) (Lockwood *et al.* 2005), might be affected by the pathway along which a species is introduced to a certain region. The pathways of species introduction might thus also affect the success of biological invasions (Perrings *et al.* 2005). Hulme *et al.* (2008) distinguished six main pathways of species introduction along a continuum from intentional to unintentional: release, escape, contaminant, stowaway, corridor, and unaided. These pathways are further classified according to three mechanisms of introduction: the import of commodities, transport vectors, and natural spread from a region where the species is already alien (Fig. 1.2).

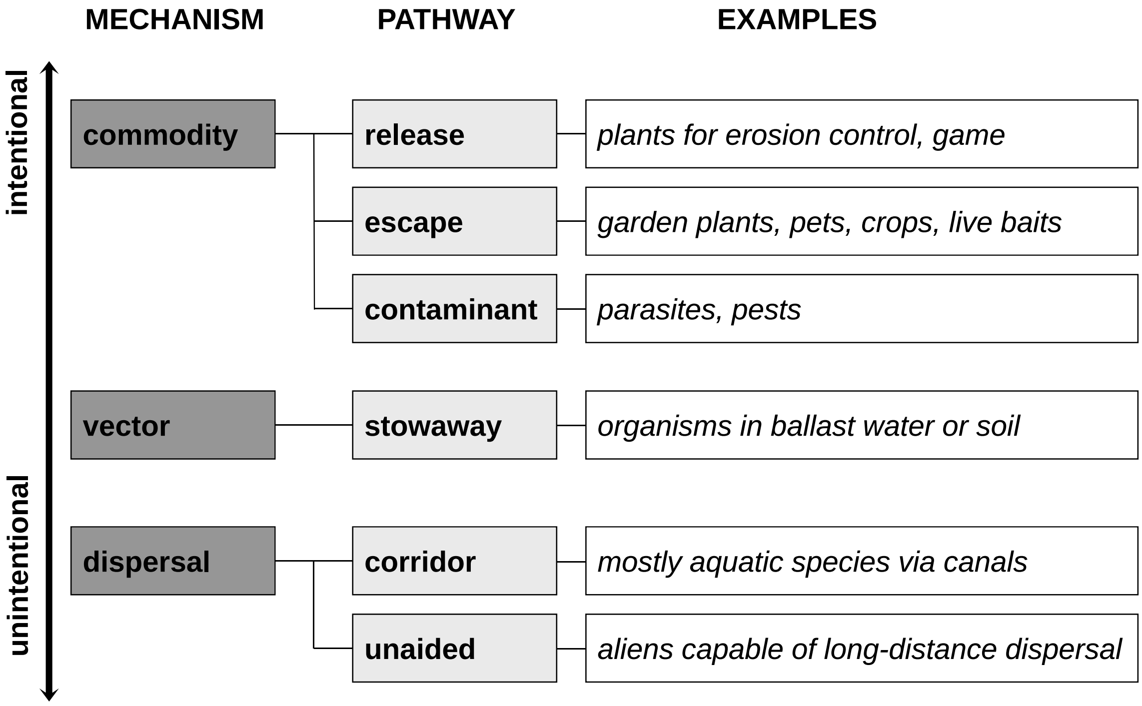


Fig. 1.2 The six main pathways of species introduction arranged along the continuum intentional-unintentional (after Hulme *et al.* 2008)

A lot of hypotheses have been used to explain invasion success or failure based on different aspects of species invasiveness, community invasibility, and propagule pressure. Recent reviews on invasion hypotheses, e.g., Inderjit *et al.* (2005), Theoharides & Dukes (2007), and Catford *et al.* (2009), pointed out that many of the hypotheses overlap or share similarities with pre-existing hypotheses and that the processes underlying the hypotheses may interact with each other. The empirical support for these invasion hypotheses is often inconsistent (Catford *et al.* 2009), and the different hypotheses are non-exclusive as they may apply to different stages of the invasion process (Inderjit *et al.* 2005, Theoharides & Dukes 2007). Below, we briefly discuss two invasion hypotheses that may be relevant for the invasive species studied in this thesis.

The **biotic resistance hypothesis** states that the biotic composition of the recipient community, e.g., the resident competitors, herbivores, and pathogens, may limit the acclimatization, establishment, and spread of an alien species (Levine *et al.* 2004). A key proposition of this hypothesis is that species-rich communities are more resistant to invasion. There is ample support for this proposition, but opposite trends, i.e., positive correlations between invasion success and species richness, have also been observed (Hooper *et al.* 2005).

The **enemy release hypothesis** states that alien plant species will experience less regulation by herbivores and other natural enemies in their introduced range, which will result in a rapid increase in distribution and abundance (Keane & Crawley 2002). The competitive release of alien species in their introduced range may not only be the result of an escape from generalist (and specialist) enemies from their native range; the impact of generalist enemies on alien species relative to the associated native species might also be lower in the introduced range (Schierenbeck *et al.* 1994, Keane & Crawley 2002, Eschtruth & Battles 2009a).

1.1.3 Consequences of biological invasions

Biological invasions affect species and ecosystems worldwide, which has resulted in ecological changes such as species extinctions, decreasing biodiversity, and biotic homogenization (McKinney & Lockwood 1999, Mooney & Cleland 2001). These ecological changes will also influence ecosystem services and human well-being (Pejchar & Mooney 2009), which will give rise to economic consequences. Yet, the impacts of invasive species are difficult to quantify (e.g., Blossey *et al.* 2001) seeing that the effect of biological invasions will depend on the characteristics of the invader as well as the invaded ecosystem (Valéry *et al.* 2008). Consequently, little data are available on the extent of the ecological and economic impact of invasive species. The database of the recent DAISIE project (Delivering Alien Invasive Species Inventories for Europe, www.europe-aliens.org) contains more than 10 000 species alien to Europe. However, for only around 10 % of the species, ecological and economic impacts were documented (Vilà *et al. in press*).

Ecological consequences of biological invasions include the impacts on native species as well as the effects on the properties of the invaded ecosystem. Invasive species have been recognized as a major driver of changes in global biodiversity (Sala *et al.* 2000). Direct effects on biodiversity result from the impact on populations of specific native species via competition for resources, via hybridization, by facilitating the spread of pathogens, or via trophic impacts such as grazing, predation or parasitism (Mack *et al.* 2000, Mooney & Cleland 2001, Hulme 2007). Invasive species affect biodiversity indirectly through the modification of ecosystem functioning via, e.g., altered rates of decomposition and evapotranspiration, reduction of the habitat quality for native species, nitrogen fixation, or altered fire regimes (Blossey *et al.* 2001, Richburg *et al.* 2001, Allison & Vitousek 2004, Brooks *et al.* 2004, Hughes & Denslow 2005).

Socio-economic consequences of biological invasions may be subtle, and they are difficult to assess. Economic impacts include both the loss in economic output, e.g., losses in crop production or a decrease in the recreational use of natural areas, and the direct costs of combating invasions, i.e., all forms of quarantine, control, and eradication (Mack *et al.* 2000). In the United States, the costs associated with invasive alien species are up to $ 120 billion per year (Pimentel *et al.* 2005). In Europe, DAISIE identified the financial costs for relevant plants and animals affecting nature conservation, agriculture, forestry, and fisheries, which will lead to an overall European cost estimate in the near future (Vilà *et al. in press*). In 2008, around € 12 billion was spent on the control of and damage caused by invasive species in the European Union; this figure certainly underestimates the real costs because many countries are only starting to record the costs (European Commission 2009).

1.2 Objectives and outline of the thesis

The North American tree species *Prunus serotina* Ehrh. is listed among the 100 worst invaders in Europe (DAISIE 2009, www.europe-aliens.org). The species grows in almost all European countries and shows a clear range expansion (Klotz 2009); it has not yet reached its potential range because its regional distribution is still limited by dispersal (Verheyen *et al.* 2007). The abundance and spread of *P. serotina* in forests and nature reserves has both ecological and economic consequences, and foresters as well as nature conservationists have invested lots of time and money in trying to control the species (Starfinger *et al.* 2003). In Flanders, the northern part of Belgium, *P. serotina* is one of the most highly invasive plant species (Verloove 2006) and the most frequently regenerating woody species in forests (Waterinckx & Roelandt 2001). People are still looking for the most effective way to control *P. serotina*, and knowledge on its biology and ecology is scattered and incomplete (Vanhellemont *et al.* 2008).

The main objective of this thesis was to gain more insight into the population dynamics of the invasive tree species *Prunus serotina* by investigating key processes in the biology of the species as well as patterns of long-term, spontaneous *P. serotina* colonization in contrasting forests. The focus of the thesis lies on pine (*Pinus sylvestris* L.) forests on sandy soil because these forests represent the habitat in which *P. serotina* occurs most often in its introduced range (Starfinger *et al.* 2003). In addition, pine plantations cover large areas in Europe, and broadleaved species have been found to establish easily in ageing pine forests (Zerbe 2002). Currently uninvaded pine stands may thus be prone to invasion by *P. serotina*, seeing the clear range expansion of *P. serotina* in Europe (Klotz 2009). The specific objectives of the thesis were:

(1) the characterization and quantification of the growth and regeneration dynamics of *P. serotina* in forest understories,

(2) the description of *P. serotina* colonization patterns in areas with an initially low propagule pressure and the identification of factors affecting the spread and establishment of the species,

(3) predicting the outcome of long-term development of pine forests in which *P. serotina* is present.

The thesis is organized in four parts (Fig. 1.3).

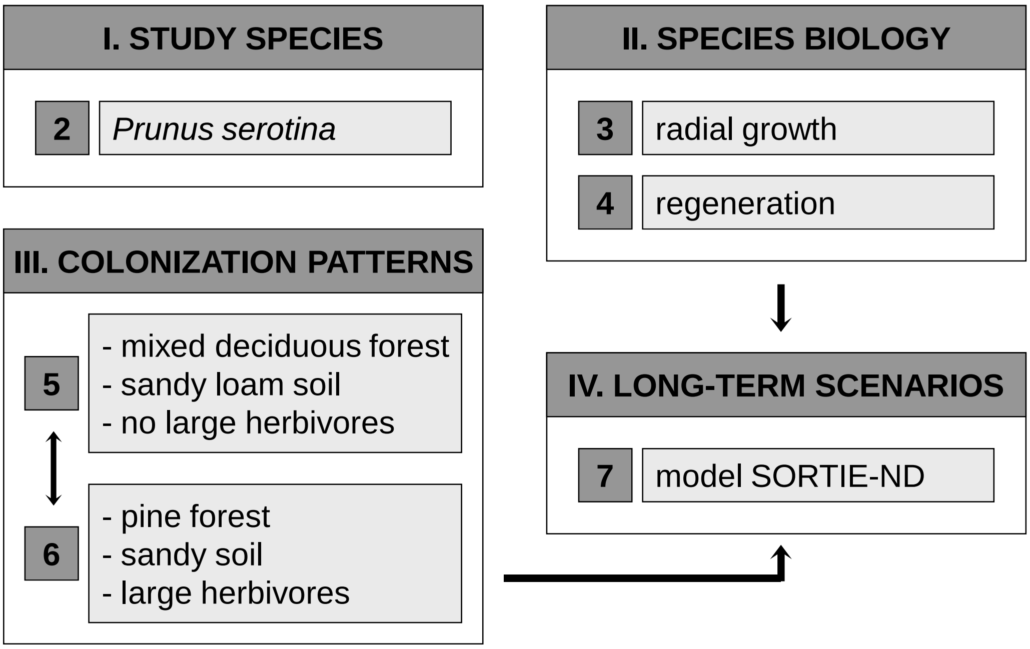


Fig. 1.3 Outline of the thesis. The four parts of the thesis are indicated with Roman numerals (I–IV); the Arabic numerals represent the chapters (2–7).

The first part (Chapter 2) is a description of the study species as well as a state of the art of the knowledge on *P. serotina* in Europe. The taxonomy and morphology, the geographic distribution and introduction history, the biology of the species, the impact of its presence in the introduced range, and the associated control measures are discussed consecutively.

The second part of the thesis deals with the growth (Chapter 3) and regeneration (Chapter 4) of *P. serotina* in the understory of pine forests on sandy soils. In Chapter 3, we quantified the radial growth of *P. serotina* in the understory of pine forests, compared the understory growth with growth in an open agricultural landscape with high light availability, and identified factors that were related to the observed variation in understory growth. Chapter 4 shows the seed set dynamics and the spatiotemporal patterns in the early regeneration stages of *P. serotina* in pine forests.

The third part consists of two case studies. We documented the colonization patterns of *P. serotina* in two contrasting forest reserves located in areas with an initially low propagule pressure of *P. serotina*. In Chapter 5, we present *P. serotina* as ‘one of the species’ in the 60-year spontaneous development of a mixed deciduous forest on sandy loam soil. Chapter 6 addresses the successful spread and the dominance of *P. serotina* in a pine forest on sandy soil that had not been managed for over 70 years and was characterized by a high density of large herbivores.

The fourth part (Chapter 7) discusses scenarios of long-term forest development with *P. serotina*. The findings of the previous parts are combined with additional data from literature to explore the long-term development of *P. serotina* in pine forests on sandy soil with the simulation model SORTIE-ND.

2 *Prunus serotina*

2.1 Taxonomy & nomenclature

2.1.1 Taxonomy

The genus *Prunus* is part of the subfamily Amygdaloideae (Prunoideae) of the family of the Rosaceae. The genus includes ca. 200 species (McVaugh 1951). Most of them grow in the temperate zone; some occur in the tropics or subtropics (Lee & Wen 2001). The most widely adopted classification of *Prunus* goes back to the 1940 work of Alfred Rehder. Rehder distinguished five subgenera: *Amygdalus*, *Cerasus*, *Laurocerasus*, *Padus*, and *Prunophora* or *Prunus* (McVaugh 1951). However, recent phylogenetic analyses identified two major groups within the genus *Prunus*: the *Amygdalus–Prunus* group and the *Cerasus–Laurocerasus–Padus* group (Lee & Wen 2001, Bortiri *et al.* 2002). The study of Lee & Wen (2001) showed that the two phylogenetic clades are not congruent with the subgeneric groups in the classification of Rehder, and they suggested a broadly defined *Prunus* genus, similar to the early work of McVaugh (1951), who recommended an 'inclusive *Prunus* genus', a world-wide and heterogeneous *Prunus* group.

Prunus serotina Ehrh. – black cherry – was classified into the subgenus *Padus* – bird cherry, along with *Prunus virginiana* L. – choke cherry – and *Prunus padus* L. – European bird cherry. *Prunus virginiana* is one of the most widely distributed tree species in North America (Preston 1961); *P. serotina* is native to the eastern part of North America (Marquis 1990); and *P. padus* is native to northern and central Europe, western Asia, and northern Africa (Leather 1996).

The species *P. serotina* contains four geographic varieties and one subspecies (USDA 2008), of which the geographic distribution is discussed in section 2.3.1:

- var. *eximia* (Small) Little – escarpment black cherry,
- var. *rufula* (Woot. & Standl.) McVaugh – southwestern black cherry,
- var. *serotina* – black cherry,
- var. *virens* (Woot. & Standl.) McVaugh – green black cherry,
- subsp. *capuli* (Cav.) McVaugh – capulí.

2.1.2 Nomenclature and etymology

Prunus serotina is sometimes named *Padus serotina* (Ehrh.) Borkh. Its common names are black cherry, wild black cherry, wild cherry, mountain black cherry, rum cherry, or cabinet cherry (Marquis 1990). In the introduced range, some of the common names refer to its native range, e.g., Amerikansk kirsebærtræ (da), merisier d'Amérique (fr), Amerikaanse vogelkers (nl), or mălin American (ro). Because of the invasive behaviour of *P. serotina*, mainly in forest understories, the species is also called 'forest pest' (en) or 'bospest' (nl).

Prunus is derived from the Latin 'prunum', i.e., plum, and 'prunus', i.e., plum tree. The Latin words were derived from the Greek προύμνον (proumnon) and προύμνη (proumné), of which the origin is unknown. The Latin word 'serotinus', i.e., coming or happening late, is a technical term from the Augustan era that replaced the classical Latin adjective 'serus', i.e., late. *Prunus serotina* thus refers to a 'plum' tree that flowers late in relation to its leaf development, cf. Spätblühende Traubenkirsche (de).

The word 'cherry' originates from the Anglo-French 'cherise', which was written down for the first time around 1236. The Old North French 'cherise' goes back to the Latin 'cerasus', i.e., cherry tree, which came from the Greek κερασός (kérasos) (Hoad 1996). The adjective 'black' refers to the colour of the ripe fruits; the adjective 'wild' refers to the fact that *P. serotina* is essentially a wild species, which is sometimes planted for its valued lumber or cultivated for its fruits (Downey *et al.* 1998).

2.2 Morphology

The morphological description of *P. serotina* is based on McVaugh (1951), Preston (1961), Sargent (1965), and Douglas *et al.* (1999).

Habit – *Prunus serotina* is a medium- to large-sized tree. In favourable conditions in the eastern United States, it can grow to a height of 30–38 m with a diameter of up to 1.5 m. However, in most of its native range, the species is much smaller, from 9 m for *P. serotina* var. *rufula*, 10 m for *P. serotina* subsp. *capuli* (Janick & Paull 2008), 15 m for *P. serotina* var. *exima*, and 12–18(–25) m with a diameter at breast height of 30–90 cm for *P. serotina* var. *serotina*. The crown is narrow, oblong or rounded, and the slender branches are arching with drooping tips (Powell & Beardmore 2002). In forests, the bole is large, branch-free, and straight to somewhat sinuous. In openings, the trunk tends to be shorter, and the crown is broad and irregular (Uchytil 1991).

Leaves – The leaves are simple, deciduous, and positioned alternately, in a single spiral, along the shoots. They are lanceolate to elliptic or ovate (Fig. 2.1, Urban *et al.* 2009). The apex is acuminate or acute; the leaf base is rounded to acute. The leaf blades are 5–12 cm long and 2.5–5 cm wide (USDA 2008), broadest near the middle or sometimes in the proximal third. The petiole is 0.8–2.2 cm long, usually with two small glands near the blade. The leaf margins are finely serrated, with simple forwardly pointing, incurving blunt teeth. The upper leaf surface is dark green with a waxy appearance; the lower surface is paler green and glabrous, sometimes with red-brown or white hairs along the basal part of the midvein. On the upper surface, the midvein and petiole are furrowed. On the lower surface, the midvein is prominent and rounded.

Flowers – The flowers appear after the leaves, at the end of March in Texas to the first week of June in Quebec. They are borne in racemes, 6–15 cm long, that develop from base to apex. The racemes appear at the end of leafy twigs that arise from last year's leafless nodes and bear 1–4 reduced leaves. A raceme can consist of 20–60 white flowers on 3–8 mm long glabrous pedicels. The calyx is cup-shaped, with five sharp-pointed oval sepals that are glabrous, 0.5–1.5 mm long. The calyx persists in the fruits. The corolla is white, saucer-shaped with five nearly circular petals that are 2.5–4 mm long (Fig. 2.1).

Fruits – Some of the flowers in a raceme form fruits: one-seeded fleshy drupes. The drupes are green to red at first, but they become a shiny dark purple or black when they ripen, in June–October. The drupes are nearly globular, with a diameter of 7–12 mm (Fig. 2.1). The subsp. *capuli* has larger cherries, with a diameter of up to 2.5 cm. The seed is an ovoid stone, which is smooth, biconvex, and often somewhat pointed. For the native range, a length of 6–8 mm is given (USDA 2008); in France, a mean length of 3.8–4.4 mm was reported (Boucault 2009).

Twigs – The twigs are slender, round, glabrous, and reddish brown. The lateral and terminal buds are small (0.5 cm), light brown, ovoid but blunt-tipped with dark-edged overlapping bud scales. The twigs have a pronounced bitter almond odour and taste.

Bark – On young stems, the bark is thin, smooth, and red-brown with conspicuous grey horizontal lenticels. On old trunks, the bark is dark brown to grey and splits up into distinctive persistent scales with upturned edges (Fig. 2.1).

Wood – The wood is diffuse-porous to semi ring-porous, close-grained, heavy, and hard. The heartwood is light to dark reddish brown. The wood density at 12 % moisture content is 500–600 kg m^{-2} (Wiselius 2001).

Roots – The roots are spreading and shallow, mostly restricted to the upper 60 cm of the soil. Occasional sinker roots extend to depths of 90–120 cm. Young *P. serotina* seedlings develop a taproot, which turns into a shallow root system before the sapling stage (Fowells 1965).

Fig. 2.1 Flowers, fruits, leaves, and bark of young and old *Prunus serotina* trees [photographs: Fien Vanhellemont]

Prunus serotina is often confused with *P. virginiana*, a mistake that probably goes back to Linnaeus' *Species plantarum* in which the type specimen for *P. serotina* was in fact a specimen of *P. virginiana*. As a result, the name *virginiana* has been used for black cherry in some botanical works of the 19th and 20th century (McVaugh 1951). *Prunus virginiana* co-occurs with *P. serotina* in much of the native range and in some parts of the introduced range. The most distinct morphological differences between the two species are the leaf margins, which are sharply serrate for *P. virginiana* and have blunt incurved teeth for *P. serotina*; the venation, with 11 pairs of secondary veins that all reach the leaf margin in *P. virginiana* and up to 60 pairs of secondary veins of which 15 pairs reach the leaf margin in *P. serotina*; the calyx, which is deciduous for *P. virginiana* and persistent for *P. serotina*; and the colour of the ripe fruits, which is mostly red for *P. virginiana* and black for *P. serotina* (Mulligan & Munro 1981, Schütz 1988).

2.3 Native range

Prunus serotina is the largest of the *Prunus* species native to North America, and it is of commercial value in some areas because of its high-quality wood. However, in most of its native range, *P. serotina* grows as small and poorly formed shrubs of low commercial value, which are nonetheless important as sources of fruit for wildlife (Marquis 1990). In some parts of the native range, *P. serotina* is listed as a weedy species (McVaugh 1951, Mulligan & Munro 1981, EPPO 2005).

2.3.1 Geographic distribution

Prunus serotina is native to the eastern part of North America (Fig. 2.2). It grows from the southern parts of Quebec and Ontario in the north to central Florida in the south. Its western boundary runs through eastern North Dakota, Minnesota, Iowa, extreme eastern Nebraska, eastern Kansas, eastern Oklahoma, and Texas (McVaugh 1951, Hosie 1969, USDA 2008). The species is also native to Mexico and Guatemala (McVaugh 1951).

The four varieties of *P. serotina* have a distinct geographic distribution (Fig. 2.2). *Prunus serotina* var. *serotina* is widespread in the eastern United States and eastern Canada and is also found in Mexico; *P. serotina* var. *rufula* and *P. serotina* var. *virens* grow in Arizona, New Mexico, and Texas; and *P. serotina* var. *eximia* occurs in central Texas on the Edwards Plateau and the Balcones Escarpment. The subspecies *capuli* is native to southern Mexico and Guatemala (McVaugh 1951, USDA 2008).

2.3.2 Habitats and communities

Prunus serotina var. *serotina* grows under a wide range of climatic and edaphic conditions (Fowells 1965). It is found from sea level to elevations of 1800–2000 m (McVaugh 1951) on a wide variety of soils, but most often on coarse, acid, and relatively infertile soils (Marquis 1990). It occurs on well-drained sites as well as on somewhat poorly drained sites, seldom in wetter conditions (Marquis 1990). *Prunus serotina* var.

serotina shows its optimum development in the cool, moist, and temperate climate on the Allegheny Plateau in Pennsylvania and New York, on sandy podzol to silt loam soils at elevations of 300–790 m. The Allegheny Plateau is characterized by a mean annual precipitation of 970–1120 mm, well-distributed throughout the year (Marquis 1990). The number of frost-free days is 100–160, and the minimum and maximum monthly mean temperatures are -7ºC in January and 20ºC in July (Fowells 1965).

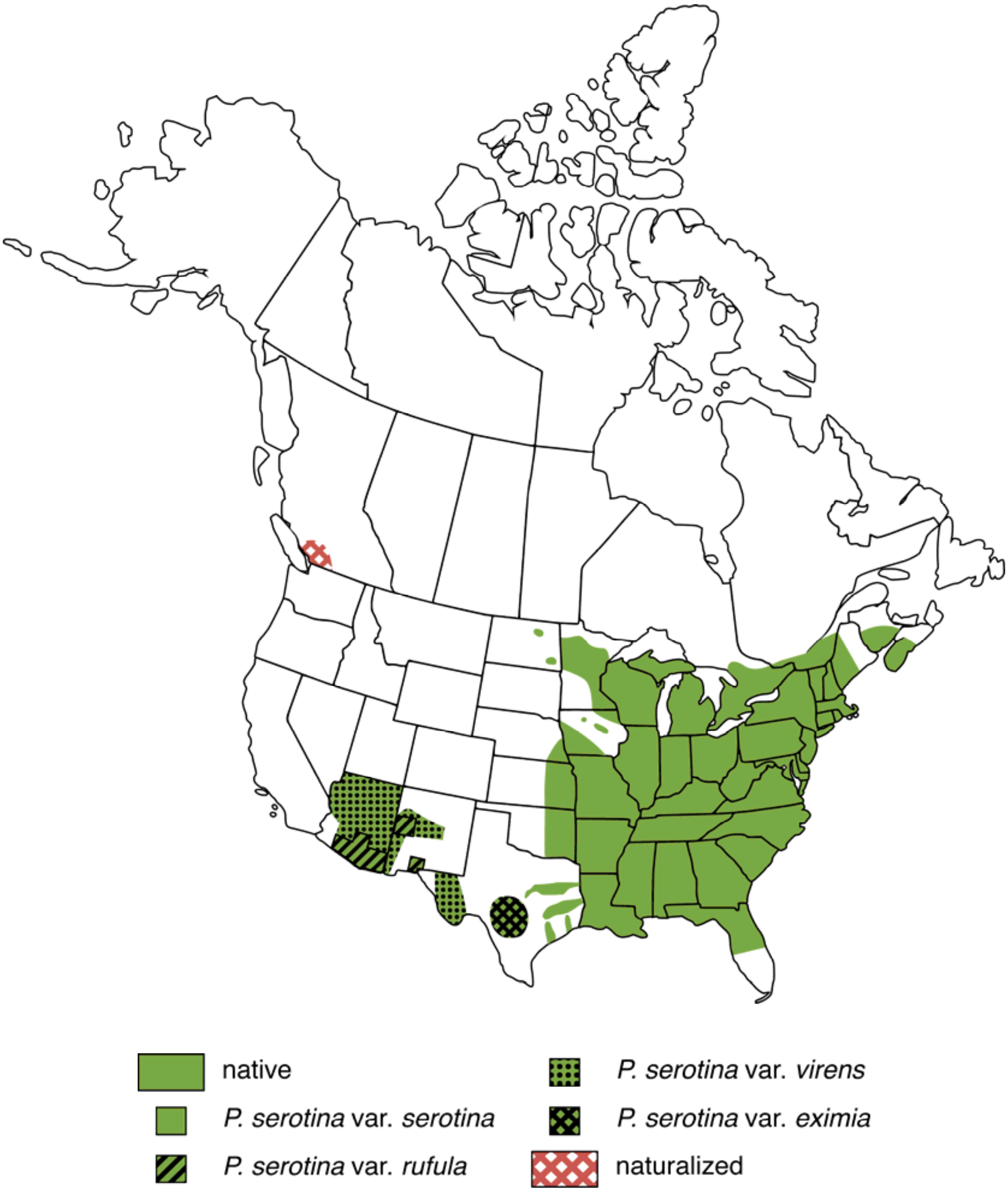


Fig. 2.2 The native range of *Prunus serotina* in North America, based on the distribution maps of the USDA (plants.usda.gov, visited 17/05/2009). Note that *P. serotina*, i.e., *P. serotina* var. *serotina*, has naturalized around Vancouver in British Columbia. [figure: Quinten Vanhellemont]

Prunus serotina mainly occurs in relatively open conditions because adult *P. serotina* trees are shade-intolerant (Powell & Beardmore 2002). It is able to colonize openings in forests and temporarily dominates forest stands during the secondary succession (Auclair & Cottam 1971). In eastern North America, the species is found as scattered individuals in many types of mesic forests and second-growth hardwood forests. In the southwestern part of its native range, *P. serotina* occurs in deciduous forests of canyons, valleys, and rich bottomlands (USDA 2008). In only one forest type, *P. serotina* is a major component, i.e., in the black cherry-maple northern hardwood forest on the Allegheny Plateau and in the Allegheny Mountain sections of Pennsylvania, New York, Maryland, and West Virginia (Marquis 1990). *Prunus serotina* var. *serotina* is also found as a weed tree in second-growth areas, old fields, and along fencerows and roadsides (McVaugh 1951, USDA 2008).

Prunus serotina var. *virens* and *P. serotina* var. *rufula* grow together with other deciduous trees mostly above 1500 m elevation, in wooded canyons in mountains in arid and semi-arid ranges (McVaugh 1951). *Prunus serotina* var. *eximia* occurs in the upper valleys and canyons of an area in central Texas (Fig. 2.2), isolated from the distributional ranges of the other *P. serotina* varieties (McVaugh 1951). *Prunus serotina* subsp. *capuli* is usually found in woods, pastures, hedges, and roadsides in anthropogenically disturbed areas (McVaugh 1951).

2.4 Introduced range

Prunus serotina had been introduced into western Canada, South America, southeastern Asia, Oceania, and Europe. The following sections on the introduction history and the present distribution of the species deal with the introduction into Europe. Nonetheless, for the sake of completeness, the other introductions are first briefly mentioned.

- *Prunus serotina* var. *serotina* has been introduced from eastern North America into British Columbia. It has naturalized at a few locations in the Vancouver area, the most densely populated area of British Columbia (Klinkenberg 2009, Fig. 2.2). Grandtner & Laplante (2009) also mention an introduction in Peru.
- *Prunus serotina* subsp. *capuli*, native to Mexico and western Guatemala, has been introduced for fruit cultivation in most of Central America, and in Venezuela,

> Colombia, Ecuador, Peru, and Bolivia, probably by the Spanish conquistadores in the 16th century (McVaugh 1951, Morton 1987, National Research Council 1989). It is naturalized in the northwestern part of South America (Morton 1987), and very common around highland villages in the Andes (National Research Council 1989). The species is unprecedented in eastern South America and the rest of the world, except for the Philippines, where the species was introduced in 1924 (Morton 1987), and northern New Zealand (National Research Council 1989).

Information on the presence, frequency, and status of *P. serotina* in European countries can be found in the 'North European and Baltic Network on Invasive Alien Species' (NOBANIS, www.nobanis.org) and the project 'Delivering Alien Invasive Species Inventories for Europe' (DAISIE, www.europe-aliens.org). Unfortunately, the information provided for some countries covered by both databases was contradictory [visited 12/05/2009]. The European and Mediterranean Plant Protection Organization (EPPO 2005) and a recent paper based on the DAISIE database (Lambdon *et al.* 2008) show yet another distribution of *P. serotina* in Europe. Additional data sources were used to resolve the contradictions and verify the similarities between NOBANIS, DAISIE, and EPPO (see Appendix 2.1).

2.4.1 Introduction history

Prunus serotina is one of the first North-American tree species that has been introduced into Europe (Starfinger *et al.* 2003). Genetic research showed that the *P. serotina* in Europe mainly comes from the United States east of the Appalachian Mountains, with the Allegheny Plateau as an important source of introduction (Petitpierre 2008, Pairon *et al. submitted*). Consequently, the introduced *P. serotina* was most probably the variety *P. serotina* var. *serotina*, which confirms the earlier statements of McVaugh (1951) and Wallis de Vries (1987). The following sections on the biology of the species and the consequences of its presence in Europe thus discuss *P. serotina* var. *serotina*. However, to improve the readability of the text, the shorter phrase '*P. serotina*' is used to refer to *P. serotina* var. *serotina* in these sections and in the remaining chapters of the thesis.

The introduction of *P. serotina* into Europe occurred via two distinct pathways: introduction for ornamental purposes (i.e., 'escape', see Chapter 1) and introduction for forestry use (i.e., 'release').

Introduction: horticulture – From the 17th century onwards, *P. serotina* has been planted in parks and gardens in Europe because of its abundant white flowers in spring and the yellow colour of its leaves in autumn (Starfinger 1997). *Prunus serotina* was planted as early as 1623 in France, 1629 in Britain, and 1685 in Germany. Afterwards, the species was introduced in almost all European countries, from the Netherlands in the 18th century; via Poland, Sweden, and Hungary in the 19th century; to Slovakia, Serbia, and Estonia in the 20th century (Appendix 2.1).

Introduction: forestry – At the end of the 18th century, *P. serotina* was recommended as a timber tree for poor soils (Starfinger *et al.* 2003). Foresters started planting the species for the production of high-quality timber around 1873 in the Netherlands (Martens 1991), around 1883 in Germany, and around 1892 in Belgium (Muys *et al.* 1992). These experimental plantations rarely produced the expected valuable timber, and most of the planted *P. serotina* showed a poor, shrub-like growth form. Nonetheless, the rapid growth and establishment of *P. serotina* and the low C/N ratio of its leaves heralded a second phase of planting (Starfinger *et al.* 2003). During the first half of the 20th century, *P. serotina* was planted massively in wind and fire breaks, as a shelter for game, and for soil improvement in the understory of pine and larch plantations (*Pinus sylvestris* L., *Pinus nigra* J.F. Arnold, *Larix* spp.) on sandy soils in northwestern Europe. It was also used for the restoration of mining land (Klotz 2009), the fixation of continental dunes, and as a competitor against grasses and heather in heathland afforestations (Bakker 1963, Starfinger & Kowarik 2003). Large-scale plantings occurred in the Netherlands between 1920 and 1950 (Van den Tweel & Eijsackers 1987), in Belgium until the 1950s (Muys *et al.* 1992), and in Germany until the 1980s (Starfinger 1997). *Prunus serotina* has also been used for forestry purposes in Hungary (Balogh *et al.* 2008), and there is one known forest plantation with *P. serotina* in Serbia (Mihailo Grbić *pers comm*). In Denmark, *P. serotina* was mainly planted in windbreaks and hedges surrounding fields (Hans Erik Svart *pers comm*). The species has also been planted along highways until the 1980s, e.g., in Germany (Starfinger 1990). The dream of producing high-quality *P. serotina* timber is still vivid, e.g., in Germany (Haag & Wilhelm 1998) and Turkey (Esen *et al.* 2007).

Establishment – A few decades after the first plantings, *P. serotina* was reported to have ‘escaped’ into the wild. The lag phase between the first introduction and the first record of establishment varies between 29 years (1796–1825) in the area of Brandenburg and

Berlin in Germany (Kowarik 1995), 87 years (1813–1900) in Poland (Tokarska-Guzik 2005), and 89 years (1870–1959) in Skåne in Sweden (Torbjörn Tyler *pers comm*). *Prunus serotina* was considered naturalized in Austria in 1970 (Maurer 1996), and near Kristiansand in the southern part of Norway in 1980 (Reidar Elven *pers comm*). For many European countries, the lag time between the first introduction of *P. serotina* and the establishment of the species is much lower than the mean lag time of 147 years that was calculated for 184 naturalized woody species in Brandenburg, Germany (Kowarik 1995).

Spread – During the second half of the 20th century, the rapid growth and spread of *P. serotina* began to worry foresters and nature conservationists in Belgium, Germany, and the Netherlands (Starfinger *et al.* 2003). The species was called a forest pest, and people switched from large-scale plantings to large-scale eradication programs. Many control measures were tested, mainly in the Netherlands (Van den Tweel & Eijsackers 1987), and several chemical, mechanical, and biological methods have been used in Belgium, Germany, and the Netherlands to eradicate the species (Starfinger *et al.* 2003). By the end of the 20th century, the aim of the control measures shifted from eradication towards control. Notwithstanding the many ongoing control measures, *P. serotina* shows a clear range expansion, and continues invading forests and abandoned fields (Klotz 2009). The species may now be considered part of the European flora (Starfinger *et al.* 2003).

2.4.2 Geographic distribution

Prunus serotina occurs in the temperate and continental regions of Europe whereas the species is rare or absent in Mediterranean areas and the northern parts of the Nordic countries (Fig. 2.3).

Prunus serotina is invasive and widespread in Belgium, Denmark, Germany, the northern part of Italy, the Netherlands, and Poland. In the Czech Republic, France, and Hungary, *P. serotina* acts as an invasive species in some areas; and the species is naturalized in England and Wales, a few locations in Luxembourg, southern Sweden, and some parts of Lithuania and Switzerland. In other European countries, *P. serotina* is not (yet) considered an invasive species. It is still rare in Austria, Bulgaria, Estonia, Norway, Romania, Serbia, Slovakia, and Ukraine. In many countries, e.g., Finland and Portugal, it is mainly found as an ornamental species in parks and (botanical) gardens. *Prunus serotina* is absent in Albania, Iceland, Ireland, Montenegro, and Turkey (Appendix 2.1).

