Botanica SERBICA 43 (2): (2019) 175-186

Original Scientific Paper

Congeneric comparison of allelopathic and autotoxic effects of four *Solidago* species

Birutė Karpavičienė[1]*, Julija Danilovienė[1] and Roberta Vykertaitė[2]

1 Institute of Botany, Nature Research Centre, Žaliųjų Ežerų 49, 08406 Vilnius, Lithuania
2 Institute of Biosciences, Life Sciences Centre, Saulėtekio 7, 10257 Vilnius, Lithuania

ABSTRACT: The invasive species *Solidago canadensis* and *S. gigantea* are known for having the potential to inhibit their neighbours through allelopathy. However, there are no data on allelopathic properties of the natural interspecific hybrid *S.* ×*niederederi* and no investigations comparing the allelopathic potential of native and invasive *Solidago* species. We therefore studied the allelopathic effect of aqueous leaf extracts of *S. virgaurea*, *S. canadensis*, *S. gigantea* and *S.* ×*niederederi* on two congeneric pairs of species (*Festuca* and *Solidago*) occurring naturally in communities with the tested *Solidago* species. Germination and seedling growth of *Festuca rubra* were inhibited by all *Solidago* extracts more than were those characteristics of *F. pratensis*, while *S. canadensis* was more sensitive to its own and congeneric extracts than was *S.* ×*niederederi*. The effect of leaf type (green or withered) on *Festuca* seedling growth was target species-specific, while seed germination was more suppressed by green leaf extracts. The results of this study do not support the hypothesis that invasive plant species have stronger persistent allelopathic effects on native plants compared to their native congeners.

Keywords: allelopathy, germination, inhibition, invasive plants, *Solidago*

Received: 19 July 2019 Revision accepted: 18 September 2019

UDC: 582.998.1:581.524.2: 581.524.13:[582.542.11: [631.547.1+581.14]]
DOI: https://doi.org/10.2298/BOTSERB1902175K

INTRODUCTION

Nowadays, approximately 6.2 new species capable of naturalisation arrive each year in Europe (Lambdon *et al*. 2008). Not all introduced species establish into new communities and, moreover, of those that successfully establish, a large number become naturalised in the resident community rather than an invasive one (Eppstein & Molofsky 2007). The success of alien species in new territories depends on multiple factors acting in all spatiotemporal stages of invasion: transport, colonisation, establishment and landscape spread (Theoharides & Dukes 2007). At the species level, success of invasion is ensured by higher values of performance-related traits characterising physiology, leaf-area allocation, shoot allocation, growth rate, size and fitness in comparison with non-invasive plant species (van Kleunen *et al*. 2010). Invasive plants tend to have small seeds, short juvenile periods and vegetative reproduction (Kolar & Lodge 2001); greater phenotypic plasticity (Daehler 2003); or allelopathic properties (Kruse *et al*. 2000).

Solidago canadensis L. and *S. gigantea* Aiton., two North American goldenrods, are highly invasive species whose rapid spread poses a threat to seminatural habitats in Europe (Weber 1998). Beyond direct competitive interactions, goldenrods have the potential to interact indirectly with their neighbours through allelopathy (Pisula & Meiners 2010). Allelopathy is defined as any direct or indirect harmful effect of one plant on another through production and release of chemical compounds (Rice 2012). Such a chemical compound or group of compounds released from invasive plant parts by leaching, root exudation, volatilisation or residue decomposition inhibits the growth and germination of members of the recipient plant community (Zedler & Kercher 2004; Abhilasha *et al*. 2008). The sensitivity to allelochemicals depends on the demographic stage, and the strongest allelopathic inhibition by exotics may occur

*correspondence: birute.karpaviciene@gamtc.lt

during germination and early establishment (Orr *et al.* 2005). Allelopathy is usually interspecific (Singh *et al.* 2010), while intraspecific allelopathy, commonly known as autotoxicity, occurs when toxic chemical substances released by a plant into the environment inhibit germination and growth of the same plant species (Singh *et al.* 2010; Li *et al.* 2016).

Commonly, in experiments on the allelopathic effect of invasive *Solidago* species, extracts from fresh or dried green leaves (Pisula & Meiners 2010; Wang *et al.* 2016), fresh or dried whole aboveground biomass (Sekutowski *et al.* 2012; Yuan *et al.* 2013; Baličević *et al.* 2015) or roots and rhizomes (Yuan *et al.* 2013; Pal *et al.* 2015) are used. However, according to Orr *et al.* (2005), the use of dead plant material in the study of allelopathic potential is considered more realistic than use of fresh or dried living plant parts. Moreover, older leaves of *Solidago* naturally die from the bottom up as the growing season proceeds (Weber 2000; Weber & Jakobs 2005), but no research has been done to ascertain the allelopathic potential of senescent plant material of *Solidago*.

