

Interaction between invasive and potentially invasive shrub species does not influence relationships between their ecological success and distance from propagule sources

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Abstract Although interactions between alien and native plant species are well studied, data on interactions between two co-existing alien species with respect to their invasibility are scarce. The aims of this study were (1) to evaluate three factors shaping abundance of the alien shrub species *Cornus alternifolia*: abundance of another alien (invasive) shrub species (*Prunus serotina*), type of tree stand (coniferous vs. broadleaved) and distance to propagule sources and (2) to assess the potential dispersal distance of the species studied. Densities of both species were assessed within 194 experimental plots (located in experimental plantations of trees) in Rogów Arboretum (Central Poland). *P. serotina* occurred on 79 and *C. alternifolia* on 33 of the 194 plots. The furthest distance of *C. alternifolia* from the propagule source was 338 m. *C. alternifolia* reached higher densities in

coniferous than broadleaved tree stands. Density of *C. alternifolia* depended on tree stand type and distance from the propagule source, but did not depend on density of *P. serotina*. Density of *C. alternifolia* decreased with increasing distance from the propagule source; however, this relationship was modified by the type of tree stand: densities were lower in broadleaved than in coniferous stands. The presence of the invasive species seems to neither facilitate nor limit the dispersal distance of *C. alternifolia*, as these two species differ in shade tolerance. The study also provided the first information about *C. alternifolia* potential invasiveness, because earlier this species was noticed only as casually escaping from cultivation in Slovakia.

Keywords Secondary invasion · *Prunus serotina* · *Cornus alternifolia* · Shade tolerance · Dispersal distance · Spread

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Introduction

Invasive species cause harmful consequences for biodiversity conservation and difficulties for management. Due to the longevity and size of woody species (Richardson and Rejmánek 2011; Rejmánek 2014), as well as their strong ability to modify habitat (transformers species sensu Richardson et al. 2000), invasive woody species can be especially damaging to the environment. Tree species (both alien and native) influence light availability (Knight et al. 2008; Niinemets 2010), mineral nutrient cycling (Augusto et al. 2002; Reich et al. 2005; Dauer et al. 2007; Mueller et al. 2012), soil acidity (Binkley and Valentine 1991; Binkley and Giardina 1998; Mueller et al. 2012), decomposition rate (Hobbie et al. 2006, 2007, 2010), fine root and leaf lifespans (Withington et al. 2006), ectomycorrhizal infections (Dickie et al. 2006; Trocha et al. 2012), and soil biota (Mueller et al. 2015, 2016). Modifying effects of invasive woody species on habitat was also reported from several biomes across the world (e.g., Vitousek 1990; Ehrenfeld 2003; Stohlgren and Rejmánek 2014; Castro-Díez et al. 2014; Menge and Chazdon 2016). Among woody species, some guilds are especially responsible for ecosystem change, e.g., nitrogen-fixing species (e.g., Ehrenfeld 2003; Rice et al. 2004; Castro-Díez et al. 2014; Jo et al. 2015) or coniferous trees planted on sites typical to broadleaved trees (e.g., Binkley and Valentine 1991; Augusto et al. 2002; Zerbe and Wirth 2006; Jagodziński et al. 2015).

Habitat invasibility depends on propagule pressure (Lonsdale 1999; Lockwood et al. 2005; Křivánek et al. 2006). This term describes availability of propagules, for example expressed as quantity of mature plants (Vanhellemont et al. 2009), cultivation intensity (Pyšek et al. 2009, 2015), distance to the nearest fruiting plant (Jagodziński et al. 2015), or propagule quality (Sinclair and Arnott 2015). Probability of occurrence and density of natural regeneration decreases with distance from the seed source (Riepšas and Straigytė 2008; Deckers et al. 2005; Terwei et al. 2013; Jagodziński et al. 2015). Propagule pressure is also connected with the presence of dispersal agents, in the case of species producing edible fruits, with presence of frugivorous birds. Behavior of dispersal agents may influence spread of some species—for example presence of coniferous tree stands as places for perching and defecation (Żywiec et al. 2013).

Accurate assessment of maximum dispersal distance is necessary for proper placement of species invasiveness within a naturalization-invasion continuum (Richardson and Pyšek 2006).