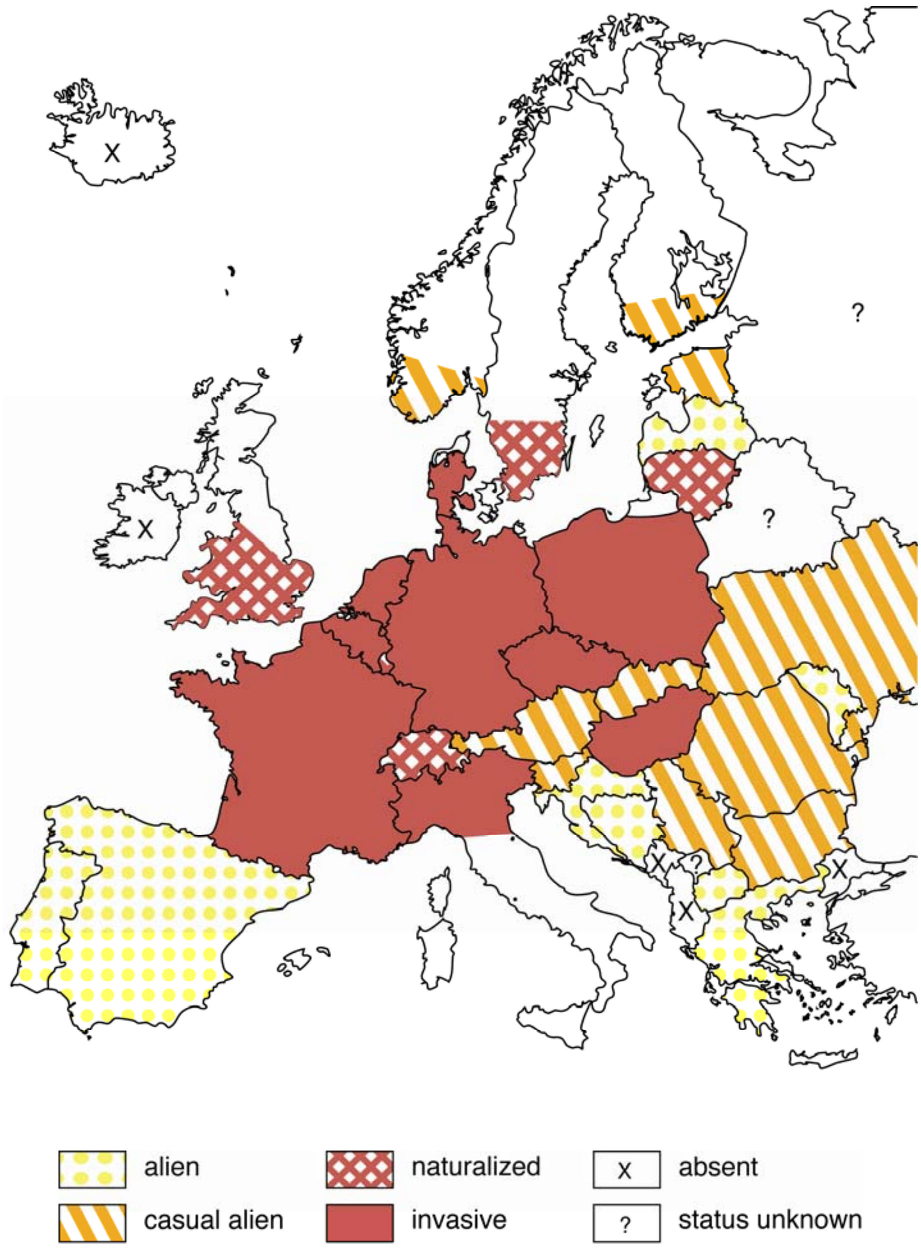


Fig. 2.3 The status of *Prunus serotina* in European countries, based on the data in Appendix 2.1 and with the status categories according to Richardson *et al.* (2000) and the definitions in Chapter 1 [figure: Quinten Vanhellemont]

The present genetic structure and geographic distribution of *P. serotina* in Europe are the result of multiple introductions via two distinct introduction pathways, i.e., introductions for ornamental purposes and introductions for forestry use (Petitpierre 2008, Pairon *et al. submitted*, Appendix 2.1). Introductions for horticulture are associated with a small initial propagule size, which may cause founder effects and genetic drift. Moreover, ornamental plantings will have occurred on geographically separated locations, which made gene flow between populations unlikely. In countries where *P. serotina* was mainly introduced as an ornamental species, e.g., the United Kingdom, *P. serotina* populations show low internal gene diversity but high inter-population genetic differentiation (Petitpierre 2008, Pairon *et al. submitted*). Planting a species repeatedly and on larger scales, e.g., for forestry purposes, implies a large initial propagule pressure and a low reduction in genetic diversity. The combination of large-scale and multiple forestry plantings with independent ornamental plantings in countries such as Germany will have enabled gene flow between adjacent populations, which has resulted in genetically more diverse populations that show little between-population differentiation (Petitpierre 2008, Pairon *et al. submitted*).

The two introduction pathways are also reflected in the status of *P. serotina* in European countries (Appendix 2.1). *Prunus serotina* is considered an invasive species in those countries in which it was introduced early and for forestry use, which is not that surprising, seeing that both residence time and propagule pressure have been found to promote the invasiveness of a species (see Chapter 1). As a consequence, the present distribution of *P. serotina* still largely reflects the former planting efforts, e.g., in the Netherlands (Van den Tweel & Eijsackers 1987), Germany (Starfinger *et al.* 2003), and the northern part of Belgium (Verheyen *et al.* 2007).

2.4.3 Habitats and communities

Prunus serotina occurs under different climatic conditions in its native and introduced range (Petitpierre 2008). In Europe, the species grows and proliferates in a climate characterized by a higher evapotranspiration and a lower annual precipitation that is more evenly distributed throughout the year than in North America. Besides, the range of climatic conditions in which *P. serotina* grows in Europe is more restricted than the climatic range in the United States with regard to the annual mean temperature, the minimum temperature of the coldest month, the maximum temperature of the warmest month, and the number of growing degree days. *Prunus serotina* does not occur abundantly in the Mediterranean region, probably because of the dry summer conditions. It is mostly found in oceanic and sub-oceanic climate conditions (Zerbe & Wirth 2006).

Prunus serotina grows on a wide range of soil conditions in Europe. The species is found on acid to nearly neutral, nitrogen poor to relatively rich, and moderately moist soils

(Zerbe & Wirth 2006). It is most common on acid and dry sandy soils, e.g., in northern Belgium (Waterinckx & Roelandt 2001), Denmark (Hans Erik Svart *pers comm*), northern Germany (Starfinger 1997), Hungary (Balogh *et al.* 2008), and the Netherlands (Bakker 1963). Podzolic soils are particularly prone to *P. serotina* invasion (Van den Tweel & Eijsackers 1987, Chabrerie *et al.* 2007, Verheyen *et al.* 2007). *Prunus serotina* also occurs in coastal dunes in the Netherlands (Ehrenburg *et al.* 2008) and on loess soils in Hungary (Balogh *et al.* 2008). On wet or calcareous soils, *P. serotina* is mostly absent (Waterinckx & Roelandt 2001, Decocq 2007, Chabrerie *et al.* 2007). On richer soils, the competition with other species may be too intense (Van den Tweel & Eijsackers 1987).

Prunus serotina is found in conditions with high light availability, mainly in semi-natural or managed plant communities: hedges in agricultural areas, tree avenues, forest edges, coppice, gaps and clearcut areas in forests, and forest stands with light-demanding tree species such as pine (*Pinus sylvestris*), larch (*Larix* spp.), birch (*Betula pendula* Roth), and oak (*Quercus robur* L. and *Q. petraea* (Matt.) Liebl.) (Starfinger *et al.* 2003, EPPO 2005, Godefroid *et al.* 2005, Decocq 2007, Verheyen *et al.* 2007, Klotz 2009). *Prunus serotina* also colonizes heathlands, dry grasslands, and fallow terrains in urban areas (Eijsackers & Oldenkamp 1976, Starfinger & Kowarik 2003, Klotz 2009). In forested areas, the species occurs most frequently in young, small, and privately owned stands because most eradication programs have been performed in public forests (Honnay *et al.* 1999, Verheyen *et al.* 2007).

2.5 Biology

In its native range, a lot of studies have considered the biology of *P. serotina* because the species is of commercial value in some parts of the eastern United States (Marquis 1990). In the introduced range, research on the ecology and biology of the species has started only recently, and most studies have been performed during the last decade.

Prunus serotina is allotetraploid and has high genetic diversity (Pairon 2007). In its native range, it has been classified as an opportunistic, fast-growing tree species with enough shade tolerance to persist in lower canopy positions (Sutherland *et al.* 2000). It is a typical gap-phase species that can regenerate in forest understories but needs more light for further growth (Auclair & Cottam 1971, Starfinger 1990, Closset-Kopp *et al.* 2007). *Prunus serotina* is known as a stress-tolerant ruderal sensu Grime (2001), and Closset-

Kopp *et al.* (2007) demonstrated that the r- and K-strategy of MacArthur & Wilson (see Grime 2001) both apply to *P. serotina*, but to different life stages of the species. *Prunus serotina* behaves as a K-strategist in its early life stages: seedlings and saplings of *P. serotina* are able to persist in forest understories. Adults of *P. serotina* can be considered r-strategists: they tend to maximize population growth and dispersal.

2.5.1 Fruit production

Prunus serotina flowers in May–June in its introduced range (Closset-Kopp *et al.* 2007, Phartyal *et al.* 2009), and the flowers are pollinated by generalist insects (Grisez *et al.* 2003) such as hoverflies and bees (Starfinger & Kowarik 2003). Self-pollinated flowers do not develop into viable seeds (Forbes 1973), and late spring frosts have been found to damage flowers (Marquis 1990). Weather conditions may affect pollination: warm and dry conditions stimulate the flowers and promote insect activity (Forbes 1973). Consequently, flower crops are not always good indicators of the size of seed crops (Bjorkbom 1979, Pairon *et al.* 2006a). Pairon *et al.* (2006a) observed up to 133 300 flowers per tree in the understory of a pine forest in Belgium, but only 3–13 % of the flowers developed into fruits and 25 % of these fruits were aborted prematurely. The number of fruits per raceme depends on light availability and varies between 1 and 8.6 (Deckers *et al.* 2005, Pairon *et al.* 2006a,b). Despite the relatively low fruit set, the absolute fruit production is high, e.g., 1500–6500 per tree in forest understories (Pairon *et al.* 2006a,b, Closset-Kopp *et al.* 2007) and 7800 per tree in open conditions (Deckers *et al.* 2008). The fruiting period lasted from August to September in an open landscape in Belgium (Deckers *et al.* 2008), and from September to November in forest understories in Belgium (Pairon *et al.* 2006a) and France (Boucault 2009). The dates of flowering and fruit ripening may differ by up to three weeks among individuals of *P. serotina* growing in the same location (Grisez 1974), and the fecundity also varies between trees (Pairon *et al.* 2006a). Some trees never produce high quantities of seeds, even in favourable conditions (Marquis 1990).

Individual *P. serotina* trees produce some seeds nearly every year (Fowells 1965). Good seed crops occur at intervals of 1–5 years across the native range (Marquis 1990), and fruit production varied between years in a forest in Germany (Starfinger 1990) and central Belgium (Pairon *et al.* 2006a). In addition, flower and fruit production are affected by the age and size of the tree and the growing conditions (Starfinger 1990). The age of first seed production was 4–7 years in areas with high light availability (in Belgium, Deckers *et al.* 2005) or 20 years in forest understories (in Germany, Starfinger 1990). Resprouts may flower even earlier in open conditions, e.g., after 3 years (Van den Tweel & Eijsackers 1987). Pairon *et al.* (2006a) also found a weak positive correlation between tree age and the number of fruits in forest understories. In the United States, seed production starts at the age of 5–10 years (Fowells 1965, Grisez *et al.* 2003), and seed set is optimal for trees of 30–100 years old (Fowells 1965). Tree size is positively correlated with fruit production in open landscapes (Deckers *et al.* 2008), but not in forest understories (Pairon *et al.* 2006a,b). Fruit production is higher in full light (Van den Tweel & Eijsackers 1987, Closset-Kopp *et al.* 2007).

2.5.2 Seed dispersal

Prunus serotina fruits are dispersed by gravity ('barochory') and by animals ('zoochory'). The bulk of the fruits, i.e., up to 95 %, fall within the first 5–10 m of the seed tree in forests (Hoppes 1988, Pairon *et al.* 2006b). Birds and mammals effectively disperse the seeds over long distances, i.e., > 100 m (Pairon 2007, Boucault 2009). Birds seem to select healthy fruits with sound seeds (Pairon *et al.* 2006a), and they disperse the fruits non-randomly to focal points in a landscape, e.g., hedgerow intersections, seed trees or roost trees (Deckers *et al.* 2005, 2008). Foxes might also be efficient dispersers of *P. serotina* seeds as they use their droppings as an olfactory demarcation of their territory and leave them mostly on open areas, appropriate for the subsequent growth of *P. serotina* seedlings (Boucault 2009). Moreover, passage through the digestive tract of birds and mammals may improve seed germinability (see section 2.5.3).

Birds distribute *P. serotina* seeds in their droppings or by regurgitation (Smith 1975). *Prunus serotina* fruits are consumed by a relatively diverse assemblage of dispersal agents, and migratory birds may have a large impact on *P. serotina* dispersal (Eijsackers & Oldenkamp 1976, Vader 2002, Boucault 2009). Wood-pigeon (*Columba palumbus* Linnaeus, 1758) and blackbird (*Turdus merula* Linnaeus, 1758) were the main *P. serotina* dispersers in an agricultural landscape in Belgium (Deckers *et al.* 2008), and Boucault (2009) observed four bird species consuming *P. serotina* fruits in a forest in France: three species from the Turdidae family, i.e., song trush (*Turdus philomelos* Brehm, 1831), redwing (*Turdus iliacus* Linnaeus, 1766), and blackbird, and one species from the Sturnidae family, i.e., starling (*Sturnus vulgaris* Linnaeus, 1758). Tree crop size and drupe ripeness positively affect frugivore visitation rates (Deckers *et al.* 2008). Deer (*Dama dama* [Linnaeus, 1758]), wild boar (*Sus scrofa* Linnaeus, 1758), red fox (*Vulpes vulpes* Linnaeus, 1758), and marten (*Martes* spp.) distribute *P. serotina* seeds in their droppings (Boucault 2009), and cattle are also reported to eat *P. serotina* fruits (Ehrenburg *et al.* 2008). Secondary dispersal of *P. serotina* seeds is exerted by small, seed-caching rodents ('dyszoochory') and by the dung beetle *Trypocopris vernalis* Linnaeus, 1758 in a forest in France (Boucault 2009).

2.5.3 Germination

Seeds of *P. serotina* exhibit physiological dormancy (Baskin & Baskin 2002, Phartyal *et al.* 2009), and they need a period of after-ripening in moist and oxic conditions (Grisez 1974). The endocarp is permeable to water, and there is no physical dormancy. When the endosperm swells at the time of germination, the seed stone is split into two halves. The germination is hypogeous, i.e., the cotyledons stay below the soil surface (Grisez 1974). Seeds germinate over a six-week period (Smith 1975).

The germinability of *P. serotina* seeds depends on the mother tree and the geographic location (Grisez 1974, Eijsackers & Van de Ham 1990), the site conditions (Closset-Kopp *et al.* 2007, Boucault 2009), the dispersal date (Smith 1975, Phartyal *et al.* 2009), and the dispersal mode. The passage of seeds through the digestive tract of birds or small mammals such as foxes improves the germinability (Krefting & Roe 1949, Smith 1975, Boucault 2009, Phartyal *et al.* 2009); seeds that passed through the digestive tract of cattle do not germinate anymore (Ehrenburg *et al.* 2008). The seedbed requirements are flexible (Fowells 1965), but germination percentages are higher in shaded and moist conditions (Marquis 1990, Burton & Bazzaz 1991) and in litter, compared to mineral soil (Huntzinger 1967, Burton & Bazzaz 1991). However, seed predation is also likely to be higher below *P. serotina* shrubs or dense fern layers than in open conditions (Smith 1975, Burton & Bazzaz 1991, Royo & Carson 2008, Boucault 2009); 12–20 % of seeds were predated by small rodents in forest understories in France (Boucault 2009). Reported germination rates vary widely and are difficult to compare or generalize because of the differences in definitions and methods (Table 2.1).

Prunus serotina seeds remain viable for 3 up to 5 years in the native (Marquis 1975, Wendel 1977) and introduced range (Eijsackers & Van de Ham 1990). In a forest in

Central Belgium, Phartyal *et al.* (2009) found only 2 % viable seed bank seeds. *Prunus serotina* seed bank seeds show a high variability in germination capacity between sites and years (Wendel 1977, Burton & Bazzaz 1991, O'Hanlon-Manners & Kotanen 2006). The short-lived persistent seed bank ensures that *P. serotina* regeneration appears abundantly almost every year (Bjorkbom 1979, Marquis 1990).

Table 2.1 Seed quality of *Prunus serotina* in its native (US, United States) and introduced range (EU, Europe)

seed quality	%	method	range	reference
soundness	7–55	embryo present/absent	EU	Boucault (2009)
soundness	91	embryo (un)damaged	US	Bjorkbom (1979)
viability	62	tetrazolium/floating tests	EU	Pairon *et al.* (2006a)
germinability	0–24	germination tests (lab)	EU	Boucault (2009)
germinability	42	germination tests (lab)	EU	Closset-Kopp *et al.* (2007)
germinability	16–62	germination tests (lab)	EU	Phartyal *et al.* (2009)
germinability	86–90	germination tests (lab)	US	Grisez (1974)
germinability	3-6	pot experiment	EU	Starfinger (1990)
germinability	1–14	pot/field experiments	EU	Eijsackers & Van de Ham (1990)
germinability	2–20	field experiments	US	Burton & Bazzaz (1991)
germinability	3–25	field experiments	US	Huntzinger (1964)
germinability	60	field experiments	US	Huntzinger (1967)

2.5.4 Seedling survival and growth

The abundance and survival of *P. serotina* seedlings are determined by soil conditions and light availability in the native (Smith 1975, Horsley 1993, D'Orangeville *et al.* 2008) and introduced range (Knight *et al.* 2008, Juhász *et al.* 2009). Seedling survival also depends on seedling age. Pairon *et al.* (2006a) found low survival, i.e., 8 %, for seedlings younger than 3 years and high survival, i.e., > 85 %, for seedlings older than 4 years in a pine forest in Belgium. Smith (1975) showed 9 % survival of 1-year old seedlings in a pine forest in Illinois. Overall, a relatively low percentage of *P. serotina* seeds will result in seedlings older than 4 years, e.g., 5 % in the understory of a pine forest in Belgium (Pairon *et al.* 2006a) and 0–47 % in germination experiments with different soil and vegetation types in the Netherlands (Eijsackers & Van de Ham 1990). In spite of the low survival rates, the high number of newly recruiting *P. serotina* seedlings ensures a dense and seemingly permanent seedling bank (Pairon *et al.* 2006a).

Prunus serotina seedlings grow fast in full light (Deckers *et al.* 2005); Godefroid *et al.* (2005) determined a threshold of 58–80 % of full light for successful seedling growth. In shaded forest understories, seedlings grow slowly but are able to survive for up to 5 years (Marquis 1990). Those understory seedlings of *P. serotina* show high morphological plasticity, and the growth of their lateral branches is high compared to the overall height growth (Paquette *et al.* 2007). The height of the suppressed seedlings and their maximum age depend on the light level (Marquis 1990, Starfinger 1990, Closset-Kopp *et al.* 2007, Knight *et al.* 2008). Seedling banks of *P. serotina* have been documented for the native range and for two sites in the introduced range (Starfinger 1990, Closset-Kopp *et al.* 2007). Silvertown & Charlesworth (2001) named stunted tree seedlings 'Oskars' after the character Oskar in *Die Blechtrommel* by Günter Grass. In the novel, Oskar decides to stop growing at the age of three. Likewise, *P. serotina* seedlings in a seedling bank age but show almost no growth. They wait for a canopy gap that will admit light (Silvertown & Charlesworth 2001), which will enable them to regain growth. The presence of a bank of 'Oskars' was the most important factor determining local *P. serotina* invasion success in a forest in France in the modelling study of Sebert-Cuvillier *et al.* (2007).

2.5.5 Resprouting

Prunus serotina readily resprouts from stumps or stems of trees which crown died back (Fowells 1965, Brommit *et al.* 2004). The stump sprouts grow faster than seedlings during the first 20–30 years, especially in full light (Fowells 1965, Closset-Kopp *et al.* 2007). The resprouting capacity enables *P. serotina* trees of all ages to delay their mortality. If the aboveground parts of a tree die off, the resprouts may survive in the understory until a canopy gap occurs and they can regain growth. Closset-Kopp *et al.* (2007) called this 'Alice behaviour' after the character Alice in *Alice's adventures in wonderland* by Lewis Carroll. Alice eats mushrooms to change her size and adapt better to the changing environment. *Prunus serotina* is also able to switch from tree to resprouts, e.g., in unfavourable light conditions, which might be seen as a way to optimize the use of resources. In their modelling study, Sebert-Cuvillier *et al.* (2007) found that the resprouting capacity sped up the local *P. serotina* invasion in a French forest although its contribution to the invasion process was weak when compared to the impact of a bank of 'Oskars' (see section 2.5.4).

2.5.6 Saplings and adults

Adults and large saplings are intolerant of shade and competition whereas they grow fast in areas with a high availability of light, water, and nutrients (Marquis 1990). In an open agricultural landscape in Belgium, Deckers *et al.* (2005) found a strong age-size relationship for *P. serotina* saplings and trees and a mean diameter growth comparable to the diameter growth on the Allegheny Plateau (Fowells 1965). The diameter growth slows down and mortality increases rapidly at the age of 50 years in Europe (Wallis de Vries 1987) and at 80–100 years in the eastern United States (Marquis 1990). Because of the shallow root system, old *P. serotina* trees are vulnerable to windthrow, particularly on wet soils (Fowells 1965).

2.5.7 Damaging agents

Prunus serotina is tolerant to air pollution (Klotz 2009), but the species is sensitive to high atmospheric ozone concentrations (VanderHeyden *et al.* 2001). Besides, *P. serotina* is highly susceptible to fire injury and intolerant of flooding (Marquis 1990). Several herbivorous and pathogeneous species have been found to affect *P. serotina*.

Mammals and birds – Severe browsing by white-tailed deer (*Odocoileus virginianus* Zimmermann, 1780) hinders the regeneration of *P. serotina* in the native range (Huntzinger 1967, Marquis 1990) although high deer densities, i.e., > 25 km^{-2}, have also been found to favour *P. serotina* over other tree species, causing dramatic shifts in the species composition of forests in the eastern United States (Horsley *et al.* 2003, Rossell *et al.* 2005). Porcupines (Erethizontidae) consume the bark of *P. serotina*, which can kill the tree if it is girdled entirely (Marquis 1990). In the introduced range, red deer (*Cervus elaphus* Linnaeus, 1758) and roe deer (*Capreolus capreolus* Linnaeus, 1758) browse on *P. serotina* (Eijsackers & Oldenkamp 1976, Boucault 2009). Rodents and pigeons damage seeds and seedlings in both the native and introduced range (Huntzinger 1967, Grisez 1974, Wallis de Vries 1987, Eijsackers & Van de Ham 1990, Boucault 2009), and nuthatches (*Sitta* spp.) and pheasants (*Phasianus colchicus* Linnaeus, 1758) were observed to predate on *P. serotina* seeds in a forest in France (Boucault 2009).

Insects – *Furcipus rectirostris* (Linnaeus, 1758), a snout beetle native to Europe and northeastern Asia, predates *P. serotina* seeds in Belgium (3 % infested seeds, Pairon *et al.* 2006a), France (1–17 %, Boucault 2009), and the Netherlands (3–17 %, Moraal 1988). The North American fruit fly *Rhagoletis cingulata* (Loew, 1862), which larvae develop in *P. serotina* fruits, is a quarantine species in Europe, but it has been found in the Netherlands (Smit 2003), Switzerland, Italy, and Germany (Lampe *et al.* 2005). A suite of native polyphagous Lepidoptera and Coleoptera feeds on the non-native *P. serotina* in Poland and France (Nowakowska & Halarewicz 2006a,b, Boucault 2009). An overview of insect damage on *P. serotina* in the United States can be found in Marquis (1990).

Pathogens – Boucault (2009) found an unidentified fungus inside the endocarp of empty seeds on moist soils in France. *Chondrostereum purpureum* (Pers.) Pouzar, a fungal plant pathogen of deciduous trees in temperate zones, causes silver leaf disease in *P. serotina* and other fruit trees (De Jong 1988). Soilborne pathogens, i.e., *Pythium* spp., caused a lower survival probability (Packer & Clay 2000) and a lower juvenile growth (Packer & Clay 2003) of *P. serotina* seedlings close to *P. serotina* seed trees in a mesic deciduous forest on silt loam soil in Indiana. *Pythium* spp. are oomycetes that cause damping-off disease in plants. They inflict the greatest damage during germination and seedling establishment, and the infections are more severe on moist soils (Martin & Loper 1999). Reinhart *et al.* (2005) suggested that these *Pythium* spp. negatively affect the survival of *P. serotina* seedlings throughout the native range, but that the soil community facilitates *P. serotina* invasion in Europe (Reinhart *et al.* 2003). Because of the differences in the studied ecosystems, e.g., dry sandy soil in Europe versus moist loamy soil in the United States, and the relatively limited range of the studies, i.e., one study site in Europe and eight study sites in the United States, these findings should be considered hypotheses rather than conclusive evidence.

2.6 Impact

As a gap-dependent species, *P. serotina* thrived in the young and relatively open forest stands in which it had been planted (Wallis de Vries 1987), and the species benefited from the regular thinnings that are part of the forest management (Starfinger *et al.* 2003). *Prunus serotina* formed dense thickets in these forests and spread to neighbouring forest stands and open areas. Its spread has undoubtedly been favoured by the repeated and large-scale plantings, i.e., the large initial propagule pressure, and the biology of the species. *Prunus serotina* seed production starts early, occurs almost every year, and the seeds are effectively distributed by birds and mammals. A seed and seedling bank are built up, and the species resprouts easily after physical damage, which makes it difficult to remove or control the species. Due to the higher seed production and the more effective dispersal by birds in open landscapes, *P. serotina* will spread faster in open landscapes than in forests (Kowarik 1995). Natural disturbances, e.g., storms, may speed up the spread of *P. serotina* (Sebert-Cuvillier *et al.* 2007, 2008). The spread and abundance of *P. serotina* in both forests and open landscapes have ecological as well as economic consequences. Because the colonization success of *P. serotina* depends on the ecosystem type, the impact will also vary. Nature conservation problems occur mainly in non-forest ecosystems (Starfinger *et al.* 2003).

2.6.1 Ecological impact

High densities of *P. serotina* may change the abiotic site conditions, alter the biodiversity, and influence the succession. One might question, however, whether these are consequences of the high densities of *P. serotina* rather than mere species effects (Verheyen *et al.* 2007).

Dense tickets of *P. serotina* alter the light conditions and modify the topsoil (Godefroid *et al.* 2005, Verheyen *et al.* 2007) although the extent and nature of the changes in topsoil properties will depend on the initial soil conditions (Koutika *et al.* 2007, Verheyen *et al.* 2007, Dassonville *et al.* 2008). *Prunus serotina* may affect the topsoil through changes in the humus conditions and reduced soil water availability due to a higher interception and transpiration. The litter of *P. serotina* is indeed characterized by high nutrient concentrations and decomposes rapidly (Maddelein *et al.* 1991, Adams & Angradi 1996, Lorenz *et al.* 2004). The phosphorus content, for instance, has been found to be higher below *P. serotina* (Anders 2005, Chabrerie *et al.* 2008). The pH of the litter layer and the upper soil layer below *P. serotina* was lower (Starfinger *et al.* 2003, Chabrerie *et al.* 2008), similar (Verheyen *et al.* 2007) or higher (Anders 2005, Vanderhoeven *et al.* 2005) than in non-invaded stands.

Studies on the relationship between *P. serotina* and understory species richness do not reveal consistent results. In several studies, species richness was negatively correlated with *P. serotina* abundance (Starfinger 1990, Honnay *et al.* 1999, Godefroid *et al.* 2005, Chabrerie *et al.* 2007). However, other studies found little impact of *P. serotina* on species diversity (Vanderhoeven *et al.* 2005, Chabrerie *et al.* 2008), and Knight *et al.* (2008) even found a positive relationship between understory species richness and abundance of *P. serotina* seedlings. Verheyen *et al.* (2007) found the sharpest decrease in species numbers on wet soils. On dry soils, the species richness was only marginally affected, but the species composition did change: stress-tolerant species disappeared, and competitors became more important (Godefroid *et al.* 2005, Verheyen *et al.* 2007). By altering the structure of the vegetation, *P. serotina* might also alter the habitat conditions for fauna: the dense *P. serotina* thickets provide shelter and produce fruits (Starfinger & Kowarik 2003, Boucault 2009). Lepidoptera seem to be attracted to ripe *P. serotina* fruits (Korringa 1947). Several arthropods typical of dead wood of broadleaved species occur in dead wood of *P. serotina*, which is often the only broadleaved species in invaded pine forests (Geudens 1997).

In open vegetation types such as dunes, heathlands, and dry grasslands, *P. serotina* accelerates the succession towards vegetation types dominated by woody species, which might cause rare and endangered species of open habitats to disappear (Starfinger *et al.* 2003, Ehrenburg *et al.* 2008). In forests, the dense shrub layer of *P. serotina* might act as a recalcitrant layer (cf. Royo & Carson 2006) that hinders the regeneration of other woody species and may have a long-lasting impact on further forest development (Starfinger *et al.* 2003).

2.6.2 Economic impact

The presence of *P. serotina* hampers the conversion of pine forests towards broadleaved forests (Lorenz *et al.* 2004), and complicates forest management measures such as thinning, timber harvesting, or planting. The *P. serotina* control preceding the regular measures will increase the overall management cost (Eijsackers & Oldenkamp 1976, Muys *et al.* 1992). Decocq (2007) indicates that attaining successful regeneration of the target tree species is 6–35 % more expensive in invaded stands. Besides, the control of *P. serotina* itself is time-consuming and expensive. The high vitality of the resprouts, the seed and seedling bank, and the recurring seed input by birds make continual control actions necessary. The different measures for *P. serotina* control cost € 50–2200 per ha and per year, depending on the abundance and size of the *P. serotina* (Starfinger *et al.* 2003, Van Raffe & De Jong 2008). Estimates of the actual expenses associated with *P.*

serotina management are rarely available. For Germany, the total annual costs were estimated to be € 25 million (Reinhardt *et al.* 2003), and in Belgium, € 126 000 were spent on *P. serotina* control in six military domains (1525 ha) in 2005 and 2006 as part of the LIFE project DANAH (www.danah.be) (De Bruyn *et al.* 2007).

Contrary to its negative economic consequences, *P. serotina* has some economic assets as well, i.e., a high recreation value and the production of valuable timber. The recreation value of the species results from its aesthetic, i.e., the abundant flowers in spring and the yellow autumn leaves (Eijsackers & Oldenkamp 1976, Javelle *et al.* 2006) and its high resprouting capacity and resistance to trampling, which made it a popular species for screen plantings at intensely used recreational areas (Bakker 1963, Eijsackers & Oldenkamp 1976). *Prunus serotina* yields firewood with a relatively high calorific value, and may also produce valuable timber such as veneer or furniture wood under appropriate management regimes, a possibility that is still discussed among some foresters (Starfinger *et al.* 2003, Nyssen 2009).

2.7 Control

Control of *P. serotina* is a costly and long-term commitment that will only be effective if the control measures are applied on large areas, if all neighbouring landowners are involved, if control measures are geared to the biology and ecology of *P. serotina*, and if other, native species are able to occupy the ecological niche appropriate for *P. serotina* prior to new *P. serotina* colonization (cf. Geudens *et al.* 2009).

Control measures – At present, *P. serotina* is mostly controlled by a combined mechanical-chemical method that consists of cutting down the *P. serotina* trees and spraying the remaining stumps with herbicides (Brehm 2004, Vanhellemont *et al.* 2008). Alternative methods that require less or no herbicides, e.g., grazing or biological control, are tested for use in water-collection areas and other vulnerable sites. Although most herbivores avoid the cyanide-containing leaves of *P. serotina*, sheep, goats, and cattle browse on young *P. serotina* leaves. These herbivores have been used to control seedlings and young resprouts of *P. serotina*, with varying success (Ehrenburg *et al.* 2008, Uiterweerd 2008). Research on the biological control of *P. serotina* with *Chondrostereum purpureum* started in the Netherlands in the 1980s (De Jong 1988) and is still going on in the Netherlands, Germany, and Switzerland (Münte 2009). In forests, planting shade-tolerant native species such as *Fagus sylvatica* L. might be a successful control measure, with long-term effects (Starfinger *et al.* 2003).

Regulation – In Germany, the use of *P. serotina* in forestry is forbidden in Niedersachsen (EPPO 2005), and *P. serotina* has to be controlled in Berlin, according to the forest management recommendations (Münte 2009). *Prunus serotina* appears on the black list in Belgium (Branquart *et al.* 2007) and Switzerland (CPS-SKEW 2006), but these lists have no regulatory consequences. The black list status indicates that *P. serotina* has a (potentially) high impact on the environment (Branquart 2007) and causes health problems and economic losses (Köhler *et al.* 2005). In some countries, e.g., Austria, Slovakia, and Spain, *P. serotina* occurs on a list with potentially invasive species (Dana *et al.* 2001, Essl & Rabitsch 2002, Cvachová *et al.* 2003). *Prunus serotina* is still sold by garden centres, e.g., in the Czech Republic (Křivánek 2006a,b), and forestry nurseries, e.g., in Belgium (www.sylva.be).

Appendix 2.1

The presence, status, and distribution of *Prunus serotina* in European countries. The year of first introduction (if known), the pathway of introduction, and the references are provided as well.

PRES (presence)

Prunus serotina is absent (-) or present (x) in a country. An ‘x’ between brackets indicates that *P. serotina* only occurs in parks and (botanical) gardens. For these countries, no data is provided on the distribution of the species (DIST: -).

STAT (status)

Prunus serotina is alien (A), casual alien (C), naturalized (N), or invasive (I). The classes are according to Richardson *et al.* (2000); see Chapter 1.

DIST (distribution)

The distribution of *P. serotina* is widespread (W, well-distributed through the entire country), local (L, present in some parts of the country), or rare (R, present at a few locations in the wild). For countries in which *P. serotina* is alien (STAT: A), no distribution is given (-). Asterisks (*) refer to certain references, which also bear an asterisk, and indicate that detailed data on the distribution of *P. serotina* in the country are available, e.g., distribution maps or species inventories.

YEAR (year of first introduction)

The year of first introduction is known for some countries; ‘> 1900’ indicates that the exact year of introduction is not known, but that the introduction probably occurred at the beginning of the 20th century.

PATH (pathway of introduction)

Prunus serotina was introduced intentionally via two different pathways: for ornamental purposes (O) or for forestry use (F). The main pathway of introduction is indicated in the table. In Denmark, *P. serotina* was mainly planted in hedges surrounding fields (‘hedges’).

