



## Ecological factors controlling the abundance of non-native invasive black cherry (*Prunus serotina*) in deciduous forest understory in Belgium

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### Abstract

The relation between invasion success of *Prunus serotina* and type of recipient habitat was studied in a large forest in central Belgium. The major emphasis in this study was the determination of factors controlling the abundance of *P. serotina* in understory strata. Environmental variables measured in 34 sample plots were slope, aspect, litter depth, soil type, pH, soil compaction, soil moisture, air humidity, soil temperature and light intensity in spring and late summer. Site conditions were also expressed indirectly for 210 sample plots using Ellenberg indicator values (soil nutrients, acidity, moisture, light conditions). Plots with *P. serotina* had lower mean indicator values for soil moisture, reaction (pH) and nitrogen, compared to plots without *P. serotina*. Twenty indicator species were identified for plots in which *P. serotina* occurs. The species richness of the herb layer was negatively correlated with the percentage cover of black cherry in the shrub layer. The percentage cover of *P. serotina* saplings in different overstory types was ranked as follows: *Quercus* > *Pinus* > *Fagus* > logging areas. Only three variables explained significant amounts of variation in *Prunus* abundance: slope, light intensity at 120 cm in April and light intensity at ground level in September. We found a positive response of black cherry seedlings to light intensity between 58 and 80% of full light (April measurements at 120 cm), while saplings showed a negative response within this range. Between 21 and 47% of full light (April measurements at 120 cm), seedlings were poorly represented whereas saplings showed a quite high cover. Between 0.3 and 1.8% light (September measurements at ground level), seedlings were almost absent while saplings maintained a high abundance. The results suggest that *P. serotina* shows a differential response to light intensity in relation to its development stage, i.e. the species is heliophilous at the seedling stage and becomes a shade plant at the sapling stage.

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## 1. Introduction

Biological invasions are clearly one of the most important impacts humans have had on the Earth's ecosystems (Rejmanek, 1996). In many biogeographical regions, some invasive species (i.e. species having the ability to establish themselves, out-compete natives and take over a new environment) have led to difficult or even uncontrollable problems and permanent vigilance is required. Therefore, we need to understand what attributes make some plant species more invasive, what are the impacts of these species on the native ecosystem and which communities or systems are receptive and which are vulnerable.

One example of a serious invader is the black cherry, *Prunus serotina* Ehrh., whose native range is eastern North America. *P. serotina* var. *serotina* was first introduced in Europe in the 17th century as an ornamental tree. From the end of the 19th century onwards, it was used in forestry as an auxiliary tree, mainly in Germany, The Netherlands (Eijsackers and Oldenkamp, 1976) and Belgium (e.g. Van den Meersschaut and Lust, 1997). After being widely cultivated in forests for improving soil quality and for fire prevention around pine plantations, the species became invasive and received for a long time the name of "wood pest" (Leclercq, 1960). In Germany, the species was still planted in the 1980s (Starfinger, 1990b). In Belgium and The Netherlands, the planting of this species for forestry applications stopped around 1950, but its synanthropic distribution is still increasing, so that the extent of the problem is not yet fully realised (Maddelein, 1990). *P. serotina* is recorded in all forest types of northern Belgium (Van den Meersschaut and Lust, 1997), although with a higher presence and abundance in *Betulo-Quercetum* and *Fago-Quercetum* associations (Waterinckx, 2001). This invasion has considerable consequences for forestry as well as for nature conservation.

Currently, *P. serotina* spreads in most of Europe, from the north of France to Poland, Hungary and Rumania, as well as from Denmark to Italy (Starfinger, 1990a). It mainly grows on sandy soil (Haeupler and Schönfelder, 1988), but the species can also germinate and establish on a wide range of other soil types (peaty to sandy) in many different plant communities

(Starfinger, 1990a; Waterinckx, 2001). In Berlin, the species mainly develops in *Quercion robori-petraeae* communities, particularly in stands of the *Pino-Quercetum petraeae* association (Starfinger, 1990b). In Belgium the massive development of *P. serotina* in pine (*Pinus nigra* and *Pinus sylvestris*) plantations seems to be due to its successful establishment strategy, in combination with anthropogenic influence (soil disturbance and eutrophication) (e.g. Eijsackers, 1990; Versteijnen, 1991; Muys and Maddelein, 1993). The species is considered intolerant of deep shade, although young seedlings usually develop in the shade of an overstorey or in partially cut stands (Horsley and Gottschalk, 1989). *P. serotina* represents a threat for the survival of numerous native woodland (tree) species, impedes the rejuvenation of the forest and is a great competitor for water and nutrients (Muys and Maddelein, 1993).

In its synanthropic range, *P. serotina* has been studied for the consequences of its spread in different countries such as Germany (Starfinger, 1990a, 1990b, 1991), The Netherlands (Eijsackers and Oldenkamp, 1976; Eijsackers and van den Ham, 1984; Eijsackers, 1990; Farjon, 1986) or Italy (Sartori, 1988). In Belgium, most studies of *P. serotina* concern management techniques focused on the control of this invasive species (Maddelein, 1990; Versteijnen, 1991; Muys et al., 1992; Muys and Maddelein, 1993; Van den Meersschaut, 1996). However, in its synanthropic range, the response of the plant to a broad range of ecological factors has not received much attention previously. An important question for understanding the invasive behaviour of *P. serotina* is what features of the environment are important to the spatial and temporal dynamics of the species. In order to understand the success of *P. serotina* and to plan possible management strategies against this species, it is necessary to compare its ecology and the characteristics of the habitats concerned.

This research is a combination of a vegetation study of a particular group of stands and an ecological study of the species, with the objectives of (1) acquiring more knowledge about microclimate and soil requirements of *P. serotina* in its synanthropic area; (2) analysing the effect of its development on the species richness in the understory; (3) exploring the possible influence of recipient forest vegetation on its invasion.

