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Seed development and germination ecophysiology of the invasive tree *Prunus serotina* (Rosaceae) in a temperate forest in Western Europe

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Abstract Seed development, dormancy and germination of the American invasive tree species, *Prunus serotina*, are described for plants growing in a large forest in Belgium. Seeds of *P. serotina* were collected following anthesis in the first week of July and thereafter at fortnightly intervals. Seed dormancy, temperature requirements for germination and the soil seed bank were investigated. At maturation (about 105 days after anthesis), seed moisture content had decreased to around 13.7%, and 44% of the seeds had attained the capacity to germinate. Mature seeds of *P. serotina* exhibited physiological dormancy, germinating only after a long cold, moist stratification period. Highest germination percentage occurred in seeds treated with gibberellic acid (GA_3), at 10°C. We found no evidence that *P. serotina* forms a persistent seed bank but noticed a persistent seedling bank in the field.

Keywords Invasive species · Black cherry · Seed dormancy · Temperature requirement · Soil seed bank

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Introduction

The understanding of seed germination ecology is enhanced by knowledge of the (i) physiological, morphological and physical states of seeds at the time they mature; (ii) changes in these states that must precede germination; (iii) environmental conditions required for these changes to take place; and (iv) environmental conditions occurring in the habitat between time of maturation and germination (Baskin and Baskin 1998). To obtain this information, observations need to be made on the reproductive life cycle. The reproductive development of plants begins with the formation of flower buds and progresses through anthesis, fruit development and accumulation of storage materials in seed and ends with physiological maturity, when the seed reaches its maximum dry weight (Tekrony and Egli 1997). In some pulpy fruits like those of *Prunus avium*, while the seed is still inside a fleshy fruit its moisture content continues to decrease as dry weight increases, and the seeds become desiccation-tolerant before they are shed from the plant (Finch-Savage 1998).

Mature seeds of some species do not germinate, because the seed or fruit coat is impermeable to water or it mechanically restricts the expansion of the hydrated embryo. Seeds of the majority of temperate species have physiological dormancy, thus physiological inhibiting mechanisms of the embryo that prevent radicle emergence (Baskin and Baskin 1998); Camacho-Morfin (1994) has reported inhibitors in seeds of *Prunus serotina* subsp. *capuli*. Chemically dormant seeds do not germinate due to the presence of inhibitors in the pericarp, and they require removal or leaching of them to break this kind of dormancy (Nikolaeva 1969, 1977). Although Baskin and Baskin (2004) do not recognize chemical dormancy as a class of dormancy, numerous studies have demonstrated that in vitro germination is inhibited by a variety of compounds found in the embryo, endosperm and seed coat, and in structures that are dispersed along with seeds in many plant families (Bewley and Black 1994). The adaptiveness of seed dormancy and germination strategies of plants have been a matter of considerable theoretical and empirical interest to biologists (Leck et al. 1989; Fenner 1992), however, many tree species lack long-term seed dormancy mechanisms, but they form a seedling bank (Harper 1977).

The seed germination ecology of *P. serotina* fruits has been studied by various researchers in its native range in North America (Huntzinger 1968; Marquis 1973; Bonner 1975). The species flowers from March to early June and fruits mature from June to October, depending on latitude (Sargent 1965). Thus, a comparative study is necessary to understand the seed germination ecology of a wide-ranging species, particularly to know what controls the timing of germination under natural and/or synanthropic conditions, since seed development, dissemination and degree of dormancy vary from one locality to the other. Seeds of *P. serotina* in the northern hardwood forest in North America exhibit delayed germination: one year's crop germinated over a period of three years or longer in artificially buried soil seed bank experiments (Wendel 1972; Marquis 1975). According to Marquis (1975), delayed germination allows *P. serotina* to bank large amounts of seed on the forest floor in Pennsylvania. In glasshouse germination experiments, Beatty (1991) and Brown (1992) did not find any seedlings of *P. serotina* from soil samples taken from natural vegetation. Accordingly, Thompson et al. (1997) categorized this species as having a transient to short-term persistent seed bank. We need further information on *P. serotina* to know its ability to form a soil seed bank in its introduced range under different land use systems. Furthermore, *P. serotina* is one of the most invasive species in European forest ecosystems. During the last few decades, the species has greatly expanded within its region of introduction, invading both forest fragments and linear woody habitat patches (Starfinger 1997). Especially on poorer soils, it often impedes nowadays natural regeneration of less competitive native species (Muys et al. 1993). Species attributes and ecosystem properties are the most important variables to explain the invasion success of a non-native species (Kolar and Lodge 2001). Numerous studies have tried to identify those ecosystem properties that play a role in the invasion of *P. serotina* (e.g. Deckers et al. 2005; Godefroid et al. 2005; Verheyen et al. 2007; Closset-Kopp et al. 2007). However, we know very few publications on the species' life cycle in its synanthropic range (but see Pairon et al. 2006). Exploring the germination ecophysiology of *P. serotina* in its synanthropic area might therefore enhance the understanding of its invasion success.