Appendix 2.1 (continued)

COUNTRY	PRES	STAT	DIST	YEAR	PATH	REFERENCES
Albania	-	-	-	-	-	Petrit Hoda *pers comm*
Austria	x	C	R		O	Essl & Rabitsch (2002), Franz Essl *pers comm*
Belarus						
Belgium	x	I	W *		F	Van Landuyt *et al.* (2006) *, Branquart *et al.* (2007), SPW-DGO3-DEMNA (2009) *
Bosnia & Herzegovina	(x)	A	-		O	Sulejman Redžić & Dubravka Šoljan *pers comm*
Bulgaria	x	C	R		O	Jerzy Zielinski *pers comm*
Croatia	x	A	-			Flora Croatica (hirc.botanic.hr/fcd/InvazivneVrste/)
Czech Republic	x	I	L	1811	O (F)	Křivánek (2006a,b)
Denmark	x	I	W		hedges	Hans Erik Svart *pers comm*
Estonia	x	C	R	1932	O	Estonian database of alien species (eelis.ic.envir.ee/voorliigid/eng)
Finland	x	C	R		O	Harry Helmisaari & Henry Väre *pers comm*
France	x	I	L *	1623	O (F)	Decocq (2007), Tela Botanica (2009) *
Germany	x	I	W *	1685	F	Starfinger & Kowarik (2003), FlorKart (2006) *
Greece	(x)	A	-		O	Filippos Aravanopoulos *pers comm*
Hungary	x	I	L *	1897	F	Balogh *et al.* (2008) *
Iceland	-	-	-	-	-	Jóhann Pálsson *pers comm*
Ireland	-	-	-	-	-	Stokes *et al.* (2006), Milbau & Stout (2008a), NBN Gateway (2009)
Italy	x	I	L *		F	Celesti-Grapow *et al.* (2009) *
Kosovo						
Latvia	(x)	A	-	1805	O	Agnese Priede & Peteris Evarts-Bunders *pers comm*

Appendix 2.1 (continued)

COUNTRY	PRES	STAT	DIST	YEAR	PATH	REFERENCES
Lithuania	x	N	R *		O	Gudžinskas (2000) *
Luxembourg	x	N	R *		O	Welter *et al.* (2008) *
Macedonia	(x)	A	-		O	Bojan Simovski *pers comm*
Moldova	(x)	A	-		O	Petru Cocirta *pers comm*
Montenegro	-	-	-	-	-	Dragan Roganović *pers comm*
Norway	x	C	R		O	Reidar Elven *pers comm*
Poland	x	I	W *	1813	F	Tokarska-Guzik (2005), Tokarska-Guzik *et al.* (2008) *
Portugal	(x)	A	-		O	Elizabete Marchante *pers comm*
Romania	x	C	R *		O	Paulina Anastasiu *pers comm* *
Russia						
Serbia	x	C	R	> 1900	O	Mihailo Grbić *pers comm*
Slovakia	x	C	R *	> 1900	O	Viera Ferakova *pers comm* *
Slovenia	x	C	R *	> 1900	O	Jogan (2001) *, Nejc Jogan *pers comm*
Spain	(x)	A	-		O	Dana *et al.* (2001)
Sweden	x	N	L *	1870	O	Hans Henrik Bruun & Torbjörn Tyler *pers comm* *
Switzerland	x	N	R *			CPS-SKEW (2006) *, Wittenberg (2006)
the Netherlands	x	I	W *	1740	F	Buis (1985), Odé *et al.* (2003) *
Turkey	-	-	-	-	-	Derya Esen *pers comm*
United Kingdom	x	N	L *	1629	O	data Hill *et al.* (2005), NBN Gateway (2009) *
Ukraine	x	C	R		O	Myroslav Shevera *pers comm*

Photo 3.1 Study plot Genk: *Prunus serotina* below *Pinus sylvestris* (July 2008)

Photo 3.2 Study plot Langdorp: dense understory of *Prunus serotina* and *Sorbus aucuparia* below *Pinus sylvestris* (July 2007)

3 Radial growth of *Prunus serotina* in the understory of Scots pine stands

After: Vanhellemont M, Verheyen K, Staelens J, Hermy M. Factors affecting radial growth of the invasive *Prunus serotina* in pine plantations in Flanders. European Journal of Forest Research, *in press*

3.1 Abstract

The invasive tree species *Prunus serotina* causes problems in Western Europe, mainly in pine forests on sandy soil. Thus far, there have been almost no studies considering the diameter growth of *P. serotina* in its introduced range. We analyzed the radial growth of *P. serotina* in seven Scots pine (*Pinus sylvestris*) plantations in Flanders (northern Belgium) with multiple linear regressions and a potential × modifier approach. The radial growth of *P. serotina* in the understory of the studied pine plantations was reduced by up to 50 % as compared to potential *P. serotina* growth in full light conditions. Size and site effects were strongly growth-reducing; crowding effects were important only for small individuals. The actual radial growth of *P. serotina* below pines was determined primarily by the diameter and age of the *P. serotina* tree and by competition with neighbouring trees.

3.2 Introduction

Biological invasions result in significant losses in the economic value, biodiversity and functioning of invaded ecosystems worldwide (Mack *et al.* 2000, Chapter 1). The altering of ecosystem functioning by invasive alien species often makes it difficult, or even impossible, and expensive to return to the prior, desired condition (Vitousek *et al.* 1997), which results in management problems and complicated restoration projects (D'Antonio & Meyerson 2002). Knowledge of the biology of the targeted invasive species is a prerogative for successful control. Moreover, a quantitative understanding of the factors affecting growth, survival, and fecundity will lead to insight into the performance of populations in invaded ecosystems (Buckley *et al.* 2003).

The invasive tree species *Prunus serotina* Ehrh. affects the biodiversity, influences the abiotic site conditions, and alters the succession of invaded ecosystems in Western and Central Europe (Starfinger *et al.* 2003, Chapter 2). Its abundance causes major disruptions in forestry and nature conservation, and controlling the species is difficult and expensive (Reinhardt *et al.* 2003, Chapter 2). In Flanders, the northern part of Belgium, large-scale and costly eradication programs have started as early as the 1950s (Muys & Maddelein 1993). Nonetheless, in 1997–1999, *P. serotina* was found to be the most frequently regenerating woody species in Flemish forests (Waterinckx & Roelandt 2001). Control of *P. serotina* is ongoing, and forest managers are still looking for the most cost-effective way to control the species (Vanhellemont *et al.* 2008).

The first studies on *P. serotina* in its introduced range focused on control measures (e.g., Jager & Oosterbaan 1979, Van Den Meersschaut & Lust 1997a, Brehm 2004). Research on the ecology of the species has only started recently, including studies on seed dispersal, impact on the invaded ecosystem, and effects of the ecosystem and landscape structure on presence/abundance and spatial spread (see Chapter 2). Studies on growth are notably absent in the published research on *P. serotina* in Europe. Even in its native range, relatively few studies have considered the diameter growth of *P. serotina* (e.g., Auclair & Cottam 1973, Auclair 1975, Auchmoody & Rexrode 1984, Schuler 2006). Nonetheless, quantification of growth is important, particularly for long-lived invasive woody species, in order to measure the rate of biomass accumulation and for the timing of control measures. Moreover, apart from understanding dispersal and recruitment, insight into growth-influencing factors is essential for predicting the future role of *P. serotina* in the development of invaded forest stands (see Chapter 7).

The objectives of this chapter were (1) the quantification of the radial growth of *P. serotina* in pine forests, (2) gaining insight into the relationship between growth of *P. serotina* in forest understories and its potential growth in an open landscape with high light availability, and (3) the identification of variables that are related to the observed variation in understory radial growth.

3.3 Materials and methods

3.3.1 Study area

In July and August 2006, data were collected in seven homogenous Scots pine (*Pinus sylvestris* L.) plantations on coarse sandy soil, distributed within the Campine region (‘Kempen’) in Flanders, the northern part of Belgium (Fig. 3.1, Table 3.1). The minimum and maximum monthly mean temperatures are 1.4°C in January and 16.7°C in July, and the mean annual precipitation is 799 mm, evenly distributed over the year (www.meteo.be). The pine stands were planted 50–70 years ago (Table 3.1), and they have not been managed during the last decades. Consequently, the pine trees still showed a fairly regular spatial pattern (Ripley’s K, Ripley 1977, figures not shown), and the basal area and stem density were high as compared to the managed stands in the yield tables of Jansen *et al.* (1996), i.e., the basal area was 36–48 % higher, the stem density 41–167 %. The understory was not planted; *P. serotina* has established spontaneously in the studied stands and has not been affected by past control management.

3.3.2 Data collection

In each stand, a 20 m x 40 m study plot had been permanently marked in 2004, and the position of all trees and saplings taller than 1 m in the study plots had been determined with a theodolite and a measuring tape. Tree diameter was measured at breast height for the canopy trees (*P. sylvestris*) and at stem base for the understory species (e.g., *P. serotina*). Site productivity was determined as the site productivity index according to the growth curves of Jansen *et al.* (1996), based on the age and height of eight dominant *P. sylvestris* trees in each stand.

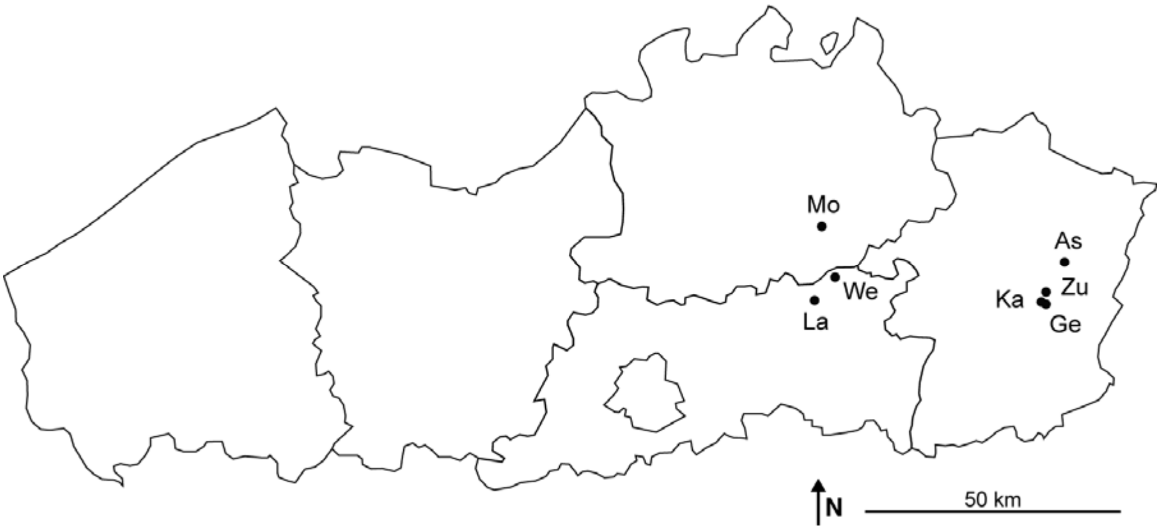


Fig. 3.1 The location of the studied pine stands in Flanders (see Table 3.1 for additional information on the study sites)

To assess the growth of *P. serotina*, 18–28 individuals (evenly distributed over the observed diameter range) were sampled in the central 10 m x 20 m of each plot (cf. Table 3.1). The height, diameter at breast height (dbh), and diameter at stem base were measured, and we took a stem cross-section or two stem cores, i.e., along two directions perpendicular to each other, at 10–20 cm above the root collar. Ring widths were measured to the nearest 0.01 mm using a positioning table (LINTAB) with associated software (TSAPWin, www.rinntech.com) and a stereomicroscope (Olympus SZX12).

Canopy openness, i.e., the percentage of open sky seen from beneath a forest canopy, was used as a measure of light availability during the growing season. Hemispherical photographs were taken above a subset of seedlings and saplings for which the diameter at the stem base was less than 3.5 cm (‘small individuals’, Table 3.2) as it was not feasible to take photographs above larger saplings and trees. A digital camera (Nikon D70S) with a Sigma 8-mm fisheye lens was mounted on a tripod (1 m height), oriented towards north, and levelled. Photographs were taken in uniformly overcast conditions. The applied combination of camera and lens produced non-circular images which were processed with Gap Light Analyzer (GLA version 2.0, Frazer *et al.* 1999) to calculate canopy openness over the zenith angle 0 to 63°. Hemispherical photographs with a wide angle of view have been shown to be an accurate method for estimating canopy openness (Paletto & Tosi 2009).

Table 3.1 The characteristics of the seven study sites: the geographic location and the site productivity (SP, the derived maximum mean annual volume increment of *Pinus sylvestris*); the stem density (N), basal area (BA), dominant height (h_d), and age of the pine (*P. sylvestris*) overstory; the stem density (N) and mean diameter at stem base (d_m) for the understory *Prunus serotina* taller than 1 m, height of the tallest *P. serotina* (h_{max}), and age of the oldest *P. serotina* determined by counting growth rings for the five tallest *P. serotina* trees in each plot (age) and the number of *P. serotina* samples per site (*n*); the other tree and shrub species in the understory, apart from *P. serotina*, in decreasing abundance and sorted into three stem density classes, i.e., N > 1000 ha^{-1} (N1), 1000 ha^{-1} > N > 100 ha^{-1} (N2), and N < 100 ha^{-1} (N3)

site					overstory (*Pinus sylvestris*)				understory (*Prunus serotina*)					understory (other species [a])		
code	location	Lat	Lon	SP	N	BA	h_d	age	N	d_m	h_{max}	age	*n*	N1	N2	N3
		(°N)	(°E)	(m^3 ha^{-1} yr^{-1})	(ha^{-1})	(m^2 ha^{-1})	(m)	(yr)	(ha^{-1})	(cm)	(m)	(yr)				
As	As	51°01’	5°34’	11.1	763	36.3	22.9	53	2388	2.3	9.7	35	*28*		Sa	Bp
La	Langdorp	51°01’	4°54’	8.7	863	36.8	20.6	55	1288	5.2	7.8	26	*20*	Sa	Al, Fa, Bp, Qro	Qru
We	Westerlo	51°05’	4°53’	10.7	1075	38.9	23.0	56	1075	7.3	9.1	22	*18*	Sa		Qro, Qru, Al, Fa, Bp, Ia
Mo	Molekens	51°10’	4°50’	9.0	813	35.7	22.1	58	1150	7.4	13.3	33	*27*		Sa	Rp, Qro, Ia, Qru, Bp
Ka	Katteven	50°57’	5°32’	9.0	663	36.6	21.6	59	1088	5.4	8.9	27	*21*	Sa	Qro, Fa	Al, Bp, Qru
Ge	Genk	50°57’	5°32’	9.6	838	38.3	24.0	72	775	9.2	13.5	44	*18*		Sa	Qro, Ia, Qru
Zu	Zutendaal	50°58’	5°33’	8.0	800	38.6	23.4	74	663	5.6	11.2	52	*24*	Sa	Qru, Fa	Qro, Ia, Al

[a] Al, *Amelanchier lamarckii* F. G. Schroed. – Bp, *Betula pendula* Roth – Fa, *Frangula alnus* P. Mill. – Ia, *Ilex aquifolium* L. – Qro, *Quercus robur* L. – Qru, *Quercus rubra* L. – Rp, *Robinia pseudo-acacia* L. – Sa, *Sorbus aucuparia* L.

3.3.3 Data analysis

For each sampled *P. serotina*, we calculated the mean past five-year (2000–2005) radial growth. Radial growth values rather than the derived basal area increments were used for the further analyses seeing the results of Dimov *et al.* (2008), who showed that diameter growth and basal area growth were both correlated with individual tree variables. In our study, e.g., the age of the sampled *P. serotina* was indeed correlated with radial growth ($r = 0.373$, $p < 0.001$) as well as basal area increment ($r = 0.533$, $p < 0.001$).

3.3.3.1 Quantification of radial growth

Since the radial growth data did not meet the ANOVA assumptions of homoscedasticity, we used non-parametric Kruskal-Wallis tests and Games-Howell post-hoc multiple comparisons to compare radial growth between sites, diameter classes, and age classes. A diameter-age relationship was used to depict the realized diameter growth of *P. serotina* at the study sites ('Kempen') in comparison with the growth at two other sites in Flanders, i.e., an open agricultural landscape ('Meerhout'; data Deckers *et al.* 2005) and a mixed deciduous forest ('Liedekerke'; data Chapter 5), and a pine forest in the Netherlands ('Ossenbos'; data Chapter 6).

3.3.3.2 Actual versus potential radial growth

We used a potential × modifier model to analyze the modifying effect of the variables size, site, and crowding on the potential growth of a target tree (cf. Canham *et al.* 2006) (Eq. 3.1):

$$\textit{radial growth} = \textit{potential radial growth} \times \textit{size effect} \times \textit{site effect} \times \textit{crowding effect} \qquad (3.1)$$

The *potential radial growth* (mm yr^{-1}) is defined as the expected radial growth of a tree at its optimal size, on the optimal site, and in the absence of competition. We calculated the potential radial growth independently in order not to lose the interpretation of the potential and modifier components and to decrease the number of parameters estimated based on the collected dataset. Using the data for the open landscape in which *P. serotina* grew in favourable light and soil conditions (Deckers *et al.* 2005), we calculated a potential radial growth of 4.891 mm yr^{-1}.

To account for the effect of (1) target tree size, (2) site conditions, and (3) crowding by neighbouring trees, we defined three unitless modifiers, ranging from 0 to 1. The *size effect* was modelled by a lognormal function (Eq. 3.2):

$$\textit{size effect} = \exp\left(-\frac{1}{2}\left(\frac{\ln\left(\mathrm{d_i}/\delta \right)}{\sigma} \right)^2 \right) \quad , \tag{3.2}$$

with d_i the diameter (cm) of the target tree, δ the diameter at which the potential radial growth occurs, and σ the parameter determining the breadth of the function (Canham *et al.* 2006).

The *site effect* was addressed by a modifier based on site productivity, assuming that growth declines monotonically as the site productivity decreases (Eq. 3.3):

$$\textit{site effect} = \exp\left(-\frac{\omega}{\mathrm{SP_i}} \right), \tag{3.3}$$

with SP_i the site productivity for tree *i*, expressed as the productivity of the site for *P. sylvestris* and calculated as described above, and ω a shaping parameter. Growth will be reduced more intensely for larger ω.

The *crowding effect* was included as a monotonically declining function (Eq. 3.4):

$$\textit{crowding effect} = \exp\left(-C\left(\mathrm{NCI_i} \right) \right), \tag{3.4}$$

with C the exponential decay factor and NCI_i the net competitive effect on subject tree *i* (Eq. 3.5):

$$\mathrm{NCI_i} = \sum_{j=1}^{n_i} \frac{\mathrm{d_j}^{\alpha}}{\mathrm{dist_{ij}}^{\beta}} \,. \tag{3.5}$$

The net competitive effect (NCI_i) of the n_i neighbours *j* on a subject tree *i* is calculated as a direct function of the diameter (d_j, in cm) of neighbour tree *j* and as an inverse function of the distance ($dist_{ij}$, in m) between subject tree *i* and neighbour tree *j*. The diameter of the subject tree was not included in Eq. 3.5 to avoid incorporating a size effect. Competitors were selected based on a fixed radius of 5 m, according to the plot size. To limit the number of parameters, all competitor species were assumed to be similar with respect to their NCI, i.e., having the same α and β values, with $0 \leq \alpha \leq 3$ and $0 \leq \beta \leq 2$ (cf. Canham *et al.* 2006).

Eqs. 3.2–3.5 form the full model described by Eq. 3.1. Maximum likelihood parameters were estimated with simulated annealing in R 2.2.0 (R Development Core Team 2005), using the likelihood package version 1.0 (Murphy 2006a). Residuals were normally distributed, but the variance increased with the mean predicted growth rate. Therefore, the error term for the observations was modelled as a simple linear function of the mean. The importance of each of the modifiers (size, site, crowding) was tested by leaving out the modifier under consideration (e.g., size) and by comparing the performance of the reduced model (e.g., 'site + crowding') with that of the full model (Eq. 3.1), using the Akaike Information Criterion corrected for small sample sizes. The R^2 of the linear regression between the observed and predicted radial growth was used to evaluate the goodness of fit. Modelling was done separately for the full dataset and for the subsets of small and large individuals (see Table 3.2 for the characteristics of the subsets).

3.3.3.3 Analysis of actual radial growth at the study sites

To gain insight into to actual radial growth of *P. serotina* in pine forests, multiple linear regressions were used to analyze the radial growth at the study sites as a function of diameter, age, competition, and site productivity, for the entire dataset and for the subsets of small and large individuals. For the small individuals, canopy openness was included in the regression analysis since light availability has been shown to be particularly important for explaining growth differences of small *P. serotina* (Closset-Kopp *et al.* 2007). In modelling the growth of the large individuals, we included ontogeny, expressed as the mean past growth for the preceding five, ten, or twenty years. Competition was determined with the competition index of Hegyi (1974), a distance-dependent index with a diameter-ratio of subject tree to competitor trees (Eq. 3.6), in which the competitors were selected based on the criterion of Daniels (1976) (Eq. 3.7):

$$CI_i = \sum_{j=1}^{n_i} \frac{d_j / d_i}{dist_{ij}} \tag{3.6}$$

$$\text{for} \quad dist_{ij} < \frac{d_i + d_j}{8}, \tag{3.7}$$

with CI_i the competition index for subject tree i; n_i the number of competitors for subject tree i, selected based on Eq. 3.7; d_j the diameter (cm) of competitor j; d_i the diameter (cm) of subject tree i; and $dist_{ij}$ the distance (m) between competitor j and subject tree i. We set the denominator to 8 in Eq. 3.7, following Martin & Ek (1984), who showed that this value produces about the same number of competitors as the 2.3 m² ha^{-1} angle gauge that gave the best correlation between competition and annual diameter growth in the study of Daniels (1976). Torus edge correction was used to avoid underestimation of competition for trees close to the borders of the plots (Monserud & Ek 1974).

Stepwise multiple linear regression was done with SPSS 12.0 (SPSS 2003) after log-transformation of the dependent variable (the mean five-year radial growth) and the CIs in order to meet the statistical assumptions. The Variance Inflation Factor was smaller than three in the studied models.

Table 3.2 Minimum, maximum, and mean values for the variables in the full dataset and the subsets of small and large individuals

	full dataset (n = 153)		small individuals (n = 50)		large individuals (n = 103)	
	min–max	mean	min–max	mean	min–max	mean
diameter (cm) [a]	0.1–22.9	8.1	0.1–3.2	1.2	3.5–22.9	11.2
height (m)	0.1–16.6	5.9	0.1–4.1	1.4	2.7–16.6	7.9
age (yr)	2–52	20	2–19	10	10–52	25
competition index [b]	0–363.8	28.7	0–363.8	76.7	0.8–20.1	6.7
canopy openness (%) [c]			10.4–26.2	19.5		
growth (mm yr^{-1}) [d]	0.04–4.33	1.16	0.04–1.76	0.41	0.18–4.33	1.53

[a] Diameter was measured at stem base.
[b] The competition index was calculated as Daniels' modification of Hegyi's competition index (see Eq. 3.6).
[c] Canopy openness was only measured for the subset of small individuals.
[d] Growth is calculated as the mean radial growth of the last five years.

3.4 Results

3.4.1 Quantification of radial growth

The mean radial growth, with the standard deviation between brackets, was 1.16 mm yr^{-1} (sd 0.84) for the full dataset, 0.41 mm yr^{-1} (sd 0.29) for small individuals, and 1.53 mm

yr^{-1} (sd 0.78) for large individuals (Table 3.2). Radial growth differed significantly between diameter ($\chi^2 = 93.774$, df = 5, $p < 0.001$) and age ($\chi^2 = 61.149$, df = 5, $p < 0.001$) classes (Fig. 3.2) while there were no significant differences between sites ($\chi^2 = 4.771$, df = 6, $p = 0.573$). *Prunus serotina* reached maximum radial growth rates at a dbh around 15 cm (Fig. 3.2). Fig. 3.3 shows that the radial growth of *P. serotina* in the understory of pine (Kempen, Ossenbos) as well as deciduous forests (Liedekerke) is reduced compared to the growth of *P. serotina* in full light conditions (Meerhout). The fitted functions for the relationship between dbh (y, in cm) and age (x, in yr) were $y = 0.27\ x^{1.35}$ ($R^2 = 0.98$) for the open landscape and $y = 0.11\ x^{1.37}$ ($R^2 = 0.51$) for the studied pine forests.

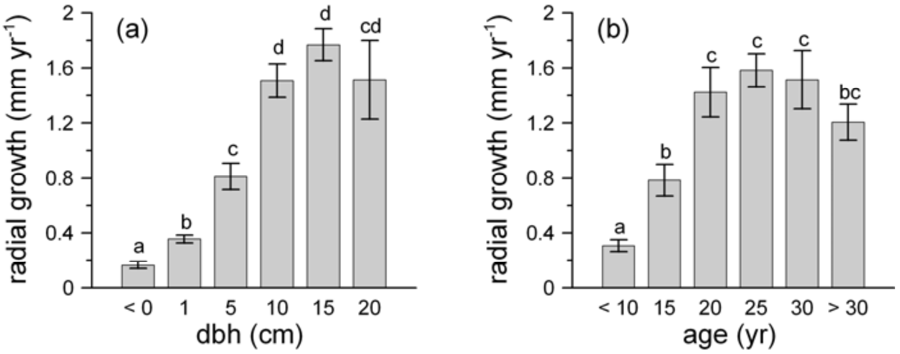


Fig. 3.2 Radial growth of *Prunus serotina* in pine plantations for different dbh (a) and age classes (b). Significant differences between the classes are indicated by the characters above the bars ($p < 0.05$). The error bars depict standard errors.

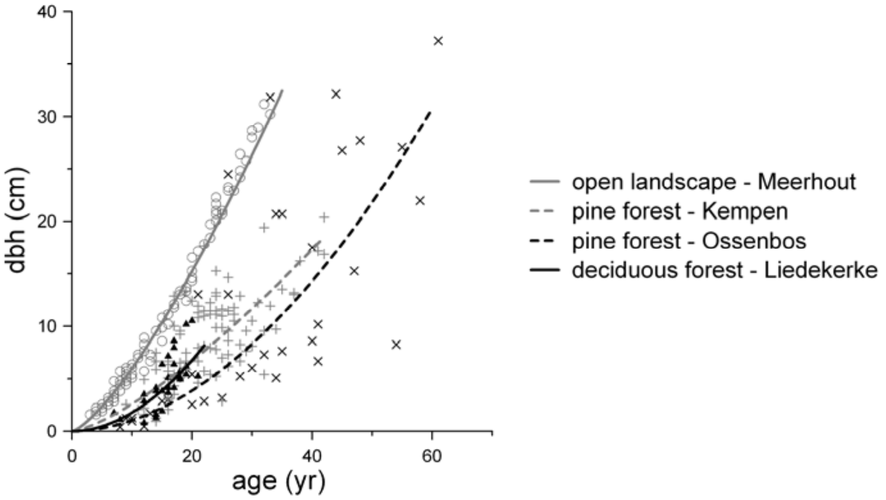


Fig. 3.3 Relationship between dbh and age for *Prunus serotina* in the studied pine stands (plus signs, ‘Kempen’), an open landscape (circles, ‘Meerhout’), another pine forest (crosses, ‘Ossenbos’) and a deciduous forest (triangles, ‘Liedekerke’)

3.4.2 Reduction of potential radial growth

The potential × modifier approach allowed us to identify the variables which modify the potential growth (Table 3.3) and to visualize their impact (Fig. 3.4). The 'size + site' model provided the best fits for the full dataset ($R^2 = 0.51$) and the large individuals ($R^2 = 0.14$) while the full model resulted in the best fit for the small individuals ($R^2 = 0.65$). Radial growth increased with diameter (Fig. 3.4a) and site productivity (Fig. 3.4b), the site effect being slightly smaller for small individuals. The crowding effect had a large impact on the actual growth for small individuals (Fig. 3.4c).

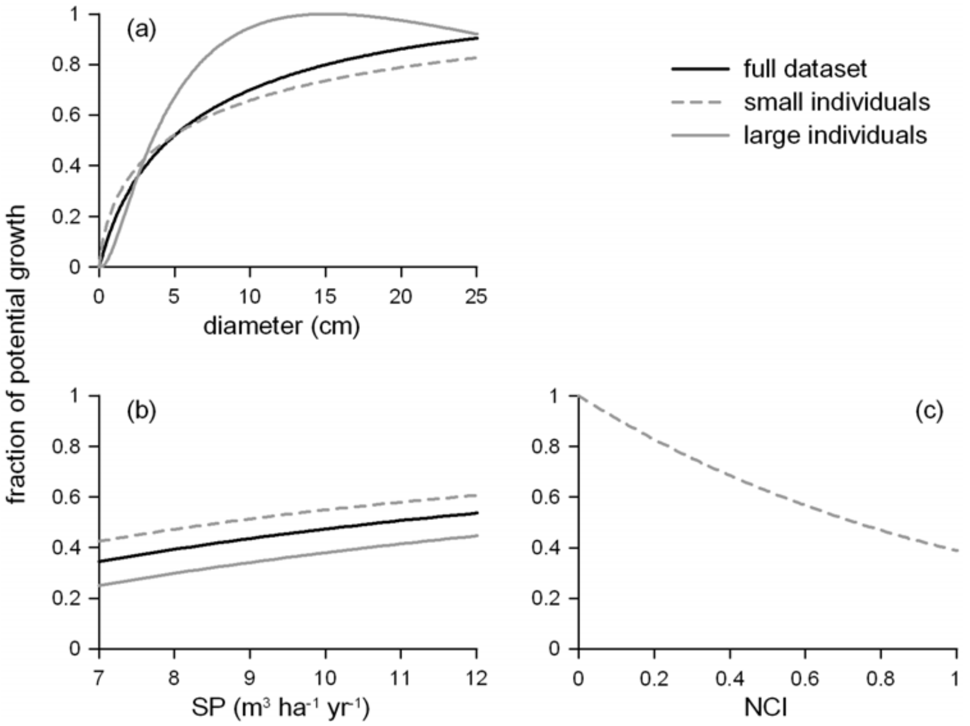


Fig. 3.4 Predicted effects of variation in (a) subject tree size, (b) site conditions (SP: site productivity), and (c) crowding on potential radial growth for the full dataset and the subsets of small and large individuals. The net competitive effect (NCI) is relative to the subject tree with the highest value of NCI.

3.4.3 Actual radial growth

The multiple linear regression explained 65 % of the variance in observed radial growth for the full dataset, 62 % for the small individuals, and 25 % for the large individuals (Table 3.4). The most important determinants of radial growth were competition (for the full dataset), tree diameter (for the three datasets), and age (for the large individuals). Competition and age had a negative impact on growth; tree diameter and site productivity were positively related to the radial growth of *P. serotina*. The impact of site productivity was small, and only relevant for the full dataset. Canopy openness was not significantly correlated with the growth of the small individuals (r = -0.167, p = 0.125), and did, consequently, not appear in the regression model. The same held true for ontogeny for the large individuals (results not shown).

Table 3.3 Comparison of alternate potential × modifier radial growth models for the full dataset, the large individuals and small individuals of *Prunus serotina* in stands of *Pinus sylvestris*

	AIC_c [a]						
	full model [b]	site + size	size + crowding	site + crowding	no. p	n	R^2
full dataset	196.23	**189.82**	211.37	363.26	4	153	0.51
small individuals	**176.47**	187.23	191.21	225.82	7	50	0.65
large individuals	214.47	**207.77**	234.29	222.10	4	103	0.14

[a] Akaike's Information Criterion corrected for small sample sizes

[b] In the full model, potential radial growth is multiplied by the three modifiers: site, size, and crowding. The other three models are reduced versions of the full model in which one of the modifiers is left out. For the best model (lowest AIC_c, indicated in bold), the number of parameters (no. p), the sample size (n), and the R^2 are given.

Table 3.4 Parameter estimates (b_i) with standard error (s.e.), standardized coefficients (β_i), goodness of fit (R^2) and the number of observations (n) for the linear radial growth models of *Prunus serotina* in stands of *Pinus sylvestris* for the full dataset and the subsets of small and large individuals

	full dataset (n = 153)			small individuals (n = 50)			large individuals (n = 103)		
	b_i	s.e.	β_i	b_i	s.e.	β_i	b_i	s.e.	β_i
intercept	-0.267	0.498		-0.003	0.436		-0.427	0.166	
diameter [a]	0.061	0.014	0.417	-0.553	0.109	-0.755	-0.072	0.013	-0.586
age	-0.024	0.008	-0.273	-0.074	0.024	-0.460	-0.037	0.008	-0.525
lnCI [b]	-0.477	0.057	-0.656	-0.269	0.077	-0.442			
SP [c]	-0.135	0.043	-0.159						
R^2	0.65			0.62			0.25		

[a] Diameter was measured at stem base.

[b] The competition index (CI) was log-transformed in order to meet statistical assumptions. Daniels' modification of Hegyi's competition index was used to calculate competition.

[c] SP is the site productivity, characterized by productivity of the study sites for *P. sylvestris*.

3.5 Discussion

Diameter, age, and competition were found to be the most important determinants of the radial growth of *P. serotina* in the understory of *P. sylvestris* plantations in northern Belgium. This finding is similar to the results of Monserud & Sterba (1996), in which tree size and competition explained most of the variance in basal area increment for the main forest species in Austria, and Doležal *et al.* (2004), who found stem size and age to be the most important determinants for radial growth of *Betula platyphylla* Sukaczev.

3.5.1 Impact of site conditions

Although site productivity had a large impact on the actual growth of *P. serotina* on sandy soil as compared to the potential growth in an open agricultural landscape (Fig. 3.4b), site productivity explained only a marginal part of the variation in growth among the seven study sites (Table 3.4), and the actual *P. serotina* growth at the study sites was similar to the *P. serotina* growth in the Ossenbos and the Liedekerke forest (Fig. 3.3), which are located on poor sandy soil and on sandy loam soil, respectively (see Chapter 5 and 6). These findings are in concordance with the characterization of *P. serotina* as a generalist species (Fridley *et al.* 2007), the wide geographic range in its native area, and the good growth on a variety of soils throughout eastern North America as long as the summer growing conditions are sufficiently moist and cool (Chapter 2).

3.5.2 Impact of competition

The crowding effect restricted growth significantly, but only for small *P. serotina* individuals (Fig. 3.4c). Closset-Kopp *et al.* (2007) found a clear growth reduction for *P. serotina* seedlings growing in the forest understory (canopy cover 75–100 %) compared to canopy gaps (canopy cover 25–75 %). The light conditions in the homogenous pine forests of our study were rather uniform (canopy openness 10–26 %, Table 3.2), and we did not find a significant correlation between canopy openness and radial growth. Therefore, the observed crowding effect is probably not entirely due to competition for light, but might result from an intensive competition for belowground resources at the infertile and dry study sites. Seedlings of *P. serotina* are indeed able to survive as ageing juveniles under the dense shade of a closed canopy (Closset-Kopp *et al.* 2007, Chapter 2), regaining growth in better light conditions (Marquis 1990). This might imply that the nutrient requirements of the species are high in shaded conditions, according to Coomes

& Grubb (2000), who stated that species with high potential growth rates, responding markedly to increased irradiance, are most sensitive to nutrient availability in low light conditions.

3.5.3 Variation in radial growth

The radial growth of the large *P. serotina* individuals in the studied pine stands was highly variable. Only a limited part of the variation could be explained based on the studied variables, and accounting for ontogeny, i.e., past diameter growth, or site productivity did not improve the models. Other factors, including genetic variability, pathogens, physical damage, weather conditions, and residual effects of past periods of suppression and release may increasingly influence the radial growth of large saplings and trees (cf. Wright *et al.* 2000, Jones & Thomas 2004). Furthermore, the gap dependence of *P. serotina* (Chapter 2) suggests that competition for light might become more important for explaining the growth of large individuals. Unfortunately, we were not able to measure the light availability above the large *P. serotina* individuals directly.

3.6 Conclusions

Mean radial growth of *P. serotina* in the understory of pine forests was 0.41 mm yr^{-1} (sd 0.29) for *P. serotina* with a diameter at stem base < 3.5 cm and 1.53 mm yr^{-1} (sd 0.78) for *P. serotina* with a diameter at stem base > 3.5 cm. Radial growth was optimal for *P. serotina* with a dbh of 10–15 cm and an age of 20–30 yr. The understory radial growth of *P. serotina* was reduced by up to 50 % as compared to the potential *P. serotina* growth in full light conditions. The effects of site productivity and tree size reduced the growth of all *P. serotina* trees; crowding effects were important only for small *P. serotina* individuals. The actual radial growth of *P. serotina* below pines was related to the diameter and age of the *P. serotina* tree and the competition with neighbouring trees.

4 Regeneration of *Prunus serotina* in the understory of Scots pine stands

After: Vanhellemont M, Baeten L, Hermy M, Verheyen K (2009) The seedling bank stabilizes the erratic early regeneration stages of the invasive *Prunus serotina*. Écoscience 16, 452–460

4.1 Abstract

We studied the regeneration dynamics of the invasive tree species *Prunus serotina* in the understory of seven Scots pine (*Pinus sylvestris*) stands in the introduced range for four years, focusing on temporal, spatial, and spatiotemporal patterns. In each 20 m x 40 m study plot, we inventoried all trees and shrubs taller than 1 m, counted seedlings in three age-height classes, trapped *P. serotina* seed rain, and identified the *P. serotina* seed trees. The seed set, seed rain density, and seedling densities of *P. serotina* all varied between the years and between the study plots, but the temporal stability of the spatial regeneration patterns increased with regeneration stage. There was a clear distinction between (1) seedlings smaller than 20 cm, younger than 6 years, occurring in very high densities and (2) seedlings between 20 cm and 1 m tall, older than 6 years, showing high spatiotemporal stability. Notwithstanding the large year-to-year variation in seed input, *P. serotina* maintained its regeneration potential in the forest understory by building up a short-lived seedling bank. The seedling bank strategy might represent an efficient way towards site occupancy of shade-tolerant alien species in forest understories with few shade-tolerant native species.

4.2 Introduction

The early life stages of tree and shrub species are important with regard to forest dynamics: they represent a blueprint of the future community structure and composition. Consequently, processes or species traits limiting or favouring recruitment of certain woody species will strongly influence forest development (Ribbens *et al.* 1994, Hille Ris Lambers & Clark 2003, Chapter 7). Many temperate tree species show annual variability in seed production (e.g., Herrera *et al.* 1998, Grime 2001), and they rarely saturate the forest floor with seed (Ribbens *et al.* 1994). Persistent seed banks are not common to temperate forest tree species, but the annual variation in seed production might be overcome by the capacity of the seedlings to survive for certain periods under unfavourable circumstances, which ensures the maintenance of the potential for regeneration (Grime 2001). Marks & Gardescu (1998) defined this 'seedling bank' as a set of seedlings older than one year, excluding shoots of sprout origin, that exhibit a restricted range of sizes in shaded conditions. By building up a seedling bank, a species can stabilize the outcome of the erratic processes of seed set and germination. Consequently, the regeneration potential of the species will no longer solely depend on its current seed set and germination. This stabilizing effect has already been shown for several native temperate tree species, e.g., *Acer pseudoplatanus* L. in France (Collet *et al.* 2008) and *Acer saccharum* Marshall in the northeastern United States (Marks & Gardescu 1998, Woods 2008). The build-up of a seedling bank might favour alien, invading tree species over native species with no, or a less effective, seedling bank strategy. Martin & Marks (2006) indeed suggested that the invasiveness of *Acer platanoides* L. in forests in the eastern United States might be partly attributed to its more effective seedling bank build-up compared to the native species including *A. saccharum*. Meiners (2005) also showed that seedlings of *A. platanoides* might compete more effectively with other seedlings than its native congener *A. saccharum*.