## 2. Study area

The research was conducted in the Sonian Forest, south of Brussels (50°47'N; 4°26'E). This area has been proposed as a Site of Community Importance (Natura 2000 area, in fulfilment of the EC-Habitat Directive). It is an ancient but intensively managed forest that was supposed to have covered the whole of Western Europe after the last Ice Age. The forest actually covers an area of 4383 ha, 1654 ha of which are situated within the administrative limits of the Brussels Capital Region, which constitutes a management unit and the area taken into consideration in the present study. Some 20,000 years ago, sandstone and flintstone formed the upper layer in the area of the Sonian Forest. After the last Ice Age, this layer was covered with loess. Today, almost the whole surface of the forest (95%) is composed of a 3–4 m thick silt layer, which corresponds to the loess deposition. The prevailing soil type has an “Abc” profile, i.e. silt loam soil with textural B horizon according to the Belgian Soil Map (Louis, 1959) (USDA: Hapludalf; FAO: Luvisol; French classification: Sol lessivé acide). The forest ranges in elevation from 65 to 130 m a.s.l. The climate of the area is temperate and humid, with a growing season of 7 months (April–October). Mean annual temperature is 9.9 °C, annual precipitation is 798 mm (Lieth et al., 1999). Originally, the Sonian Forest was an oak-hornbeam forest (dominated by *Quercus robur* and *Carpinus betulus*). Since the plantation work of the Austrian administration at the end of the 18th century, it is now composed of 85% of beech (*Fagus sylvatica*). Except beech, few other woody species are found. Seven percent of the forest surface is occupied by oak stands (*Quercus robur*) and 8% is represented by introduced conifer stands (*P. sylvestris*, *Larix decidua*, *Picea abies*). A few decades ago, black cherry (*P. serotina*) was experimentally introduced at one location in the Sonian Forest, from which it spread in the vicinity. Seed bearers are also present near the study area, which created many seed sources for the colonisation of the rest of the forest far from the stand where the black cherry was initially planted. Currently, *P. serotina* develops spontaneously as seedling, sapling or adult tree in many stands throughout the study area, although preferentially in those nearby the forest edge. Up to now, the species has not been managed in the area taken into consideration in the present contribution.

## 3. Methods

### 3.1. Vegetation sampling

The method used combined systematic and stratified sampling, in order to avoid the risk of omitting specific forest stations which would be located between the grid of systematic sampling. For the stratified sampling, the relevés were distributed according to a pre-established framework on the basis of forest stands, pedological, topographical, geological and vegetation maps. After demarcation of spatial units with comparable combinations of factors (forestry, pedological, geological, geographical, botanical aspects), we carried out a systematic sampling within each of these sectors. For the systematic sampling, the relevés were distributed with arbitrarily fixed systematic interval, i.e. an approximate density of one relevé per 8 ha.

A total of 210 relevés (20 m × 20 m) were made according to the Braun–Blanquet method (e.g. Westhoff and van der Maarel, 1978). Those habitats into which the spontaneous invasion by *P. serotina* was observed were further investigated for environmental variables.

### 3.2. Recording of explanatory variables

Ecological measurements were taken in each of the 34 relevés where *P. serotina* was recorded. The quantitative variables listed in Table 1 were used for the present study. Soil compaction, pH, humidity, temperature and light intensity were recorded using a systematic sampling scheme (Fig. 1).

#### 3.2.1. Stand basal area

Stand basal area of the overstorey species within each plot ( $G$ ) was calculated by measuring the circumference of all trees (>10 cm) at breast height (130 cm).  $G$  is the sum of the basal area of all living trees in a stand, expressed in m<sup>2</sup>/plot of fixed dimensions (20 m × 20 m in the present study).

#### 3.2.2. Available light quantity

In each relevé, four measurements of light intensity were taken using a Lutron LX-105 light-meter at 5 m distant locations along an east–west

Table 1  
Quantitative explanatory variables

Number	Code	Variable	Range	Methods of recording
1	soilTa	Soil temperature in April	8.3–12.1 (°C)	Soil temperature (mean of four values) measured at 3 cm depth in April
2	soilTs	Soil temperature in September	13.5–15.6 (°C)	Soil temperature (mean of four values) measured at 3 cm depth in September
3	AirHa	Air humidity in April	27–49 (%)	Air humidity (mean of four values) measured in April
4	AirHs	Air humidity in September	45–73 (%)	Air humidity (mean of four values) measured in September
5	pHH <sub>2</sub> O	pH H <sub>2</sub> O	3.6–4.5	Reaction pH measured with a pH meter after mixing 5 g of soil with 10 ml of deionized water and left for 30 min
6	pHKCl	pH KCl	3.3–4.0	Reaction pH measured with a pH meter after mixing 5 g of soil with 10 ml of 1 M KCl and left for 30 min
7	Comp	Compaction	77–237 (N)	Soil compaction (mean of four values) at 20 cm depth, measured by a cone-penetrometer
8	L120A	Light intensity at 120 cm in April	6–80 (%)	Proportion of full light in the stand (mean of four values) measured by a luxmeter in April at 120 cm height
9	L120S	Light intensity at 120 cm in September	<1–54 (%)	Proportion of full light in the stand (mean of four values) measured by a luxmeter in September at 120 cm height
10	L0S	Light intensity at 0 cm in September	<1–13 (%)	Proportion of full light in the stand (mean of four values) measured by a luxmeter in September at the ground level
11	G	Stand basal area (G)	0.32–3.61 (m <sup>2</sup> )	Area of the stand in the plot (400 m <sup>2</sup> ), calculated from measurements of tree circumference at 130 cm height
12	soilM	Soil moisture	24–58 (%)	Water content (mean of four values) of soil cores (0–10 cm) calculated by the gravimetric method
13	Alt	Altitude	80–125 (m)	Height of the sample plot above sea level
14	slope	Slope	0–40 (%)	Slope of the ground compared to the horizon, measured with a clinometer
15	N	Mean nitrogen index	3–7	Nitrogen availability in the sample plot obtained by calculating the weighted average of the Ellenberg's index for each species present in the sample plot

transect on two dates in the spring (without overstory canopy) and in the summer (with overstory canopy). Because of the spectral characteristics of the understory, light varies according to weather circumstances (Federer and Tanner, 1966), and all measurements were taken during clear days. Paired measurements were made below herb cover and above herb cover 120 cm above the ground, with the sensor surface horizontal, between 11.00 and 15.00 h, to get uniform and comparable radiation data (Geiger, 1965; Aude and Lawesson, 1998). Each measurement was represented by the average value of a continuous light record during 30 s. For each season and each position, the four measurements of each sampling area were averaged for the multivariate analyses (CCA/RDA). The percentage of light transmission into the stand was calculated as the inside intensity divided by the average of outside light intensity recorded before entering and after leaving the stand.