One of the most important consequences is higher competitive performance of alien species, which displace native species (Vitousek 1990; Lövei 1997; Rejmánek 2014). There are many studies concerning competition between alien and native plant species (Gorchov and Trisel 2003; Saccone et al. 2010; Robakowski and Bielinis 2011; Kawaletz et al. 2014; Sanderson and Antunes 2013; McShane et al. 2015). On the other hand, Davis (2003) argued that competition from introduced species is not an important cause of native species extinctions. However, in studies concerning relationships between invasive and native species, authors frequently focused only on competition between the alien and native species, and intraspecific competition, neglecting relationships between two invaders (e.g., Mangla et al. 2011; Rodríguez-Echeverría et al. 2013). Studies concerning relationships between two alien species are relatively rare, but essential to better understanding the competitive interactions among alien species, and increase our knowledge of secondary invasions (Gioria and Osborne 2014). It is especially important when occurrence of earlier-established invaders modifies environments in ways which facilitate dispersal distance of secondary alien species, according to the invasional meltdown concept (Simberloff and Von Holle 1999; Simberloff 2006; Gioria et al. 2011). In one case of herbaceous invasions, there is evidence of higher competitive ability of the secondary invader *Fallopia japonica*, over the primary invader *Gunnea tinctoria*, which was displaced by *F. japonica* over a few years (Gioria et al. 2011). In cases of competition between two invaders, higher morphological plasticity is one of the reasons for superior competitive ability of one species (Mony et al. 2007).

The aim of this study was to assess the performance of the alien shrub *Cornus alternifolia*. We investigated interactions among three factors: effects of plantations of ecologically alien (coniferous) tree species, competition with invasive shrub (*Prunus serotina*), and distance from propagule source. We hypothesized that the relationship between density of *C. alternifolia* and distance from the propagule source will be modified by density of *P. serotina* and by the type of the tree stand, which reflects habitat modification by forest

management. Our secondary aim was to evaluate the maximum dispersal distance of *C. alternifolia* to assess its potential invasiveness.

Materials and methods

Species studied

Cornus alternifolia L. f. is a member of the Cornaceae family with a natural range in eastern North America. *Cornus alternifolia* is a small tree, reaching heights up to 9 m. Within its native range *C. alternifolia*, due to its shade tolerance, occurs in the understory of several types of forests, both deciduous (especially with *Acer rubrum*, but also with *Betula alleghaniensis*, *Ulmus americana*, *Fraxinus* spp., *Populus* spp., and *Quercus* spp.) as well as mixed and coniferous (usually with *Abies balsamea*, *Picea rubens* and *Pinus taeda*) most frequently on well-drained deep soils. Usually *C. alternifolia* co-occurs with *Prunus serotina*. This species can reproduce by root suckers and seeds, which are dispersed by gravity and animals (Coladonato 1994). Wide geographical and climatic range, together with its ornamental value, allows *C. alternifolia* to be cultivated in several countries, which can favor risk of invasion (Pyšek et al. 2009; Rejmánek 2014). However, this species was never found escaping from cultivation, except in Slovakia (Medvecká et al. 2012), where it was treated as casual and not invasive in natural ecosystems.

Prunus serotina Ehrh. is a tree in the Rosaceae family from eastern North America. *P. serotina* occurs mainly in deciduous and mixed forests with *Acer rubrum* and *A. saccharum*, *Betula alleghaniensis*, *B. lenta*, *Carya* spp., *Picea* spp., *Pinus taeda*, *P. strobus* and other *Pinus* spp., *Populus* spp., and *Quercus* spp. (Burns and Honkala 1990). This species was introduced into Europe as an ornamental shrub and for production of high quality timber. When timber production failed, it was widely planted to improve soil quality. It most frequently has a shrub form, in contrast to its native range, where it grows into a tall tree able to produce valuable timber (Burns and Honkala 1990; Starfinger et al. 2003; Halarewicz and Żolniercz 2014). *Prunus serotina* is one of the most widespread invasive woody species in Europe, especially in coniferous forests (e.g., Chabrerie et al. 2008;

Knight et al. 2008; Vanhellemont et al. 2009; Jagodziński et al. 2015).