The present work describes the seed development and dormancy of *P. serotina* Ehrh. in a temperate forest in Belgium, in order to understand its germination eco-physiology. We ask the following questions: (i) When do fruits mature? (ii) When do fruits/seeds begin to disperse? (iii) When do seeds acquire germinability? (iv) What is the dormancy state of seeds at the time of dispersal? (v) What are the environmental conditions required to break dormancy? (vi) What is the density of *P. serotina* in the buried soil seed bank? and (viii) Does the species form a persistent soil seed bank or only a transient one?

Materials and methods

Study area

Prunus serotina Ehrh. seeds were collected from the Sonian Forest, south of Brussels (50°47′N; 4°26′E). The forest area (4,383 ha) ranges in elevation from 65 to 130 m a.s.l. Climate of the area is temperate and humid, with a growing season of 7 months (April–October). Mean annual temperature is 9.9°C,

and annual precipitation is 798 mm (Lieth et al. 1999). Beech (*F. sylvatica*) has been widely planted since the end of the 18th century; as of now, this forest consists of 74% *F. sylvatica*, 16% oak (*Quercus robur*), 8% introduced conifers (*Pinus sylvestris*, *Larix decidua* and *Picea abies*) and 2% diverse broadleaved species, such as chestnut (*Castanea sativa*), ash (*Fraxinus excelsior*), maple (*Acer pseudoplatanus*) and wild cherry (*P. avium*). *P. serotina* appears mainly in conifer, oak and beech stands, where it occurs in the understory, as a tree, shrub, sapling or seedling. It is also recorded in logging areas (open clear-felled areas).

Seed development

Fruits of *P. serotina* were collected following anthesis (when most flowers had bloomed) in the first week of July from four representative, marked trees growing in light conditions under moderate canopy cover, and thereafter collection was made at biweekly intervals between July and September 2002. The initial harvests were done 30 days after anthesis (DAA) on 3rd July 2002. At each harvest, approximately 1000 fruits were collected in the morning from different parts of the tree crown and samples from all four trees were mixed after being brought to the laboratory in polythene bags. Data were recorded for changes in fruit colour, fresh weight of 100 fruits, and dry matter percentage. Moisture content of fruits and seeds was determined on a fresh weight basis after drying samples at 103°C for 17 h (International Seed Testing Association 1999). For all the above parameters, four replicates of 50 seeds were used except for determination of fresh weight of 100 fruits. Sixty days after anthesis and onwards, germination ability of the seeds was determined. One set of seeds from each harvest was incubated at constant 20°C without a cold, moist stratification to check their germinability. Another set of seeds from each harvest were mixed into potting soil and then subjected to a cold, moist stratification for one month at 2–3°C in the laboratory. Thereafter, 50 seeds from each harvest were sown in the garden (outdoors) in natural light/dark conditions and germination was monitored regularly. On final harvest, about 200 de-coated seeds were also collected from four abundantly found faeces of herbivorous mammals. These seeds were washed and separated from faeces and four replications of 50 seeds were subjected to a cold, moist stratification and were used for germination. Seeds that produced a radicle about 1 cm long were considered germinated.