For the most part, target species used to evaluate the potential allelopathic effects of invaders have been predominantly crop species and other exotic weeds rather than native species (Hierro & Callaway 2003). Similarly, in studies of the allelopathic properties of *Solidago* species, crop species and weeds are predominant, while native species are rarely involved (Abhilasha *et al.* 2008; Yuan *et al.* 2013).

In most cases, single invasive *Solidago* species, *S. canadensis* (Abhilasha *et al.* 2008; Yuan *et al.* 2013; Wang *et al.* 2016) or *S. gigantea* (Sekutowski *et al.* 2012; Baličević *et al.* 2015; Ravlić *et al.* 2015), have been studied for their allelopathic properties, and more rarely two or more invasive species were compared (Butcko & Jensen 2002; Gruľová *et al.* 2016). The congeneric approach involving comparative studies of exotic species with natives in the same genus may provide circumstantial evidence for allelopathy in exotic invasions (Inderjit *et al.* 2008). However, there is only one congeneric study on the inhibitory effect of invasive *Solidago canadensis* and native *S. decurrens* (Zhang *et al.* 2010). Moreover, allelopathic properties of native *S. virgaurea* have been tested only on germination of some crop species (Kaczmarek *et al.* 2012), while allelopathic properties of the natural interspecific hybrid *S. ×niederederi* have not been studied at all.

We conducted a congeneric-based test of the allelopathic effect of native and invasive *Solidago* species on two congeneric pairs of target species occurring naturally in communities with the tested *Solidago* species. One pair of target species included two native *Festuca* species, while the second pair consisted of invasive *Solidago canadensis* and its interspecific hybrid *S. ×niederederi*. We used aqueous extracts of green and withered leaves in the *Festuca* germination experiment and aqueous extracts of green leaves in the *Solidago* germination experiment.

The following questions were addressed: (1) Does the inhibitory effect differ between extracts from dried green and withered leaves? (2) Do the invasive *Solidago* species differ from the native ones in their allelopathic potential? (3) Are germination and early seedling growth of invasive *Solidago* species sensitive to extracts of intraspecific and intrageneric origin?

MATERIALS AND METHODS

Plant material. Four species of goldenrods were included in this study: *Solidago canadensis*, *S. gigantea*, *S. ×niederederi* Khek and *S. virgaurea*. Two of these (*S. canadensis* and *S. gigantea*), the North American species, belong to the most common invasive plant species of Europe and have achieved a large range since their introduction (Weber 2011). *Solidago ×niederederi* is a natural hybrid between *S. canadensis* and *S. virgaurea*, which is the only *Solidago* species native to Europe (Szymura & Szymura 2013). According to Pyšek *et al.* (2004), natural hybrids of native and invasive species are considered as alien in the sense of not having been in the region before agriculture.

The plant material was collected from abandoned fields in the northern part of Vilnius. Coordinates of sampling locations were N 54°44'59", E 25°13'51" for *S. gigantea*; and N 54°48'13", E 25°16'35" for all other species. Two types of leaves were sampled from the stems of each *Solidago* species: live green leaves located on the upper part of stems (green), and withered dark-brown leaves located on the lower part of stems (withered). For each species, leaves from at least 15 plants were collected and air-dried. Seeds of *S. canadensis* and *S. ×niederederi* were collected, air- dried and kept in paper bags until the *Solidago* germination experiment.

Extract preparation. Extracts were made from 25 g of dried and grinded leaves placed in 250 mL of distilled water and kept for 24 h at room temperature. Extracts were strained through muslin cloth and after that through filter paper. Stock solutions of 100 and 50% concentration of both types of leaves were used in the *Festuca* germination experiment, while only extracts of green leaves were used in the *Solidago* germination experiment.

***Festuca* germination experiment.** Two common native species (*Festuca pratensis* Huds. and *F. rubra* L.) were used as the target species. Three replicates were used for each treatment combination (four extract species × two leaf types × two extract concentrations × two test species × three replicates) and three replicates of distilled water × two test species served as a control. A total of 102 sterile Petri dishes (9 cm in diameter) were prepared, 51 dishes per each *Festuca* species. Fifty seeds (caryops-

es) of *Festuca* were spread on two-layer filter paper in each Petri dish. At the beginning, 5 mL of each of the treatment solutions was added. Throughout the entire experiment, distilled water was added as necessary to keep the filter paper moist. The germinated seeds in each Petri dish were counted after 14 days. All germinated seeds and seedlings of each Petri dish were air-dried and weighed with an accuracy of 0.0001 g.