Area of the study

Rogów Arboretum (51°49'N, 19°53'E; 189 m a.s.l.) is the Forest Experimental Station of Warsaw University of Life Sciences (SGGW) with collections of ornamental woody plants and experimental forestry stands of 75 species of trees (Jagodziński et al. 2015). Within the Rogów Arboretum, all plots are located in potential habitat of fertile deciduous forest (potential natural vegetation is *Tilio-Carpinetum*, a subcontinental oak-lime-hornbeam forest). Soil parental material in the arboretum is homogenous. In the study area, there are gray-brown podzolic forest soils with horizons O-A-Eet-Bt-C (Czępińska-Kamińska et al. 1991; Jagodziński and Banaszczak 2010). Nevertheless, plantation of ecologically and geographically alien, usually coniferous species (Jagodziński et al. 2015), has led to increased litterfall of acidic needles, decreased soil pH, leaching of soil nutrients (e.g., Binkley and Valentine 1991; Augusto et al. 2002) and increased light availability (Knight et al. 2008). The nearest meteorological station in Strzelno (covering the last 55 years) had a mean annual temperature of 7.2 °C (mean January temperature was −3.2 °C and mean July temperature was 17.3 °C), mean annual precipitation of 596 mm, and mean growing season length of 212 days (Jagodziński and Banaszczak 2010).

The original and unique propagule source of *Prunus serotina* in Rogów Arboretum is a tree stand planted in 1932 in one plot in the central part of the arboretum that had 63 mature trees in 2012 (Jagodziński et al. 2015; Fig. 1). From this one stand (0.14 ha), *P. serotina* dispersed through the arboretum and beyond. This process was clearly visible because this species has not been planted in the surrounding neighborhood (within 500 m) of the arboretum. *Cornus alternifolia* was planted in three plots. The primary propagule source of *C. alternifolia* was a 0.07 ha tree stand of *Acer saccharum* and *Castanea sativa*, where *C. alternifolia* was planted in 1973. In 2012, 747 *C. alternifolia* shrubs were present within this plot, including 583 up to 0.5 m, and 164 over 0.5 m height. This species was also planted in 1976 (four plants) and in 1977 (three plants) in two different

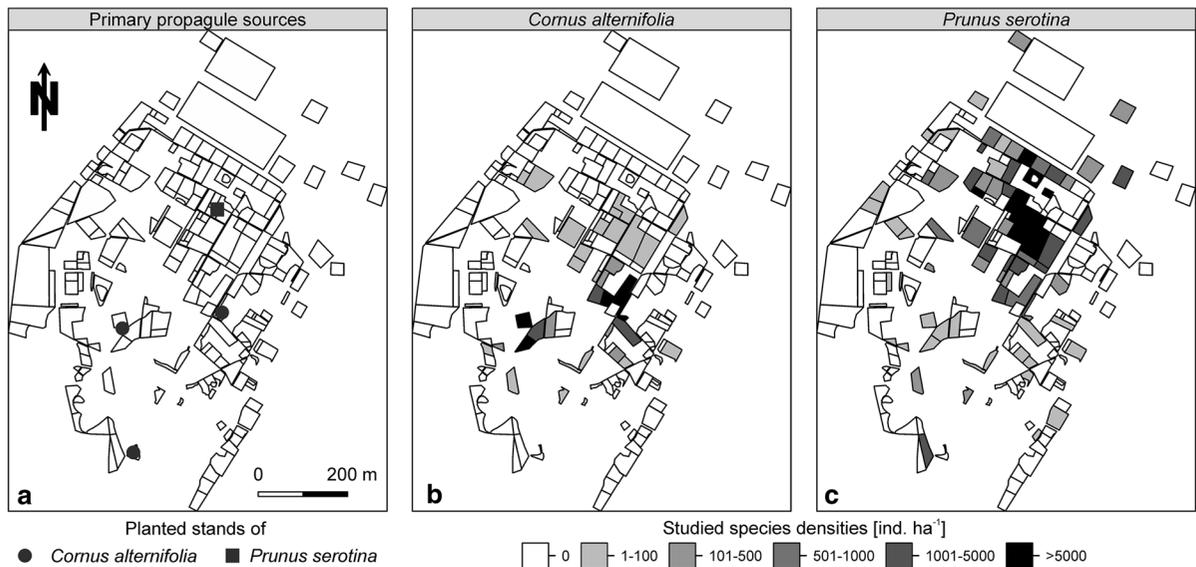


Fig. 1 Study plots in Rogów Arboretum: **a** localities of first introduction of *Prunus serotina* (square) and *Cornus alternifolia* (circles); **b** and **c** densities of both species studied

stands, located c.a. 300 m from each other, but not within study plots (Fig. 1).

Both species studied were introduced at different times and with different numbers of seedlings, which resulted in different propagule pressures; thus, one may be concerned that this influenced the results and their interpretation. However, due to the high number of cultivated taxa, providing a wide range of modifications of environmental conditions by alien tree species, historical documentation and homogenous soil conditions, Rogów Arboretum is a very good place to study alien species of trees. Previous studies have examined the dispersal distance of alien species (Jagodziński et al. 2015) and how they drive species diversity of plants, fungi, and invertebrates (Jagodziński et al. 2011; Kasprowicz et al. 2011; Skorupski et al. 2011; Wojterska et al. 2012; Kałucka et al. 2013).