Pretreatment to overcome dormancy

In experiment 1, approximately 3,000 fresh, mature seeds were collected on final date of harvest and subjected to the five treatments according to Phartyal et al. (2003) with modification, viz. intact seeds soaked in distilled water (T_1), soaked in 500 ppm gibberellic acid (GA_3) (T_2), soaked in 500 ppm cytokinin (T_3), soaked in a combination of equal (v/v) solution of 500 ppm GA_3 + cytokinin (T_4), and soaked in distilled water following acid (65% H_2SO_4) scarification (T_5). Soaking time was 72 h for all treatments. The soaked seeds were placed in polythene bags after draining excess water, and the sealed bags were inflated with air to supply sufficient oxygen. Seeds were stratified at 2–3°C for 120 days and at 15-day interval, the bags were opened and checked for moisture. On 45 days of stratification and thereafter on every 15-day interval, 100 seeds (four replicates of 25 seeds) from each of five treatments were incubated at 10°C to observe release from dormancy. Seeds that produced a radicle about 1 cm long were considered germinated. Seeds that germinated during the course of stratification within the polythene bags were also recorded at 15-day interval. The experiment 2 investigated the temperature and time required for stratification to break dormancy and obtaining germination in a fresh seed lot. For this experiment, approximately 2,500 mature seeds were collected on final date of harvest. Seeds were initially soaked in 500 ppm GA_3 (since this treatment has shown better results in experiment 1) and in distilled water (control) for 72 h and then stratified for 8 weeks at 2–3°C in polythene bags; thereafter they were moved to incubate at 5, 10 and 15°C. For incubation, four replicates of 100 seeds were inserted into wet potting soil mixture kept in loosely sealed plastic pots. Seeds were examined at weekly intervals, and those that produced a radicle of about 1 cm long were considered germinated. The data were expressed as cumulative germination percentages.

Soil seed bank study

To determine whether *P. serotina* forms a buried soil seed bank, soil samples were collected from eight

representative stands in the Sonian forest that contain *P. serotina*, i.e. two pure *Fagus*-stands, two pure *Quercus*-stands, two pure *Pinus*-stands and two logged areas (at least four years old).

For each stand, we chose two plots, one in which *P. serotina* cover was <5% and another in which cover was >75%. Within each stand, a total of 32 soil samples were collected in June from eight randomly selected blocks of 20 cm × 20 cm in four layers (litter and 0–5, 5–10 and 10–15 cm soil depth).

The reason for sampling in June was to collect seeds that did not germinate during spring and before new seeds were dispersed in autumn; thus to sample for a persistent seed bank (see Walck et al. 2005). A total of 256 (8 × 8 × 4) soil samples were collected. Each sample was air-dried for 48 h and then subdivided into three equal parts, and each subsample was assigned to one of the following three methods for estimating the soil seed bank: (i) direct germination of seeds in trays in a greenhouse at 20–25°C with 12/12 h artificial light/dark conditions; (ii) germination in the same environmental conditions after three months cold, moist stratification (in soil) at 5°C and (iii) direct counting of seeds following washing of soil samples. Seed viability was determined by the Triphenyl Tetrazolium Chloride (TTZ) test (International Seed Testing Association 1976) only in subsample 3.

Statistical analysis

Fresh weight of 100 fruits, percentage of fruit and seed moisture content, dry matter and seed germination were analyzed using one-way ANOVA followed by the least significance difference (LSD) test ($P < 0.05$). Final percentage values were arcsine square-root transformed for statistical analysis, but non-transformed data are shown in table and figures. Pearson's correlation coefficient was calculated to determine the relationship between seed germination and other parameters of seed development with one-tailed test to see the significance level.

Results

Seed development

Prunus serotina began flowering in the last week of May and was in full bloom in the first week of June. The entire process of seed development was completed within approximately 105 DAA, i.e. in late summer/early autumn. During the entire course of seed development, fruits underwent a series of colour changes. At the first harvest, on July 3rd (30 DAA), fruits were green and firmly attached to the mother plant, and they remained in this state until August 2nd (60 DAA). Colour of fruits gradually changed from dark green to blackish red and then to completely black by August 17th (75 DAA), by which time the mesocarp was soft. At this stage, fruits were relatively easy to detach from mother plants. At the final harvest, on September 16th (105 DAA), the majority of fruits had turned dark black, had developed a more succulent mesocarp, and began to disperse.