The tree species *Prunus serotina* Ehrh. is considered an invasive species in Europe (see Chapter 2). Its invasiveness has been attributed to the combination of traits that enables the species to persist as a juvenile in shaded conditions and to exhibit rapid growth in open habitats and forest gaps (Closset-Kopp *et al.* 2007). Up till now, the studies on *P. serotina* seed dispersal (Deckers *et al.* 2005, Pairon 2007, Deckers *et al.* 2008) and regeneration (Starfinger 1990, Closset-Kopp *et al.* 2007) in Europe nearly all used data for only one year and one site, which has prevented examining the spatiotemporal variability in the early life stages of *P. serotina* in its introduced range. Studies on the regeneration dynamics of woody species should, ideally, exceed a single growing season and cover a series of consecutive early life stages. We wanted to investigate the temporal and spatial variability in the seed rain and seedling dynamics of *P. serotina* in its introduced range. Therefore, we studied the properties of *P. serotina* regeneration in seven Scots pine (*Pinus sylvestris* L.) plantations on sandy soil for four years.

The objectives of this chapter were the characterization of (1) the seed set dynamics and (2) the temporal and spatial variability in seed rain and seedling densities of *P. serotina* in the understory of pine forests in its introduced range.

4.3 Materials and methods

4.3.1 Study area

The study plots were located in seven homogenous *Pinus sylvestris* stands on coarse sandy soil in the Campine region, the northern part of Belgium (see Chapter 3: section 3.3.1 and Table 3.1). The pine trees were planted 50–70 years ago, and they have not been managed during the last decades. The understory was not planted and has developed spontaneously. *Prunus serotina* was present in high densities, but native shrub species such as *Sorbus aucuparia* L. have also been able to establish (see Chapter 3: Table 3.1). Seedlings were found for three alien species, i.e., *P. serotina*, *Quercus rubra* L., and *Amelanchier lamarckii* F. G. Schroed., and for the native species *S. aucuparia*, *Quercus robur* L., *Ilex aquifolium* L., *Frangula alnus* L., and *Betula pendula* Roth.

4.3.2 Data collection

In each of the seven pine stands, we used the permanently marked 20 m x 40 m study plot from Chapter 3 (section 3.3.2) as well as the data on position and diameter for all trees and saplings taller than 1 m in the study plot. Tree diameter was measured at breast height for the canopy trees (*P. sylvestris*) and at stem base for all the woody species in the understory. In 2006, 2007, and 2008, we recorded which *P. serotina* trees and shrubs were bearing seeds.

To sample the seedlings of tree and shrub species, each 20 m x 40 m study plot was subdivided into 32 contiguous plots of 5 m x 5 m, i.e., the seedling plots (Fig. 4.1). We distinguished between seedlings resulting from seeds germinated in the year of sampling (stage I), seedlings smaller than 20 cm (stage II), and seedlings between 20 and 100 cm tall (stage III). In general, for *P. serotina*, stage II seedlings were younger than 6 years while stage III seedlings were older than 6 years (see Appendix 4.1). Seedlings were counted in June 2004 (stage I+II vs. stage III) and in July 2006, 2007, and 2008 (stage I, stage II, and stage III).

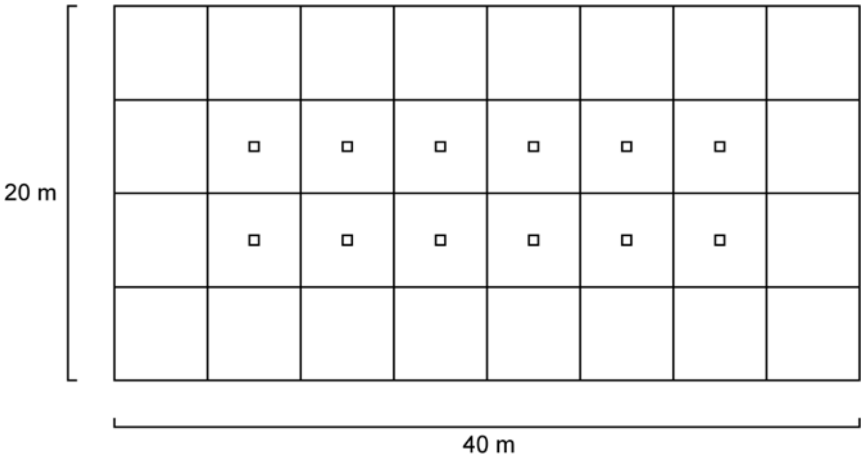


Fig. 4.1 The design of the 20 m x 40 m study plot with the 32 contiguous 5 m x 5 m seedling plots and the 12 central 0.5 m x 0.5 m seed plots

Prunus serotina seed densities were sampled in the central twelve seedling plots of each study plot. At the centre of these twelve plots, we marked 0.5 m × 0.5 m plots, i.e., the seed plots (Fig. 4.1). In June 2004, litter was collected in the seed plots to sample the seed bank. The volume of the litter samples was measured, and the *P. serotina* seeds were sorted out. Seeds were considered potentially viable if they were still firm and did not show any sign of predation or physical damage. In 2006, 2007, and 2008, we sampled the seed rain of *P. serotina* with seed traps (Photo 4.1). The seed traps were made of a 0.5 m × 0.5 m wooden frame, with a depth of 5 cm. The bottom of the traps consisted of a nylon screen; the top was made of a hardware cloth with openings of 2 cm. The traps were placed on the seed plots in July, and they were left out until mid-December. Every two weeks, seeds were collected from the traps, the fruit pulp was washed away, and the percentage of seeds showing signs of predation by the bird-cherry weevil *Furcipus* *rectirostris* (Linnaeus, 1758) was determined (cf. Pairon *et al.* 2006a, Boucault 2009). For the study plot Katteven, seed rain was only sampled in 2006 and 2007.

Photo 4.1 Seed traps in study plot Molekens (July 2008)

4.3.3 Data analysis

We examined the seed set, seed rain, and seedling densities of *P. serotina*. For the analysis of the seed rain and seedling densities, we consecutively investigated temporal, spatial, and spatiotemporal patterns. The spatial variation was studied on two spatial scales: between and within the study plots. We mainly focused on the period 2006–2008, using the 2004 data primarily for further illustration of the findings. Data analysis was performed in SPSS 15.0 (SPSS 2006) and R 2.8.0 (R Development Core Team 2008).

4.3.3.1 Seed set dynamics

To study the seed-bearing dynamics of *P. serotina* trees, we distinguished between trees that set seed in the three studied years (2006, 2007, and 2008), trees that did not set seed in any of the studied years, and trees that showed year-to-year variability in seed set. For the latter, we performed χ^2 tests on a tree's seed set (0/1 variable) between subsequent years to examine whether seed set in a year was associated with seed set in the previous year. Logistic regression was used to relate the presence/absence of seeds to the diameter of the tree and the competition with neighbouring trees. Competition between trees was calculated with the competition index of Hegyi (1974), based on the diameter of and the distance to neighbouring trees that meet the criterion of Daniels (1976) (cf. Eq. 3.6 in Chapter 3).

Next, the mean observed seed production per tree (SP_o) was calculated for each study plot based on the observed seed rain density and the number of seed-bearing trees per study plot with Eq. 4.1 (cf. Pairon *et al.* 2006b):

$$SP_o = \frac{\frac{A_{plot}}{A_{traps}} \sum_{k=1}^{12} S_k}{n_{st}} \qquad (4.1)$$

with A_{plot} the surface area of the study plot, A_{traps} the summed surface area of the 12 seed traps in the study plot, S_k the number of seeds in trap k, and n_{st} the number of seed-bearing trees in the study plot.

4.3.3.2 Seed rain and seedling dynamics

Prunus serotina seed rain data were available for the seven study plots in 2006 and 2007, i.e., for 84 seed plots per year, and for six study plots in 2008, i.e., for 72 seed plots. Seedling data were analyzed for six of the study plots, i.e., for 192 seedling plots, because we found almost no *P. serotina* seedlings in study plot Langdorp. The consecutive analyses on the temporal, spatial, and spatiotemporal variation were done separately for the seed rain densities and for the seedling densities. The temporal variation at the study plot level, i.e., the differences in overall seed rain or seedling densities between years, was investigated with non-parametric k related samples Friedman tests. Spatial variability was studied between and within the study plots. First, to examine the differences in seed rain or seedling densities between the study plots, we used non-parametric k independent samples Median tests. Second, to compare the variation in seed rain (n = 12) or seedling densities (n = 32) within each study plot, we calculated coefficients of variation. Spatiotemporal patterns were studied to determine whether the observed spatial patterns of seed rain or seedling densities within a study plot remained stable between the studied years. For that purpose, we performed Mantel tests on the matrices in which the data for the grid of seed plots (n = 12) or the grid of seedling plots (n = 32) were used as the matrix entries. Separate matrices were compiled for each of the studied years.

4.4 Results

4.4.1 Seed set dynamics

Fifty-five percent of the *P. serotina* taller than 1 m in the study plots did not set seed in the period 2006–2008 (399 individuals); 27 % bore seeds in each of the three years (196 individuals); and 18 % set seed in one or two years (132 individuals). For the latter trees, seed set in a year lowered the chance to set seed in the following year. The χ^2-test was significant for 2006–2007 ($\chi^2 = 18.34$, df = 1, $p < 0.001$) and tended towards significance for 2007–2008 ($\chi^2 = 3.56$, df = 1, $p = 0.06$). Both tree diameter and competition with neighbouring trees were significant in explaining the seed-bearing status of *P. serotina* (Table 4.1). The probability of seed set increased with diameter and decreased with competition. The range of the observed seed production per tree across the study plots was 0–493 in 2006, 481–5245 in 2007, and 46–134 in 2008.

Table 4.1 The effect of tree diameter and competition on the seed-bearing status of *Prunus serotina* in the studied plots (logistic regression): parameter estimates (b), parameter significance (p), and odds ratio (o.r.) for 2006, 2007, and 2008

	2006			2007			2008		
	b	p	o.r.	b	p	o.r.	b	p	o.r.
intercept	-2.15	< 0.001	0.12	-1.75	< 0.001	0.17	-1.84	< 0.001	0.16
diameter [a]	0.35	< 0.001	1.42	0.35	< 0.001	1.41	0.30	< 0.001	1.35
competition [b]	-0.03	0.011	0.97	-0.08	< 0.001	0.92	-0.05	0.001	0.95
R^2		0.50			0.57			0.48	

[a] Diameter was measured at stem base.

[b] Competition was calculated as Daniels' modification of Hegyi's competition index (see Eq. 3.6 in Chapter 3).

4.4.2 Seed rain dynamics

The insect predation level of the trapped seeds differed between the study plots and between the years, ranging from 7 % in 2007 to 23 % in 2006 (mean values for the seven study plots) and from 2 % for study plot Genk to 21 % for study plot Langdorp (mean values for the period 2006–2008). Of the seeds found in the litter layer (2004 data), 0–30 % was still potentially viable.

Seed rain densities (Fig. 4.2a) were significantly different between the years for all study plots together (k related samples $p < 0.001$, $n = 72$) as well as for each of the study plots separately (all $p < 0.001$, $n = 12$). Seed rain densities differed significantly between the study plots for 2006 (k independent samples $p < 0.001$, $n = 84$) and for 2007 ($p < 0.001$, $n = 84$), but not for 2008 ($p = 0.079$, $n = 72$). The spatial variability of the seed rain densities within the study plots was significantly larger in 2006 than in 2007 but similar for 2007 and 2008 (Fig. 4.3). The spatiotemporal variation in seed rain densities was high: the spatial patterns within the study plots showed no temporal stability (no significant correlations in the Mantel tests).

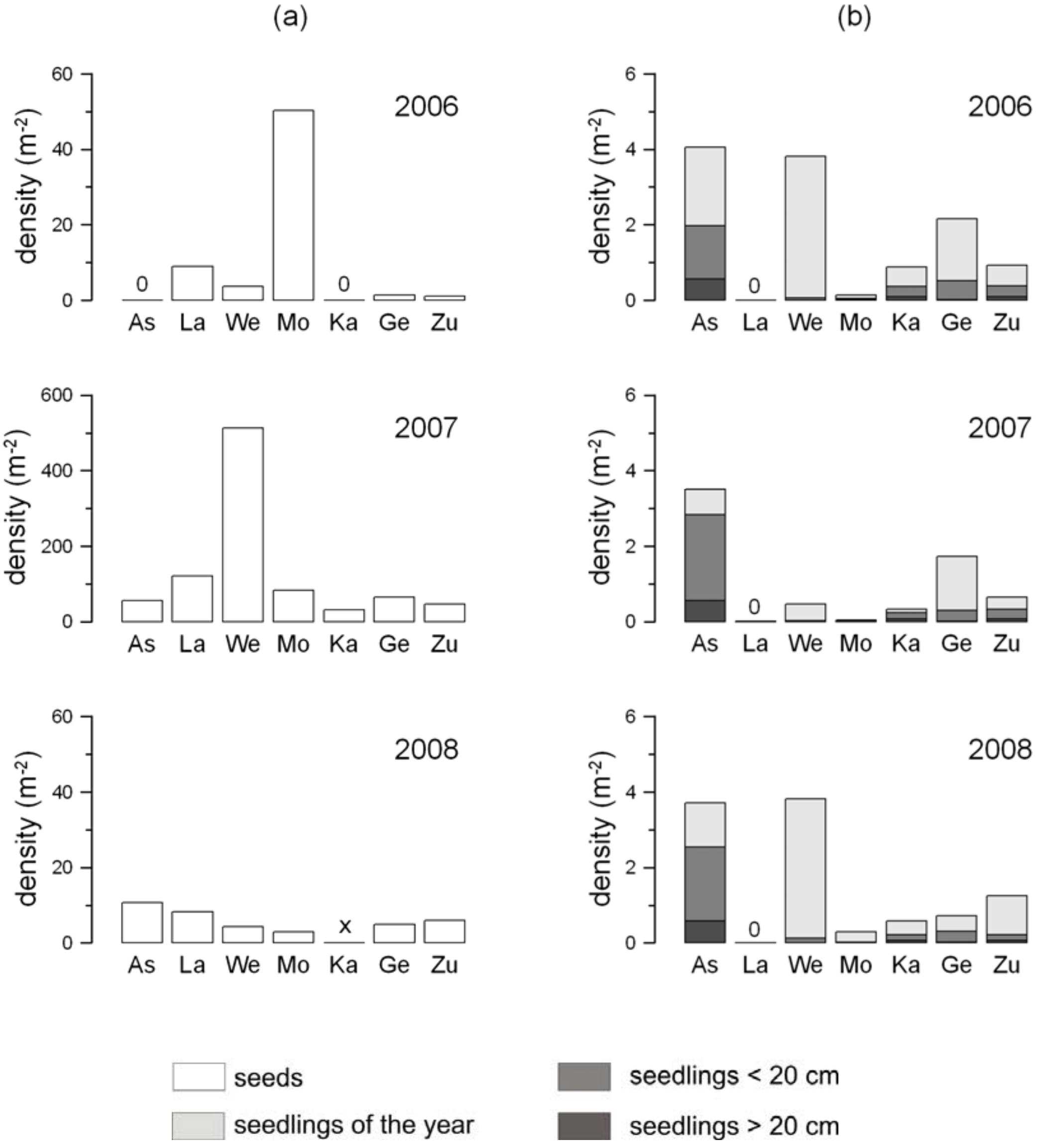


Fig. 4.2 Seed rain (a) and seedling (b) densities of *Prunus serotina* in the seven study plots (see Chapter 3: Table 3.1) in 2006, 2007, and 2008. Very low or zero densities are labelled with zero; the cross indicates that there are no data. Note that the scale of the vertical axis in figure a is 10 times as large for 2007 as for 2006 and 2008.

4.4.3 Seedling dynamics

In study plot Langdorp, we found only two *P. serotina* seedlings, and we excluded the plot from the seedling analysis. For the other plots, the observed mean seedling densities ± standard errors were, with the full density range between brackets: 10287 ± 2675 ha^{-1} for stage I (163–37575 ha^{-1}), 4608 ± 1611 ha^{-1} for stage II (100–22763 ha^{-1}), and 1253 ± 481 ha^{-1} for stage III seedlings (25–5775 ha^{-1}). The mean observed stage II seedling densities were 3–25 times higher than the stage III seedling densities, except for one plot, in which the stage II/stage III density ratio equalled 1. The ratio of native tree species seedling abundance versus *P. serotina* seedling abundance increased from stage I seedlings (7 ± 2 % native species) to stage II seedlings (47 ± 4 %) and stage III seedlings (68 ± 8 %), except for one study plot in which only 20 % of stage III seedlings were native.

The seedling densities of *P. serotina* varied between the years and between the study plots (Fig. 4.2b). The temporal variability in seedling densities declined with seedling stage. Seedling densities differed significantly between the years in all the study plots for the stage I seedlings (all k related samples $p < 0.001$, $n = 32$), in three study plots for the stage II seedlings ($p < 0.001$, $p = 0.001$, $p = 0.012$, $n = 32$), and in one study plot for the stage III seedlings ($p = 0.006$, $n = 32$). Spatial variability occurred between and within the study plots. For each of the seedling stages, the seedling densities differed significantly between the study plots, in 2006, 2007 as well as 2008 (all $p < 0.001$, $n = 192$). The spatial variability within the study plots increased with seedling stage (Fig. 4.3).

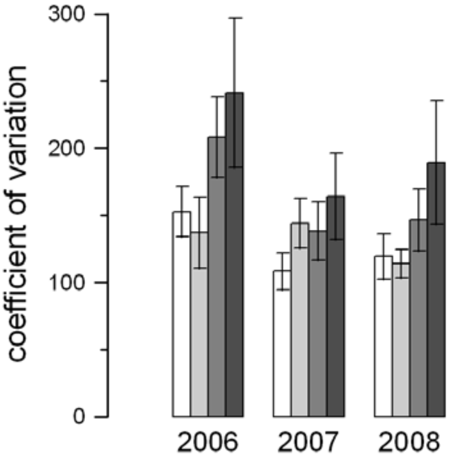


Fig. 4.3 The mean coefficient of variation for the seed rain (n = 12) and seedling densities (n = 32) of *Prunus serotina* within the study plots in 2006, 2007, and 2008. The error bars show standard errors.

The spatiotemporal variability was higher for stage I and stage II seedlings than for stage III seedlings, which is shown by the lower correlation coefficients for stage I and stage II seedlings in Fig. 4.4. All correlations of the Mantel tests were significant for stage III seedlings (p values between 0.001–0.025, n = 32). For the stage I+II seedlings, almost no significant correlations were found for the 2- and 4-year intervals (Fig. 4.4a). Both the stage I and stage II seedlings did not show significant correlations for the 1-year and 2-year intervals (Fig. 4.4b) except for one study plot, for which all correlations were significant for stage I and stage II seedlings, and for two study plots that showed significant correlations for both the stage I and stage II seedling densities between 2006 and 2007.

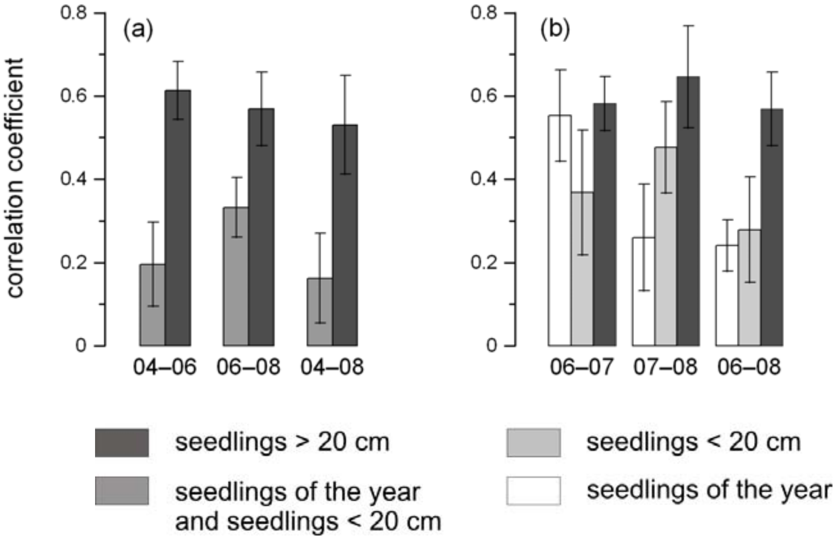


Fig. 4.4 The temporal stability of the spatial patterns of *Prunus serotina* seedling abundances depicted as mean correlations between the years for the study plots (Langdorp excluded). The error bars show standard errors. Figure a: correlations for the 2-year intervals 2004–2006 and 2006–2008 and the 4-year interval 2004–2008. Seedlings resulting from seeds germinated in the year of sampling and seedlings smaller than 20 cm are combined because the distinction between the two classes was not made in 2004. Figure b: correlations for the 1-year intervals 2006–2007 and 2007–2008 and the 2-year interval 2006–2008.

4.5 Discussion

Although the early life stages of *P. serotina* in the understory of the studied pine stands showed a high spatial and temporal variability, the temporal stability of the spatial regeneration patterns increased with seedling stage. The spatial positioning of stage III seedlings, i.e., seedlings taller than 20 cm and older than 6 years, showed a much higher correlation between years than the spatial arrangement of the stage I and stage II seedlings, i.e., the seedlings smaller than 20 cm and generally younger than 6 years. The continuous presence of small *P. serotina* seedlings in the understory enabled *P. serotina* to maintain its regeneration potential in the sampled pine stands despite the large year-to-year variation in seed input.

4.5.1 Seed set and germination

Prunus serotina seed production per tree showed annual variation, similar to the findings of a 2-year study in a pine stand in Central Belgium (Pairon *et al.* 2006a) and the reported variation in seed production in its native range (Grisez 1974, Bjorkbom 1979, Martin & Canham *in press*). The temporal and spatial variation in seed set observed within the study plots might have resulted from variable weather conditions in combination with differences in flowering and fruit-ripening dates among the *P. serotina* individuals in a plot (cf. Forbes 1973, Grisez 1974). Besides, the spatial seed rain patterns will have been influenced by the spatial pattern of trees and shrubs in the study plots seeing that seed set probability was affected by *P. serotina* tree diameter and competition with neighbouring trees. Next to variation in seed set, we also observed differences in the proportion of seeds predated by *Furcipus rectirostris*. Predation levels differed between sites, similar to the findings of Boucault (2009) for three forests in France, and between years. The lowest proportional predation levels occurred in the best seed year, i.e., 2007, which might be the result of predator satiation. Although only a small percentage of the seed rain density, e.g., 0.3–1.2 % for 2007, turned into new seedlings the following year, stage I seedling densities were extraordinarily high in some of the study plots, similar to the findings of Closset-Kopp *et al.* (2007), who found *P. serotina* stage I seedlings to be much more numerous than the other seedling stages in forest understories.

4.5.2 A short-lived seedling bank

The high densities of seedlings smaller than 20 cm that can be up to 6 years old are in concordance with our observations in a pine forest in the Netherlands (see Chapter 6) and the observations of Closset-Kopp *et al.* (2007) in Compiègne forest in France. Thus, *P. serotina* is able to build up a short-lived seedling bank in forest understories. In its native range, *P. serotina* frequently co-occurs with species that are known to build up a seedling bank, such as *Acer saccharum*, *Fagus grandifolia* Ehrh., *Tsuga canadensis* (L.) Carrière, and *Quercus alba* L. (Marks & Gardescu 1998). In the introduced range, on the other hand, persistent seedling banks are not a common feature of tree and shrub species. Seedling banks have been documented for *Ilex aquifolium*, *Picea abies* (L.) H. Karst. (Marks & Gardescu 1998), *Fagus sylvatica* L., and *Acer pseudoplatanus* (Collet *et al.* 2008), of which only *Ilex aquifolium* occurred sporadically in the studied stands (see Chapter 3: Table 3.1). *Sorbus aucuparia* may also build up a seedling bank (Żywiec & Ledwoń 2008), but its establishment is negatively affected by the presence of herbivores (Raspé *et al.* 2000). The massive presence of *P. serotina* seedlings in the understory of the studied stands may ensure future site occupancy to the detriment of the native species present.

4.5.3 *Prunus serotina* versus the native species

It should be noted that seedlings of native species did occur in our study plots despite the absence or paucity of seed sources of native species near the study plots. Moreover, the ratio of seedling densities of native species versus *P. serotina* increased with seedling stage. Although seedlings-of-the-year were much more numerous for *P. serotina* as compared to native species, 50–90 % of the seedlings larger than 20 cm were native, except for 1 study plot in which only 20 % of the stage III seedlings were native. Yet, this trend did only partly continue into the shrub layer. *Prunus serotina* made up 28–44 % of the shrub layer in four of the study plots, but the *P. serotina* densities were 1.5–19.1 times higher than the summed densities of all the native species in the shrub layer of the other three study plots. The relatively low light levels below the *P. serotina* shrubs might impede the release of *P. serotina* seedlings from the seedling bank and might have a negative impact on the growth of the stage III seedlings of *P. serotina* (cf. Marquis 1990, Starfinger 1990). Indeed, *P. serotina* seedlings might only be able to grow taller than 20 cm in areas where they experience low levels of competition, which is illustrated by the negative relationship between competition and seedling biomass in our study (Appendix 4.1). Likewise, Knight *et al.* (2008) found higher abundances of tall *P. serotina* seedlings in areas with a higher light availability and less competition with other species in the herb layer. Contrary to *P. serotina*, the native shrub species *Sorbus aucuparia*, which was the most frequently occurring native species in the study plots (cf. Chapter 3: Table 3.1), is known to be reasonably shade tolerant in its early life stages (Raspé *et al.* 2000). Consequently, *S. aucuparia* seedlings larger than 20 cm might show a higher survival and growth than *P. serotina* stage III seedlings below *P. serotina* shrubs (cf. Chapter 5).

4.6 Conclusions

The seed set, seed rain density, and seedling densities of *P. serotina* varied between the years, between the study plots, and within the study plots. Although the seed input differed markedly between years, *P. serotina* maintained its regeneration potential in the forest understory by building up a short-lived seedling bank, characterized by high densities of small seedlings. These seedlings grew taller and thus into the next seedling stage in areas with low levels of competition. Two seedling stages could be distinguished:

(1) seedlings smaller than 20 cm, younger than 6 years, occurring in very high densities,

(2) seedlings between 20 cm and 1 m tall, older than 6 years, showing high spatiotemporal stability.

The seedling bank strategy seemed to favour the invasive *P. serotina* over the native tree and shrub species in the studied forest stands. The seedling bank might ensure site occupancy when canopy gaps occur. In that case, regeneration of *P. serotina* will not solely depend on seed input since high densities of seedlings will be present to profit from the increase in light availability. Yet, long-term data will be necessary to demonstrate whether the abundant presence of *P. serotina* seedlings and saplings will lead to a persistent, alternative plant community on the sandy soils that are now covered with pine plantations in its introduced range.

The observed variation in seed production and seedling densities across years and sites in our study indicates that conclusions drawn from one-year and one-site observations of *P. serotina* seed set, seed dispersal, or recruitment should be considered with care.

Appendix 4.1

To investigate the characteristics of the *Prunus serotina* seedling layer in the studied pine stands, *P. serotina* seedlings older than 1 year were sampled destructively in four of the stands, i.e., As, Genk, Katteven, and Zutendaal (see Chapter 3: Table 3.1), in August 2008. We used the 20 m x 40 m study plot in each of the stands and sampled up to four seedlings smaller than 1 m in each of the thirty-two 5 m x 5 m seedling plots. For each seedling (n = 440), we measured position within the study plot, height, and diameter at the root-shoot boundary. Oven-dry biomass of the leaves, stems, and large roots was measured for 364 of the seedlings.

The age of the seedlings was determined by counting terminal bud scars and growth rings. The terminal bud scars could be identified easily for 340 of the sampled seedlings. To count growth rings, 202 of the sampled seedlings were cut at the root-shoot boundary and 15–20 µm thick sections were cut with a sliding microtome. The sections were stained with an aqueous 1 % safranin solution, rinsed with water, dehydrated with a series of 50 %, 75 %, and 95 % alcohol, and mounted in Euparal on slides for microscopic examination. Growth rings could be identified for 72 of the 202 seedlings, and the relationship between age (y) and diameter at stem base (x) for these 72 seedlings, i.e., $y = 3.045 \ln x + 3.106$ ($R^2 = 0.69$), was used to estimate the age of the other seedlings. The estimated age was compared with the age based on the bud scar counting, which lead to a reliable age estimate for 340 seedlings.

Based on the height and age distributions, we distinguished two seedling classes. Seedlings smaller than 20 cm were, on average, 4.0 ± 0.1 years old, and 90 % of them was younger than 6 years (n = 222). Seedlings larger than 20 cm were 7.5 ± 0.1 years old, 90 % being older than 6 years (n = 118). Total seedling biomass (y) was affected by age (x_1) and competition (x_2): $\ln y = 4.639 + 0.468\, x_1 - 0.360 \ln x_2$ ($R^2 = 0.71$, n = 206), in which competition was calculated with the competition index of Hegyi (1974), based on the diameter of and the distance to all neighbouring trees that meet the criterion of Daniels (1976) (see Chapter 3: Eq. 3.6).

5 Patterns of *Prunus serotina* colonization in a mixed deciduous forest in an area with a low propagule pressure

After: Vanhellemont M, Verheyen K, De Keersmaeker L, Vandekerkhove K, Hermy M (2009) Does *Prunus serotina* act as an aggressive invader in areas with a low propagule pressure? Biological Invasions 11, 1451–1462

5.1 Abstract

Most studies on *Prunus serotina* in Western Europe have focused on heavily invaded areas, where the presence and abundance of *P. serotina* still reflect its introduction history. Because propagule pressure is an important driver of invasion success, we wanted to investigate whether *P. serotina* would still be labelled an aggressive invader in an area with a far lower propagule pressure, in which the species had not been favoured through deliberate human introduction. We reconstructed the *P. serotina* colonization in the Liedekerke forest reserve, a mixed deciduous forest in central Belgium, based on aerial photographs (1944–1986), forest inventory data (for 1986, 1996, and 2006), and tree ring analysis. Connectivity to seed sources and light availability were the major drivers of *P. serotina* presence. In 2006, *P. serotina* could not be considered an aggressive invader in the studied forest. The rate of spread had slowed down rather quickly, and the establishment of native shrub and tree species seemed not to be hampered by the *P. serotina* presence. Furthermore, understory *P. serotina* showed low growth and seed production while further germination and establishment of *P. serotina* were probably hampered by the high *Rubus* cover. Nonetheless, calamities opening up the canopy layer in the few areas with high *P. serotina* sapling density may alter the course of the invasion process. Our results suggest that long-distance dispersal events and ‘windows of opportunity’, i.e., spots with high light availability, direct *P. serotina* colonization. When these ‘windows’ close, it is difficult for *P. serotina* to thrive, and the invasion process slows down. Closing the windows of opportunity for invasive species might be an effective measure to mitigate their aggressive behaviour.

5.2 Introduction

Invasive woody plant species that alter the vegetation structure and the species composition of native communities, i.e., aggressive invaders (Chapter 1), pose conservation problems world-wide, both in forest and non-forest ecosystems (e.g., Martin 1999, Richburg *et al.* 2001, Tassin *et al.* 2006, Meiners 2007, Martin *et al.* 2009). Shade-tolerant woody species are a particular challenge because they typically have long generation times and experience multiple lag phases during the invasion process (Martin & Marks 2006, Wangen & Webster 2006). This makes the early detection of the invasiveness of shade-tolerant species difficult, and may allow a species to consolidate its position (and its impact on the ecosystem) long before the need for control measures becomes obvious. To gain insight into the patterns and ecosystem consequences of such protracted invasion processes, it would be interesting to study the colonization of invasive species in areas where the history of introduction and ecosystem disturbance are known. Because high propagule pressure and ecosystem disturbance have both been found to facilitate invasion processes (Lozon & MacIsaac 1997, Křivánek *et al.* 2006), research should focus on areas in which the invasive species has not been planted or managed. The widespread control measures in highly invaded regions often preclude the study of the ecological processes that govern the rate of invasion.

Studies on the invasive tree species *Prunus serotina* Ehrh. in Europe focused mainly on areas that are already heavily invaded. The presence and abundance of *P. serotina* in these areas might be explained primarily by its introduction history and by anthropogenic disturbance (see Chapter 2). It would be useful to study the spread of *P. serotina* in an area characterized by a far lower propagule pressure, in which the species has not been introduced deliberately, and to investigate whether the species would still be labelled an aggressive invader. After all, *P. serotina* has not yet fully occupied its potential range, e.g., in Flanders, the northern part of Belgium (Verheyen *et al.* 2007), and shows a clear range expansion in Europe (Klotz 2009). Therefore, the species will likely spread to new, uninvaded areas in the future. Identification of the factors that control the rate of colonization of new sites by *P. serotina* and the consequences of the establishment of *P. serotina* for native populations and ecosystem processes will be critical to the development of appropriate management strategies.

To study the spontaneous spread of invasive tree species in forests, long-term data are needed (cf. Wangen & Webster 2006). Strict forest reserves, acting as references for nature-oriented forest management, represent an opportunity to study the spontaneous development of forests and the possible impact of invasive species. In Flanders, however, the monitoring of strict forest reserves only started in 2000. Consequently, no long-term data are available. The Liedekerke forest reserve is unique in this respect because inventory data were available for three moments in time, i.e., 1986, 1996, and 2006. Besides, the Liedekerke forest reserve is situated in a forest-poor region in which little *P. serotina* has been planted. The Liedekerke forest reserve therefore offers an opportunity to study the colonization of *P. serotina* in an environment in which the species has not been favoured through deliberate human introduction.

The objectives of this chapter were (1) the description of the spread of *P. serotina* in a developing deciduous forest in an area with a low propagule pressure, (2) the identification of factors that are related to the observed colonization pattern, and (3) predicting the future role of *P. serotina* in the studied forest.

5.3 Materials and methods

5.3.1 Study area

The Liedekerke forest reserve (20.9 ha) is situated in central Belgium (N50°52’ E004°07’) on well-drained sandy loam soil, 25 m above sea level (Fig. 5.1). Minimum and maximum monthly mean temperatures are 2.5°C in January and 17.2°C in July, and the mean annual precipitation is 821 mm (www.meteo.be). The forest reserve borders on the Liedekerke state forest (55 ha, west and north), the rivulet Hollebeek (east), and agricultural fields and pasture (south). The area remained forested until 1891, when a few small parcels were cut. In 1926, all trees and shrubs were cut for the installation of a transmitting station. The subsequent management regime with regular cutting and mowing resulted in the development of heathland and coppice. After the dismantlement of the transmitting station during WWII, management practices ceased and the vegetation developed to a mixed deciduous forest, consisting of nineteen native and two alien tree and shrub species. At present, the mean basal area in the study area is 31 m^2 ha^{-1}, of which *Betula* spp. (*B. pendula* Roth and *B. pubescens* Ehrh.) represent 43 %, *Quercus rubra* L. 20 %, and native *Quercus* spp. (*Q. robur* L. and *Q. petraea* [Matt.] Liebl.) 25 %

(Table 5.1). The herb layer was dominated by *Rubus fruticosus* agg. (Photo 5.1 and 5.2); species such as *Dryopteris carthusiana* (Vill.) H.P.Fuchs, *Lonicera periclymenum* L., *Dryopteris dilatata* (Hoffm.) A.Gray, *Athyrium filix-femina* (L.) Roth, *Holcus lanatus* L., and *Teucrium scorodonia* L. occurred in low abundance and frequency.