### 3.2.3. Soil compaction

In each sampling area, four measurements of soil compaction were performed at 20 cm depth and at 5 m-distant locations along a north–south transect using a cone penetrometer (Eijkkelkamp Agrisearch Equipment, The Netherlands), a device forced into the soil to measure its resistance to vertical penetration. When the cone-shaped tip is pushed into the soil, the penetrometer provides a continuous plotting of soil strength and soil depth, unless impenetrable stone or wood is encountered (Miller et al., 2001). The readings are expressed in newton (N), the SI unit of force. Cone penetrometers are frequently used to measure soil resistance (e.g. Seixas and McDonald, 1997; Jansson and Wasterlund, 1999). The average value was used for the multivariate analyses.

### 3.2.4. Soil pH and moisture

Soil samples were taken for pH. Each sample is a composite of four 0–10 cm deep cores taken at 5 m-

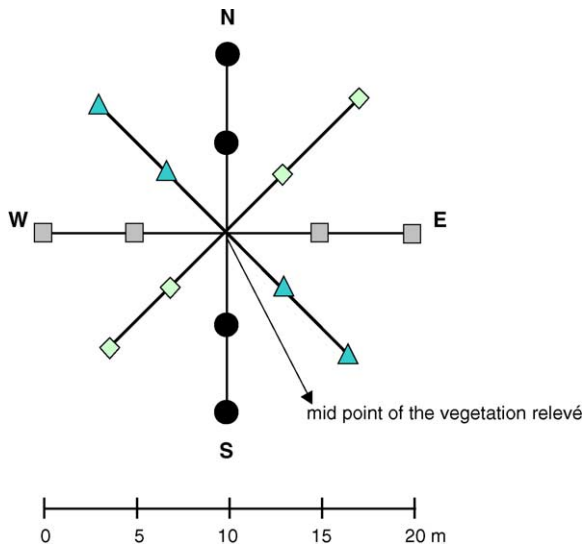


Fig. 1. Diagram showing the respective position of repeated measurements of soil compaction (filled circles), light intensity (squares), soil pH and humidity (diamonds) and soil temperature (triangles), within each vegetation sampling.

distances from the mid point of the vegetation plot. The surface of each soil core was discarded to avoid litter. Fresh soil was passed through a 1 mm sieve. Five grams of soil were mixed with 10 ml of deionised water or 1 M KCl and left for 30 min, after which the reaction pH was measured with an ISFET IQ150 pH meter (IQ Scientific Instruments Inc., USA). Soil moisture was determined gravimetrically on composited samples.

### 3.2.5. Other environmental variables

An overlay of the published soil map (Louis, 1959) with the sample plots was made. This allowed the sample plots to be assigned to one of the following soil types: silt, sandy silt, silty sand and disturbed soil.

For the complete data set (plots with and without *P. serotina*;  $n = 210$ ), the nitrogen availability (N), soil reaction (R), soil moisture (F) and light (L) in the sample plots were estimated using Ellenberg's species indicator values. Because species are not always constant in their ecological requirements and ought in principle to have different indicator values in different parts of their range (Hill et al., 1999), we used the recalibrated Ellenberg's indicator values for the British Isles (closer to our study area), instead of the original

ones which were defined for Central Europe (Ellenberg et al., 1991). Weighted averages were calculated for each sample plot.

Since Braun–Blanquet cover-abundance values are not suitable for mathematical treatment, raw data were transformed by the correspondent cover percentage value (median of each scale interval): 87.5, 62.5, 37.5, 15, 2.5, 0.5 and 0.2, accounting respectively for 5, 4, 3, 2, 1, + and  $r$  (arbitrary values were taken for  $r$ , + and 1).

### 3.3. Data analyses

To investigate whether *P. serotina* is restricted to particular microhabitats within the study area, we first compared the mean Ellenberg's indicator values of soil nitrogen, reaction, humidity and light between plots with and without *P. serotina*, with a Mann–Whitney  $U$ -test. Indicator species for the two types of sites (with and without *P. serotina*) were derived by the method of Dufrière and Legendre (1997), as available in the PC-ORD package (McCune and Mefford, 1997). The method combines information on the concentration of species abundance in a particular group and the fidelity of occurrence of a species in a group. It produces indicator values for each species in each group, which are tested for statistical differences using a Monte Carlo technique (Dufrière and Legendre, 1997).

Relationships between the species richness in herb layer and the percentage cover of *P. serotina* were analysed by linear regression analyses (Spearman rank correlation coefficient,  $r_s$ ). In order to get more insight on the nature of lost species, we calculated separate correlations with plant functional groups such as CSR strategies according to Grime et al. (1988). Intermediate strategies were pooled according to Graae and Sunde (2000) using the following categories:

- C+ (competitors): C, C/CR, C/CSR, C/SC;
- CSR+ (competitive and stress-tolerant ruderals): CR, CR/CSR, CSR, SC, SC/CSR, SR, SR/CSR;
- R+ (ruderals): R, R/CR, R/CSR, R/SR;
- S+ (stress tolerants): S, S/CSR, S/SC, S/SR.

A Kruskal–Wallis test was used to investigate whether *P. serotina* is restricted to a particular overstorey type. For this analysis, five mixed stands were

removed because of a lack of sufficient samples for statistical tests. The 29 remaining pure stands were grouped as followed: *Fagus* stands ( $n = 9$ ), *Quercus* stands ( $n = 8$ ), *Pinus* stands ( $n = 6$ ) and logging areas ( $n = 6$ ). One-way analysis of variance was then used to test whether there were significant differences in environmental variables between the different overstorey types.

In order to detect the patterns of variation in the abundance of *P. serotina* that can be explained by environmental variables, we calculated a Canonical Correspondence Analysis (CCA; Ter Braak and Gremmen, 1987) using Canoco 4.5 for Windows (Ter Braak and Šmilauer, 2002). This initial analysis provided a check on how unimodal the data were. Because the lengths of the gradient was 0.69 S.D., we assumed that the response curve would be monotonic and we considered a redundancy analysis (RDA). The advantage of using RDA is that in its biplot it provides more quantitative information than CCA in its joint plot (Jongman et al., 2000). Three explanatory variables were categorical variables, representing the soil type, litter thickness and aspect. The other variables were quantitative (altitude, slope, soil moisture, pH, compaction, light intensity, stand basal area). In order to investigate the contribution of soil temperature and air humidity as explanatory variables, a second RDA using air temperature as a covariate was necessary, because these two variables depend on it.