Methods

During the study in September 2012, we assessed the density of both *C. alternifolia* and *P. serotina* within 194 plots, all of which were experimental stands of 110 tree species (Online Resource 1). Of these 194 plots, 95 were plots with coniferous tree species, 53 with broadleaved species, and 46 were mixed tree stands. The total area studied was 25.2 ha, with an average plot size of 0.13 ± 0.02 ha (minimum plot

size: 0.01 ha; maximum plot size: 2.1 ha). Plot sizes differed, as experimental stands have been established over time since the 1920s, and during establishment of the arboretum, it had not been considered as a site for studies on dispersal distance of alien species. Plot sizes and localities were obtained from Arboretum land survey documentation. We excluded from the study plots where the understory was mowed, as well as those with single trees and shrubs and ornamental collections. The density of both *C. alternifolia* and *P. serotina* was calculated in two height classes: low shrubs (i.e., plants up to 0.5 m height) and tall shrubs (over 0.5 m). This division was applied after Jagodziński et al. (2015), where plants lower than 0.5 m performed differently than tall shrubs.

We examined whether density of *C. alternifolia* depends on dispersal limitation, competition with *P. serotina* and tree stand type. Dispersal limitation was described by distance to the nearest seed source, which was assumed to be one of the localities of introduction mentioned above, because only at those locations has fruiting and seed dispersal been observed and maintained for a relatively long time. Competition with *P. serotina* was measured by its abundance (density) on each plot. Habitat type, due to high variability of tree species planted in the arboretum, was described by tree stand type (broadleaved, coniferous, or mixed tree stand). Due to non-normal distributions, uneven

variance and high number of zero values, nonparametric Kruskal–Wallis tests were performed to check significance of differences in mean density of *C. alternifolia* between coniferous and broadleaved stands. Mixed tree stands were excluded from further analysis due to lack of *C. alternifolia*. We also assessed the influence of all these factors using generalized linear models based on the negative binomial distribution, as this approach is less biased than traditional linear models computed from log-transformed variables (O’Hara and Kotze 2010) and can overcome problems with long-tailed distributions. We tested models with all combinations of the three factors studied, both additive and interaction variants for low shrubs, for tall shrubs and for the overall density (low + tall shrubs). The best fitted model was chosen based on Akaike’s Information Criterion (AIC). All analyses were performed in R software (R Core Team 2015), and the negative binomial model was performed using the *glm.nb()* function from the MASS package (Venables and Ripley 2002).

Results

Cornus alternifolia occurred in 33 of 194 experimental plots, including 27 of 95 coniferous tree stands and six of 53 broadleaved tree stands (Table 1). *Cornus alternifolia* was not found in mixed tree stands. In total, 4330 individuals of *C. alternifolia* were counted, of which 78.3% were low shrubs and

21.7% were tall shrubs. The highest densities were found in a stand of *Acer saccharum* and *Castanea sativa*, which was the place of first introduction (12,450.0 ind. ha⁻¹), *Carya laciniosa* (9140.0 ind. ha⁻¹; 16 m from the propagule source), *Abies koreana* (5813.3 ind. ha⁻¹; 19 m), and two stands of *Abies cephalonica* × *nordmanniana* (5166.7 and 2225.0 ind. ha⁻¹, and 17 and 47 m from the propagule source, respectively). The furthest distance from the seed source at which *C. alternifolia* was found and was the stand of *Abies alba* at 338 m, and its density in this plot was 16.7 ind. ha⁻¹.

Density of *C. alternifolia* was statistically significantly higher in coniferous than in broadleaved tree stands ($P < 0.05$; Table 1). Although mean densities were higher in broadleaved tree stands, medians were equal in both types of tree stands (0 ind. ha⁻¹), and the 3rd quartile was higher in coniferous tree stands (0 ind. ha⁻¹ in broadleaved tree stands and 9 ind. ha⁻¹ in coniferous tree stands).

Overall density of *C. alternifolia* was explained by the model with four factors: distance from the propagule source, type of tree stand, *P. serotina* density, and interaction between these last two factors (Table 2). All factors except *P. serotina* density were statistically significant ($P < 0.001$). Density of *C. alternifolia* low shrubs was explained by the same parameters. The density of tall shrubs was best explained by a simpler model, including only distance from the propagule source and *P. serotina* density; however, effects of these covariates were low.