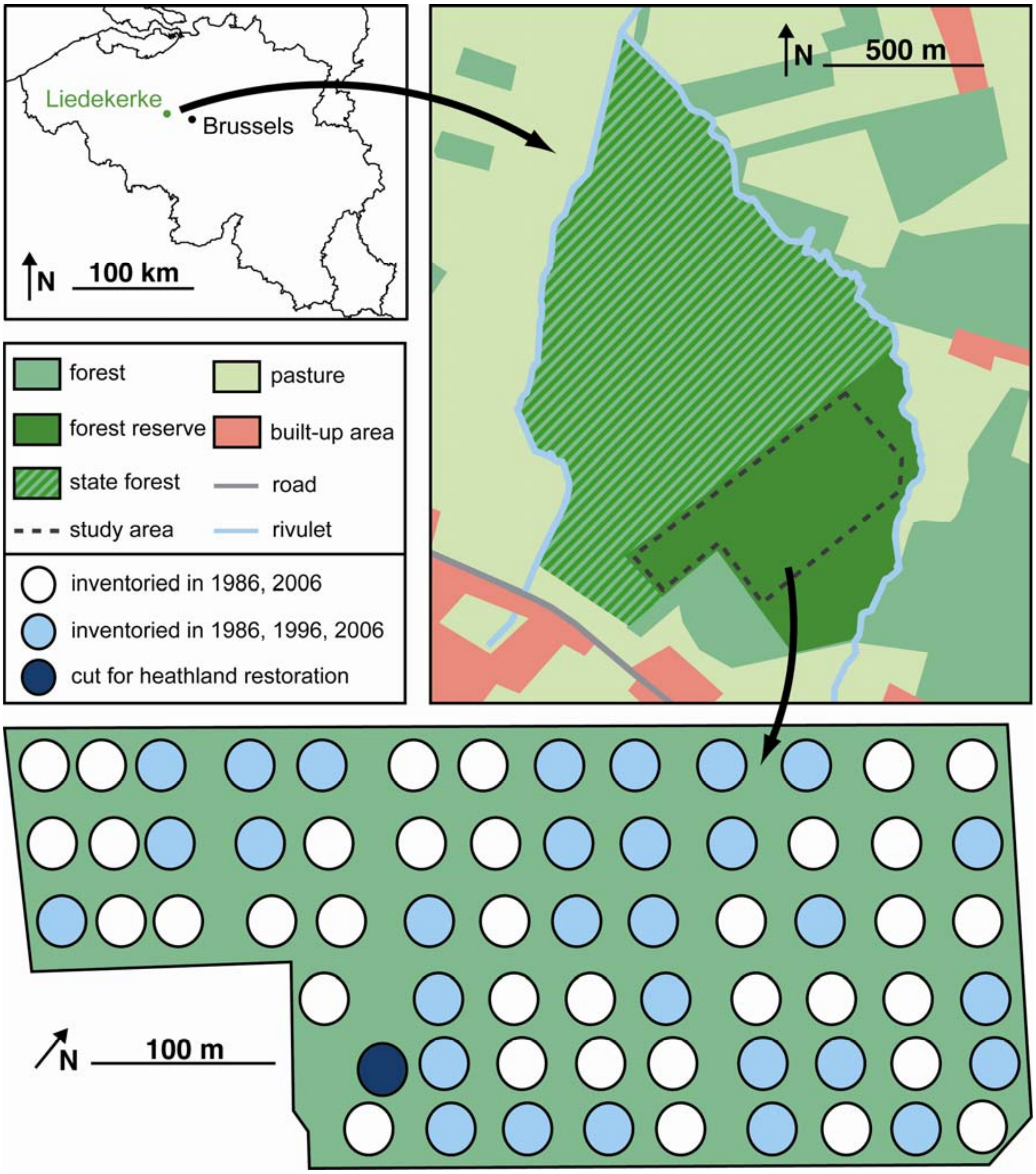


Fig. 5.1 Top: the location of the study area in Belgium and in the Liedekerke state forest Bottom: the study area with the 66 circular study plots [figure: Quinten Vanhellemont]

In 1986, a 12.9 ha study area was defined, and 66 circular plots with radius 15 m, covering 36 % of the study area, were installed at the intersections of a 40 m x 50 m grid (Fig. 5.1). The permanently marked plot centres (cf. Photo 5.1) were relocated and positioned by GPS in 2006.

Photo 5.1 Circular plot no. 49 in the Liedekerke forest reserve: dense layer of *Rubus fruticosus* agg. below *Betula* spp. [photograph: Luc De Keersmaeker, October 2006]

5.3.2 Data collection

The aforementioned circular plots were used to study the changes in structure and species composition of the forest stand, based on ten-year interval data (Fig. 5.1). Since long-term data on forest development in Flanders are quite rare, they offer unique possibilities for the study of, for instance, invasion processes. Still, it should be stressed that the use of such past inventory data requires a thorough examination of the former methodologies (see Appendix 5.1) as even subtle methodological distinctions might influence the interpretation of the results. In 1986, all 66 plots were included in the forest inventory, whereas in 1996, only 31 of the plots were sampled. In 2006, all plots were studied again, except for one plot (no. 45), which had been cleared during a project of heath restoration in 2005 (De Coster *et al.* 2006). For the 2006 data collection, the standard protocol for the inventory of forest reserves in Flanders (De Keersmaeker *et al.* 2005), consistent with the European recommendations of Hochbichler *et al.* (2000), was modified in order to get data comparable with the data of 1986 and 1996.

Table 5.1 Stem density (N) and basal area (BA) for the tree and shrub species in the study area of the Liedekerke forest reserve, based on the inventory of the 65 circular plots measured in 1986 and 2006. The p-values show the significance of the change in N or BA between 1986 and 2006. Trees and shrubs with a basal area smaller than 0.01 m^2 ha^{-1}, i.e., *Malus sylvestris* (L.) Mill., *Cornus sanguinea* L., and *Ilex aquifolium* L., were not included in the table.

	N (ha^{-1})			BA (m^2 ha^{-1})		
species	1986	2006	p	1986	2006	p
Betula spp. [a]	785	353	< 0.001	12.72	13.35	0.084
Quercus spp. [b]	174	135	< 0.001	3.97	7.76	< 0.001
Quercus rubra L. (alien)	44	48	0.177	1.82	6.24	< 0.001
Castanea sativa Mill.	30	35	0.002	0.65	2.04	0.004
Fraxinus excelsior L.	12	12	0.532	0.28	0.47	0.288
Populus spp. [c]	74	7	< 0.001	0.94	0.33	< 0.001
Prunus serotina Ehrh. (alien)	7	25	0.006	0.11	0.22	0.018
Sorbus aucuparia L.	14	18	0.191	0.21	0.22	0.747
Frangula alnus Mill.	49	16	< 0.001	0.18	0.08	0.003
Salix spp. [d]	44	4	< 0.001	0.60	0.12	< 0.001
Corylus avellana L.	8	23	< 0.001	0.11	0.16	0.068
Alnus spp. [e]	49	6	< 0.001	0.42	0.10	< 0.001
Crataegus monogyna Jacq.	1	5	0.004	0.01	0.02	0.008
Sambucus nigra L.	1	6	0.026	0.01	0.03	0.026
Total	1296	695	< 0.001	22.04	31.13	< 0.001

[a] *Betula pendula* Roth and *Betula pubescens* Ehrh.; [b] native *Quercus* species: *Quercus petraea* (Matt.) Liebl. and *Quercus robur* L.; [c] *Populus × canescens* (Ait.) Smith and *Populus tremula* L.; [d] *Salix caprea* L. and *Salix aurita* L.; [e] *Alnus glutinosa* (L.) Gaertn. and *Alnus incana* (L.) Moench

To gain insight into the vegetation development after WWII, aerial photographs of 1944 (The Aerial Reconnaissance Archives), 1951, 1969, 1978, and 1986 (National Geographical Office, www.ngi.be) were imported in a GIS-environment, geo-referenced and assigned to land cover classes, i.e., herbaceous vegetation, scattered shrubs and trees, dense shrubs, and closed forest patches. For each plot, plot history (HIST) was calculated as the minimum number of years the plot had been 'closed forest'.

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.

The initial points of invasion were identified as *P. serotina* trees that were part of the canopy layer and/or had a diameter at breast height (dbh) larger than 25 cm, further on called the source trees of *P. serotina*. Stem cores were used to estimate the age of the source trees. A connectivity measure (CON), based on the Incidence Function Model connectivity measure of Hanski (1994), was calculated for each plot (Eq. 5.1):

$$CON_i = \sum_{j \neq i} \exp\left(-\alpha dist_{ij}\right) dbh_j \tag{5.1}$$

with $dist_{ij}$ the distance (in m) between source tree j and the centre of plot i, dbh_j the dbh (in cm) for source tree j, and α the scaling parameter for the effect of distance to seed dispersal. Parameter α was set to 0.033 as α^{-1} represents the average migration distance and Pairon (2007) reported a 30 m dispersal distance for bird-dispersed *P. serotina* drupes. The seed production capacity of each source tree was assessed by incorporating the dbh of the tree, seed production being related to tree size (Greene *et al.* 2004). Plots were classified into five classes, based on their connectivity, i.e., CON 0–15 (class 1), CON 15–25 (class 2), CON 25–35 (class 3), CON 35–45 (class 4), and CON > 45 (class 5). Plots with a low connectivity, e.g., class 1 plots, are located further from seed sources than plots with a high connectivity, e.g., class 5 plots. The minimum distance to a seed source was, on average, 72 m (class 1), 50 m (class 2), 36 m (class 3), 31 m (class 4), and 17 m (class 5).

Fifty-four subcanopy *P. serotina* individuals were sampled, distributed within the diameter range of *P. serotina* in the inventory data, and their diameter at stem base, dbh, and height were measured. Stem cross sections (for small individuals) or tree cores (for large individuals) were taken at 10–20 cm above the root collar to determine age and growth, based on ring width measurements (see Chapter 3: section 3.3.2). For each individual, competition was calculated with the competition index of Hegyi (1974), based on the diameter of and the distance to all neighbouring trees that meet the criterion of Daniels (1976) (see Chapter 3: Eq. 3.6).

In addition to connectivity (CON) and plot history (HIST), six variables describing the available growth space were used to predict presence/absence of *P. serotina* in the 65 inventory plots in 2006: the summed basal area of all trees with a dbh > 5 cm, for 1986 (BA86) and 2006 (BA06); the percentage of basal area made up by shade-casting species (defined according to Ellenberg 1996), for 1986 (%BAS86) and 2006 (%BAS06); the change in total basal area between 1986 and 2006 (ΔBA); and the percentage of cover by *Rubus* in the herb layer in 2006 (%Rubus). The shade-casting species in the Liedekerke forest reserve were *Castanea sativa* Mill., *Corylus avellana* L., *Ilex aquifolium* L., and *Quercus rubra*.

Canham *et al.* (1994) demonstrated a very strong relationship between the shade tolerance of a species and its light-extinction characteristics. While we wanted to investigate the impact of shade – and thus: shade-casting tree species – on the presence of *P. serotina*, further on in this chapter, we will use the term 'shade-tolerant' instead of 'shade-casting' to match the use of 'light-demanding'.

5.3.3 Data analysis

5.3.3.1 Forest development

Forest development was studied based on the number of trees (N) and the basal area (BA) in 1986, 1996, and 2006, for both shade-casting (NS and BAS) and light-demanding species (NL and BAL). Paired t-test were used to compare the 1986 and 2006 data (65 plots), while the 30 plots that had been measured thrice were analysed with a repeated-measures GLM, with year of inventory as within-subjects factor. The multivariate approach to test for within-subject effects (Pillai's trace test statistic) was used to avoid the assumption of sphericity among the repeated measurements (O'Brien & Kaiser 1985).

Particular attention was given to the changes in presence (number of plots occupied) and abundance (N and BA) of *P. serotina*, the study species, and *Sorbus aucuparia* L., a native shrub which frequently co-occurs with *P. serotina* in Flemish forests (Verheyen *et al.* 2007). As the ecology of *S. aucuparia* and *P. serotina* are similar and *P. serotina* was only planted sporadically near the Liedekerke forest, both species might have a similar colonization history within the forest reserve.

5.3.3.2 Analysis of growth and age relationships for Prunus serotina

The curve estimation procedure in SPSS 15.0 for Windows (SPSS 2006) was used to evaluate different types of models to describe the allometric relationships age–diameter and age–height. Based on the age–diameter relationship and the inventory data, an age distribution was set for the *P. serotina* in the study area. Mean diameter growth of *P. serotina* for the past five years (2000–2005) was analyzed with multiple linear regression (stepwise variable selection) using tree-related variables (height, diameter, age) and competition with neighbouring trees (CI). Growth was ln-transformed, CI square-root-transformed.

5.3.3.3 Presence/absence of Prunus serotina *in the study plots*

Plots with or without *P. serotina* in 2006 were compared with respect to the plot characteristics (t-tests) and the change in basal area (repeated-measures GLM with year of inventory as within-subjects factor and presence/absence of *P. serotina* as between-subjects factor). Subsequently, multiple logistic regression with forward variable selection was used to predict the presence/absence of *P. serotina* in the plots in 1986 and 2006. The change in -2 loglikelihood was used to assess the relative importance of the variables included in the model. The analysis was done for *P. serotina* irrespective of life stage and, separately, for trees (age > 20 yr), shrubs (age > 12 yr), and saplings/seedlings (age < 12 yr), classes that were based on the age distribution of *P. serotina* within the study plots (see below). The age classes roughly correspond with the following size classes: dbh < 2 cm for seedlings/saplings, 2 cm < dbh < 5 cm for shrubs, 5 cm < dbh < 25 cm for trees, and 25 cm < dbh for source trees.

5.4 Results

5.4.1 Forest development

Fig. 5.2 shows the changes in land cover within the study area. The herbaceous vegetation has been colonized fast: solitary shrubs and dense shrub patches were found in ca. 90 % of the area by 1951. In 1986, 96 % of the area was forested, and the remaining herbaceous vegetation was restricted to the forest tracks, which were mown yearly till 2003.

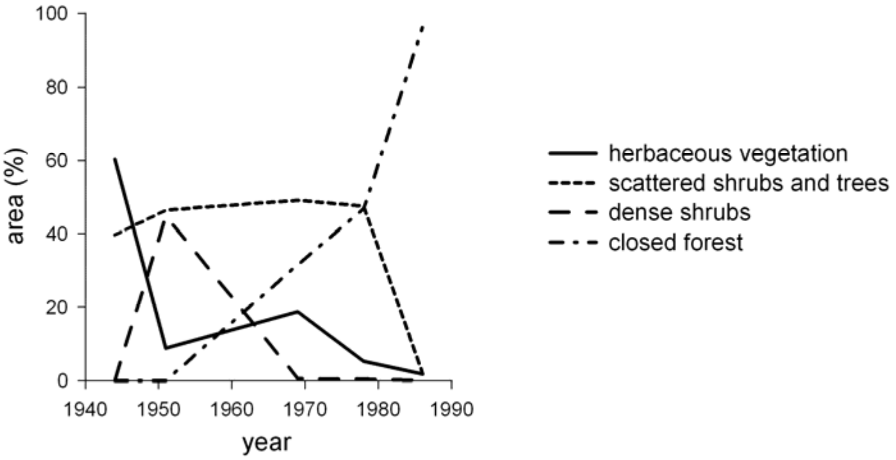


Fig. 5.2 Changes in land cover in the study area between 1944 and 1986

The changes in stem density (N) and basal area (BA) between 1986 and 2006 are presented in Fig. 5.3. Both N and NL dropped significantly ($p < 0.001$) between 1986 and 2006 whereas NS was larger in 2006 than in 1986 ($p < 0.001$). BA and BAS rose significantly ($p < 0.001$) between 1986 and 2006, but the increase in BAL was only significant between 1986 and 1996 ($p < 0.001$, $p = 0.054$ for 1996–2006). The percentage cover of *Rubus* in the study plots was correlated negatively with BAS ($r = -0.360$, $p = 0.003$).

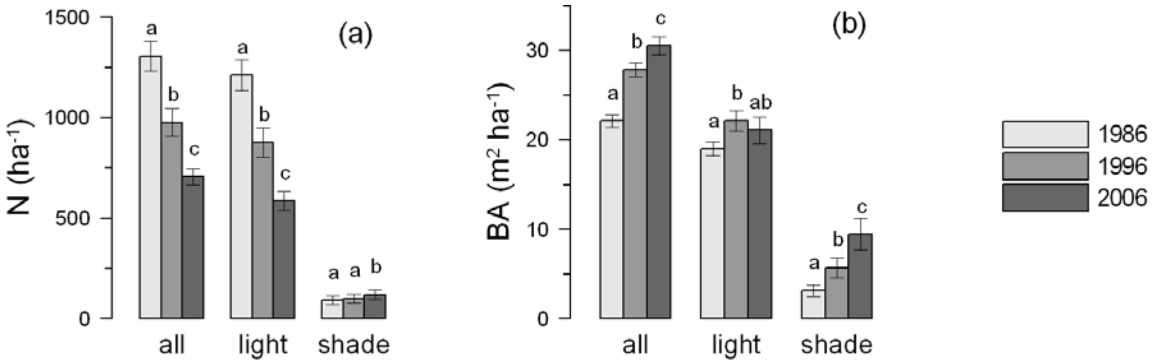


Fig. 5.3 Changes in stem density (N, figure a) and basal area (BA, figure b) for all species ('all'), light-demanding species ('light'), and shade-tolerant species ('shade') in the Liedekerke forest reserve between 1986 and 2006. The characters above the bars indicate significant differences between the years ($p < 0.001$, repeated measures GLM); the error bars represent standard errors.

Within the entire forest reserve, 50 trees of *P. serotina* were identified as source trees. These source trees (age > 30 yr) established around 1970–1975 at spots that were still not classified as 'closed forest' on the aerial photograph of 1969 (Fig. 5.4). In 2006, the vitality of 56 % of the source trees was poor, and even the healthy-looking trees often turned out to have a rotten core.

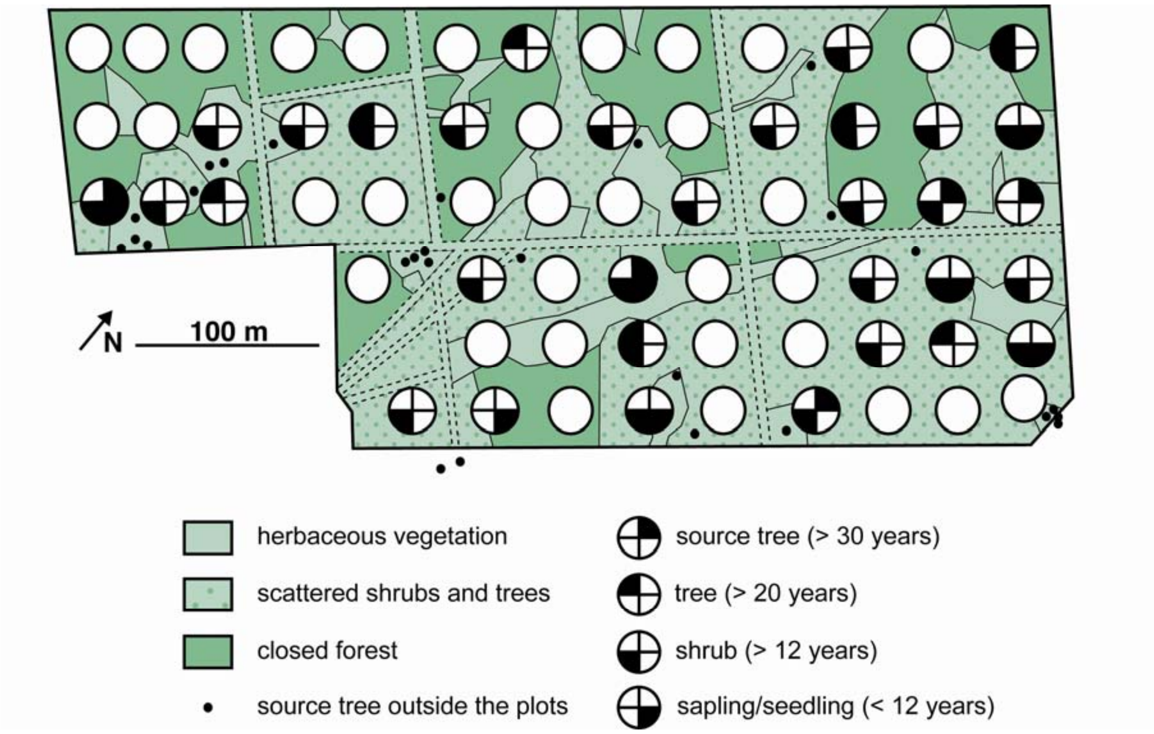


Fig. 5.4 Presence of *Prunus serotina* in the study plots in 2006. The presence of source trees, trees, shrubs, and saplings/seedlings is shown for each plot by means of the black quadrants. Empty circles indicate that no *P. serotina* was present. The black dots indicate the position of the source trees, i.e., the initial points of the *P. serotina* invasion, that occurred outside the study plots. The background colours indicate the land cover in 1969: herbaceous vegetation, scattered shrubs and trees, and closed forest. [figure: Quinten Vanhellemont]

Prunus serotina spread through the study area, from 14 plots (out of 65) colonized in 1986 to 33 plots in 2006, also establishing in plots further away from the source trees (Fig. 5.5). In 1986, 8–17 % of plots with a low to intermediate connectivity were colonized by *P. serotina*; in 2006, *P. serotina* was present in 23–71 % of these plots. The number of plots with *S. aucuparia* also increased: from 38 plots in 1986 to 60 plots in 2006. The data of the 30 plots which were inventoried thrice showed a large increase in number of plots occupied between 1986 and 1996: from 6 to 15 plots for *P. serotina* and from 17 to 28 plots for *S. aucuparia*. Yet, between 1996 and 2006, *P. serotina* only evolved from 15–17 and *S. aucuparia* from 28–29 plots. Stem density and basal area of both *P. serotina* and *S. aucuparia* were higher in 2006 than in 1986, but the changes were significant only for *P. serotina* ($p = 0.006$ and $p = 0.018$, Table 5.1).

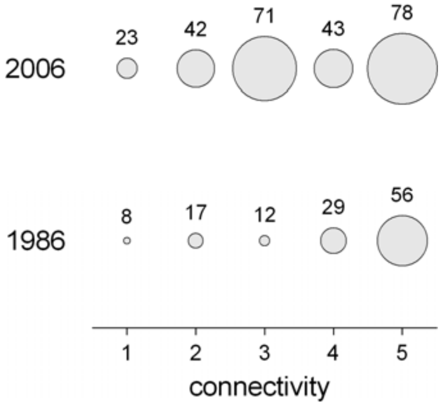


Fig. 5.5 The frequency of plots in each connectivity class colonized by *Prunus serotina*, in 1986 and 2006. The five classes of connectivity are based on the connectivity measure CON (see Eq. 5.1). Plots with a low connectivity (class 1) are located further from seed sources than plots with a high connectivity (class 5).

5.4.2 Growth and age relationships for *Prunus serotina*

In 2006, the subcanopy *P. serotina* in the inventory had a dbh < 15 cm; 11 % of them bore inflorescences or fruits; and mean diameter growth for the last five years (2000–2005) was 2.8 ± 0.2 mm yr^{-1}. Diameter growth (y, in mm yr^{-1}) of *P. serotina* was determined predominantly by the diameter at stem base (x_1, in cm) and the age (x_2, in yr) of the tree and competition with neighbouring trees (x_3): $y = 4.911 + 0.487\ x_1 - 0.028\ x_1^2 - 0.077\ x_2 - 0.071\ x_3$ ($R^2 = 0.80$).

The curve estimation procedure revealed that the relationship between age (y, in yr) and diameter at stem base (x, in cm) was described most accurately by a power model: $y = 7.25\ x^{0.40}$ ($R^2 = 0.80$). The age distribution showed a continuous colonization process, starting when the source trees had reached 10–15 years of age and, presumably, started producing seed. In 2006, seedlings and saplings (age < 12 yr) occurred in one tenth of the plots (Fig. 5.4).

5.4.3 Presence/absence of *Prunus serotina* in the study plots

In 2006, plots with *P. serotina* were characterized by a higher connectivity (p = 0.023), BA (p = 0.017), BAS (p = 0.005), and ΔBA (p = 0.002). The increase in BA and BAS was greater in plots with *P. serotina* (p interaction 0.008 and 0.005, respectively, Table 5.2). Plots without *P. serotina* had a higher BAL (p = 0.024).

Table 5.2 The significance (p-values) of the differences in basal area (BA), basal area of light-demanding species (BAL), and basal area of shade-tolerant species (BAS) between plots with or without *Prunus serotina* (presence) in 1986 or 2006 (year)

source of variation	BA	BAL	BAS
year	< 0.001	0.001	< 0.001
year x presence	0.005	0.600	0.008
presence	0.362	0.024	0.005

Plots with a high connectivity to the *P. serotina* source trees, i.e., the initial points of invasion, were more likely to be colonized by *P. serotina* (Table 5.3), in 1986 as well as in 2006 (Fig. 5.5). Whereas in 1986, only connectivity and history of the plots were related to *P. serotina* presence/absence, in 2006, the presence of *P. serotina* was found to be correlated with a high increase in BA and a low cover of *Rubus* (Table 5.3). Moreover, plots with *P. serotina* trees (age > 20 yr) were characterized by a high basal area; shrubs (age > 12 yr) grew in plots with a high amount of shade-tolerant species in 1986; and seedlings/saplings (age < 12 yr) seemed to be present in plots in which the vegetation remained open longer and with a high share of shade-tolerant species in 2006 (Table 5.3).

Table 5.3 Logistic regression of the presence/absence of *Prunus serotina* in the inventory plots (n = 65) in 1986 (overall presence) and in 2006 (overall presence; presence of trees, shrubs, and saplings/seedlings). The sign (+/-), the significance p (based on the Wald statistic) and the relative importance -2LL (-2 loglikelihood) are presented for the significant factors.

	1986			2006											
	overall			overall			tree			shrub			sapling/seedling		
	22 %			51 %			37 %			37 %			11 %		
	($R^2 = 0.34$)			($R^2 = 0.39$)			($R^2 = 0.24$)			($R^2 = 0.19$)			($R^2 = 0.52$)		
	(misclass: 17 %)			(misclass: 25 %)			(misclass: 15 %)			(misclass: 23 %)			(misclass: 21 %)		
factor [a]	sign	p	-2LL	sign	p	-2LL	sign	p	-2LL	sign	p	-2LL	sign	p	-2LL
CON	+	0.036	5.678	+	0.028	6.766	+	0.02	6.493	+	0.071	3.501	+	0.064	3.582
HIST	-	0.024	6.616										-	0.023	7.726
%BAS86										+	0.012	6.987			
%BAS06													+	0.007	9.049
BA06							+	0.025	5.952						
ΔBA				+	0.007	8.382									
%Rubus				-	0.037	5.407									

[a] CON the connectivity of a plot (see Eq. 5.1), HIST the minimum number of years a plot had been ‘closed forest’, %BAS86 and %BAS06 the percentage of basal area made up by shade-tolerant species in 1986 or 2006, BA06 the basal area (m^2 ha^{-1}) of the plot in 2006, ΔBA the difference in BA between 1986 and 2006 (m^2 ha^{-1}), %Rubus the percentage cover of *Rubus* spp. in the herb layer in 2006

5.5 Discussion

Combining the 2006 data with prior inventories, aerial photographs, and tree ring analysis made it possible to study the colonization and spread of *P. serotina* in the Liedekerke forest reserve, to infer the underlying mechanisms, and to make predictions on the future role of *P. serotina* within the forest reserve.

5.5.1 Establishment

Long-distance seed dispersal events (cf. Cain *et al.* 2000) in combination with patches with high light availability, representing windows of opportunity (DeGasperis & Motzkin 2007), may have been responsible for the establishment of the first *P. serotina* individuals, i.e., the source trees (Fig. 5.4), in the Liedekerke forest reserve around 1970. In Meerhout, the study area of Deckers *et al.* (2005), the first *P. serotina* individuals also established around 1970. It is not clear which seed source has been responsible for the initial colonization of the Liedekerke forest reserve, but due to the high dispersal capacity of *P. serotina*, a few seed sources in the neighbourhood would have been enough for a sufficient propagule pressure (cf. D’Orangeville *et al.* 2008). The subsequent forest development, characterized by an increase in basal area (Fig. 5.3, Table 5.1) and a decrease in light availability, has probably reduced the opportunities for the establishment of newly arriving *P. serotina* propagules. Further colonization of the area started around 1984 and presumably coincided with the beginning of seed production of the *P. serotina* individuals established in 1970. These trees have acted as seed sources throughout the invasion process, which is pointed out by the high impact of connectivity to source trees on the present distribution of even young individuals of *P. serotina* (Table 5.3).

5.5.2 Colonization patterns

Prunus serotina occurrence was more likely in plots with a high basal area, particularly of shade-tolerant species (Table 5.2). Yet, seedlings of *P. serotina* have been shown to need some light, i.e., 58–80 % of full light (Godefroid *et al.* 2005). Plots with a high share of light-demanding species, however, were characterized by a high *Rubus* cover and a scarce incidence of *P. serotina*. This trade-off between light availability and *Rubus* abundance with regard to seedling and sapling densities was also found by Mountford *et al.* (2006). In plots with a low canopy cover, *Rubus* formed a recalcitrant understory layer (cf. Royo & Carson 2006), hampering the germination and establishment of *P. serotina* as well as other tree and shrub species (cf. Van Uytvanck *et al.* 2008). In plots with a high basal area, the low *Rubus* cover left some possibilities for *P. serotina* establishment. Likewise, D'Orangeville *et al.* (2008) found that *P. serotina* presence was associated with open, relatively young forests where light availability was sufficient for *P. serotina* seedlings to exhibit rapid growth and overcome woody and herbaceous competition.

Although *P. serotina* saplings are able to survive low light conditions (Starfinger 1990), light is essential for further growth (Verheyen *et al.* 2007) and seed production (Closset-Kopp *et al.* 2007). Growth of subcanopy *P. serotina* in the Liedekerke forest reserve was affected by competition with neighbouring trees as well as the age and dimensions of the tree, which has also been shown for the growth of *P. serotina* in the understory of Scots pine (*Pinus sylvestris* L.) forests in the Campine region, Flanders ('Kempen', Chapter 3). Mean understory diameter growth in Liedekerke (2.8 mm yr^{-1}) and the Kempen (3.3 mm yr^{-1}, Chapter 3) were similar and rather low as compared to the 6.3 mm yr^{-1} *P. serotina* growth in an open agricultural landscape that was characterized by a high nutrient availability and full light conditions (Deckers *et al.* 2005). Furthermore, only 10 % of the subcanopy *P. serotina* in Liedekerke showed some sign of flowering/fruiting whereas *P. serotina* in full light conditions has been shown to start producing seeds already at the age of four (Deckers *et al.* 2005).

5.5.3 A forest pest?

The spread of *P. serotina* in the Liedekerke forest reserve occurred mainly between 1986 and 1996, and the invasion process slowed down between 1996 and 2006. Besides, the putative adverse effects of *P. serotina* on the regeneration of native tree and shrub species were not confirmed by our results. *Sorbus aucuparia* was omnipresent in the study area (60 out of 65 plots) and other shrub species, e.g., *Corylus avellana*, have been able to increase (Table 5.1). The high shade-tolerance of *C. avellana* (Niinemets & Valladares 2006) and *S. aucuparia* adults (Raspé *et al.* 2000) might favour these species, as compared to *P. serotina*. Moreover, Jonášová *et al.* (2006) found that *S. aucuparia* presence is relatively independent of the presence of source trees, which contrasts with the impact of the connectivity to source trees on *P. serotina* presence. Therefore, we could not consider *P. serotina* an aggressive invader in the Liedekerke forest reserve in 2006. Our results are consistent with the findings of Starfinger *et al.* (2003): the invasive potential of *P. serotina* is affected by preceding human introductions and the ecosystem conditions at hand.

In contrast with the currently limited impact of the *P. serotina* invasion, *Quercus rubra*, the other alien species in the studied forest reserve, might exert a huge impact on the future development of the forest, seeing the threefold increase in basal area during the last twenty years (Table 5.1), its omnipresence in the canopy layer, and the areas with high densities of seedlings smaller than 50 cm.

5.5.4 Future development

The further development of *P. serotina* in the forest reserve might not be as dramatic as was postulated in the report of Van Den Meerschaut & Lust (1997b). First, the seed rain might decrease because of the poor vitality of the source trees and the low seed production by subcanopy *P. serotina*. In addition, a further increase in basal area, particularly of shade-tolerant species, will enhance competition so that subcanopy *P. serotina* might not easily reach the canopy, where the high light conditions would promote seed production. Second, the presence of the recalcitrant *Rubus* layer might continue to hamper the establishment of *P. serotina* seedlings and saplings. Even if the increase in shade-tolerant species diminishes the cover of *Rubus* spp., the shade associated with the increase in basal area of shade-tolerant species might, as well, hamper the further establishment of *P. serotina*.

Nonetheless, the few areas with high *P. serotina* sapling density imply a large potential in case of calamities opening up the canopy layer since the build-up of a persistent bank of seedlings and saplings of *P. serotina* has been pointed out an effective strategy for ensuring site-occupancy (Closset-Kopp *et al.* 2007, Sebert-Cuvillier *et al.* 2007). Moreover, *P. serotina* might simply experience a prolonged establishment phase in areas with a low propagule pressure, as has been shown for *Acer platanoides* L. (Wangen & Webster 2006). The invasion of *A. platanoides* in the temperate forests of eastern North America is comparable with that of *P. serotina* in Western Europe: *A. platanoides* has widely been planted, is categorized as an aggressively colonizing species, and is able to build a seedling bank in shaded conditions (Martin & Marks 2006). Long-distance dispersal events and gap dynamics were shown to be responsible for the invasion success of *A. platanoides* (Wangen & Webster 2006), similar to our findings for *P. serotina*.

Photo 5.2 The basal area of the shade-tolerant *Quercus rubra* increased whereas the stem density of light-demanding *Betula* spp. decreased in the Liedekerke forest reserve during the 20-year study period. [photograph: Luc De Keersmaeker, October 2006]

5.6 Conclusions

At present, *P. serotina* cannot be considered an aggressive invader in the Liedekerke forest reserve: (1) the spread of the species occurred mainly between 1986 and 1996 while the invasion process slowed down between 1996 and 2006; and (2) its presence does not seem to hamper the establishment of native shade-tolerant shrub and tree species.

Connectivity to seed sources and light availability were the most important determinants of *P. serotina* presence in the Liedekerke forest reserve. The establishment and growth of shade-tolerant shrub and tree species and the recalcitrant herb layer probably slowed down the spread of *P. serotina*. Long-distance dispersal events in combination with windows of opportunity and gap dynamics seem to direct the colonization of uninvaded areas by *P. serotina*.

Appendix 5.1

Characteristics of the inventory data for the Liedekerke forest reserve: year of inventory (year), number of plots (n), description of the plot size and the data (with dbh: diameter at breast height), source of data

year	n	data description	data source
1986	66	dendrometric data (dbh > 2 cm) - plot radius = 15 m - species and dbh	data Bart De Cuyper
1996	31	dendrometric data (dbh > 2 cm) - plot radius = 15 m - species and dbh	data Diego Van Den Meersschaut
1998	31	regeneration data - plot radius = 2.5 m: species (height < 0.5 m) - plot radius = 15 m: species (dbh < 2 cm, height > 0.5 m)	data Diego Van Den Meersschaut
2006	30 [a]	dendrometric data (dbh > 5 cm) - plot radius = 15 m - species and dbh regeneration data - plot radius = 2.25 m (height < 0.5 m) - plot radius = 4.5 m (dbh < 2 cm, height > 0.5 m) - plot radius = 15 m (dbh < 2 cm, height > 0.5 m, and 2 cm < dbh < 5 cm) - species vegetation data - plot 16 m x 16 m - species and cover	data Research Institute for Nature and Forest (INBO)
2006	35	dendrometric data (dbh > 2 cm) - plot radius = 15 m - species and dbh regeneration data - plot radius = 2.25 m (height < 0.5 m) - plot radius = 4.5 m (dbh < 2 cm, height > 0.5 m) - species vegetation data - plot 16 m x 16 m - species and cover	own data

[a] Plot no. 45 was involved in a program of heath restoration: all trees and shrubs were cut and the litter was removed.

Photo 6.1 The core area of the Ossenbos forest reserve: dense regeneration of *Prunus serotina* (August 2007)

Photo 6.2 The mound that runs through the Ossenbos forest reserve with the *Prunus serotina* shrub layer (August 2007)

6 Patterns of *Prunus serotina* colonization in a Scots pine forest in an area with an initially low propagule pressure

After: Vanhellemont M, Wauters L, Baeten L, Bijlsma R-J, De Frenne P, Hermy M, Verheyen K. *Prunus serotina* unleashed: invader dominance after 70 years of forest development. Biological Invasions, *in press*

6.1 Abstract

Propagule pressure and disturbance have both been found to facilitate invasion. Therefore, knowledge on the history of introduction and disturbance is vital for understanding an invasion process, and research should focus on areas in which the invasive species has not been deliberately introduced or managed to study unconfounded colonization patterns. We focused on the 70-year spontaneous spread of the invasive tree species *Prunus serotina* in a Scots pine (*Pinus sylvestris*) forest in the Netherlands. To reconstruct the invasion process, we combined historical maps, tree ring analysis, spatially explicit tree inventory data, seed density data, and regeneration data for both native and alien species. *Prunus serotina* was the only species that showed successful regeneration: the species was present throughout the forest in the tree, shrub, and herb layer. Native species were not able to outgrow the seedling stage. Our data demonstrate that *P. serotina* is a gap-dependent species with high seed production that builds up a seedling bank. We also compared the results of this study with a similar study on *P. serotina* colonization in a deciduous forest in Belgium (Chapter 5), where the *P. serotina* invasion was not successful. The sharp contrast between the outcomes of the two invasion processes shows the importance of studying an invasive species and the recipient ecosystem jointly and made us raise the hypothesis that herbivore pressure may facilitate *P. serotina* invasion.