As an alternative approach to assessing the importance of factors controlling the abundance of *P. serotina*, we employed an analytical procedure for the selection of optimal combinations of explanatory variables. The program TWINSPAN (Two-way indicator species analysis; Hill, 1994), which is the most widely used technique for polythetic divisive classification (Kent and Coker, 1992), was chosen. Although it was initially developed for the classification of species and samples, it is geared towards ecological data and we found it useful for classifying environmental variables. Twinspan was run only with the variables which significantly contributed to the variation of *Prunus* abundance, as highlighted by the RDA procedure. This analysis could only be performed since the selected variables were measured on the same scale (%). Cut-levels were set to 0, 1, 3, 10, 20, 35, 50, 65 and 80. The number of final groups is dependent on the rules used to stop the splitting

processes. On the basis of the algorithm, final groups may result because of too few observations or too little variation in the group to warrant an attempt to split it, or because of no significant differences in the *Prunus* cover between the groups.

Nomenclature and species life forms are given by Lambinon et al. (1998). *Rubus fruticosus* was considered as a single species.

If not stated otherwise, all statistical analyses were carried out with Statistica Version 6.0 (Statsoft Inc., 2001). The 0.05 level of probability was accepted as significant throughout the work.

## 4. Results

### 4.1. Habitat characteristics

Plots with *P. serotina* had lower mean indicator values for soil moisture (5.38 versus 5.92,  $P < 0.0001$ , Mann–Whitney *U*-test), reaction (4.55 versus 5.02,  $P = 0.0134$ , Mann–Whitney *U*-test) and nitrogen (4.63 versus 5.12,  $P = 0.0092$ , Mann–Whitney *U*-test), compared to plots without *P. serotina*. These differences indicate that black cherry was restricted to particular environmental conditions. The mean light index was higher for plots with *P. serotina* (5.31 versus 5.20), but the difference was not significant ( $P = 0.2090$ , Mann–Whitney *U*-test). The composition of vegetation in plots with *P. serotina* was significantly different from that of plots without the species, in the sense that 20 indicator species were typical for plots in which *P. serotina* occur (Table 2), from which *Castanea sativa*, *Maianthemum bifolium*, *P. sylvestris*, *Pteridium aquilinum*, *Quercus rubra* and *Robinia pseudacacia* are the best indicators ( $P < 0.01$ ). *R. fruticosus* was the only indicator species for plots without *P. serotina* (results not shown: indicator value = 37;  $P = 0.04$ ).

### 4.2. Impact of *P. serotina* on the herbaceous species richness

The species richness of the herb layer was negatively correlated with the percentage cover of *P. serotina* in the shrub layer but not in the herb layer (Fig. 2a, b). Separate correlations made with plant functional types showed that stress-tolerants are

Table 2  
Indicator species for plant communities with *P. serotina*

<i>P. serotina</i>	Relative abundance		Relative frequency		Observed indicator value (IV)	IV from randomized groups		<i>P</i> -value
	+	–	+	–		Mean	S.D.	
<i>Carpinus betulus</i> (H)	32	4	6	1	17.0	6.1	4.74	0.025
<i>Castanea sativa</i> (S)	33	2	23	3	42.5	8.5	5.50	0.001
<i>Corylus avellana</i> (H)	33	0	6	0	16.7	2.0	3.77	0.035
<i>Corylus avellana</i> (S)	31	7	22	5	25.8	9.5	6.02	0.023
<i>Deschampsia cespitosa</i>	25	25	15	12	26.4	12.2	6.22	0.038
<i>Dryopteris dilatata</i>	52	16	75	35	38.5	25.6	4.97	0.016
<i>Larix decidua</i> (T)	31	6	15	2	18.3	7.2	4.75	0.037
<i>Lonicera periclymenum</i>	32	5	29	9	26.8	10.4	6.47	0.027
<i>Maianthemum bifolium</i>	28	16	19	4	37.5	8.4	5.12	0.001
<i>Pinus sylvestris</i> (T)	33	2	33	3	42.6	8.5	5.39	0.002
<i>Prunus avium</i> (S)	31	6	6	1	16.6	6.3	5.02	0.023
<i>Pseudotsuga menziesii</i> (S)	33	0	6	0	16.7	2.0	3.73	0.031
<i>Pteridium aquilinum</i>	30	11	52	22	41.1	15.5	6.76	0.005
<i>Quercus petraea</i> (S)	33	1	22	1	25.3	7.8	5.28	0.021
<i>Quercus rubra</i> (S)	33	2	11	1	32.8	4.8	5.03	0.004
<i>Robinia pseudacacia</i> (S)	33	1	15	1	23.9	5.7	4.84	0.004
<i>Salix caprea</i> (S)	29	12	10	4	25.9	8.6	5.35	0.018
<i>Sorbus aucuparia</i> (H)	32	3	55	6	26.7	11.5	6.79	0.033

The table shows the relative abundance (average abundance of a given species in a given group of relevés over the average abundance of that species in all relevés expressed as a %) and relative frequency (% of relevés in given group where given species is present) of the species in plant communities with (+) and without (–) *P. serotina*, as well as indicator values (% of perfect indication, based on combining the values for relative abundance and relative frequency) and results of the Monte Carlo test of significance (1000 permutations). The layer is mentioned for tree species (H = herb layer; S = shrub layer; T = tree layer).

significantly reduced, while competitors are not affected by an increasing cover of *P. serotina* (Fig. 2c, d). Furthermore, there was an overall difference in species richness between invaded and non-invaded plots (8.39 versus 11.09,  $P = 0.0311$ , Mann–Whitney *U*-test).

#### 4.3. Relationship between the abundance of *P. serotina* and overstory species

The percentage cover of *P. serotina* in different overstory types was ranked as follows: *Pinus* > *Quercus* > *Fagus* > logging, for the herb layer, and *Quercus* > *Pinus* > *Fagus* > logging, for the shrub layer (Fig. 3). Differences were significant for the shrub layer only ( $\chi^2 = 18.68$ ; d.f. = 3;  $P = 0.0003$ ; Kruskal–Wallis test followed by a Student Newman Keuls test), indicating that *P. serotina* was more abundant in *Quercus* and *Pinus* stands than in *Fagus* stands or in logging areas. Table 3 gives the mean values of environmental variables in these four

overstory types. Mean nitrogen index, pH and, as expected, light intensity in April, were significantly lower in *Pinus* stands than in other overstory types, while soil compaction was significantly higher in *Fagus* stands (ANOVA followed by a Student Newman Keuls test).