The fresh weight of 100 fruits, fruit moisture content, percent dry matter, and seed moisture content differed significantly ($P < 0.001$, data not shown) between harvests. Fruit weight increased steadily until 75 DAA (23.1 g) and then increased significantly ($F_{5,18} = 546.03$, $P < 0.001$) to 45.5 g at around 90 DAA (Fig. 1a). Fruit moisture content declined from 78.9% to 49.7% until 75 DAA, and then it increased significantly ($F_{5,18} = 268.50$, $P < 0.001$) to 54.6% at 90 DAA. Fruit dry matter percentage showed a reverse trend, with an increase from 20.2% (30 DAA) to 50.4% (75 DAA), after which there was a significant decline ($F_{5,18} = 298.18$, $P < 0.001$). In contrast, moisture content of seeds (without mesocarp/pericarp) declined significantly ($F_{4,15} = 3216.49$, $P < 0.001$) at regular intervals, from 77.3% (45 DAA) to 13.7% at the time of final harvest 105 DAA, which coincided with natural seed fall (Fig. 1b).

Germination was not observed in seeds from any harvest when incubated at constant 20°C in the absence of a cold, moist stratification pre-treatment. During the last three harvests, there was a progressive increase in the proportion of seeds that were able to germinate after exposure to a cold, moist stratification. However, total time from the beginning of germination to the emergence of seedlings did not differ between the harvest dates (data not shown). Seeds acquired the capacity to germinate by August 17th (75 DAA), when the difference between dry matter percentage and fruit moisture content began to level off (Fig. 1b). However, only 16% germination was recorded at this stage of seed development, increasing up to 28% on September 1st (90 DAA). A