Table 1 Occurrence and density of height classes of *Cornus alternifolia* in the Rogów Arboretum experimental plots ($n = 194$) within coniferous and broadleaved tree stands

Features	Overall	Low shrubs (<0.5 m height)	Tall shrubs (>0.5 m height)
Number of plots with <i>C. alternifolia</i>	33	31	19
Mean density [ind. ha ⁻¹]	210.1	168.2	41.9
SE	89.9	73.0	19.0
Max density [ind. ha ⁻¹]	12,450.0	9716.7	2733.3
Mean density [ind. ha ⁻¹] in			
Coniferous stands	198.5 ^a	164.8 ^a	33.6 ^a
SE	87.7	80.4	15.3
Broadleaved stands	398.4 ^b	308.7 ^b	89.7 ^a
SE	278.2	216.6	61.6
<i>P</i>	0.0186	0.0115	0.1675
χ^2	5.5404	6.3858	1.9049

Values (mean ± SE) with the same letter within rows are not statistically different, according to Kruskal–Wallis tests

Table 2 Results of generalized linear models (GLM) with negative binomial distributions explaining relationships between density of *Cornus alternifolia*, distance (from the propagule source), tree stand type (coniferous or broadleaved), and *Prunus serotina* density

Variable	Estimated	SE	<i>t</i> -value	<i>P</i>
Overall density				
(Intercept)	6.9660	0.7755	8.983	<0.001
Distance	−0.0196	0.0035	−5.622	<0.001
<i>P. serotina</i> density	0.0000	0.0001	0.159	0.874
Tree stand type	−5.5270	0.8870	−6.231	<0.001
<i>P. serotina</i> density × tree stand type	0.0141	0.0016	8.946	<0.001
AIC = 609.13	Log-likelihood = − 289.6			
Low shrubs (<0.5 m height)				
(Intercept)	6.6890	0.7946	8.418	<0.001
Distance	−0.0187	0.0036	−5.231	<0.001
<i>P. serotina</i> density	0.0000	0.0001	0.067	0.947
Tree stand type	−6.0250	0.9496	−6.344	<0.001
<i>P. serotina</i> density × tree stand type	0.0148	0.0016	9.087	<0.001
AIC = 570.51	Log-likelihood = − 279.3			
Tall shrubs (>0.5 m height)				
(Intercept)	7.4732	0.9081	8.229	<0.001
Distance	−0.0671	0.0095	−7.082	<0.001
<i>P. serotina</i> density	0.0004	0.0001	3.107	0.002
AIC = 336.08	Log-likelihood = − 164.0			

Discussion

Our findings show that *C. alternifolia* is able to self-reproduce, because on five plots we found plants which were fruiting with small seedlings present. This species spreads successfully within Rogów Arboretum. Therefore, according to alien species classifications (Richardson et al. 2000; Pyšek et al. 2004), *C. alternifolia* is an invasive species, because it is able to reproduce and spread >100 m over <50 years. However, this definition come from invasion ecology, and contrary to the definition provided by the IUCN, and does not take into account economical/environmental impact of an invasive species (Richardson et al. 2011). Surrounding forests could be able to host *C. alternifolia*, as they are also mostly plantations of coniferous or mixed tree stands in habitats of deciduous forests, despite the fact that they are dominated by a native species—*Pinus sylvestris*. However, *C. alternifolia* has not yet colonized natural plant communities in the neighborhood of the arboretum, and has not been seen at all outside the arboretum. In addition, *C. alternifolia* was not found in plots with mixed tree stands, especially those similar to surrounding forests. Therefore, according to the conservation biology definition, *C. alternifolia* may not be considered invasive, due to

lack of confirmed impact on biodiversity. Nevertheless, its ability to spread due to its dispersal mode (zoochory) and ornamental value, resulting in its popularity in horticulture, and therefore increasing propagule pressure, are traits indicative of invasiveness (Pyšek et al. 2009; Rejmánek 2014). It is also possible that the *C. alternifolia* in Rogów represents the end of the ‘lag phase’ of biological invasion, as this last for an average of 131 years in cases of alien shrub species (Kowarik 1995). The main factor limiting the dispersal distance of *C. alternifolia* may be dispersion of seed sources from three scattered locations of only a few specimens; thus, the rate of dispersal distance may increase when more individuals start reproducing. Similarly, dispersal distance of *P. serotina* in Europe was more connected with planting intensity than with its dispersal traits (Starfinger et al. 2003; Vanhellemont et al. 2009).