#### 4.4. Relationship between the abundance of *P. serotina* and environmental variables

The arrangement of the 34 samples with *P. serotina* in the RDA ordination is shown in Fig. 4. Eigenvalues of first and second axis were 0.530 and 0.121, respectively. Table 4 shows the variance explained by each of the variables tested and the cumulative variance explained. The variance explained by all variables was 67%. Only three variables explained significant amounts of variation in *Prunus* abundance: slope (12%), light intensity at 120 cm in April (L120A; 11%) and light intensity at ground level in September (LOS; 11%). The litter thickness class 5–

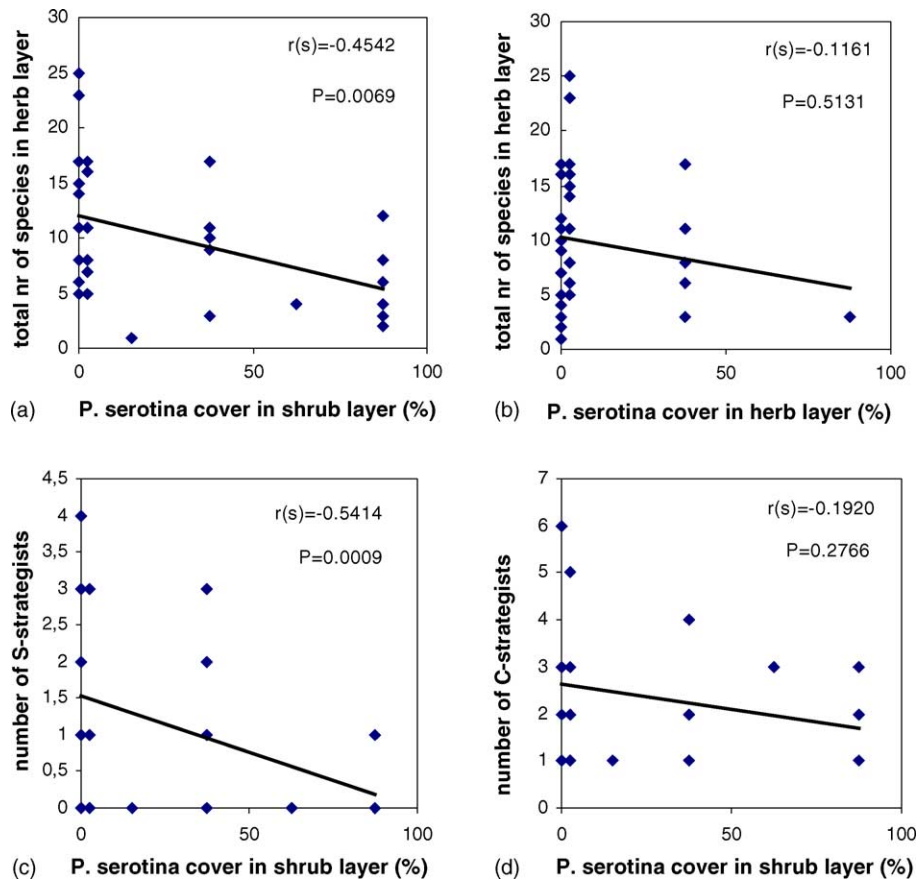


Fig. 2. Relationship between the total species richness in herb layer and the percentage cover of *P. serotina* in (a) the shrub layer and (b) the herb layer. Separate correlations are drawn for stress-tolerants (c) and competitors (d).  $r_s$  = Spearman rank correlation coefficient.

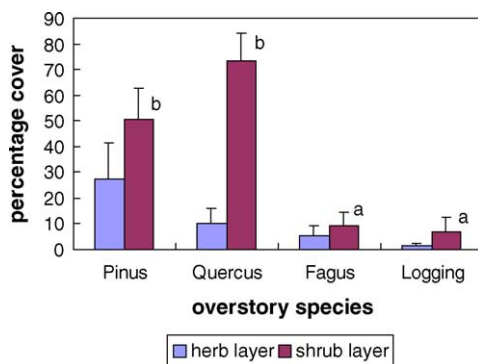


Fig. 3. Mean percentage cover (+S.E.) of *P. serotina* in shrub layer and herb layer, under four overstory species. Differing letters indicate significant differences using a Kruskal–Wallis test followed by a Student Newman Keuls test. Differences are significant for the shrub layer ( $\chi^2 = 18.68$ ; d.f. = 3;  $P = 0.0003$ ), but not for the herb layer ( $\chi^2 = 5.30$ ; d.f. = 3;  $P = 0.1511$ ).

10 cm explained 6% of the variation, but was above the significance level ( $P = 0.08$ ). Ordinations involving soil temperature and air humidity as explanatory variables, where the effect of air temperature was removed (partialled out) by using the air temperature as a covariable, are not shown because these variables did not significantly explain the variation in *Prunus* cover (Table 3). In this analysis, the soil temperature in September highly contributed to the explained variation (22%), but was not significant ( $P = 0.07$ ).

Optimal combinations of explanatory variables are shown diagrammatically by a series of binary splits (Fig. 5). Slope was the most powerful single predictor of the *Prunus* abundance. This variable was partitioned into flat areas (slope = 0%) and sloping areas (slope = 3–40%). Average *Prunus* cover of the former group in the herb and in the shrub layers is 0.77 and

Table 3  
Mean values (+S.E.) of environmental variables in four overstory types

	Significance	Overstory			
		<i>Fagus</i>	<i>Pinus</i>	<i>Quercus</i>	Logging
Soil temperature in September (°C)	NS	14.58 ± 0.22	14.92 ± 0.18	14.64 ± 0.14	14.40 ± 0.14
Air humidity in September (%)	NS	57.33 ± 2.37	57.17 ± 1.96	62.88 ± 2.50	55.50 ± 2.49
Soil temperature in April (°C)	NS	9.02 ± 0.39	9.10 ± 0.24	9.76 ± 0.20	9.12 ± 0.24
Air humidity in April (%)	NS	35.11 ± 1.92	35.00 ± 1.37	30.75 ± 0.94	35.67 ± 2.91
pH H <sub>2</sub> O	<i>P</i> < 0.01	4.16 ± 0.06 a	3.78 ± 0.06 b	4.07 ± 0.06 a	4.10 ± 0.07 a
pH KCl	<i>P</i> < 0.01	3.74 ± 0.05 a	3.45 ± 0.04 b	3.67 ± 0.04 a	3.71 ± 0.06 a
Compaction (N)	<i>P</i> < 0.01	162.25 ± 15.25 a	112.74 ± 9.53 b	104.82 ± 7.43 b	117.12 ± 15.94 b
Light intensity at 120 cm in April (%)	<i>P</i> < 0.01	55.19 ± 6.16 a	23.98 ± 4.88 b	41.70 ± 4.35 a	50.54 ± 6.91 a
Light intensity at 120 cm in September (%)	NS	5.64 ± 3.30	2.34 ± 1.01	4.02 ± 1.75	10.96 ± 8.66
Light intensity at 0 cm in September (%)	NS	1.97 ± 0.92	1.20 ± 0.40	2.53 ± 1.46	0.88 ± 0.22
Stand basal area ( <i>G</i> ) (m <sup>2</sup> )	NS	1.40 ± 0.20	1.68 ± 0.21	1.04 ± 0.13	1.44 ± 0.45
Soil moisture (%)	NS	32.97 ± 1.61	37.23 ± 4.82	33.01 ± 1.09	37.18 ± 3.46
Altitude (m <sup>2</sup> )	NS	91.89 ± 3.81	96.83 ± 4.61	93.88 ± 3.55	98.50 ± 6.04
Slope (%)	NS	2.67 ± 1.14	9.17 ± 6.25	5.75 ± 3.54	5.33 ± 2.46
Mean nitrogen index	<i>P</i> < 0.01	4.75 ± 0.23 a	3.53 ± 0.29 b	5.31 ± 0.39 a	4.26 ± 0.18 a