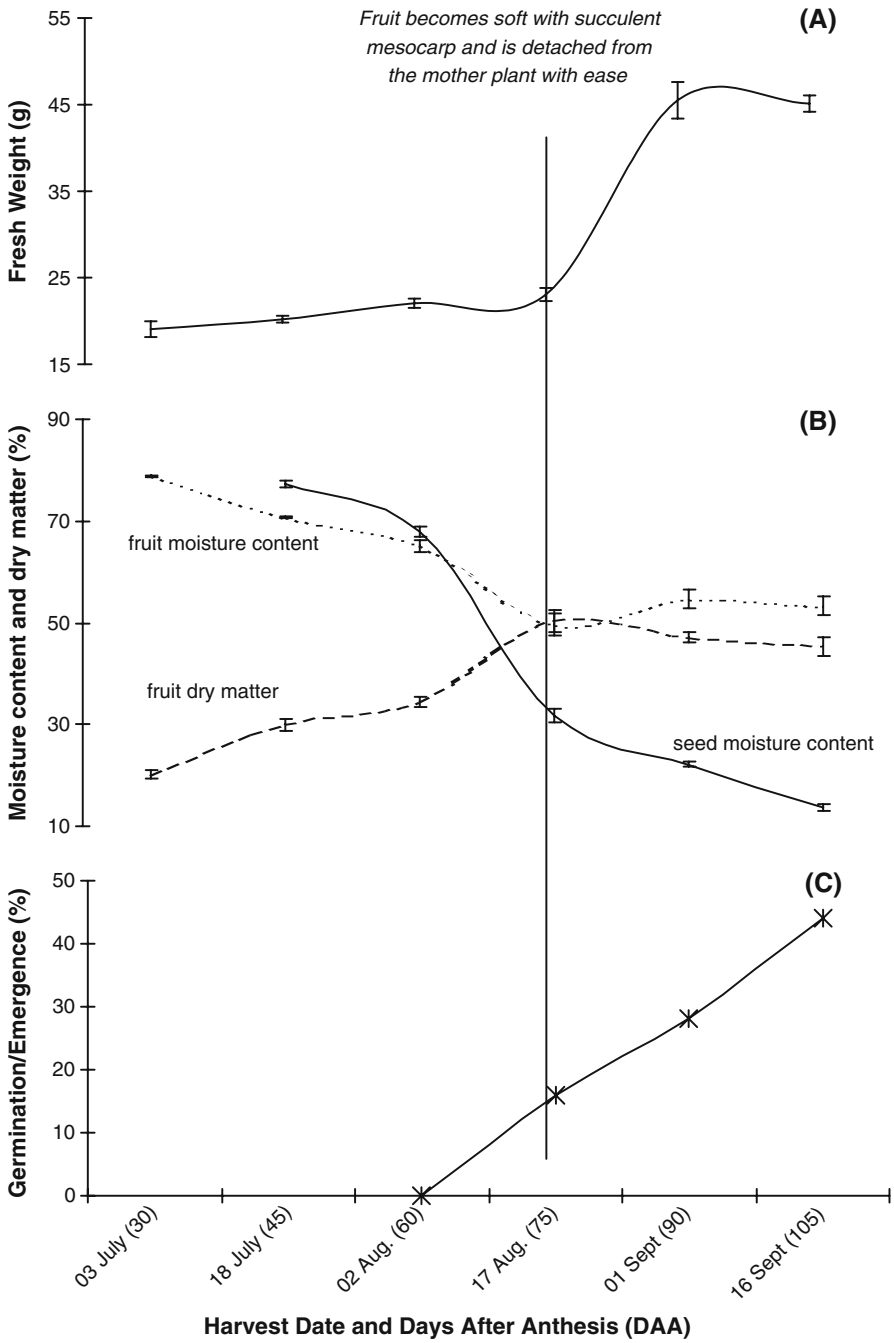

Fig. 1 Chronological changes in **a** fresh weight of 100 fruits, **b** fruit moisture content, fruit dry matter percentage, seed moisture content, and **c** seed germination percentage in *Prunus serotina* during the seed development. The vertical bars represent means ± SE

maximum of 44% germination was attained at the time of final harvest, on September 16th (105 DAA). Seed germination tends to increase with harvest date (Fig. 1c) as seed moisture decreased naturally from 31.8% to 13.7%. During the later stages of seed development, herbivorous mammals consumed black cherry seeds, eroded their seed coat (mesocarp), and dispersed them away from parent trees in faeces. These de-coated seeds were collected from faeces on the final date of harvest and subjected to cold, moist stratification; 55% of them germinated. Germination showed a significant negative correlation with seed moisture content ($r = -0.94$, $P = 0.03$) and a significant positive correlation with DAA ($r = 0.99$,

$P = 0.001$). Other parameters such as fresh weight, fruit moisture content, and dry matter percentage did not correlate significantly with seed germination during maturation.

Pre-treatment to overcome dormancy

No fresh mature seeds of *P. serotina* germinated when they were incubated in the growth chamber without pre-chilling treatment. The highest cumulative germination (62%) was obtained in seeds treated with 500 ppm GA_3 that were cold-stratified for 120 days (Table 1). Soaking seeds in 500 ppm cytokinin resulted in only 16% germination. The combination of GA_3 and cytokinin resulted in 21% germination. This is still lower than the 34% germination of the untreated seeds. Seeds rotted when stratified after initial scarification with 65% H_2SO_4.

Temperature had a marked effect on germination. Highest germination was at 10°C throughout the observation period (Fig. 2). In general, GA_3-treated seeds had higher cumulative germination than untreated seeds at all three temperatures tested. The GA_3-treated seeds began to germinate 13 weeks after stratification and reached the highest percentage in 21, 22 and 24 weeks of incubation at 10, 5 and 15°C, respectively. Contrary to GA_3-treated seeds, germination percentage and rate in untreated seeds were low. The first germination occurred on the 13th week of incubation at 5 and 10°C and on the 14th week at 15°C, and reached the highest germination percentage on the 24th week in all three temperatures. Prolonging the incubation period beyond 24 weeks resulted in rotting of the seeds in all the treatments.