6.2 Introduction

Propagule pressure and ecosystem disturbance are both considered important drivers of invasion success (Richardson & Pyšek 2006, Chapter 1). Consequently, studies focusing on heavily invaded areas in which the invasive species has been planted or managed might overestimate the invasiveness of a species. With respect to the development of long-term strategies for the control of invasive species, it is important to know whether a species is able to invade new areas because of its own invasiveness or because of recurrent introductions by humans. Addressing the underlying causes of a successful invasion rather than simply trying to eradicate particular invasive species will lead to a more effective control of biological invasions (Mack *et al.* 2000).

The study presented in Chapter 5 was probably the first to investigate patterns of long-term spontaneous spread of the invasive tree species *Prunus serotina* Ehrh. in its introduced range. Yet, biological invasions are context-dependent and the invasion success of alien species depends on the invasiveness of the species as well as the invasibility of the ecosystem (Facon *et al.* 2006, Chapter 1). Consequently, the colonization patterns of a particular alien species may depend on the characteristics of the recipient ecosystem. Comparing the outcomes of spontaneous colonization processes in different ecosystems can provide a useful framework for setting management priorities for invasive species that enter new, uninvaded areas. Therefore, we studied patterns of long-term *P. serotina* colonization in another forest in the introduced range, i.e., a pine forest on sandy soil, and compared the results with those of the study on the *P. serotina* spread in a mixed deciduous forest on sandy loam soil (Chapter 5). The Ossenbos forest reserve is a Scots pine (*Pinus sylvestris* L.) forest in the Netherlands, located in an area with an initially low propagule pressure of *P. serotina*. It provided a unique opportunity for our study because it has not been managed for over 70 years and *P. serotina* has not been planted nor managed.

The objectives of this chapter were (1) the identification of factors related to the abundance and growth of *P. serotina*, (2) the characterization of *P. serotina* seed dispersal patterns, (3) the comparison of the demography of *P. serotina* and the other tree and shrub species in the Ossenbos forest reserve, and (4) the comparison of the colonization patterns of *P. serotina* in this chapter and Chapter 5.

6.3 Materials and methods

6.3.1 Study area

The Ossenbos forest reserve (54 ha) lies within the 3600 ha artillery training camp De Harskamp in the Natura 2000 site Veluwe, the Netherlands (N52°08’ E005°48’), in a landscape matrix that includes forest patches, heathlands, and bare sand (Fig. 6.1). The site lies 39 m above sea level on poor wind-borne sand deposits. The minimum and maximum monthly mean temperatures are 2°C in January and 17°C in July, and the mean annual precipitation is 850 mm (www.knmi.nl). The forest developed spontaneously around an east–west running mound that had been installed around 1832 to protect the heathlands, south of the mound, from the drifting sands north of the mound (Fig. 6.1). Pine (*Pinus sylvestris*) and oak (*Quercus robur* L.) establishment close to the mound started around 1850 and 1900, respectively. Further tree colonization of the former heathland occurred between 1926 and 1965 while the former drift sand did not appear as forested until 1976. The first *P. serotina* plantings at De Harskamp, at 3 km from the Ossenbos, occurred in 1973 (Arthur Varkevisser *pers comm*). Yet, *P. serotina* first became established in the Ossenbos around 1940, which indicates that the earliest colonization came from outside De Harskamp. By 2003, the mean stem density (N) of the forest was 1169 ha^{-1}, and the mean basal area (BA) was 26.6 $m^2\ ha^{-1}$, with *P. sylvestris* (53 % of N, 85 % of BA) and *P. serotina* (44 % of N, 11 % of BA) as the main tree species. Other tree and shrub species, present in low densities, were *Betula pendula* Roth, *Betula pubescens* Ehrh., *Q. robur*, *Quercus rubra* L., *Sorbus aucuparia* L., and *Frangula alnus* Mill. The forest reserve is the only area in the Harskamp in which hunting is prohibited and therefore acts as a safe site, which results in a high game density, i.e., around 1 ha^{-1} (Arthur Varkevisser *pers comm*). The estimated number of individuals for the three ungulate species that occur in the area are 25 red deer (*Cervus elaphus* Linnaeus, 1758), 25 wild boar (*Sus scrofa* Linnaeus, 1758), and 10 roe deer (*Capreolus capreolus* Linnaeus, 1758).

6.3.2 Data collection

Forty circular plots of 500 m² were located randomly on a 50 m x 50 m grid in the entire forest, and, in addition, a study area of 70 m x 140 m, i.e., the core area, was installed in the oldest part of the forest reserve (Fig. 6.1). In the 40 circular plots, dendrometric and regeneration data were collected for each tree species in March 2003: position, diameter at breast height (dbh), and height (h) were measured for all living trees (dbh > 5 cm) in a circle with radius 12.6 m; and the height and number of saplings (dbh < 5 cm, h > 0.5 m) were recorded in an inscribed square plot of 18 m x 18 m.

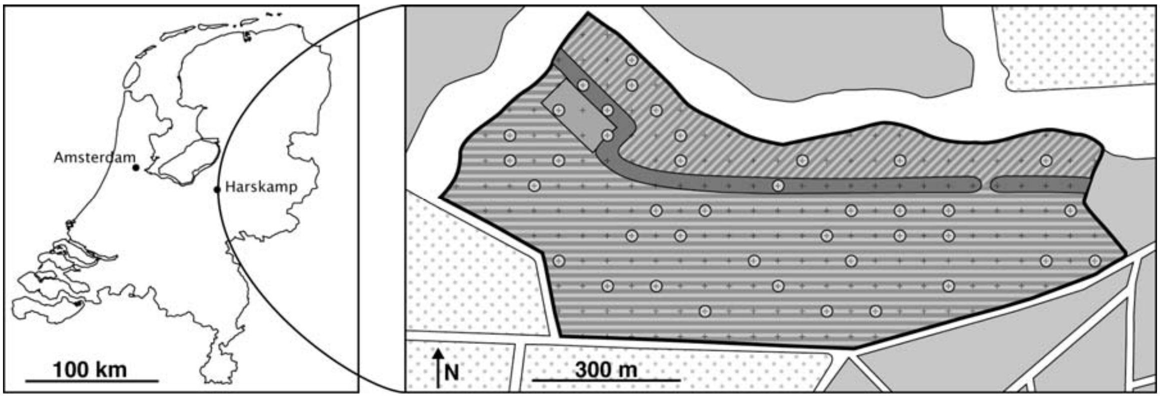


Fig. 6.1 Left: location of Harskamp and the Ossenbos forest reserve (54 ha) in the Netherlands; right: the Ossenbos (black contour line) with the 40 circular plots and the core area (plain grey), surrounded by open sand and sandy tracks (white), heathlands (grey dots), and forest patches (dark grey). The northern part of the Ossenbos, which developed on drift sand (shaded with right-slanting lines), is separated from the southern part, which developed on heathland (shaded with horizontal lines), by a mound that runs from west to east through the forest (deep dark grey) [figure: Quinten Vanhellemont]

In the core area, position, dbh, and height were measured for all living and dead trees with a dbh larger than 5 cm in March 2003. In addition, in August 2007, data were collected on *P. serotina* growth and establishment as well as on regeneration of other tree and shrub species. To study the growth of *P. serotina* in the core area, we sampled 33 *P. serotina* individuals, distributed within the diameter range of *P. serotina* in the inventory data and located below the intimately mixed native tree species *P. sylvestris* and *Q. robur* (13 individuals), below the alien *P. serotina* (11), or in a canopy gap (9). Diameter and height were measured, stem cross sections (for small individuals) or tree cores (for large individuals) were taken at 20–30 cm above the root collar, and ring widths were measured (see Chapter 3: section 3.3.2). For each individual, competition was calculated with the competition index of Hegyi (1974), based on the diameter of and the distance to all neighbouring trees that meet the criterion of Daniels (1976) (see Chapter 3: Eq. 3.6).

The core area was subdivided into 96 squares of 10 m x 10 m. At the centre of each square, we took a hemispherical photograph to calculate canopy openness (see Chapter 3). The central 60 squares were used to study regeneration of tree and shrub species. In the centre of each of these plots, a 4 m x 4 m regeneration plot and a 0.4 m x 0.4 m litter plot were defined. Since the forest reserve is located in an artillery training camp and fieldwork was only possible during a two-week shooting-free period in summer, we could not quantify the seed rain of *P. serotina* directly. Instead, we collected litter in the 60 litter plots, measured the volume of the litter samples, and sorted out the seeds. Both intact seeds, representing a potential seed bank, and seed halves, representing germinated seeds, were counted. Since seeds of *P. serotina* found in the litter layer of forests have been shown to have a low germinability (O'Hanlon-Manners & Kotanen 2006, Phartyal *et al.* 2009), we only used the data for the germinated seeds for further analysis. In addition, the spatial position of the seed-bearing *P. serotina* trees in the core area was noted. For all tree and shrub species, regeneration was counted in the 60 regeneration plots. Seedlings were divided into four classes (classification after Closset-Kopp *et al.* [2007] and Chapter 4): seedlings resulting from seeds germinated in 2007 (stage I), seedlings < 20 cm (stage II), 20 cm < seedlings < 120 cm (stage IIIa), and seedlings > 120 cm (stage IIIb).

6.3.3 Data analysis

For our analysis of the colonization patterns and the demography of *P. serotina*, we focused on the core area, located in the oldest part of the forest, where *P. serotina* was present in the tree, shrub, and herb layer. In addition, the regeneration data for the circular plots were used to check whether the regeneration patterns that were observed in the core area also held for the younger portions 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* in the developing pine forest. Second, to examine the demography of *P. serotina*, we successively studied the growth and seed densities of *P. serotina* in the core area, and the presence and abundance of the seedlings in the core area and the saplings in the circular plots. Third, we also studied the regeneration of native tree and shrub species, in the core area and in the circular plots, to compare the colonization potential of *P. serotina* with that of the native species. Data analysis was performed in SPSS 15.0 (SPSS 2006) and R 2.7.0 (R Development Core Team 2008).

6.3.3.1 *Spatial patterns*

The 2003 data for individuals with a dbh > 5 cm were used to calculate basal area (m^2 ha^{-1}) and stem density (ha^{-1}) for living and dead trees in the core area. Based on the frequency histogram of the tree height data, the dataset was divided into trees (h > 10 m) and shrubs (h < 10 m). The frequency histograms for the dbh data of the *P. serotina* trees and shrubs were studied to gain further insight into the structure of the *P. serotina* tree and shrub layer. We used the add-on R library spatstat version 1.14-4 (Baddeley & Turner 2005) to evaluate the stem density for the main tree and shrub species spatially with isotropic Gaussian smoothing kernels, and we analyzed the patterns of interactions between the spatial point patterns of the different tree species in the shrub and tree layer with bivariate Ripley's K (Ripley 1977). We calculated Ripley's L, a square root transformed Ripley's K, using Ripley's isotropic edge correction. The pointwise 5 % upper and lower critical envelopes for testing the hypothesis of complete spatial randomness, i.e., L(d) = 0, were based on 999 Monte Carlo simulations of a uniform Poisson process. Observed L(d) values lying within the envelopes indicate a random spatial association; observed L(d) values larger than the upper envelope indicate a positive spatial association; L(d) values smaller than the lower envelope indicate a negative spatial association.

6.3.3.2 *Growth of* Prunus serotina

For the sampled *P. serotina* trees and shrubs, multiple linear regressions were used to analyze the mean radial growth for the years 2001–2006 as a function of dbh, height, age, canopy openness, and competition. Next, the curve estimation procedure in SPSS was used to study the relationships between age and dbh and between age and height for *P. serotina* growing below *Q. robur* and *P. sylvestris*, below *P. serotina*, or in gaps. Interactive effects between the canopy tree neighbourhood and the age of the studied *P. serotina* on the achieved dbh or height were investigated with ANCOVA analysis (Scheiner & Gurevitch 2001).

6.3.3.3 *Dispersal kernels of* Prunus serotina

We used inverse modelling (Ribbens *et al.* 1994) to relate our data on the seed and seedling densities in each plot to data on the location of seed-bearing trees. Overlapping seed shadows were used to model the density of seeds or seedlings with distance from the source tree, calculated as the product of fecundity, i.e., seed production, and the dispersal kernel, i.e., the probability density describing the scatter of seeds/seedlings about the source tree (Clark *et al.* 1999). Since Greene *et al.* (2004) found the lognormal dispersal kernel to be the best fit to observed dispersal curves, which was confirmed for *P. serotina* by Pairon *et al.* (2006b), we used the lognormal seed dispersal kernel (Eq. 6.1), multiplied by the seed production (Eq. 6.2), which was modelled as a function of the dbh of the source tree:

$$\frac{1}{(2\pi)^{1.5}\, S\, dist_{pt}^{\;2}} \exp\left(-\frac{\left(\ln\left(dist_{pt}/L\right)\right)^{2}}{2S^{2}} \right) \tag{6.1}$$

$$a\,(dbh_t)^{b} \tag{6.2}$$

with S the shape parameter, L the scale parameter, $dist_{pt}$ the distance between plot p and source tree t, dbh_t the dbh of source tree t, and a and b translating the dbh of the source tree into seed production. We determined kernels for seeds, for seedlings smaller than 20 cm (stage I and stage II), and for seedlings taller than 20 cm (stage IIIa and stage IIIb) in order to evaluate the local efficiency of the seed rain with regard to the subsequent regeneration stages. Calculating the dispersal kernels was done with maximum likelihood methods, using the R packages neighlikeli and likelihood version 1.0 (Murphy 2006a,b). Pearson correlations and the slope between observed and predicted seed/seedling densities were used to estimate the goodness of fit of the models.

6.3.3.4 Regeneration of tree and shrub species

We used the same approach for the study of the regeneration patterns for the seedlings in the core area and for the saplings in the circular plots. First, presence/absence of a species was modelled with binary logistic regressions based on the plot characteristics, i.e., basal area of the tree and shrub layers ($m^2\ ha^{-1}$), stem density (ha^{-1}), and, for the core area, canopy openness (%). For *Q. robur* in the core area, we also used the minimum distance to a seed tree (m) because *Q. robur* seed trees were present in the core area and local *Quercus* dispersion is mainly barochorous (Johnson *et al.* 2002). Next, to explain the abundance of a species' seedlings in the core area or its saplings in the circular plots, we performed a data reduction (PCA) on the plot characteristics, and calculated Pearson correlations between the seedling/sapling densities and the principal components. For the circular plots, we used the data on basal area of the tree and shrub layer, stem density, and maximum tree height (m). For the regeneration plots in the core area, we additionally used data on canopy openness and, for *P. serotina*, seed density (m^{-2}).

6.4 Results

6.4.1 Spatial patterns and forest structure in the core area

In the core area, *Pinus sylvestris* accounted for ca. 70 % of the basal area, both for living and dead trees, while *P. serotina* showed the highest stem densities for living trees (71 %) and for standing dead trees (79 %) (Table 6.1). The tree layer was made up of *P. sylvestris* (62 %, 177 ha^{-1}), *P. serotina* (28 %, 82 ha^{-1}), and *Quercus robur* (10 %, 29 ha^{-1}), while the shrub layer consisted almost completely of *P. serotina* (97 %, 503 ha^{-1}), with only a few *Q. robur* (3 %, 16 ha^{-1}) present.

Shrubs (h < 10 m) of *P. serotina* showed a reverse J-shape frequency distribution across dbh classes, and had a dbh between 5 cm (62 % of the shrubs) and 25 cm (1 %). The histogram for the dbh of *P. serotina* trees (h > 10 m) was bell-shaped and ranged from a dbh of 5 to 35 cm, with 60 % of the trees having a dbh between 15 and 25 cm (Fig. 6.2).

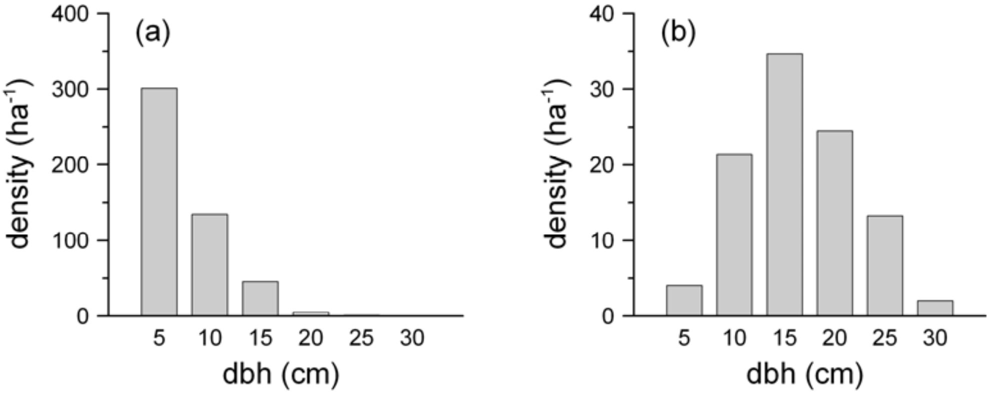


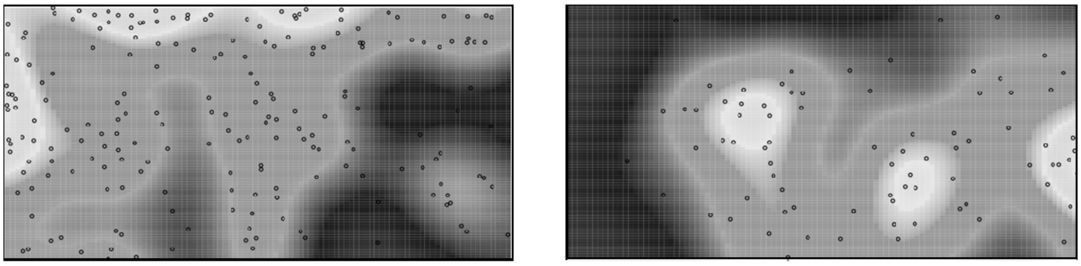
Fig. 6.2 Stem density of the *Prunus serotina* shrubs (a) and trees (b) in the core area for different dbh classes

Table 6.1 Stem density (N) and basal area (BA) for the main tree species in the core area: living trees, standing dead trees, and lying dead trees. Percentages of the total stem density or basal area are given between brackets.

	living		dead			
			standing		lying	
	N	BA	N	BA	N	BA
species[a]	(ha^{-1})	($m^2\ ha^{-1}$)	(ha^{-1})	($m^2\ ha^{-1}$)	(ha^{-1})	($m^2\ ha^{-1}$)
Pinus sylvestris L.	188 (*23*)	23.5 (*72*)	54 (*20*)	3.6 (*65*)	89 (*51*)	2.1 (*74*)
Prunus serotina Ehrh.	586 (*71*)	6.7 (*20*)	215 (*79*)	1.9 (*34*)	83 (*47*)	0.7 (*24*)
Quercus robur L.	46 (*6*)	2.5 (*8*)	4 (*1*)	0.03 (*1*)	4 (*2*)	0.05 (*2*)
total	821 (*100*)	32.8 (*100*)	273 (*100*)	5.5 (*100*)	176 (*100*)	2.8 (*100*)

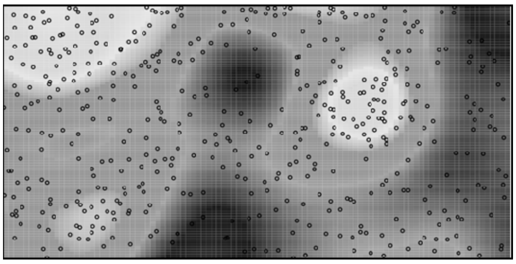
[a] *Sorbus aucuparia* L. (0.01 $m^2\ ha^{-1}$) and *Betula* spp. (0.03 $m^2\ ha^{-1}$), i.e., *Betula pendula* Roth and *Betula pubescens* Ehrh., were not included in the table because of their low contribution to the basal area.

Fig. 6.3 shows the spatial patterns of stem density for the main tree and shrub species in the core area. Areas with high densities of *P. serotina* trees (Fig. 6.3b) corresponded to areas with low densities of *P. sylvestris* and *Q. robur* trees (Fig. 6.3a) whereas *P. serotina* shrubs (Fig. 6.3c) were more abundant below *P. sylvestris* and *Q. robur* trees (Fig. 6.3a) than below *P. serotina* trees (Fig. 6.3b). These observations are further demonstrated in Fig. 6.4. Negative spatial dependence occurred between *P. serotina* trees and the two most common native species – *P. sylvestris* and *Q. robur* – for distances larger than 1.8 m (Fig. 6.4a), and between *P. serotina* shrubs and *P. serotina* trees for distances larger than 1 m (Fig. 6.4c). The positions of shrubs of *P. serotina* were independent of the positions of *P. sylvestris* and *Q. robur* trees at distances up to 16.3 m, but showed a positive spatial association for larger distances (Fig. 6.4b). Spatial associations between living and dead trees were random for all distances and all species, except for dead pines/oaks and shrubs of *P. serotina*, which showed clustering between 3.7 m and 18.2 m (figures not shown).



(a) tree *Pinus – Quercus*

(b) tree *Prunus serotina*



(c) shrub *Prunus serotina*

Fig. 6.3 The spatial position (black dots) and stem density (background colour from dark grey for low densities to light grey for high densities) of *Pinus sylvestris* and *Quercus robur* trees (a), *Prunus serotina* trees (b), and *P. serotina* shrubs (c) in the 70 m x 140 m core area

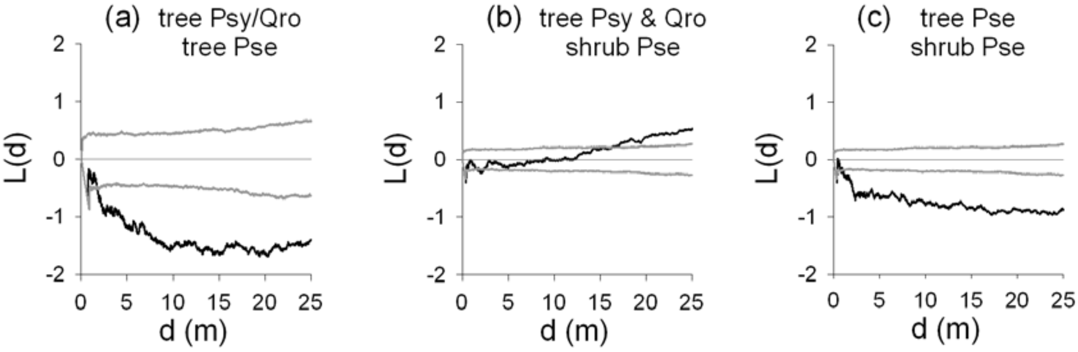


Fig. 6.4 Bivariate Ripley’s L for the point patterns of *Pinus sylvestris* (Psy) and *Quercus robur* (Qro) trees on the one hand and *Prunus serotina* (Pse) trees (a) or *P. serotina* shrubs (b) on the other hand, and for *P. serotina* trees and shrubs (c). The observed L(d) values are indicated in black; the 5 % upper and lower critical envelopes for the hypothesis of complete spatial randomness are indicated in grey.

6.4.2 Growth of *Prunus serotina*

Radial growth of *P. serotina* (y) showed a significant relationship with dbh (x): ln y = 0.083 + 0.491 x (R^2 = 0.66, $p < 0.001$). Adding height, age, competition, or canopy openness did not improve the regression. *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). For *P. serotina* below *P. sylvestris* and *Q. robur*, the fits were worse: R^2 = 0.61 for dbh–age and R^2 = 0.37 for height–age (Table 6.2). Interactions between the growing situations and age on the achieved dbh and height were significant ($p = 0.013$ and $p = 0.034$): the increases of dbh and height with age were higher in gaps than below *P. serotina* (Fig. 6.5).

Table 6.2 Equations of the linear and power regressions for the relationships dbh–age and height–age for *Prunus serotina* growing in gaps, below *Pinus sylvestris* or *Quercus robur*, and below *P. serotina* (cf. Fig. 6.5)

relationship [a]	equation	R^2	p
dbh (y) – age (x)			
in gaps	$y = -8.149 + 0.584\ x$	0.96	< 0.001
below *P. sylvestris–Q. robur*	$y = 0.070\ x^{1.335}$	0.61	0.003
below *P. serotina*	$y = -3.1 + 0.275\ x$	0.86	< 0.001
height (y) – age (x)			
in gaps	$y = -2.498 + 0.318\ x$	0.94	< 0.001
below *P. sylvestris–Q. robur*	$y = 0.482\ x^{0.752}$	0.37	0.037
below *P. serotina*	$y = -0.625 + 0.164\ x$	0.83	< 0.001

[a] dbh, diameter at breast height (cm); height, tree height (m); age, tree age (yr)

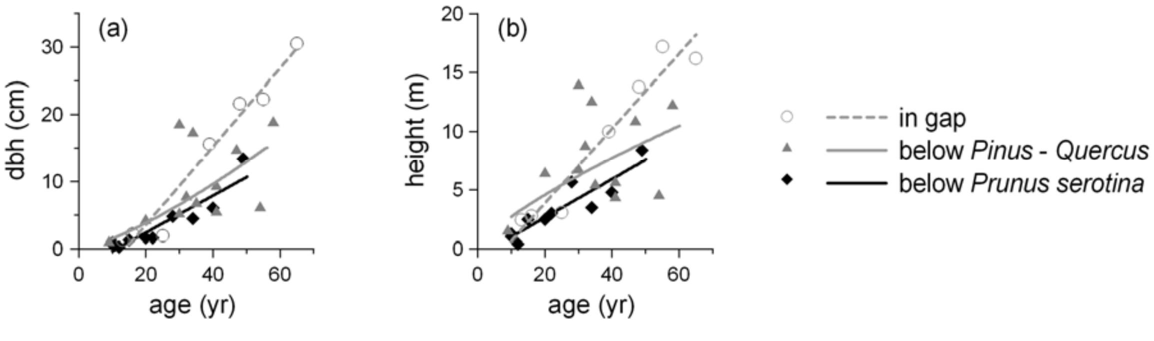


Fig. 6.5 Relationships between dbh–age (a) and height–age (b) for *Prunus serotina* growing in gaps (open circles), below *Pinus sylvestris* or *Quercus robur* (grey triangles), or below *P. serotina* (black diamonds)

6.4.3 *Prunus serotina* dispersal kernels

In the entire core area, 347 *P. serotina* trees and shrubs were found to be bearing fruits, of which 208 were in the central 60 plots. In the litter samples, we found 2374 intact *P. serotina* seeds (247.3 m^{-2}) and 1996 germinated seeds (207.9 m^{-2}). The observed mean seed production per tree was 6984 for intact seeds and 5872 for germinated seeds. Fig. 6.6 shows the dispersal kernels for *P. serotina* seeds (r = 0.27, slope = 0.97), small seedlings (stage I and stage II; r = 0.43, slope = 0.96), and large seedlings (stage IIIa and stage IIIb; r = 0.17, slope = 0.95). Seeds and small seedlings both displayed maximum probability densities close to the source tree while large seedlings showed a maximum around 13 m from the source tree.

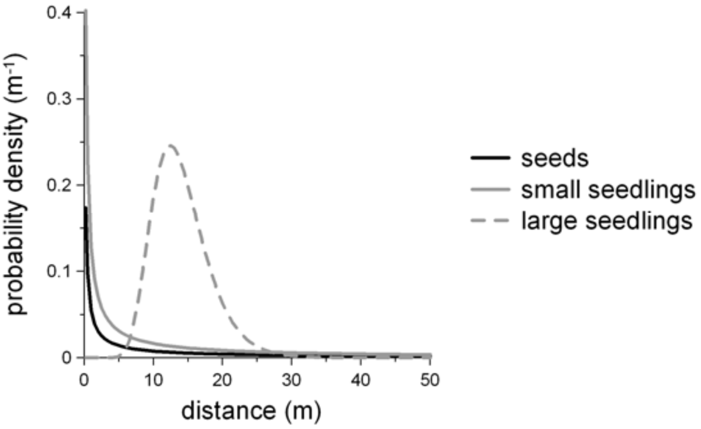


Fig. 6.6 Probability density of seeds (solid black line), seedlings smaller than 20 cm (solid grey line), and seedlings taller than 20 cm (dashed grey line) of *Prunus serotina* in the core area as a function of the distance from the source tree

6.4.4 Regeneration of tree and shrub species

Table 6.3 shows the seedling data for the tree and shrub species in the core area. *Prunus serotina* was by far the most abundantly regenerating species and the only species with stage IIIb seedlings, i.e., seedlings taller than 120 cm. For *P. sylvestris*, only stage I seedlings, i.e., seedlings resulting from seeds germinated in the year of sampling, were found. *Prunus serotina*, *Sorbus aucuparia*, and *Q. robur* showed the highest densities for stage II seedlings: most seedlings of these species were smaller than 20 cm. Logistic regressions for presence/absence of the species' regeneration, based on the characteristics of the tree and shrub layer, were not significant. The abundance of *P. serotina* seedlings smaller than 20 cm increased with seed density (stage I: r = 0.50, $p < 0.001$; stage II: r = 0.44, p = 0.001), and the abundance of *P. serotina* seedlings taller than 20 cm (stage IIIa:

r = -0.50, p < 0.001; stage IIIb: r = -0.42, p = 0.001) was correlated with the principal component 'competition' (eigenvalue = 1.352), which contrasted basal area (r = 0.77) and stem density (r = 0.73) with canopy openness (r = -0.48). Thus, the abundance of the seedlings taller than 20 cm was higher in plots with high canopy openness and low basal area and stem density. For the other species, no significant correlations were found between seedling abundance and plot characteristics.

Table 6.3 Regeneration of tree and shrub species in the 60 sample plots in the core area: density (ha^{-1}) and the number (n) and percentage (%) of plots. Total regeneration per species is subdivided into seedlings resulting from seeds germinated in the year of sampling (stage I), seedlings smaller than 20 cm (stage II), seedlings between 20 and 120 cm (stage IIIa), and seedlings taller than 120 cm (stage IIIb).

species [a]	density	plots	
	(ha^{-1})	n	%
Prunus serotina Ehrh.	*182646*	*60*	*100*
- stage I	10875	60	100
- stage II	149656	60	100
- stage IIIa	20771	59	98
- stage IIIb	1344	38	63
Pinus sylvestris L.	*7844*	*56*	*93*
- stage I	7844	56	93
Sorbus aucuparia L.	*1833*	*44*	*73*
- stage I	42	3	5
- stage II	1396	39	65
- stage IIIa	396	21	35
Quercus robur L.	*542*	*31*	*52*
- stage I	83	7	12
- stage II	385	23	38
- stage IIIa	73	7	12
Frangula alnus Mill.	*323*	*18*	*30*
- stage I	10	1	2
- stage II	135	9	15
- stage IIIa	177	12	20
Ilex aquifolium L.	*73*	*7*	*12*
- stage II	73	7	12

[a] Regeneration of *Taxus baccata* L. (stage II), *Betula pendula* Roth (stage II), and *Amelanchier lamarckii* F.G. Schroed. (stage IIIa) did only occur in 1 or 2 plots and in densities between 10 and 20 ha^{-1}.

Saplings (h > 0.5 m, dbh < 5 cm) were found in all circular plots. The most frequently present species were, with the number of plots and mean density in these plots between brackets: *P. serotina* (40 plots, 5477 ha^{-1}), *S. aucuparia* (23 plots, 168 ha^{-1}), *P. sylvestris* (10 plots, 762 ha^{-1}), *Frangula alnus* (9 plots, 158 ha^{-1}), and *Q. robur* (9 plots, 65 ha^{-1}). Saplings of *Betula* spp. and *Ilex aquifolium* L. occurred in only three plots and in very low numbers. We found no significant relationships between presence/absence and abundance of tree species regeneration on the one hand and the characteristics of the tree and shrub layer of the circular plot on the other hand, except for *P. serotina*. Ln-transformed abundances of *P. serotina* saplings smaller than 2 m ($r = 0.35$, $p = 0.037$) and taller than 2 m ($r = 0.55$, $p = 0.001$) were significantly correlated with the principal component (eigenvalue = 1.166) that combined maximum tree height, basal area of tree and shrub layers, and stem density. *Prunus serotina* saplings were more abundant in plots with a high stem density and with a high basal area for both the tree and the shrub layer.

6.5 Discussion

Our results show that spatial abundance data for different life stages can be a powerful tool to reconstruct patterns of tree species colonization and to unveil factors influencing the invasion process of a long-lived invasive species.

6.5.1 Colonization and demography

The first *P. serotina* establishment in the Ossenbos in 1940 was most probably the result of long-distance dispersal by birds because by that time, the pine and oak trees in the developing Ossenbos were large enough to have acted as focal trees in the open heathland landscape (cf. Deckers *et al.* 2008). By 2003, the Ossenbos had developed into a *Pinus sylvestris–P. serotina* forest, with high *P. serotina* abundances in well-structured forest plots characterized by a high basal area and stem density. *Prunus serotina* was the only species present in the tree and shrub layer as well as in (extremely) high seedling and sapling densities.

Prunus serotina trees occurred mainly in gaps of the pine/oak canopy (Fig. 6.4a), and the growth of *P. serotina* was highest in gaps (Fig. 6.5), which supports the gap dependence of *P. serotina* as reported in both its native (Auclair & Cottam 1971) and introduced range (Starfinger 1990, Closset-Kopp *et al.* 2007). The gap dependence of *P. serotina* was further illustrated by the high density of *P. serotina* shrubs below light-demanding *P.*

sylvestris and *Quercus robur* trees (Fig. 6.4b), the relatively low density of *P. serotina* shrubs below shade-casting *P. serotina* trees (Fig. 6.4c), and the positive correlation between canopy openness and the abundance of *P. serotina* seedlings taller than 20 cm.

Seed production per tree and seed densities in the litter layer were high and similar to other studies in forests in the introduced range (Pairon *et al.* 2006a,b, Closset-Kopp *et al.* 2007), but much higher than values observed in the native range (Smith 1975). The extremely high densities of *P. serotina* seedlings smaller than 20 cm indicate the build-up of a persistent seedling bank (cf. Closset-Kopp *et al.* [2007] and Chapter 4 for the introduced range and Marquis [1990] for the native range), and the higher abundance of *P. serotina* seedlings taller than 20 cm in plots with a higher canopy openness (Photo 6.1) suggests that the height of suppressed *P. serotina* seedlings depends on the light level (cf. Knight *et al.* 2008). The observed increase in mean distance from the source tree for taller seedlings (Fig. 6.6) fits in with the Janzen-Connell hypothesis (Janzen 1970, Connell 1971), which has already been shown to hold for *P. serotina* in its native range (e.g., Packer & Clay 2000). Our data also suggest some kind of ‘shrub bank’, with *P. serotina* shrubs of up to 60 years old and still less than 10 m high growing below *P. sylvestris* or *Q. robur* (Photo 6.2).

6.5.2 The herbivory hypothesis

Prunus serotina was omnipresent in the forest reserve whereas native deciduous species occurred only sporadically and most native seedlings did not grow taller than 20 cm (Table 6.3). Consequently, one would be tempted to consider *P. serotina* a prolific and successful invasive species. Nonetheless, in a similar study in a mixed deciduous forest in Belgium, *P. serotina* did not act as a prolific invader (see Chapter 5). For both the Ossenbos (this study) and the Liedekerke forest reserve (Chapter 5), the propagule pressure was low at the beginning of the invasion process. Roe deer were only rarely observed in the Liedekerke forest reserve whereas game densities were exceptionally high in the Ossenbos (i.e., 1 ha^{-1}). The two alien species that occurred in both forests, i.e., *P. serotina* and *Quercus rubra*, showed contrasting colonization patterns. *Prunus serotina* successfully invaded the Ossenbos, but did not show a rapid spread in Liedekerke. *Quercus rubra* did not show successful regeneration in the Ossenbos although seed trees were present in the forest and *Q. rubra* had been planted next to the forest in 1914 (Arthur Varkevisser *pers comm*). In the Liedekerke forest reserve, on the other hand, *Q.*

rubra regeneration was locally abundant and the species had been able to triple its basal area during the twenty-year study period (see Chapter 5).

Seeing the differences in colonization for *P. serotina* and *Q. rubra* in these two forests, we hypothesize that the high herbivore pressure in the Ossenbos forest reserve has favoured *P. serotina* colonization over colonization of the tree and shrub species that would naturally occur on the poor sandy soils of the Ossenbos, e.g., *Q. robur*, and *Sorbus aucuparia* (Van der Werf 1991). First, even at much lower ungulate densities, i.e., ca. 0.15 ha^{-1}, in similar forests in the Veluwe ecoregion, Kuiters & Slim (2000, 2002) found equally low regeneration densities for native species, with almost no seedlings growing above the height of the herb layer, i.e., 30–50 cm. Second, although wild boar feed on *P. serotina* fruits (Starfinger 1990), most *P. serotina* seeds are defecated unharmed. Acorns, on the other hand, are consumed completely and are a preferred food source for red deer and, particularly, wild boar (Groot Bruinderink *et al.* 1994, Gómez *et al.* 2003), which might explain the low densities of *Q. robur* (and *Q. rubra*) seedlings despite the presence of seed trees. Third, the leaves of *P. serotina* contain cyanogenic glycosides that form the toxin cyanide after wilting or ingestion (McVaugh 1951), and ingestion of *P. serotina* leaves has been found to cause sickness or death in animals (e.g., Radi *et al.* 2004). Leaves of species such as *Q. robur* and *S. aucuparia*, on the other hand, are preferred by deer (e.g., Götmark *et al.* 2005). Fourth, in its native range, *P. serotina* is less affected by deer browsing than its associated species, with the result that the species may dominate seedling and sapling layers (Marquis 1990, Horsley *et al.* 2003). Fifth, Eschtruth & Battles (2009a) recently showed that generalist native herbivores, e.g., white-tailed deer (*Odocoileus virginianus* Zimmermann, 1780), can facilitate, and even accelerate, the invasion of an alien shrub species in forests.