Differing letters within a row indicate significant differences using a one-way ANOVA followed by a Student Newman Keuls test. NS = no significant differences.

Table 4  
Percentage variation explained by explanatory variables and level of significance (Monte Carlo test)

Explanatory variable	Variance explained by single variable (%)	Cumulative variance explained (%)	<i>P</i> -level
Slope	12	12	0.0200
Light intensity at 120 cm in April	11	23	0.0250
Light intensity at 0 cm in September	11	34	0.0350
Silty sand	4	38	0.1350
Litter 5–10 cm	6	44	0.0800
Mean nitrogen index	3	47	0.2150
Compaction	2	49	0.3700
pH KCl	2	51	0.3050
Litter >10 cm	3	54	0.1550
Altitude	4	58	0.2100
North slope	2	60	0.3150
Light intensity at 120 cm in September	1	61	0.5050
Litter = 0 cm	1	62	0.6800
Litter 0–5 cm	2	64	0.2700
Silt	1	65	0.7300
Soil moisture	0	65	0.7600
pH H <sub>2</sub> O	1	66	0.8300
Stand basal area ( <i>G</i> )	0	66	0.8900
Sandy silt	0	66	0.9250
South slope	0	67	0.9400
Soil temperature in September	22	22	0.0750
Air humidity in September	5	27	0.3350
Soil temperature in April	1	1	0.6900
Air humidity in April	1	2	0.9750

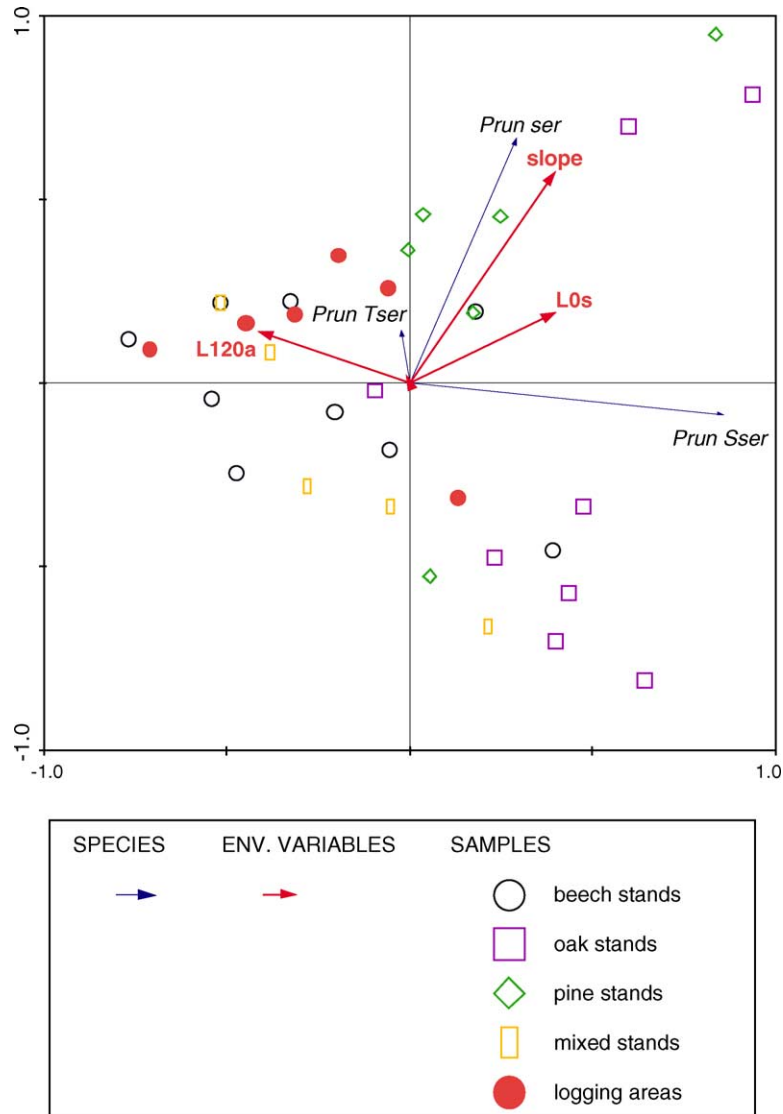


Fig. 4. RDA ordination of *P. serotina* in the herb, shrub (S) and tree (T) layers of 34 plots. Only the variables contributing significantly to the explained variation are shown. Sample plot positions along axis 1 (horizontal) and axis 2 (vertical). Both axes scaled in SD-units. Vectors indicate direction of largest change in explanatory variables and *Prunus* cover; see Table 1 for explanation and abbreviations.

20.96% respectively, compared to 18.13 and 46.25% for the sloping area group. If the flat area group was held constant in further analysis, light intensity in April at 120 cm accounted for more variation in *Prunus* cover than any other predictor. Similarly, holding constant light intensity in April and flat topography of group 2, light intensity in September (at ground level) was further partitioned and explained more variation in cover than other variables.