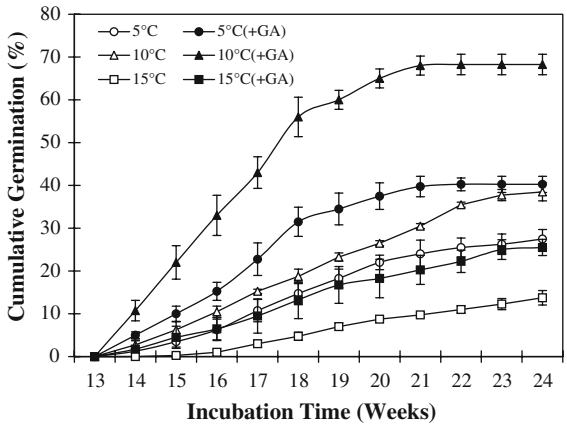

Fig. 2 Cumulative germination percentages of *Prunus serotina* seeds as a function of temperature and time. Seeds were initially soaked in GA_3 and distilled water (control) for 72 h, and then stratified at 2–3°C for 8 weeks, after which they were moved to 5, 10 and 15°C for incubation. The vertical bars indicate means ± SE. Data points are based on four replications of 100 seeds

Soil seed bank

During one year of observations, no *P. serotina* seedlings emerged from the soil samples in the greenhouse, even following 3 months of cold, moist stratification of the soil samples. Only four seeds were viable out of 196 seeds detected (mostly either in litter or 0–5 cm layer) through direct counting in soil samples (Table 2).

Discussion

Changes in seed physical characteristics have a definite advantage as indices of seed maturity since

Table 1 Effect of different treatments on cumulative germination percentages (mean ± SD) of *Prunus serotina*

Treatments		Cumulative germination (%)*
T_1	Seed soaked in distilled water	34.0 ± 5.1^b
T_2	Seed soaked in 500 ppm GA_3	62.0 ± 2.3^a
T_3	Seed soaked in 500 ppm cytokinin	16.0 ± 3.2^d
T_4	Seed soaked in combination of equal (v/v) solution of 500 ppm GA_3 + cytokinin	21.0 ± 3.8^c
T_5	Seed soaked in distilled water after acid scarification	0.0 ± 0.0^e
	SE (±)	1.61
	Critical difference at 5%	3.41

In all the treatments, seeds were soaked for 72 h then subjected to cold, moist stratification for 120 days

* Values not followed by the same letter differ significantly at $P = 0.05$

Table 2 Number of *Prunus serotina* seeds counted in the soil seed bank (total sampled surface area 0.64 m^2)

Overstory vegetation	Number of seeds
Logged areas	1 (0)*
Fagus sylvatica	2 (0)
Pinus sylvestris	149 (3)
Quercus robur	44 (1)
Total	196 (4)

* Values in parentheses show the number of viable seeds estimated by the TTZ test

they can be assessed easily in the field. In temperate mixed forest of Brussels region, *P. serotina* fruits began to disperse after three and half months from the date of anthesis and this period coincided with late summer and early autumn (mid September). Similarly in temperate deciduous forest of Northern France, *P. serotina* fruits mature in early September (Closset-Kopp et al. 2007); Pairon et al. (2006) showed that in understory pine plantation, although fruits of *P. serotina* mature in early September, they continue to disperse until the beginning of December, with a peak in the beginning of October. Seed dispersal in autumn allowed seeds to be pre-chilled enough on the forest floor over winter to break their dormancy before emerging in spring. Pericarp colour of *P. serotina* fruits changed from blackish red to dark black as seeds matured. Similar changes in fruit colour have been reported in seeds of *P. avium* (Finch-Savage et al. 2002). During seed development, fruit weight of *P. serotina* increased sharply between 75 and 90 DAA. During the same period, fruit moisture content increased significantly after an initial decline. Fruit dry matter percentage showed a reverse trend. This different behaviour of fruit weight, moisture content, and dry matter percentage may be due to the abrupt increase in mesocarp, which becomes watery and succulent at this stage. Bonner (1975) reported similar trends in *P. serotina* fruits in Central Mississippi, USA. In fruits of *P. avium*, moisture content of seeds (while still inside the fleshy fruit) continues to decrease with an increase in dry weight, and seeds acquire desiccation-tolerance before being shed from the tree (Finch-Savage 1998). In *P. serotina*, maximum dry matter percentage was reached around 75 DAA, which indicates the ability of seed to germinate (mass maturation). It is obvious that physiological maturation continued beyond the point at which the fruit is soft and ripe. On the contrary, seeds without mesocarp lost a significant amount of water at regular intervals as the endocarp became hard and the embryo changed from a soft dough-like stage to a firm white tissue.