The relationship between two alien species tested here could not be interpreted without taking into account other factors limiting their dispersal distance, e.g., distance from the propagule source (Deckers et al. 2005, 2008; Pairon et al. 2006). If *C. alternifolia* density was positively correlated with *P. serotina* density, it could be interpreted as the occurrence of one alien species facilitating secondary invasion,

following the invasional meltdown concept (Simberloff and Von Holle 1999; Simberloff 2006). However, in the final model, density of *P. serotina* was not statistically significant. Densities of both species studied depended on distance from propagule source and tree stand type (Jagodziński et al. 2015), indicating that both species colonize similar plots; however, there were no interactions between them. This may show that the effect of invasional meltdown (Simberloff and Von Holle 1999; Simberloff 2006) is rather connected with tree stand species. Both *C. alternifolia* (this study) and *P. serotina* (Jagodziński et al. 2015), reached higher densities in plantations of coniferous species. Introduction of coniferous species, which are ecologically alien (according to potential natural vegetation) and in most cases geographically alien, is also an introduction of alien species, which resulted in changes of ecosystem properties (transformers sensu Richardson et al. 2000). Although we did not measure this transformation, there are a lot of studies describing how coniferous trees planted in habitats of broadleaved forests affect light conditions (e.g., Knight et al. 2008; Niinemets 2010; Mueller et al. 2016) or soil chemistry (e.g., Binkley and Valentine 1991; Reich et al. 2005; Mueller et al. 2012), which generally facilitated invasion of alien species (Obidziński and Symonides 2000; Chmura 2004, 2014; Zerbe and Wirth 2006; Paritsis and Aizen 2008).

Both species studied coexist in the arboretum, similar to their native range (Burns and Honkala 1990; Coladonato 1994). However, *C. alternifolia* naturally occurs only in the same habitats in which *P. serotina* also occurs, often under its canopy, and has a higher shade tolerance (Burns and Honkala 1990; Uchytíl 1991; Coladonato 1994; Niinemets and Valladares 2006), which may explain its ecological success in plots invaded by *P. serotina*. Different shade tolerance of the species studied explains lack of significant influence of *P. serotina* on *C. alternifolia* density.

Although due to a high number of zero values, information about *C. alternifolia* ecological preferences for tree stands is misleading, and densities of *C. alternifolia* are statistically significantly higher in coniferous tree stands (Table 1). Together with higher frequency in coniferous tree stands (27/95 vs. 6/56), this may show that *C. alternifolia* occurs in coniferous tree stands rather than in broadleaved stands, similar to

P. serotina (Jagodziński et al. 2015). It also confirms observations of Zerbe and Wirth (2006), which found that tree stands of *Pinus sylvestris* host numerous alien species, including many invasive species. This case may also be considered as an invasional meltdown—plantations of ecologically (and mostly also geographically) alien coniferous species facilitate dispersal distance of secondary invaders—*P. serotina* (Jagodziński et al. 2015) and *C. alternifolia*, and both species invade the most invisable stands. Tree stand invisibility is mainly connected with resource availability (Richardson et al. 2011), especially light (Knight et al. 2008). Moreover, habitats with high levels of resource availability are more colonized by both native, as well as alien species (Stohlgren et al. 2006). This theory may explain why both species studied colonized similar tree stands.

Conclusions

The study found that both alien species coming from the same geographical range and from similar plant communities (Burns and Honkala 1990) colonize similar tree stand types, despite the spatiotemporal difference in propagule pressure. Density of the secondary invader, *C. alternifolia*, depends on tree stand type, distance from the propagule source, and does not depend on density of invader—*P. serotina*. Density of *C. alternifolia* decreased with the increasing distance from the propagule source, and in broadleaved stands, it was lower than in coniferous stands. *C. alternifolia* has shown the same pattern of relationships between distance from the propagule source and tree stand type as for *P. serotina* in an earlier study (Jagodziński et al. 2015); habitats invaded by the primary invader seem to be also suitable for the secondary potential invader. The primary invader seems to neither facilitate nor limit the dispersal distance of *C. alternifolia*, as these two species differ in shade tolerance. *C. alternifolia* is able to spread up to 338 m from the introduction place within 39 years, which fulfills the criterion of invisibility, according to Richardson et al. (2000). The study also provided the first information about spontaneous spread of *C. alternifolia*, because earlier this species was noticed only as a casual escape from cultivation in Slovakia, and only in ruderal habitats (Medvecká et al. 2012).

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