## 5. Discussion

### 5.1. Ecology of *P. serotina* in the study area

The presence of *P. serotina* in the study area was strongly correlated with environmental conditions. The species was restricted to the driest areas, which is consistent with the findings of Eijsackers and Oldenkamp (1976), showing that it never appears

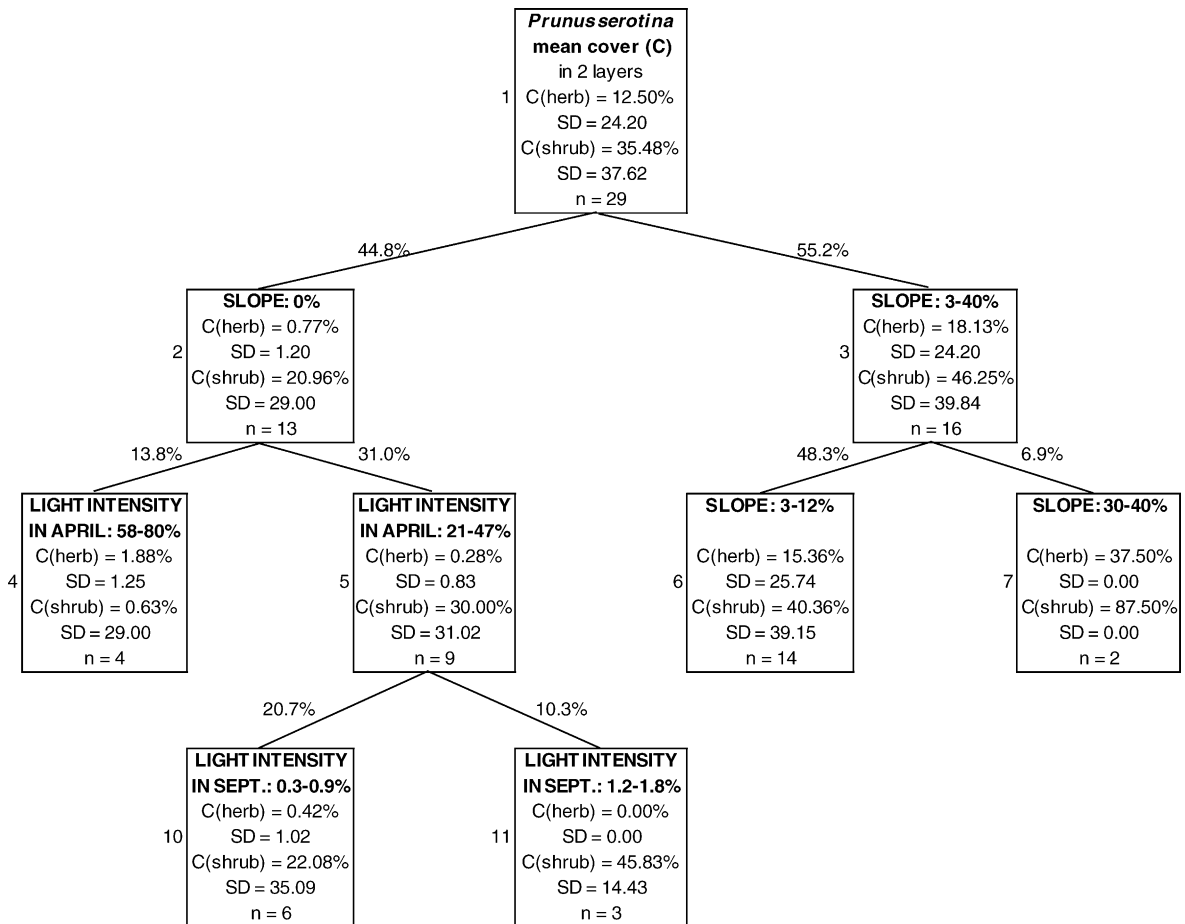


Fig. 5. Analytical model of studied predictor variables explaining variation in cover of *P. serotina*. C(herb) = cover in % in the herb layer; C(shrub) = cover in % in the shrub layer; S.D. = standard deviation in cover;  $n$  = number of stands. Percentages on the flow lines are the percentages of the total stands in each group.

on wet soils. The species was also restricted to the more acidic areas, with a lower nitrogen index. Versteynen (1991) also found that the opportunistic behaviour of the species is particularly striking on relative nutrient poor and acid soils which were disturbed (e.g. turned up, enriched, dried out). This is the case in our study area, where the acidic ( $3.5 < \text{pH H}_2\text{O} < 4.5$ ) and nutrient poor soil suffers from eutrophication, drainage and dramatic mechanical disturbance caused by modern forest management in all stands.

The abundance of black cherry in the shrub layer had a strong negative influence on the species richness of the herb layer, especially on the stress-tolerants,

while competitors were not significantly affected. Sartori (1988) also found a clear regression, if not disappearance, of the majority of indigenous species from the shrub and herbaceous layers under a *P. serotina* canopy, and he attributes this to the competition, however without specifying what kind of competition. According to Starfinger (1990b), this phenomenon may be either due to allelopathic interference between *P. serotina* and the herbaceous ground-cover plants, or the shade caused by this species, making the development of the ground flora more difficult.

*P. serotina* was found to be associated with many planted non-native trees, such as *C. sativa*, *L. decidua*,

*P. sylvestris*, *Pseudotsuga menziesii*, *Q. rubra* and *R. pseudacacia*. This is probably due to the fact that all of these are planted on the most acidic and nutrient poor soils. One of the most reliable indicator species was also the fern *P. aquilinum*. This was very frequently found together with *P. serotina*, although Horsley (1977) found that foliage extracts of *P. aquilinum* inhibited seed germination of black cherry. This suggests that soil from the upper horizons can moderate the toxicity of the herbaceous foliage extracts or that allelochemicals might be leachable instead of being bound on the soil complex. *R. fruticosus* was recognised as an indicator species for plots without *P. serotina*, which might be due to poor light conditions under the dense *Rubus* cover shading out *Prunus* seedlings, although this could also happen under a *Pteridium* canopy. In another study, Horsley (1993) highlighted that some fern cover had a dramatic impact on both the quantity and the quality of available light and that black cherry seedlings survived and grew poorly in the presence of fern foliage shade. In our study, light intensity was, together with slope, the most powerful predictor of the abundance of *P. serotina*. This substantiates the species' light requirement already mentioned in previous studies in its native range (Cottam, 1963; Auclair and Cottam, 1971; Gottschalk, 1985, 1987), but it does not validate the observations of Hough (1960) on the gap-phase behaviour of *P. serotina* as, in our study, the abundance of seedlings and saplings was much less in logging areas than under *Pinus* and *Quercus* stands, in spite of a higher light intensity. However, findings of Hough (1960) are not always supported. For instance, Husch (1954) observed that a complete removal of the forest on wide areas as in large-scale clear-cuttings resulted in far less *P. serotina*. The low abundance of *P. serotina* in the logging areas is not due to cutting as there is no active management of this species in the study area. We believe that competition with the lush herb vegetation developing in logging areas might play an important role in explaining the phenomenon. Indeed, the most abundant species in these areas is *R. fruticosus*, which shows a huge development, together with *Dryopteris dilatata*, *Holcus lanatus*, *Deschampsia cespitosa* and *Juncus effusus*. It could be that *P. serotina* seedlings are outcompeted by these species.