Seeds of *P. serotina* acquire the ability to germinate when they enter the desiccation phase, as evidenced by the rapid loss of seed moisture between 60 and 75 DDA. Desiccation appears to play some role in the switch from the developmental process to that essential for germination (Bewley and Black 1994), and this is evident in *P. serotina*, where germination percentage has a significant and negative correlation with seed moisture content. Stimulation of germination by drying appears to be universal, since even in recalcitrant seeds a small reduction in moisture content has this effect (Probert and Brierly 1989). Thomsen (1997) reported a decline in mean germination time (including cold stratification time) with decreased moisture content in *Fagus sylvatica* as seeds matured. A strong correlation of germination with seed moisture content in developing sugar maple (*Acer saccharum*) fruits has been reported by Carl and Snow (1971). Farmer (1997) described seed development patterns in *Prunus* species as a two-phase event. The full-size endocarp was formed in late spring. Thereafter, the embryo gradually became firm, and seed moisture content was reduced as the pericarp expanded and ripened. In general, seed development in *P. serotina* appears to be similar to that of most orthodox seeds and in particular to those enclosed within a moist fruit (Bewley and Black 1994; Finch-Savage et al. 2002; Jensen and Eriksen 2001).

The essential metabolic/developmental processes of most seeds are inactive by the time the seed reaches maturity. Water easily re-activates some of these processes, such as those in mitochondria, during imbibition (Ching 1973; Schmidt 2000). In general, seeds imbibe water rapidly at first, and then reach a plateau (lag phase) where water uptake is very slow or stops. Dormant seeds, where moisture uptake is not limited by a hard (water-impermeable) seed coat, tend to remain in this lag phase until dormancy is broken by treatment (Finch-Savage 1998). The above trend of water imbibition (lag phase) may also be true for *P. serotina* seeds. The endocarp may offer some mechanical resistance to germination, but it is permeable to water, thus the species is not truly

hard-seeded. Even though the seed coat is water-permeable, seeds did not germinate at any point during development without a low temperature treatment, which indicates that they have some kind of dormancy. Our results show that long-term cold, moist stratification help to overcome dormancy of intact seeds, which may categorize *P. serotina* seeds as those having physiological dormancy. Inhibitors in seeds of *P. serotina* subsp. *capuli* have been reported by Camacho-Morfin (1994). Wild mammals consumed large numbers of black cherry fruits. However, their role as seed dispersers has not been well studied (LoGiudice and Ostfeld 2002), except for birds (Pairon et al. 2006; Deckers et al. 2008). Our study shows that de-coated seeds collected from faeces of herbivorous mammals were vigorous and germinated to a higher percentage compared to seeds collected directly from the tree. Thus, any inhibitors present in seeds may have been leached out during passage of seeds through the digestive system of these animals. As a wide range of birds species highly contribute to the dispersal of *P. serotina* (Pairon et al. 2006; Deckers et al. 2008), its high germinability after passage in the digestive system of animals might have facilitated the establishment and, consequently, the invasiveness of the species.

A cold, moist stratification at 2–3°C of *P. serotina* seeds resulted in a higher germination percentage, when moved at 10°C as compared to 5 or 15°C. Similar temperature requirement for seed germination had been reported in seeds of *Prunus amygdalus* (Therios 1982), which had a low temperature requirement for stratification and a higher temperature requirement for germination. Farmer and Barnett (1972) reported that *P. serotina* seeds first develop germination capability at low temperature (3–4°C) in total darkness, after long chilling periods. Seeds of *P. virginiana* develop a high-temperature requirement for germination after an initial period of chilling treatment at 3°C, but the majority of seeds had acquired germination ability at same the temperature if kept for more than 24 weeks (Lockley 1980). Contrary to this study, Closset-Kopp et al. (2007) incubated Gibberellin-treated seeds of *P. serotina* at 20/16°C for 40 weeks and reported moderate germination percentage without any cold, moist stratification. The International Seed Testing Association (1999) rule for testing seeds at alternate 30/20°C or constant 20°C does not appear to be the optimum for germination of *P. serotina*.