6.6 Conclusions

Although the initial propagule pressure of *P. serotina* in the Ossenbos forest reserve will have been low, the forest has developed into a *Pinus sylvestris–P. serotina* forest. *Prunus serotina* was present in the tree and shrub layer and in extremely high seedling densities. *Prunus serotina* successfully established in gaps in the pine–oak canopy in the Ossenbos forest reserve, and the height of the *P. serotina* seedlings in the seedling bank was related to light availability. *Prunus serotina* also occurred in a ‘shrub bank’ with shrubs less than 10 m tall and up to 60 years old.

The outcome of the *P. serotina* colonization in the Ossenbos forest reserve clearly differs from the *P. serotina* colonization in the deciduous forest on sandy loam soil of Chapter 5, which illustrates that invasion processes are idiosyncratic and context dependent (cf. Chapter 1). We hypothesize that the high herbivore pressure in the Ossenbos forest reserve has favoured *P. serotina* over native species, which has resulted in *P. serotina* dominance.

Photo 7.1 *Pinus sylvestris* and *Prunus serotina* in the core area of the Ossenbos forest reserve (August 2007)

7 Long-term development of a pine-oak forest with *Prunus serotina*: scenarios with low and high densities of large herbivores

7.1 Abstract

The spread of shade-tolerant invasive tree species in forests can be slow because of their long life span and the lag phases that may occur during the invasion process. Models of forest succession are a useful tool to explore how these invasive species might affect long-term forest development. We used the spatially explicit individual tree model SORTIE-ND to gain insight into the long-term development of a gap-dependent invasive tree species, *Prunus serotina*, in a pine-oak forest on sandy soil, the forest type in which *P. serotina* occurs most often in its introduced range. Forest inventory data, tree ring data, and photographs of the tree crowns were collected in a forest reserve in the Netherlands characterized by high game densities. The collected data were then combined with data from literature to parameterize the model. We ran the model for two different scenarios in order to evaluate the impact of differences in the regeneration success of the native *Quercus robur* and the invasive *P. serotina*, which we attributed to differences in densities of large herbivores. The outcome of the simulations shows two differing courses of forest development. The invasive *P. serotina* became the dominant species when high herbivore densities hindered the regeneration of *Q. robur*. When *Q. robur* was able to regenerate, e.g., because of low herbivore densities, *Q. robur* became the most abundant species in the long term. We hypothesize that the relatively short life span of *P. serotina* precludes its dominance if other long-lived tree species are present and able to regenerate.

7.2 Introduction

Shade-tolerant invasive plant species can have adverse and long-lasting effects on forest ecosystems worldwide, but their invasion often remains unnoticed for a long time because of their relatively low invasion rates (Martin *et al.* 2009). Perennial woody invaders may indeed experience prolonged establishment phases between initial introduction and subsequent spread because of their long generation times and the multiple lag phases that can occur during the invasion process (Martin & Marks 2006, Wangen & Webster 2006). Studying the patterns and consequences of such protracted invasions therefore requires long-term data, which are, however, rarely available. Model simulations of long-term forest development represent an additional tool for gaining insight into the possible outcomes of various scenarios of forest development with invasive species.

We used *Prunus serotina* Ehrh., a tree species native to North America, as a case to explore the long-term invasion patterns of a gap-dependent invasive tree species (cf. Chapter 2). The relatively short period in which *P. serotina* has been present in European forests and the widespread attempts to control the species have largely precluded the investigation of long-term, spontaneous development of *P. serotina* in its introduced range (but see Chapter 5 and 6). Efforts to model the spread of *P. serotina* are also scarce (Sebert-Cuvillier *et al.* 2007, 2008, *in press*). The results of these recent studies suggest that ecosystem disturbances, e.g., wind storms (Sebert-Cuvillier *et al.* 2007, *in press*) or grazing by large herbivores (Chapter 6), may facilitate *P. serotina* invasion.

We simulated the long-term development of a pine-oak (*Pinus sylvestris* L., *Quercus robur* L.) forest in which *P. serotina* was present, i.e., the Ossenbos forest reserve (Chapter 6), with SORTIE-ND (www.sortie-nd.org), a spatially explicit individual tree model of forest dynamics. The original version of the model SORTIE was developed in the 1990s for forests in the northeastern part of the United States (Pacala *et al.* 1996), but the model has been successfully parameterized and used for modelling forest development in, e.g., northern British Columbia (see Coates *et al.* 2003) and southern New Zealand (Kunstler *et al.* 2009). The Ossenbos forest reserve represented a unique opportunity for this study because it is a forest in which *P. serotina* has spread and developed spontaneously for almost 70 years, opposite to most other forests in Western Europe where *P. serotina* has been planted or managed. In Chapter 6, we showed that the establishment and growth of *P. serotina* in the Ossenbos forest reserve were related to light availability, and based on the comparison of the patterns of the *P. serotina* invasion in Chapter 5 and 6, we hypothesized that a high density of large herbivores may favour *P. serotina* over native tree and shrub species such as *Q. robur*. The regeneration of *Q. robur* is indeed hampered by high densities of animal species that consume acorns and browse on small seedlings (Groot Bruinderink *et al.* 1994, Gómez *et al.* 2003) whereas *P. serotina* has been found to dominate seedling and sapling layers in areas with high deer densities in its native range (Horsley *et al.* 2003).

The objectives of this chapter were (1) investigating whether SORTIE-ND can be a useful tool to simulate the development of invasive woody species, (2) the visualization of long-term development of the invasive *P. serotina* and the invaded forest, and (3) exploring the impact of differences in the regeneration success of the native *Q. robur* versus the invasive *P. serotina*, which may be attributed to differences in herbivore densities.

7.3 Materials and methods

7.3.1 Study area

For a detailed description of the study area, study plot, and data collection, we refer to Chapter 6 (section 6.3.1 and 6.3.2). In this section, we provide only a brief description of the study area and the collection of the data used for the parameterization of the model.

The Ossenbos forest reserve is a spontaneously developed forest with pine (*Pinus sylvestris*) and oak (*Quercus robur*) on sandy soil in the Netherlands, in which *P. serotina* established around 1940. From 1990 onwards, the forest has been characterized by a high density (ca. 1 ha^{-1}) of ungulates, i.e., red deer (*Cervus elaphus* Linnaeus, 1758), roe deer (*Capreolus capreolus* Linnaeus, 1758), and wild boar (*Sus scrofa* Linnaeus, 1758).

Data were collected in a study plot of 70 m x 140 m in March 2003 and August 2007. For trees with a diameter at breast height (dbh) > 5 cm, the position, species, dbh, height, crown radius, and crown length were measured in 2003. In 2007, additional data were collected on age and crown openness for the three main tree species. For 49 *P. sylvestris* trees, 33 *P. serotina* trees, and 25 *Q. robur* trees, we measured dbh and height and took a stem cross section (for small individuals) or tree core (for large individuals) at 20–30 cm above the root collar. The age of the sampled trees was determined by counting the growth rings using a stereomicroscope (Olympus SZX12). We made photographs of the crown for 20 trees of each of the species using a Nikon D70S with a AF-S Zoom-Nikkor ED 18-70mm f/3.5-4.5G IF DX and following the methods of Beaudet *et al.* (2002). In addition, for each of the three species, we randomly chose 25 individuals with dbh < 5 cm and measured their dbh, height, and diameter at 10 cm above the root collar (diam10).

7.3.2 Model

We used the model SORTIE-ND version 6.09 (www.sortie-nd.org), which is based on the earlier SORTIE model (Pacala *et al.* 1996). SORTIE-ND is (1) individual-based – the basic unit of data is a tree, (2) spatially explicit – each tree has a unique location, (3) dynamic – the model shows how a forest changes during a certain time span, and (4) empirical – the model functions are fitted based on field data (Tremblay *et al.* 2005). The original, basic version of SORTIE consisted of four submodels with species-specific equations that calculate the local light availability (Canham *et al.* 1994); predict the growth and mortality of individual seedlings, saplings, and adults (Pacala *et al.* 1994, Kobe *et al.* 1995); and determine seedling recruitment (Ribbens *et al.* 1994). SORTIE-ND simulates the life cycle of individual trees for a certain number of 5-year time steps. Light is considered the limiting resource, and for each time step in a simulation or model run, SORTIE-ND first calculates an index of light availability for each tree. This Global Light Index (GLI) is based on the tree's neighbourhood, i.e., the density, size, position, and species of all the neighbouring trees. The calculated light availability is subsequently used to determine the growth of the subject tree, which is then translated into probability of mortality. Living trees with a dbh above the Minimum DBH for Reproduction produce seedlings that will be dispersed according to a given dispersal kernel.

7.3.3 Parameterization

We determined parameters for the allometry relationships for *P. sylvestris*, *P. serotina*, and *Q. robur* and for the four submodels, i.e., light, growth, mortality, and dispersal, based on the data collected in the Ossenbos forest reserve (section 7.3.1) and on literature. The complete parameter file used for the simulations is provided in Appendix 7.1; in the following sections, we indicate how we derived the parameter values.

7.3.3.1 *Allometry*

In SORTIE-ND, each tree is a discrete individual with a given spatial location and with attributes that describe its size and shape. Allometry refers to the relationships between the different components of the size and shape of a tree. We used the standard SORTIE-ND functions for the relationships crown radius–dbh, crown length–height, height–dbh for saplings and adults; dbh–diam10 for saplings; and height–diam10 for seedlings (see Table 7.1). For each of these relationships, the parameters were estimated based on the 2003 data for the study area (Table 7.1). Non-linear and linear regressions were performed in R 2.8.0 (R Development Core Team 2008). For the parameter Maximum Tree Height (see Appendix 7.1), we used the maximum tree height as reported in Brzeziecki & Kienast (1994) in combination with data from Chapter 5 and 6.

7.3.3.2 *Light*

For each individual, SORTIE-ND simulates a hemispherical photograph and uses this simulated photograph to calculate GLI, i.e., the percentage of full light received by the tree. We adjusted the region-specific light parameters that determine the local sky brightness and the seasonality to the local situation. The Beam Fraction of Global Radiation (0.32; Hemming *et al.* 2007) and the First and Last Day of Growing Season (81 and 284; Jacobs *et al.* 2008) were taken from literature; the Clear Sky Transmission Coefficient (0.526) was calculated for a clear summer day in Wageningen (N51°58' E005°38'), close to the study area (Adrie Jacobs *pers comm*). We then determined the crown openness for each of the three species, based on our photographs of the tree crowns and following the methods described in Beaudet *et al.* (2002). The mean crown openness, with the standard error between brackets, was 29.9 % (2.0) for *P. sylvestris*, 23.8 % (1.7) for *P. serotina*, and 25.1 % (1.7) for *Q. robur*. Crown openness differed between species (one-way ANOVA: $F = 5.7$, $df = 2$, $p < 0.005$). The crown openness of *P. sylvestris* was higher than that of *P. serotina* (Tukey post-hoc: $p = 0.006$) and *Q. robur* ($p = 0.036$); the crown openness of *P. serotina* and *Q. robur* did not differ ($p = 0.796$). The other parameters for the calculation of GLI (see Appendix 7.1), which are not region-specific, were taken from the standard parameter file (www.sortie-nd.org).

Table 7.1 Estimates of the parameters a and b in the allometry relationships for the *Pinus sylvestris*, *Prunus serotina*, and *Quercus robur* in the Ossenbos forest reserve

		Pinus sylvestris				*Prunus serotina*				*Quercus robur*			
relationship [a]	function	a	b	R²	n [b]	a	b	R²	n	a	b	R²	n
crown radius (y) – dbh (x)	$y = ax^b$	0.35	0.64	0.23	183	0.78	0.5	0.40	573	0.55	0.62	0.71	46
crown length (y) – h (x)	$y = ax^b$	0.71	0.78	0.24	183	0.42	1.13	0.78	573	0.56	1.06	0.27	49
h (y) – dbh (x)	$y = 1.35 + a(1-e^{-bx})$	18. 6	0.06	0.45	183	22. 7	0.03	0.61	573	16.9	0.05	0.51	49
dbh (y) – diam10 (x)	$y = ax$	0.78	-	0.99	25	0.80	-	0.93	25	0.75	-	0.97	25
h (y) – diam10 (x)	$y = 0.1 + 30\ (1-e^{-ax})$	0.021	-	0.77	25	0.024	-	0.90	25	0.022	-	0.73	25

[a] dbh, diameter at breast height (cm); h, tree height (m); diam10, diameter at 10 cm above the root collar (cm). The relationships with diam10 are based on data for individuals with a dbh < 5 cm. Crown radius and crown length are both expressed in m.

[b] n, the number of sample trees

7.3.3.3 *Dispersal*

The dispersal submodel creates seedlings and disperses them across the plot according to a given seed dispersal kernel.

The Minimum DBH for Reproduction for *P. sylvestris* and *Q. robur* was calculated based on the minimum age for first reproduction reported by Brzeziecki & Kienast (1994) and the relationships between age and dbh based on the data for the study area (see section 7.3.3.4) and another forest reserve in the Netherlands (data Goris *et al.* 2007). For *P. serotina*, we used the minimum diameter at which 90 % of the *P. serotina* set seed in the understory of pine forests on sandy soil in Flanders (data Chapter 4).

The Standardized Total Recruits (STR) is defined as the number of new seedlings that would be produced by a tree with a dbh of 30 cm. Because we did not have good long-term data on seed rain and recruitment for the three species, we determined STR based on mean annual fecundity, seed germination and 1-year seedling survival following Papaik & Canham (2006). Mean annual fecundity was calculated with the empirical relationship between seed mass and seed number formulated by Greene & Johnson (1994, 1998) and using seed mass data from Brzeziecki & Kienast (1994) for *P. sylvestris* and *Q. robur* and from Grisez (1974) for *P. serotina*. Seed germination and 1-year seedling survival were determined based on literature for *P. sylvestris* (Castro *et al.* 2004), *P. serotina* (Pairon *et al.* 2006a, Chapter 4), and *Q. robur*, for which we used the data on *Q. petraea* (Matt.) Liebl. in Degen (2006).

For the spatial placement of the seedlings around the seed trees, we chose the Weibull probability density function with the parameters provided by Charles Canham (*pers comm*). We used the North American parameters provided for *Pinus strobus* L., *Quercus rubra* L., and *P. serotina* for the *P. sylvestris*, *Q. robur*, and *P. serotina* in the Ossenbos forest reserve. *Pinus strobus* and *P. sylvestris* are both wind-dispersed, their seeds have similar dimensions, but the seeds of *P. strobus* are somewhat heavier than those of *P. sylvestris* (Brzeziecki & Kienast 1994, Noland *et al.* 2006). Both *Quercus* species are mainly barochorous, and the weight and dimensions of their seeds are similar (Brzeziecki & Kienast 1994, Kostel-Hughes *et al.* 2005).

7.3.3.4 Growth and mortality

The parameters for the submodels growth and mortality were determined indirectly, based on the data collected in 2003/2007 and a reconstruction of the forest in 1953. First, we counted the number of tree rings to estimate the age of the sampled trees. Second, we determined the relationships between age (y) and dbh (x) for the three species: $y = 8.85 + 2.15\ x$ for *P. sylvestris* ($R^2 = 0.71$, $n = 49$), $y = 10.90 + 10.80\ \ln(x)$ for *P. serotina* ($R^2 = 0.68$, $n = 33$), and $y = 35.3 + 1.09\ x$ for *Q. robur* ($R^2 = 0.65$, $n = 25$). Third, we used these relationships together with the 2003 inventory of living and dead trees to reconstruct the 1953 forest. Fourth, we ran SORTIE-ND for ten time steps, i.e., 50 year, with the 1953 situation as the model input and the parameters for allometry, light, and dispersal set as in the sections 7.3.3.1, 7.3.3.2, and 7.3.3.3. We adjusted the parameters for growth and mortality iteratively so that the output of the simulation approximated the real 2003 situation. For that purpose, we compared the maximum age and dbh as well as the diameter distribution (see Fig. 7.1) for the model output and the 2003 inventory data. Seeing the high impact of large herbivores on the regeneration of *Quercus* species (Groot Bruinderink *et al.* 1994, Gómez *et al.* 2003), we used different parameter values for the Juvenile Background Mortality Rate for *Q. robur* for the period 1953–1993 (with a low density of large herbivores) and 1993–2003 (with a high density of large herbivores). The growth values calculated based on the estimated parameters were in concordance with growth ranges reported in literature for the three species in this study (see Table 7.2).

Table 7.2 The range of radial growth rates, i.e., minimum and maximum radial growth, calculated based on the growth functions in this study compared to ranges of radial growth rates reported in the literature for *Pinus sylvestris*, *Prunus serotina*, and *Quercus robur* on sandy soil in the Netherlands or Flanders (the northern part of Belgium)

species	this study ($mm\ yr^{-1}$)	literature data ($mm\ yr^{-1}$)	reference
Pinus sylvestris L.	0.5–2.7	0.9–3.2	Goris *et al.* (2007)
Prunus serotina Ehrh.	0.5–4.1	0.1–4.3	Chapter 3, 5, and 6
Quercus robur L.	0.1–3.4	0.1–6.4	Haneca (2005)

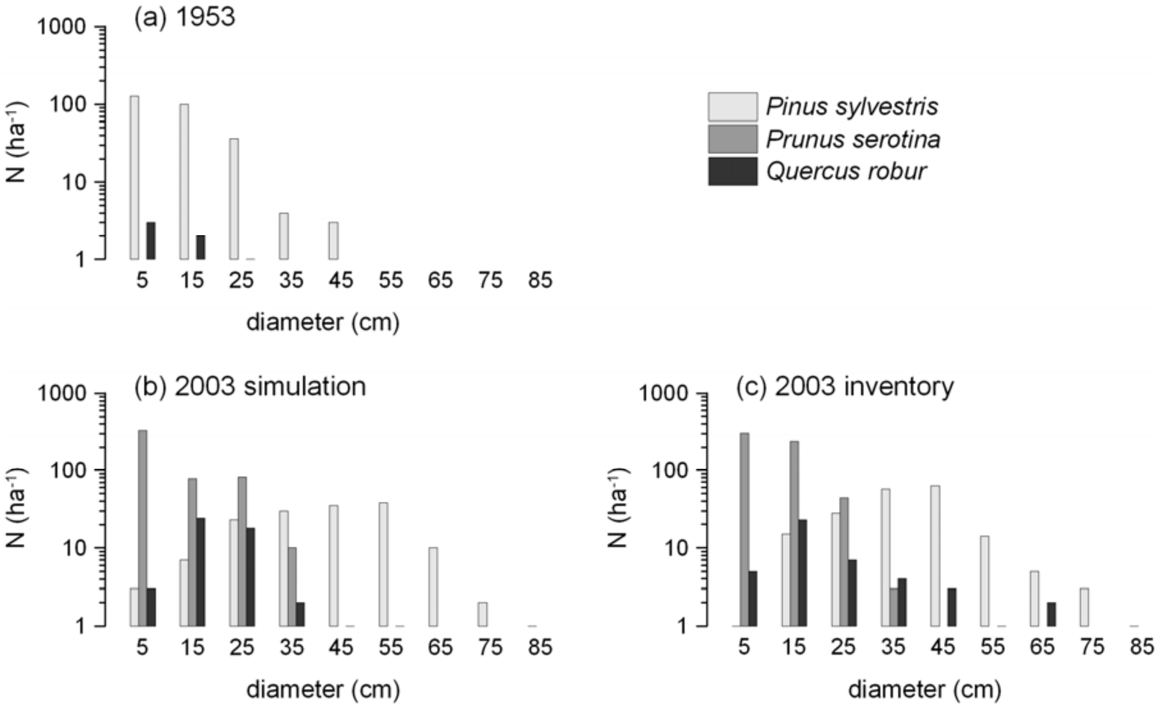


Fig. 7.1 Diameter distribution for (a) the reconstructed 1953 situation, (b) the simulated 2003 situation, and (c) the real 2003 situation in the Ossenbos forest reserve. Note that the stem densities (N, ha^{-1}) for the different diameter classes are depicted on a logarithmic scale.

7.3.4 Model input and scenarios

We used the 2003 inventory data for the Ossenbos to define the initial tree population parameters for the SORTIE-ND simulations. The Minimum Adult DBH was set to 5 cm. The initial seedling densities were set to the densities in the shrub layer (tree height < 10 m) because working with the high seedling densities that occur in reality (cf. Chapter 6) slows down SORTIE-ND and most of these seedlings will die anyway (Charles Canham *pers comm*). The model input, which is called the 'tree map', i.e., the x, y-coordinates, the species, the dbh, and height for all trees, was also based on the 2003 inventory data.

We ran the model for 100 time steps, i.e., 500 years, to study the long-term development of the pine-oak forest reserve with *P. serotina* for two scenarios that differed in the regeneration success of the invasive *P. serotina* and the native *Q. robur*. Since the extremely high herbivore densities in the Ossenbos forest reserve (see section 7.3.1) seemed to hamper the regeneration of *Q. robur* and facilitate the regeneration of *P. serotina* (Chapter 6), we attributed the regeneration differences between the two scenarios to a difference in large herbivore densities. We distinguished between a scenario with high densities of large herbivores, in which *Q. robur* showed no successful regeneration, and a scenario with low densities of large herbivores, in which *Q. robur* was able to regenerate. The two scenarios were implemented by changing the parameters that describe seedling establishment and juvenile mortality. The juvenile mortality rates for the two scenarios were taken from the simulations in section 7.3.3.4. The seedling establishment parameter, i.e., the STR values derived in section 7.3.3.3, were lowered for *Q. robur* and *P. serotina* in the scenario with high densities of large herbivores (see Appendix 7.1), according to the seedling and sapling densities recorded for the two species in Chapter 6. For *P. sylvestris*, we used the same values for the two scenarios because *P. sylvestris* is less affected by herbivory and is not able to recruit below a canopy anyhow. We repeated the simulation ten times for each scenario to account for the stochasticity in the mortality and dispersal submodels in SORTIE-ND (cf. Deutschman *et al.* 2000, Ménard *et al.* 2002). Based on the output of the ten simulations, we then calculated mean stem density (N, ha^{-1}) and mean basal area (BA, m^2 ha^{-1}) for each species and each time step.

7.4 Results

Fig. 7.2 shows the output of the 500-year SORTIE-ND simulations for the scenario with high densities of large herbivores in which *Q. robur* showed no successful regeneration (Fig. 7.2a,c) and the scenario with low densities of large herbivores in which *Q. robur* was also able to regenerate (Fig. 7.2b,d). The changes in stem density (N) and basal area (BA) of *P. sylvestris* were similar for the two scenarios: N and BA both decreased until no *P. sylvestris* stems were left after 200 years. For *P. serotina*, N showed a sharp initial decline (Fig. 7.2a,b). Between year 100 and 200, *P. serotina* N and BA remained relatively stationary, and they were similar for the two scenarios. After the year 250, the changes in N and BA of *P. serotina* differed between the scenarios: both N and BA increased steadily in the scenario with many large herbivores (Fig. 7.2a,c) whereas they decreased in the scenario with few large herbivores (Fig. 7.2b,d). For *Q. robur*, the two scenarios resulted in clearly differing patterns for the changes in N and BA. In the scenario with high densities of large herbivores, *Q. robur* was not able to regenerate, N showed a steady decline (Fig. 7.2a), and BA followed a bell-shaped curve (Fig. 7.2c). In the scenario with few large herbivores, N and BA of *Q. robur* both showed a steady increase after year 100 (Fig. 7.2b,d). After 200 years, the difference in N and BA of *Q. robur* between the two scenarios became apparent.

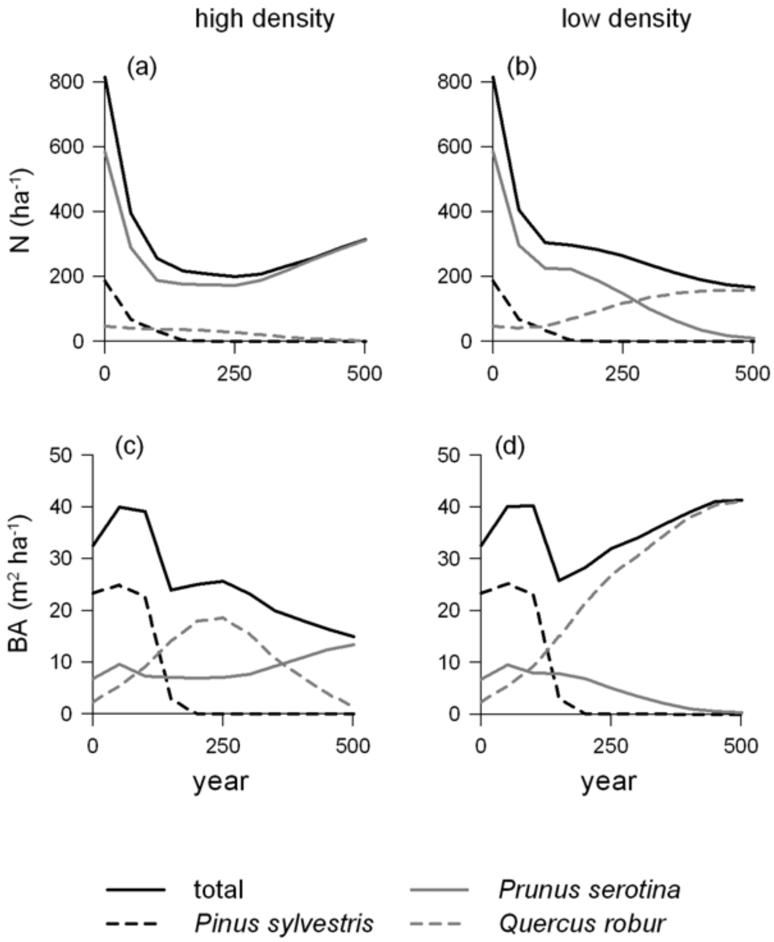


Fig. 7.2 Output of the SORTIE-ND simulations for the Ossenbos forest reserve over a 500-year simulation period showing the stem density (N, ha^{-1}) and basal area (BA, m^{2} ha^{-1}) of the adult trees (dbh > 5 cm) of *Pinus sylvestris*, *Prunus serotina*, and *Quercus robur*. The mean stem density and basal area of ten model runs are given for the scenario with high densities of large herbivores in which *Q. robur* showed no successful regeneration (a, c) and for the scenario with low densities of large herbivores in which *Q. robur* was also able to regenerate (b, d).

7.5 Discussion

7.5.1 Modelling *Prunus serotina* invasion

The spatially explicit individual-based model SORTIE-ND enabled us to explore the future development of a highly invaded, unmanaged forest reserve in which *P. serotina* occurred in the tree, shrub, and herb layer (see Chapter 6). Due to the neighbourhood dynamics ('ND') incorporated in SORTIE-ND, the course of the simulated development of one of the species in the forest and of the entire forest stand is affected by the simulated development of all the species and their mutual interactions. Thus, SORTIE-ND simulates the development of a *P. serotina* tree in association with the development of the neighbouring trees. This approach clearly differs from the models that have been used previously to better understand and predict the spread of *P. serotina*. These models only looked at *P. serotina* and did not account for changes in the invaded vegetation. Pairon (2007), for instance, used a spatially explicit individual-based model that included both demographic patterns and the spatial genetic structure of a *P. serotina* population to predict the local spread of *P. serotina* in patches of heathland and dry grassland. Sebert-Cuvillier *et al.* (2007) used a stage-classified demographic matrix population model to explore the local population dynamics of *P. serotina* in a managed forest stand and identified the life history stages with the greatest impact on population growth using elasticity analysis. This matrix model was then used to model the spatial spread of *P. serotina* in a heterogeneous landscape (Sebert-Cuvillier *et al.* 2008, *in press*). In the matrix model of Sebert-Cuvillier *et al.* (2007), all *P. serotina* individuals in a certain life stage were considered equal, e.g., each seedling has the same chance to die, to remain in the seedling stage, or to become a sapling. In addition, once a forest patch got invaded, it remained invaded for the rest of the simulation run (Sebert-Cuvillier *et al.* 2008). Although Sebert-Cuvillier *et al.* (2007) did include disturbances that changed the environmental conditions from 'shade' to 'light', canopy gaps created by the model only affected *P. serotina*. In SORTIE-ND, changes in light availability affect all the species present. Moreover, each seedling, sapling, or tree is treated as a separate individual with its growth and mortality dependent on its neighbourhood, and, as shown by the model output for the studied forest reserve in Fig. 7.2, an invaded forest patch does not have to remain invaded in the long-term. It should be noted, however, that we did not include recurrent disturbance events in our model because we studied a forest reserve in which management measures such as regular thinnings do not occur. Sebert-Cuvillier *et al.* (2007, 2008, *in press*) studied a managed forest, and they found that the frequency of disturbance affects the invasiveness of *P. serotina*. Nonetheless, SORTIE-ND may provide a useful addition on the models that predict the spread of *P. serotina* as it enables to explore the future development of forest stands that get invaded, taking into account the changes in the invader as well as in the invaded stand.

7.5.2 Does herbivory matter?

Modelling forest development with SORTIE-ND made it possible to depict the long-term development of the Ossenbos forest reserve according to two specific scenarios that differed in the regeneration success of the invasive *P. serotina* and the native *Q. robur*. We called those the scenarios with low or high herbivore densities because the extremely high game density in the study area might be the most important factor influencing the regeneration of tree species in the Ossenbos forest reserve. We simulated the impact of high herbivore pressure on tree seedlings and saplings by lowering the establishment of seedlings and by increasing the mortality of juveniles in SORTIE-ND. The outcome of the simulations for the two scenarios clearly differed. In the scenario in which the regeneration of *Q. robur* was hindered, *P. serotina* became the dominant species. When *Q. robur* was able to regenerate, e.g., because of low herbivore densities, *Q. robur* became more abundant than *P. serotina* on the long term. Processes or factors that limit the regeneration of native tree species such as *Q. robur*, e.g., a high density of large herbivores, may thus increase the invasibility of a particular ecosystem for *P. serotina* (cf. Chapter 6).

The observation that *Q. robur* gained ascendancy over *P. serotina* in the scenario with low densities of large herbivores might be the result of the longer life span of *Q. robur*. Von Holle *et al.* (2003) proposed biological inertia within a plant community as a component of the community's resistance to invasion and considered the longevity of tree species as a component of the biological inertia of forests. The life span of *P. serotina* in forests in its introduced range is relatively short, i.e., 50–80 years (Wallis de Vries 1987, Sebert-Cuvillier *et al.* 2007), as compared to the life span of *Q. robur*, i.e., several centuries and even up to 500 years (Brzeziecki & Kienast 1994). The life span of *Pinus sylvestris* is similar to that of *Q. robur* (Brzeziecki & Kienast 1994), but *P. sylvestris* is less shade tolerant than *Q. robur* (Niinemets & Valladares 2006) and is not able to regenerate in forest understories. In addition, the shade-casting ability of *Q. robur* is higher than that of *P. sylvestris* (cf. Baeten *et al.* 2009), which makes the invasion of *P. serotina* in a *Q. robur* forest less likely (cf. Sebert-Cuvillier *et al.* 2008). In a model simulation for a developing, mixed deciduous forest in its native range, the basal area of *P. serotina* also declined (Deutschman *et al.* 2000). Thus, the relatively short life span of *P. serotina* might preclude its dominance in the course of forest succession when other tree and shrub species are also able to regenerate, e.g., because large herbivores are absent.

The two scenarios used in our study simulated the effects of a continuously low or high impact of large herbivores on forest development. However, fluctuations in herbivore densities can be expected over time due to, e.g., harsh versus mild winter conditions (Melis *et al.* 2009) or differences in hunting effort (Klopcic *et al. in press*). These fluctuations in herbivore densities may affect the regeneration of particular tree species and influence the structure and species composition of forests (Klopcic *et al. in press*). Yet, the ungulate densities in the Ossenbos forest reserve are thus high that even a moderate decrease in ungulate density might not have dramatic impacts on the course of succession seeing that *Q. robur* did not even show successful regeneration at ungulate densities of one tenth of the present densities (Kuiters & Slim 2002).

7.5.3 Improving the present model?

Although forest succession models such as SORTIE-ND remain a valuable tool for exploring the possible outcomes of long-term forest development (cf. Royo & Carson 2006), some ecological mechanisms have not yet been implemented. Two issues that might be important with regard to simulations of *P. serotina* invasion are (1) its ability to delay mortality by building up a seedling bank or by resprouting when its crown dies back (Closset-Kopp *et al.* 2007, Chapter 4) and (2) the negative impact of dense herb layers on *P. serotina* seedling survival (Horsley 1993, Royo & Carson 2008, Chapter 5). Similarly, Beaudet *et al.* (2002) and Tremblay *et al.* (2005) pointed out that integrating a herb layer in the submodel 'light' of SORTIE-ND will improve the predictions for forests with dense understory vegetation, and Caplat & Anand (2009) recently showed the importance of incorporating the resprouting ability of tree species in individual-based forest development models.

To model the development of forests characterized by recurrent disturbances that create canopy gaps and increase the availability of light in the understory, including a submodel on harvest and disturbance (see www.sortie-nd.org) might be essential for a gap-dependent species such as *P. serotina*. Sebert-Cuvillier *et al.* (2007, *in press*) indeed showed that disturbances opening up the canopy layer may speed up the *P. serotina* invasion.

7.6 Conclusions

Although the simulations in this study were based on one specific site and the parameters were mostly derived indirectly, our results clearly show the usefulness of spatially explicit individual tree models such as SORTIE-ND in exploring possible outcomes of long-term development in forests in which (invasive) alien species are present. Based on the output of the simulations, it seems that the relatively short life span of *P. serotina* prevents its overall dominance if other tree species are also able to regenerate. Starfinger *et al.* (2003) have already indicated that ‘wait and see’ might be an efficient strategy for managing *P. serotina* in European forests characterized by a low degree of disturbance because *P. serotina*’s dominance will decrease, even in forests without shade-tolerant trees. Indeed, next to differences in shade tolerance, differences in life span also play a part in the coexistence of species over the course of forest development (Lusk & Smith 1998). Likewise, Cunard & Lee (2009) stated that managing the invasive *Frangula alnus* P. Mill. in forests in New Hampshire will be less effective than allowing the natural forest succession to run its course.

Appendix 7.1

Parameter file used for the SORTIE-ND simulations in the Ossenbos forest reserve

For the meaning of the different parameters, see www.sortie-nd.org. The superscript characters indicate whether a parameter was (a) set according to the characteristics of the model runs given in section 7.3.4, (b) estimated based on own data as described in section 7.3.3.1 and 7.3.3.2, (c) based on the calibration of the submodels discussed in section 7.3.3.4, (d) derived from literature or via personal communication, or (e) taken from the sample parameter file provided on www.sortie-nd.org.

Species: *Pinus sylvestris* L. (PISY), *Prunus serotina* Ehrh. (PRSE), *Quercus robur* L. (QURO)

Plot parameters

Parameter	
Number of time steps [a]	100
Random Seed [a]	0
Number of years per time step [e]	5
Plot Length in the X (E-W) Direction, in meters [a]	280
Plot Length in the Y (N-S) Direction, in meters [a]	280
Plot Latitude, in decimal degrees [a]	52.13

Allometry parameters

Parameter	PISY	PRSE	QURO
New Seedling Diameter at 10 cm, in cm [e]	0.2	0.2	0.2
Maximum Tree Height, in meters [b/d]	26	25	22
Slope of Asymptotic Crown Radius [b]	0.347	0.777	0.547
Crown Radius Exponent [b]	0.638	0.503	0.617
Slope of Asymptotic Crown Height [b]	0.709	0.417	0.559
Crown Height Exponent [b]	0.772	1.132	1.058
Slope of DBH to Diameter at 10 cm Relationship [b]	0.766	0.799	0.751
Intercept of DBH to Diameter at 10 cm Relationship [e]	0	0	0
Slope of Asymptotic Height [b]	0.061	0.029	0.053
Slope of Height-Diameter at 10 cm Relationship [b]	0.021	0.024	0.022

Appendix 7.1 (continued)

Tree population parameters

Parameter	PISY	PRSE	QURO
Minimum Adult DBH [a]	5	5	5
Seedling Height Class 1 Upper Bound, in cm [a]	20	20	20
Seedling Height Class 2 Upper Bound, in cm [a]	120	120	120
Initial Density (#/ha) - Seedling Height Class 1 [a]	0	503	16
Initial Density (#/ha) - Seedling Height Class 2 [a]	0	503	16

Light parameters

Parameter	
Beam Fraction of Global Radiation [d]	0.32
Clear Sky Transmission Coefficient [d]	0.526
First Day of Growing Season [d]	81
Last Day of Growing Season [d]	284
Number of Altitude Sky Divisions for Quadrat Light Calculations [e]	18
Number of Azimuth Sky Divisions for Quadrat Light Calculations [e]	12
Minimum Solar Angle for Quadrat Light, in rad [e]	0.779
Height at Which GLI is Calculated for Quadrats, in meters [e]	0.675
Height of Fisheye Photo [e]	Mid-crown
Number of Azimuth Sky Divisions for GLI Light Calculations [e]	18
Number of Altitude Sky Divisions for GLI Light Calculations [e]	12
Minimum Solar Angle for GLI Light, in rad [e]	0.779
Light Transmission Coefficient - PISY [b]	0.299
Light Transmission Coefficient - PRSE [b]	0.238
Light Transmission Coefficient - QURO [b]	0.251

Growth parameters

Parameter	PISY	PRSE	QURO
Shaded Linear - Diam Intercept in mm/yr [c/d]	4.4	5.53	4.8
Shaded Linear - Diam Slope [c/d]	-0.016	-0.06	-0.029
Shaded Linear - Diam Shade Exponent [c/d]	0.7	0.4	0.5

Appendix 7.1 (continued)

Mortality parameters

The Juvenile Background Mortality Rates were different for the scenario with low herbivore densities (L) and with high herbivore densities (H).