In the present study, we found a positive response of black cherry seedlings to light intensity between 58

and 80% of full light (April measurements at 120 cm), while saplings showed a negative response within this range. Between 21 and 47% of full light (April measurements at 120 cm), seedlings were poorly represented whereas saplings showed a quite high cover. Between 0.3 and 1.8% light (September measurements at ground level), seedlings were almost absent while saplings maintained a high abundance. This means that *P. serotina* shows a differential response to light intensity in function of the development stage, which would suggest that the species is heliophilous at the seedling stage and becomes a shade plant at the sapling stage. We can also assume that black cherry seedlings take advantage of the absence of overstory leaves in the early spring and that most of their development occurs during this short period without canopy. This is supported by the results of Horsley and Gottschalk (1993) who have pointed out that most height growth and leaf development of these seedlings occur during the several weeks between the appearance of leaves on understory seedlings and those of overstory trees.

According to Starfinger (1990b), who has studied *P. serotina* in its native and synanthropic range, the species can form a close shrub layer with only 10% of the daylight, and Oosterbaan (1977) observed in The Netherlands that, even with a light intensity of only 5%, its survival chance is scarcely influenced. In his study from Pennsylvania, Gottschalk (1985) observed that seedlings grow poorly under 8% light, that increasing light to levels above 20% will increase seedling growth, and that there were few differences between 20 and 94% light. Forest models of Pacala et al. (1996) showed that adult black cherry grows better than many other trees at only 10% light. Since these studies are based on growth rate, some differences with our results are expected. Furthermore, it might be that *P. serotina* does not only respond to light intensity but also to light quality. As the spectral distribution of light was certainly different in April (before the development of the canopy) than in September, because of selective spectral absorption of leaves, it may influence understory photosynthesis, growth and germination (Federer and Tanner, 1966). This seems to be confirmed by the different response of *P. serotina* to the overstory species. Black cherry was found to be significantly more abundant in *Pinus* stands compared to *Fagus* stands, and this in spite of a

significantly higher light intensity under the *Fagus* canopy. This may suggest that the spectral distribution of light would not be the same under the cover of *Pinus* or *Fagus*. This phenomenon has been pointed out for other tree species by Federer and Tanner (1966) in different oak, maple, pine and spruce stands in Wisconsin. The link between *P. serotina* and the overstory species could also be indirect, via birds and mammals which distribute seeds in their droppings and may have different behaviour patterns, frequenting different canopies to varying degrees. This relation is however not obvious in the present case because it does not explain why overstory types which are less visited by animals (pine stands) contain nevertheless more black cherry. Comparing Table 3 with Fig. 3, we can assume that *P. serotina* prefers pine and oak stands because soil pH and compaction, as well as mean light intensity in April, are somewhat lower in these stand types. This conclusion for light intensity seems worrying at first sight, knowing (from the literature) that *P. serotina* is a light-loving plant. Actually, it is not contradictory at all, and it confirms the usefulness of our cluster analysis, showing that black cherry in the shrub layer has a preference for a particular range of light intensity in April, i.e. 21–47% of full light. The mean values of light intensity calculated for pine and oak stands (where *P. serotina* is the most abundant) are precisely situated within this range.

Soil temperature in September accounted for 22% of the variance (although just below the significance level), with *P. serotina* showing a higher abundance when this parameter increases. One possible explanation is that it reflects its climatic requirements in its native range. In the Eastern United States, black cherry is known to have a better growth when July temperatures average a maximum of 27–29 °C and a minimum of 11–16 °C (Lull, 1968). These temperature ranges are much higher than what we have in our study area, which could explain the positive response of *P. serotina* to higher soil temperatures in our dataset.

In our study, *Prunus* abundance did not significantly vary with aspect. This might be due to a lack of data (8 plots versus 5 plots for north and south facing slopes, respectively), and because the somewhat higher light intensity on south facing slopes was not significantly different from this on north facing slopes (data not shown). However, this does not mean that the higher abundance of black cherry on sloping areas is

not related to light intensity. Indeed, the difference in light intensity between sloping and flat areas was globally much more pronounced and closer to the significance level (data not shown). So, there was globally more light on our sloping plots, which could explain the response of *P. serotina* for sloping areas.

## 5.2. Implications for forestry practices

The relationship between some environmental conditions and the presence or abundance of *P. serotina* has important implications for the control of this invasive species. The observed positive effect of increased light intensity on the abundance of *P. serotina* seedlings indicates that the species might benefit from stand thinning. This requirement for high light is of primary importance in applying regeneration cuttings if *P. serotina* is to be fought. The light requirement of the species suggests that *P. serotina* is unable to survive and mature without natural or man-made disturbance of the forest canopy (Cottam, 1963). Disturbance is known to enhance invasion of plant communities, but frequently it is the interaction between different disturbances that has the largest effect (Hobbs and Hueneke, 1992). In our study area, trees are usually planted in monocultural even-aged stands, thinned many times during the tree generation and harvested when mature. This forest management produces a combination of different kinds of disturbance, e.g. changes in soil water and nutrient content and a mechanical disturbance of the forest floor. So, one might expect *P. serotina* to be a very successful species in these circumstances. Management measures to reduce light level are necessary to ensure recruitment and enable the conservation of the native species pool. At present, stands are thinned every 4 years in the study area. It is thus suggested to increase this interval between two interventions. Black cherry's light requirement, however, limits its success in ecosystems that contain tree species with dense canopies such as beech or some maples (Starfinger, 1991). Although the light intensity is known to be much lower under a beech canopy than under pine and oak stands (Starfinger, 1990b), the present study exemplified that this is not always true as it depends on the structure and the age of the stands. In our study area, some of the monospecific *Fagus* plantations are old (between 150 and 200 years) even-aged stands,

where the light intensity is higher than in younger closer stands. This stand structure should be avoided. Adoption of a silvicultural system of irregular stands with mixed species with a dense canopy might hamper the development of *P. serotina* and allow a better conservation of indigenous forest species in the herb layer.

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