We assumed that *P. serotina* seeds would dominate the soil seed bank in areas where plants of this species were present in varying degrees of abundance in the tree or shrub layer. However, the results of the present study do not support this assumption. During one year of observation, no *P. serotina* seedlings emerged in the glasshouse from soil samples even following 3 months of cold, moist stratification, and only four viable seeds reported in direct counting. Thus, *P. serotina* does not form a persistent soil seed bank in temperate forests of Western Europe, analogous to in its native range in North America (Beatty 1991; Brown 1992) but opposite to Marquis (1975). The lack of viable seeds in soil seed bank may be because new seeds of *P. serotina* germinate every year on the forest floor, as shown by Pairon et al. (2006) in central Belgium. Contrary to the black cherry, *Prunus pensylvanica* (pin cherry) forms a buried soil seed bank in Northern Hardwood Ecosystems in New Hampshire, USA, where they found 40 viable seeds per square metre. These seeds deposited in situ during the development of the pin cherry stand and then probably remain dormant in soil and germinate in response to a major disturbance (Marks 1974). Thus, the buried seeds' strategy ensures the colonisation of pin cherry at a particular site. In the case of black cherry, fresh, mature, dormant seeds are shed in early autumn, they release their physiological dormancy over the long cold and moist winter period, and germination and seedling establishment occur in the next growing season, which leads to a persistent seedling banks. Closset-Kopp et al. (2007) concluded that seeds of *P. serotina* are able to enter a closed-canopy forest and to form a long-living sapling bank that typically develop a 'sit-and-wait' strategy so that the invader has a head start on native species when disturbance-induced gap occurs. This is a very common strategy in forest trees in which even-aged populations of tree seedlings persist for long periods in an extremely stunted or etiolated condition and function in a way that in some respects is analogous to that of a seed bank (Grime 2001). Indeed, in many forest trees, seeds are not produced each year, and the capacity of the seedlings to survive for long periods under unfavourable circumstances ensures that the potential for regeneration is maintained (Grime 2001). This ability to respond with accelerated growth to a sudden gap formation (so-called "Oscar syndrome" sensu Silvertown 1987), and

characteristics that would enable individuals to decrease in size, delay mortality and locally self-maintain in the understories by a strong resprouting capacity ("Alice behaviour" sensu Closset-Kopp et al. 2007) have likely contributed to the success of the species in the largely anthropized forests from Western Europe where logging frequently occurs.

Thompson (2000) reported a negative relationship between physiological dormancy and long-term soil seed persistence in some plant species. As pointed out by Baskin and Baskin (1998), species regarded as having a long-term persistent seed bank are not characterized by particular dormancy behaviour. They may (1) undergo repeated seasonal cycles of dormancy (e.g. *Lamium purpureum*), (2) be initially dormant but soon become and remain non-dormant (e.g. *Rumex crispus*), or (3) be non-dormant from the outset (e.g. *Digitalis purpurea*). Indeed, most types of dormancy (including the most frequent one, physiological dormancy) play a limited role in seed persistence in the soil (Thompson 2000). The only kind of dormancy that plays a major role in seed persistence is hard-seeded or physical dormancy (Baskin and Baskin 1998), which is not the case for *P. serotina* seeds. Recently, Thompson et al. (2003) concluded that there is no close relationship between seed dormancy and persistence in the soil. Although non-dormant seeds have a slight tendency to be less persistent, dormancy is neither a necessary nor a sufficient condition for the accumulation of a persistent seed bank. Thus, there is no realistic prospect of predicting persistence from dormancy; almost all combinations of persistence and dormancy exist (Thompson et al. 2003).

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