Parameter	PISY	PRSE	QURO
Senescence Mortality Alpha [c]	-20.0	-5.0	-25.0
Senescence Mortality Beta [c]	0.7	0.45	0.65
DBH at Onset of Senescence, in cm [c]	85.0	50.0	85.0
Juvenile Background Mortality Rate (L) [c]	0.25	0.015	0.06
Juvenile Background Mortality Rate (H) [c]	0.25	0.015	0.9
Mortality at Zero Growth [c]	0.35	0.2	0.3
Light-Dependent Mortality [c]	1.0	1.5	5.0
Adult Background Mortality Rate [c]	1.0E-4	0.018	1.0E-4
Juvenile Self-Thinning Slope [c]	-	0.008	0.012
Juvenile Self-Thinning Intercept [c]	-	0.001	0.0015

Dispersal parameters

The STR values were different for the scenario with low herbivore densities (L) and with high herbivore densities (H).

Parameter	PISY	PRSE	QURO
Minimum DBH for Reproduction, in cm [b/d]	6.7	11.5	26.7
Canopy Function Used [d]	Weibull	Weibull	Weibull
Weibull Canopy Annual STR (L) [d]	0.005	0.15	0.05
Weibull Canopy Annual STR (H) [a/d]	0.005	0.1	0.001
Weibull Canopy Beta [d]	2.0	2.0	2.0
Weibull Canopy Theta [d]	3.0	3.0	3.0
Weibull Canopy Dispersal [d]	1.03E-05	7.75E-05	1.46E-04

8 General discussion & conclusions

Invasive species cause ecological and economic problems throughout the world (Chapter 1). The majority of studies on invasive alien plant species have focused on herbaceous communities and on early-successional species that exhibit high growth rates in disturbed ecosystems (Martin *et al.* 2009). Forests have long been considered relatively resistant to invasion by alien plants (e.g., Von Holle *et al.* 2003). Yet, the apparently low number of invasions in closed-canopy forests might be the result of the lower number of shade-tolerant invasive species that have been introduced into new areas and the comparatively slow rate of invasion of these shade-tolerant invaders (Martin *et al.* 2009). Forests are certainly not immune to invasion (e.g., Martin 1999, Fagan & Peart 2004, Gilbert & Lechowicz 2005, Martin & Marks 2006), and shade-tolerant invasive species can have a strongly negative, long-lasting impact on the understory structure and species diversity of forest ecosystems (Woods 1993, Leicht *et al.* 2005).

This thesis dealt with one particular invasive tree species, i.e., *Prunus serotina* Ehrh., which was introduced from North America into Europe for the first time in the 17th century. The species has been planted for several reasons and has been considered a forest pest in Western Europe since the 1950s (Chapter 2). Studies on *P. serotina* in Europe have mainly focused on control measures while the ecology of the species has only been studied during the last decade. The genetics of the species, its seed dispersal, the effects of ecosystem and landscape structure on presence/abundance and spatial spread of *P. serotina*, and the impacts on invaded ecosystems have already been investigated (see Chapter 2). With this thesis, we wanted to fill some gaps in the knowledge of the ecology of *P. serotina* in Europe. Therefore, we investigated (1) two vital processes in the biology of the species, i.e., growth and regeneration, in Chapters 3 and 4, (2) patterns of spontaneous *P. serotina* colonization in two forest reserves in Chapters 5 and 6, and (3) the outcome of model runs for two scenarios of long-term development of a forest in which *P. serotina* was present in Chapter 7. The results of this study have lead to a more in-depth understanding of the dynamics of gap-dependent invasive tree species and *P. serotina* in particular. In addition, the findings enabled us to formulate some suggestions for management and raised several questions to be addressed in further research.

8.1 *Prunus serotina*: a gap-dependent invasive tree species

8.1.1 The seedling bank strategy

We found high densities of *P. serotina* seedlings smaller than 20 cm in the understory of Scots pine (*Pinus sylvestris* L.) stands (Fig. 4.2b, Table 6.3). Pairon *et al.* (2006a) and Closset-Kopp *et al.* (2007) also found high densities of small seedlings of *P. serotina* in a forest in Central Belgium and France. These findings indicate that *P. serotina* is able to build up a seedling bank in forest understories in its introduced range, just like in its native range (Marquis 1990). The *P. serotina* seedling bank in the pine stands in our study was relatively short-lived: seedlings smaller than 20 cm were, in general, less than 6 years old (Appendix 4.1). In areas with a higher light availability or low levels of competition with neighbouring trees and shrubs, we found seedlings growing taller than 20 cm (Appendix 4.1, section 6.4.4), which fits in with the findings of some recent studies that showed that the height of *P. serotina* seedlings is related to light availability (Closset-Kopp *et al.* 2007, Knight *et al.* 2008). Even though the seed set and seed rain densities varied considerably between the years and within the studied stands, the continuous presence of the small seedlings in the seedling bank stabilized the regeneration potential of *P. serotina* (Chapter 4).

Several shade-tolerant tree species have been found to build up a seedling bank, e.g., *Picea abies* (L.) H. Karst. (Marks & Gardescu 1998), *Acer platanoides* L. (Grime 2001), and *Acer saccharum* Marshall (Martin & Marks 2006). Such a seedling bank is an efficient strategy towards site occupancy for tree species with irregular seed production and no persistent seed bank (cf. Silvertown & Charlesworth 2001). Martin & Marks (2006) suggested that the invasiveness of the shade-tolerant *Acer platanoides* in forests in the eastern United States was partly determined by its ability to build up a seedling bank. The seedling bank strategy also fits in with the slow and creeping invasion process of shade-tolerant invasive tree and shrub species (Martin *et al.* 2009) and the lag phases typical of their colonization process (Wangen & Webster 2006). The ability of *P. serotina* to build up a seedling bank in forests in the introduced range might favour the species over the native tree and shrub species that would naturally occur on the poor sandy soils in Western Europe. Few native tree and shrub species typical of these sandy soils build up a seedling bank, with the exception of the shade-tolerant *Ilex aquifolium* L. (Marks & Gardescu 1998) and *Fagus sylvatica* L. (Collet *et al.* 2008) on the somewhat richer sites.

Sorbus aucuparia L. may also build up a seedling bank (Żywiec & Ledwoń 2008), but its seedlings are readily eaten or browsed by large herbivores (Linder *et al.* 1997). The modelling study of Sebert-Cuvillier *et al.* (2007) indeed showed that the seedling bank of *P. serotina* was the most important factor determining its local invasion success in a forest in France. The small *P. serotina* of the seedling bank are present all over the forest floor, and they will have a lead on other species that have to regenerate from seed if a calamity opens up the canopy.

Yet, *P. serotina* does not form a seedling bank in each invaded community (cf. Starfinger 1990). Small *P. serotina* seedlings were almost absent under the tall and abundant brambles (*Rubus fruticosus* agg.) in the forest reserve studied in Chapter 5. Dense herb layers have indeed been found to hamper establishment and survival of *P. serotina* seedlings due to the high seed and seedling predation by small mammals (Royo & Carson 2008) and the low light levels (Horsley 1993, Royo & Carson 2008) below the herb layer.

8.1.2 Growth and seed production

Although the early life stages of *P. serotina* are fairly shade tolerant, the species needs light for successful growth and seed production (Chapter 5 and 6), which matches the classification of *P. serotina* as an opportunistic gap phase species in its native range (Auclair & Cottam 1971, Sutherland *et al.* 2000, Chapter 2). Radial growth of *P. serotina* saplings and trees in the understory of pine stands was highly variable (Table 3.3 and 3.4) and strongly reduced compared to the growth in an open landscape with high light availability (Fig. 3.3 and 3.4b). Competition with neighbouring trees decreased the growth (and biomass) of *P. serotina* seedlings (Fig. 3.4c, Appendix 4.1), saplings, and adults (section 5.4.2). In addition, few *P. serotina* in the understory of the studied forests set seed (section 4.4.1 and 5.4.2), and understory seed set was also affected by competition with neighbouring trees (Table 4.1). In the understory of the studied pine stands, seed production started relatively late: only the *P. serotina* trees older than 20–25 years showed a high seed set probability (i.e., 90 %), similar to the findings of Starfinger (1990) for pine-oak forests in Germany. Conversely, in an open agricultural landscape with high light availability in Flanders, Deckers *et al.* (2005) found *P. serotina* growth to be rather uniform: the diameter of a *P. serotina* tree was strongly correlated with its age. Besides, fruit production started already at the age of 4 years, and more than 90 % of the *P. serotina* older than 7 years produced fruits (Deckers *et al.* 2005).

8.1.3 Colonization patterns

Propagule pressure has been found to affect both species invasiveness and habitat invasibility (cf. section 1.1.2), and colonization patterns in areas that are highly invaded by *P. serotina* can often be traced back to former planting efforts (cf. section 2.4.2). Yet, prior studies on the ecology of *P. serotina* have focused mainly on heavily invaded sites (e.g., Godefroid *et al.* 2005, Sebert-Cuvillier *et al.* 2007). Investigating patterns of spontaneous *P. serotina* colonization, unconfounded by effects of former planting and control measures, is therefore a valuable way for gaining additional insights into the ecology of the species. We studied forest development in two forest reserves located in areas with an (initially) low propagule pressure of *P. serotina* in which the species had not been controlled, i.e., the Liedekerke forest reserve (Chapter 5) and the Ossenbos forest reserve (Chapter 6). The forests differed in soil conditions (sandy loam vs. sand), tree species composition (oak-birch vs. pine), and game densities (few large herbivores vs. extremely high densities). The two forest reserves were similar in that they had not been managed for over 60 years and that *P. serotina* had not been introduced intentionally. Therefore, 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.

The colonization of *P. serotina* was triggered by long-distance dispersal events and windows of opportunity, i.e., areas with high light availability. *Prunus serotina* seeds that were dropped at spots with high light availability were able to establish and grow into seed-producing adults. Further spread of *P. serotina* was directed by connectivity to these seed sources (Table 5.3) and light availability (section 5.5.2, Fig. 6.3 and 6.5). 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: *P. serotina* was just one of the species in the forest. Conversely, in the Ossenbos, *P. serotina* became very abundant and was omnipresent in the understory (Table 6.1 and 6.3).

Light availability and seed input were the most important factors for explaining the establishment success and the further spread of *P. serotina* in the studied forest reserves. Likewise, Wangen & Webster (2006) identified long-distance dispersal events and gap dynamics as the drivers of the invasion success of the shade-tolerant *Acer platanoides* in the Mackinac Island State Park in Michigan. Competition with native shrub and herb species may have slowed down the spread of *P. serotina* in the Liedekerke forest reserve

(Chapter 5). The invasion success of *P. serotina* in the Ossenbos forest reserve (Chapter 6) might be the result of the high densities of large generalist herbivores that favoured *P. serotina* over the native species. Eschtruth & Battles (2009a) also showed that generalist herbivores such as *Odocoileus virginianus* Zimmermann, 1780 can accelerate the invasion of alien woody shrubs in forests. The contrasting outcomes of the *P. serotina* colonization in the two forest reserves illustrate that the invasiveness of a species, e.g., *P. serotina*, may depend on the characteristics of the invaded ecosystem (cf. Facon *et al.* 2006). Even in areas with a low propagule pressure, plant invasions might be successful, e.g., because of ecosystem disturbance (cf. Lozon & MacIsaac 1997).

8.1.4 Invasion success

The findings of this thesis concerning the invasion success of *P. serotina* are summarized in Table 8.1. We distinguished between factors related to the invasiveness of the species, the invasibility of the ecosystem, and the introduction effort (cf. section 1.1.2).

Table 8.1 Factors that were found to be positively or negatively related to the invasion success of *Prunus serotina* in the different chapters of this thesis.

factor	effect	chapter
invasiveness: species traits		
- frequent seed production	+	4
- effective seed dispersal	+	2, 5
- relatively high germination capacity	+	2
- low survival of seedlings of 1–2 years old	-	2, 4
- seedling bank strategy	+	4, 6
- high potential growth rate	+	3, 6
- relatively short life span	-	7
invasibility: environmental conditions		
- high light availability	+	3, 5, 6
- presence of competing shrubs/trees	-	3, 4, 5, 6
- dense herb layer	-	5
- high densities of large herbivores	+	6, 7
propagule pressure		
- planting effort	+	2
- residence time	+	2
- connectivity to seed sources	+	5

Prior studies on *P. serotina* in Europe also attributed the invasiveness of the species to its ability to build up a seedling bank (Sebert-Cuvillier *et al.* 2007), as well as its effective seed dispersal (Deckers *et al.* 2008) and resprouting capacity (Sebert-Cuvillier *et al.* 2007). The susceptibility to *P. serotina* invasion has been connected with ecosystem disturbance, e.g., due to windstorms (Sebert-Cuvillier *et al.* 2007) or forest management measures such as thinning (Starfinger *et al.* 2003). Besides, soil conditions appear to affect *P. serotina* invasion success: *P. serotina* appears most often on podzolic soils while the species is rarely found on wet or calcareous soils (Chabrerie *et al.* 2007). The relationship between planting effort and the present distribution of *P. serotina* has already been shown for the Netherlands (Van den Tweel & Eijsackers 1987), Germany (Starfinger *et al.* 2003), and Flanders (Verheyen *et al.* 2007).

Traits of successful invaders are idiosyncratic and context-dependent, and it seems to be impossible to identify general species or habitat traits that promote invasion (Moles *et al.* 2008, Chapter 1). Nonetheless, some of the characteristics listed in Table 8.1 have often been found to be related to the invasion success of plant species, e.g., effective dispersal and high reproductive success (Richardson & Rejmánek 2004, Lloret *et al.* 2005, Küster *et al.* 2008), high light availability and ecosystem disturbance (Milbau *et al.* 2003, Chytrý *et al.* 2008, Eschtruth & Battles 2009b), and introduction history, i.e., propagule pressure and residence time (Von Holle & Simberloff 2005, Küster *et al.* 2008, Bucharova & Van Kleunen 2009).

8.2 Management consequences

A recent survey with structured interviews of forest managers in Flanders (Vanhellemont *et al.* 2008) showed that control management of *P. serotina* can be cost-effective if volunteers are prepared to cut *P. serotina* in exchange for firewood. The requisite dimensions of the *P. serotina* firewood will depend on the volunteer. In this respect, knowledge on the age-diameter relationships for *P. serotina* will be valuable with regard to the timing of control measures. Regression fits between diameter and age such as the ones in Chapter 3 (Fig. 3.3) may be used to calculate expected diameter values for *P. serotina* trees of a given age. For example, in the studied pine stands, *P. serotina* reached a diameter of 5–10 cm after 20 years and a diameter of 15–20 cm after 40 years. In open situations, on the other hand, the diameter was 5–10 cm after 12 years and 15–20 cm after

22 years. Such data may be useful for forest managers that are drawing up a management plan for forest complexes in which *P. serotina* is present.

Grazing has been proposed as a control measure for *P. serotina* (see Chapter 2). Nonetheless, the omnipresence and high abundance of *P. serotina* in the Ossenbos forest reserve (Chapter 6) show that *P. serotina* is able to thrive under extremely high ungulate densities if the herbivores have access to other sources of food, e.g., the surrounding heathlands in the case of the Ossenbos. The results of Chapter 6 and 7 suggest that high densities of large herbivores may facilitate *P. serotina* invasion and may thus increase the invasibility of a community for *P. serotina*. Consequently, the invasiveness of *P. serotina* in the species-poor pine forests of Flanders and the Netherlands might be, in part, caused by high game densities that may negatively affect herb layer development (Rooney 2001) and hamper the regeneration of native species such as *Sorbus aucuparia* (cf. Linder *et al.* 1997) and *Quercus robur* L. (cf. Kuiters & Slim 2002). Densities of large herbivores have indeed increased in Europe throughout the last century, e.g., for roe deer (*Capreolus capreolus* Linnaeus, 1758) (Linnell *et al.* 1998), red deer (*Cervus elaphus* Linnaeus, 1758), and wild boar (*Sus scrofa* Linnaeus, 1758) (Kuiters 1997). Similarly, in North America, the generalist herbivore white-tailed deer (*Odocoileus virginianus*) has known a dramatic increase in population densities since 1900 (Rooney 2001), and herbivory by *O. virginianus* has been found to accelerate the invasion of an alien shrub species, i.e., *Berberis thunbergii* DC., in forests in northeastern Pennsylvania (Eschtruth & Battles 2009a).

The patterns of *P. serotina* colonization contrasted sharply between the two studied forest reserves, i.e., the mixed deciduous forest on sandy loam soil (the Liedekerke forest reserve, Chapter 5) and the pine-oak forest with high game densities on sandy soil (the Ossenbos forest reserve, Chapter 6). After ca. 70 years, *P. serotina* was omnipresent in the Ossenbos forest reserve (Fig. 6.3, Table 6.1 and 6.3) whereas *P. serotina* was just one of the species in Liedekerke, ca. 40 years after its first establishment (Table 5.1). Although *P. serotina* has had an extra 30 years to spread in the Ossenbos forest reserve, there were no indications for a sudden increase in the future spread of *P. serotina* in Liedekerke (Chapter 5). Consequently, it is not likely that *P. serotina* will become the main understory species in the Liedekerke forest reserve, even after an additional 30-year period. The observed difference in invasion outcome illustrates that invasion processes may differ between ecosystems (cf. Facon *et al.* 2006). Consequently, the sheer occurrence of *P. serotina* in a forest stand does not necessitate intensive control measures, also seeing that the ecosystem impact of *P. serotina* varies between sites (e.g., Verheyen *et al.* 2007, Chapter 2). Management approaches should therefore be preferably formulated conditional upon the characteristics of the recipient ecosystem (cf. Fig. 8.1).

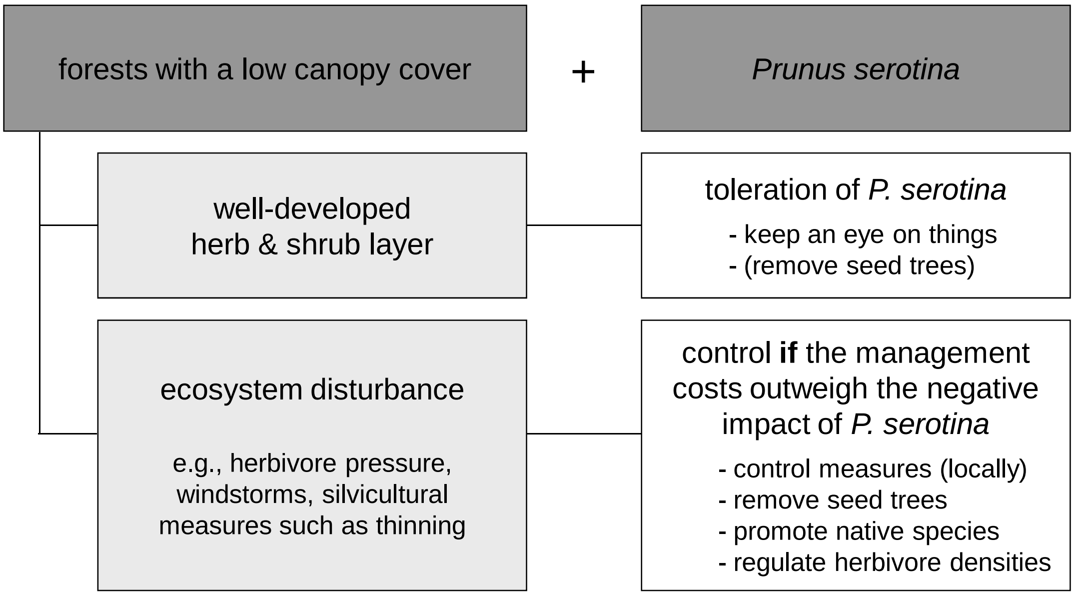


Fig. 8.1 Active control measures against *Prunus serotina* are not always necessary or cost-effective. The forest pest status of *P. serotina* should not result in intensive large-scale control in all cases, and forest managers should keep questioning why and how they control the species, relative to the desired characteristics of the forest (cf. Geudens *et al.* 2009).

The main management goal should be the creation of forest stands that are resistant to *P. serotina* invasion. The ‘windows of opportunity’ for *P. serotina* establishment and spread may be closed by promoting well-developed shrub and herb layers (Geudens *et al.* 2009, Fig. 8.1). After all, the presence of native shrub species or dense herb layers has been found to hamper the establishment and spread of *P. serotina* (Horsley 1993, Royo & Carson 2008, Chapter 5). The high invasiveness of *P. serotina* in uniform stands of light-demanding pines can be attributed to the past introduction efforts and the excellent conditions for further establishment and growth of the introduced *P. serotina.* The understory of these pine plantations is often poorly developed and poor in species, and the thinning regimes regularly admit light (Starfinger *et al.* 2003). Therefore, the colonizing *P. serotina* received increased light levels at set intervals, experienced little competition with other understory species, and was able to attain high abundances. Sebert-Cuvillier *et al.* (2007) recently also demonstrated that ecosystem disturbance speeds up the spread of

P. serotina. If other tree species are also able to regenerate, the relatively short life span of *P. serotina* in forests in Europe (cf. Wallis de Vries 1987, Sebert-Cuvillier *et al.* 2007) might prevent its overall dominance (Chapter 7). In this respect, Starfinger *et al.* (2003) proposed the 'wait and see' strategy as a cost-effective but promising way for dealing with *P. serotina*.

8.3 Suggestions for further research

Understory growth of *P. serotina* was highly variable in our study (Chapter 3). Tree size, age, and site productivity explained but a small part of the variability. Seeing the renewed interest in growing quality wood of *P. serotina* (Haag & Wilhelm 1998, Nyssen 2009), more insight into additional growth-influencing factors such as light availability and genetic provenance might be advantageous.

Building up a seedling bank is an effective strategy towards site occupancy (Silvertown & Charlesworth 2001) and has been linked with the invasiveness of *P. serotina* (Sebert-Cuvillier *et al.* 2007) and *Acer platanoides* (Meiners 2005, Martin & Marks 2006). It would be interesting to study the early regeneration stages of other shade-tolerant invasive tree or shrub species, e.g., the Asian species *Sapium sebiferum* (L.) Roxb. (Rogers & Siemann 2002) and *Berberis thunbergii* (Silander & Klepeis 1999) in the United States, in order to investigate whether the seedling bank strategy is a life-history trait that supports a species' invasiveness, especially in regions in which the seedling bank strategy is not common to the native species.

The comparison of the *P. serotina* colonization patterns in the two forest reserves in Chapter 5 and 6 illustrates that invasion processes may differ between ecosystems and stresses the importance of studying an invasive species in combination with the resident community in the recipient ecosystem (cf. Facon *et al.* 2006, Chapter 1). A suite of similar studies on patterns of *P. serotina* invasion at sites where the history of introduction and disturbance are documented could provide new insights into factors affecting the vulnerability of particular communities to *P. serotina* invasion. Besides, comparing the outcome of the *P. serotina* colonization pattern at different study sites might result in a framework for formulating management priorities.

The results of Chapter 6 and 7 suggest that high densities of generalist large herbivores can favour *P. serotina* over native species such as *Quercus robur* and may thus facilitate *P. serotina* invasion. In order to investigate the possible impact of positive feedback mechanisms associated with herbivory on *P. serotina*, it would be interesting to study spontaneous *P. serotina* colonization at sites with different ungulate densities. Besides, exclosures might be installed in the forest reserve studied in Chapter 6 to compare the further development of the forest with and without ungulates. Situating the exclosures in patches where seed sources or large saplings of other species are already present might provide answers on the following questions. Are native tree and shrub species able to compete with *P. serotina* in the absence of herbivory? Will *P. serotina* continue to recruit below *P. serotina*? Particular attention should be dedicated to patches in which both *P. serotina* and the native shrub species *Sorbus aucuparia* are present because the ecology of these species is similar and they often co-occur (Starfinger 1990, Verheyen *et al.* 2007, Chapter 5). Since seedlings and saplings of *S. aucuparia* cannot grow into the tree/shrub layer under high grazing pressure (Linder *et al.* 1997), the species might profit from a decrease in herbivore pressure. Besides, *S. aucuparia* seedlings are shade tolerant (Raspé *et al.* 2000), which might enable *S. aucuparia* to survive in shaded conditions, e.g., below *P. serotina*.

We showed that the spatially explicit individual-based model SORTIE-ND can be a useful tool to explore different scenarios of forest development (Chapter 7). Nonetheless, we studied but a relatively simple forest system with only three species: the native *Pinus sylvestris* and *Quercus robur* and the alien *P. serotina*. Parameterizing the model for some additional species, e.g., *Sorbus aucuparia*, *Ilex aquifolium*, or *Fagus sylvatica*, will enable simulating scenarios in which *P. serotina* has to compete with other shrub species and with shade-tolerant species. One might as well explore the long-term effects of planting *F. sylvatica*, which has been suggested as a measure for controlling *P. serotina* (Starfinger *et al.* 2003). The usefulness of the model SORTIE-ND might be improved by integrating some new submodels that simulate the build up of seedling banks, the resprouting capacity of tree species (Caplat & Anand 2009), and the effects of dense herb layers (cf. Beaudet *et al.* 2002, Tremblay *et al.* 2005).

Summary

This thesis focused on one particular invasive species: the North American tree species *Prunus serotina* Ehrh., which is considered one of the 100 worst invaders in Europe. The species has been introduced and planted widely in many European countries for different reasons. Because of the adverse effects of dense *P. serotina* shrub layers on biodiversity and forest management, the species was called a forest pest and became the subject of intensive and costly control measures. The success of the various control methods has remained limited, and researchers have recently started to investigate the ecology of *P. serotina* in its introduced range because more insight into the biology of invasive species may eventually lead to more effective control measures.

The number of studies on *P. serotina* in Europe has increased sharply during the last decade, but several aspects of the species have remained unstudied, most notably its growth in forest understories. Moreover, most studies have focused on heavily invaded areas. We wanted to gain insight into (1) the radial growth and the spatiotemporal variation in the regeneration of *P. serotina* in forest understories, (2) the patterns of long-term spontaneous *P. serotina* colonization in areas where the species had not been introduced intentionally, and (3) long-term forest development wíth *P. serotina*. Therefore, we collected a wide range of data using tree cores, hemispherical photographs, seed traps, seedling counts, forest inventories, historical topographic maps, and aerial photographs. The main focus of the thesis lay on Scots pine (*Pinus sylvestris* L.) forests on sandy soil, the forest type in which *P. serotina* occurs most often in its introduced range. In addition, we studied a mixed deciduous forest on sandy loam soil.

Radial growth and regeneration dynamics of *P. serotina* were studied in the understory of seven pine stands on sandy soil in Flanders, the northern part of Belgium. Radial growth of *P. serotina* was related to the diameter and age of the *P. serotina* tree and competition with neighbouring trees. Understory radial growth of *P. serotina* was up to 50 % less than potential growth of *P. serotina* in full light conditions. The reduction in growth was related to site productivity, tree size, and crowding, the latter being important only for small *P. serotina* individuals. Seed set, seed rain and seedling densities were recorded for 3–4 years, and we measured age, size, and biomass for a subset of seedlings. We found a

short-lived seedling bank, with high densities of seedlings smaller than 20 cm that were up to 6 years old. The early life stages of *P. serotina* showed high spatial and temporal variability, but the temporal stability of the spatial regeneration patterns increased with seedling age.

We reconstructed the patterns of *P. serotina* colonization in two forest reserves in areas with an initially low propagule pressure of *P. serotina*. The Liedekerke forest reserve (Flanders) is a mixed deciduous forest with birch (*Betula* spp.) and oak (*Quercus* spp.) on sandy loam soil; the Ossenbos forest reserve (the Netherlands) is a Scots pine forest with pedunculate oak (*Quercus robur* L.) on sandy soil, characterized by a high density of large herbivores. The two forests had not been managed for 60–70 years, which enabled us to study spontaneous *P. serotina* development. The outcomes of the *P. serotina* colonization contrasted sharply between the 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. 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. The presence of native shrub species, the dense herb layer, and the quick canopy closure hampered further establishment of *P. serotina* in Liedekerke whereas the high herbivore densities in the Ossenbos may have favoured *P. serotina* over native species such as *Q. robur*.

To explore the future development of the Ossenbos forest reserve, we simulated 500 years of forest succession using SORTIE-ND, a spatially explicit individual-based model of forest dynamics. We defined two scenarios, i.e., with low or high herbivore densities, that differed in the regeneration success of *P. serotina* and *Q. robur*. If *Q. robur* was able to regenerate, i.e., in the scenario with low herbivore densities, *Q. robur* became more abundant than *P. serotina* on the long term. The relatively short life span of *P. serotina* may preclude its dominance if other tree species are able to regenerate.

Our results provide insight into the growth and regeneration dynamics of a gap-dependent invasive tree species, i.e., *P. serotina*, in the understory of invaded forests. We also showed that the invasiveness of a species depends on the characteristics of the invaded ecosystem and that forest development models such as SORTIE-ND can be a useful tool to explore the future role of invasive tree species in forests.

Samenvatting

De Noord-Amerikaanse boomsoort *Prunus serotina* Ehrh. werd (en wordt) in grote delen van Europa aangeplant om verschillende redenen. De soort vormt vaak dichte struiklagen die een negatieve invloed kunnen hebben op biodiversiteit en bosbouw. *Prunus serotina* kreeg de bijnaam ‘bospest’ en men schakelde over van het aanplanten naar het bestrijden van de soort, weliswaar met beperkt succes. *Prunus serotina* wordt nu beschouwd als een van de 100 invasieve soorten met de grootste impact en verspreiding in Europa. De laatste tien jaar wordt steeds meer onderzoek verricht naar de ecologie van *P. serotina* in Europa: een beter begrip van de soort zal leiden tot een meer efficiënte bestrijding.

Onderzoek naar *P. serotina* in Europa gebeurde tot nog toe meestal in gebieden waarin de soort al massaal aanwezig was. Bovendien ontbreken gegevens over de groei van de soort en is de ontwikkeling op langere termijn nog niet gedocumenteerd. Met het onderzoek in deze thesis wilden we meer inzicht krijgen in (1) de variabiliteit in groei en verjonging van *P. serotina* in onderetages, (2) de spontane kolonisatie van *P. serotina* in bossen waar de soort niet aangeplant of beheerd werd, en (3) de langetermijnontwikkeling van bossen met *P. serotina*. Hiervoor gebruikten we groeiringanalyse, fisheyefoto’s, zaadvallen, bosinventarisatiegegevens, historisch kaartmateriaal en luchtfoto’s. Het grootste deel van het onderzoek is uitgevoerd in dennenbossen (*Pinus sylvestris* L.) op zandgrond, het bostype waarin *P. serotina* het meest frequent voorkomt in Europa. Ter vergelijking keken we ook naar een gemengd loofbos op zandleem.

De groei en verjonging van *P. serotina* werden bestudeerd in de onderetages van zeven dennenbossen op zandgrond in Vlaanderen. We vonden een verband tussen de radiale groei van *P. serotina*, de diameter en leeftijd van de boom en de competitie met naburige bomen. De groei in de bestudeerde onderetages was 50 % lager dan de potentiële groei in condities met een hoge lichtbeschikbaarheid. Deze groeireductie was gerelateerd aan de kwaliteit van de standplaats en de grootte van de boom. Voor kleine *P. serotina* was ook de nabijheid van buurbomen een groeireducerende factor. In dezelfde bossen volgden we de zaadzet voor drie jaar, de zaadregen en het aantal zaailingen voor vier jaar. Voor een subset van de zaailingen bepaalden we ook hoogte, leeftijd en biomassa. De hoge aantallen zaailingen van *P. serotina* kleiner dan 20 cm en tot 6 jaar oud wijzen op de aanwezigheid van een kortlevende zaailingbank. De bestudeerde verjongingsfasen van *P. serotina* vertoonden variatie in zowel ruimte als tijd. Voor oudere zaailingen bleef de ruimtelijke spreiding evenwel meer stabiel doorheen de tijd dan voor jonge zaailingen.

De invasie van *P. serotina* werd gereconstrueerd in twee bosreservaten: Liedekerke (Vlaanderen) en Ossenbos (Nederland). Beide bossen werden de voorbije 60–70 jaar niet beheerd en zijn gelegen in een gebied waar initieel weinig *P. serotina* aanwezig was. Bosreservaat Liedekerke is een eiken/berkenbos (*Betula* en *Quercus* spp.) op zandleem; het Ossenbos is een dennenbos met zomereik (*Quercus robur* L.) op zandgrond met een hoog aantal grote grazers. De ontwikkeling en verbreiding van *P. serotina* verschilden sterk voor de twee bossen: *P. serotina* was een van de vele soorten in Liedekerke terwijl de soort in het Ossenbos zeer abundant aanwezig was. De eerste vestiging van *P. serotina* gebeurde op plaatsen met veel licht, waarschijnlijk als gevolg van zaden achtergelaten na langeafstandsverbreiding door vogels of zoogdieren. De latere kolonisatie werd bepaald door lichtbeschikbaarheid en de afstand tot zaadbronnen. De ontwikkeling en verbreiding van *P. serotina* in Liedekerke werden geremd door de aanwezigheid van inheemse boom- en struiksoorten, de hoge bedekking van de kruidlaag en de snelle kroonsluiting. De hoge abundantie van *P. serotina* in het Ossenbos is waarschijnlijk het gevolg van de hoge graasdruk die inheemse soorten als *Q. robur* onderdrukt heeft.

Om te kijken hoe het Ossenbos verder zou ontwikkelen als ook de inheemse *Q. robur* zou kunnen verjongen, bv. wanneer grote herbivoren afwezig zouden zijn, gebruikten we SORTIE-ND. SORTIE-ND is een ruimtelijk expliciet bosontwikkelingsmodel dat de levenscyclus van individuele bomen simuleert. We lieten het model lopen voor twee scenario's, met en zonder verjonging van *Q. robur*. In het scenario met lage graasdruk kon de inheemse *Q. robur* verjongen en werd deze op termijn de dominante soort. De relatief korte levensduur van *P. serotina* in vergelijking met *Q. robur* zorgde er waarschijnlijk voor dat *P. serotina* niet dominant kon worden in dit scenario.

De resultaten over de groei en verjongingsdynamiek van *P. serotina* in deze thesis leiden tot een beter begrip van het gedrag van (half)schaduwtolerante invasieve boomsoorten in de onderetage van bossen. We toonden ook aan dat de invasiviteit van een uitheemse soort mede bepaald wordt door de eigenschappen van het geïnvadeerde ecosysteem en dat bosontwikkelingsmodellen zoals SORTIE-ND een nuttig instrument kunnen zijn om de toekomstige rol van invasieve boomsoorten in bossen te simuleren.

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Curriculum vitae

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MSc thesis

Vanhellemont M (2004) Bosontwikkeling en natuurbeheer in het riviergebied. Een studie van wederzijdse invloedsfactoren in natuurterreinen langs de Grensmaas. MSc thesis, Ghent University, Ghent, Belgium

Scientific activities

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27–30 October 2009. The invasive *Prunus serotina* stabilizes its erratic early regeneration by building up a seedling bank. World Conference on Biological Invasions and Ecosystem Functioning. Porto, Portugal

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11 May 2009. Patterns of *Prunus serotina* invasion in two contrasting forests. 2nd Belgian Conference on Biological Invasions. Brussels, Belgium

17 October 2007. Modelling radial growth of *Prunus serotina* in pine forests. 13th PhD Symposium on Applied Biological Sciences. Leuven, Belgium

22 March 2007. Groei van Amerikaanse vogelkers (*Prunus serotina*) onder scherm van grove den. Starters in het Bosonderzoek. Brussels, Belgium

Participation with poster presentation

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30 May 2008. Does *Prunus serotina* act as an aggressive invader in areas with a low propagule pressure? Symposium Aardse Zaken. Leuven, Belgium

27–30 September 2006. Population dynamics of the invasive *Prunus serotina* in pine forest on poor sandy soils in Flanders (Belgium). 4th European Conference on Biological Invasions. Vienna, Austria

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14–15 September 2009. 4th international symposium on dispersal. Ghent, Belgium

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