***Solidago* germination experiment.** Two *Solidago* species (*S. canadensis* and *S.* ×*niederederi*) were used as target species. Four replicates were used for each treatment combination (two target species × four extract species × three/six extract concentrations × four replicates) and four replicates of distilled water for each target species served as a control. Stock solutions of green leaves of 100, 50, 10, 5, 1 and 0.5% concentration were used in the *S. canadensis* germination experiment, while stock solutions of only 5, 1 and 0.5% concentration were used in the *S.* ×*niederederi* germination experiment. The scope of this experiment was limited by scarce production of seeds in this hybrid species (Migdałek *et al.* 2014). A total of 152 sterile Petri dishes (9 cm in diameter) were prepared. Thirty seeds (cypselae) of target species were spread on two-layer filter paper in each Petri dish. At the beginning, 5 mL of each of the treatment solutions was added. Throughout the entire experiment distilled water was added as necessary to keep the filter paper moist. The number of germinated seeds in the control and variants with the highest extract concentrations (100, 50, 10%) was counted daily, a seed being considered to have germinated when the radicle emerged. After 10 days, the total percentage of germination (PG), length of radicles (RL) and length of hypocotyls (LH) of seedlings were measured under a Nikon SMZ 800 stereomicroscope with Nis Elements 3.22 software. Values of RL and LH were measured only for control and samples treated with the lowest extract concentrations (0.5, 1 and 5 g L^{-1}) because of the small number of seedlings in the treatments with higher extract concentrations.

Data analysis. In performing data analysis, PG, RL, HL and seedling biomass (SB) were standardised with the mean of the control treatment (distilled water) of each *Festuca* species by calculating natural logarithmic response ratios (LnRR) according to Goldberg & Scheiner (2001):

$$LnRR = \ln (PT/MC);$$

where PT is the parameter value of the treated sample and MC is the mean value of the control treatment.

Response ratios (RR) without calculation of the natural logarithm were used for results of the *Solidago* germination experiment because of zero-value occurrence among the results.

To compare LnRR or RR among the treatments, we used a factorial ANOVA to analyse the effect of *Solidago* species, leaf type, concentration and target species. Additionally, in all cases, to detect treatment effects, we performed a separate factorial ANOVA for each target species. In case of significant interactions, the t-test was used to test differences between mean values of treatments.

RESULTS

Effect on *Festuca* germination. Values of PG did not differ between *Festuca* species in the control (mean ± SE: 84.5 ± 2.1 and 88.7 ± 4.8% for *F. rubra* and *F. pratensis*, respectively, $p = 0.475$ t-test). However, target species had a significant effect on PG when *Solidago* leaf extract solutions were added (Table 1). It turned out that PG was also affected by leaf type and extract concentration, while the effect of the *Solidago* species used for extracts was insignificant.

When *Festuca* species were analysed separately, the effect of the *Solidago* species was significant for PG of *F. pratensis* (Table 2) and insignificant for PG of *F. rubra* (Table 3). However, when leaf type was taken into account, a significant difference in extract effect on PG was found between *Solidago* species only for withered leaves. The inhibitory effect of *S. virgaurea* and *S.* ×*niederederi* withered leaf extracts was significantly stronger than the effect of *S. canadensis* extracts ($Z = 2.96$, $p = 0.031$ and $Z = 2.86$, $p = 0.042$, respectively). The effects of leaf type and extract concentration were significant for both target species (Table 2). The green leaf extracts had a stronger inhibitory effect on PG than the withered leaf extracts [Figs. 1 & 2; $p = 0.007$ and $p = 0.001$ (t-test) for *F. pratensis* and *F. rubra*, respectively]. The highest concentration of green leaf extracts of all *Solidago* species significantly reduced PG of *F. rubra* from 36.1 to 42.8% on average (extracts of *S. canadensis* and *S.* ×*niederederi*, respectively), while the highest concentration of green leaf extracts reduced PG of *F. pratensis* from 17.9 to 30.1% on average (extracts of *S. gigantea* and *S.* ×*niederederi*, respectively). The effect of withered leaf extracts was insignificant for PG of *F. pratensis*, while the highest concentration of withered leaf extracts significantly reduced PG of *F. rubra* from 16.3 to 22.7% on average (extracts of *S.* ×*niederederi* and *S. canadensis*, respectively).

Effect on *Festuca* seedling biomass. Seedling biomass (SB) differed between *Festuca* species in the control (mean ± SE: 1.54 ± 0.17 and 2.27 ± 0.19 mg for *F. rubra* and *F. pratensis*, respectively; $p < 0.001$, t-test) and in variants where *Solidago* leaf extract solution was added. The value of SB was also affected by leaf type and extract concentration (Table 1). However, the effect of *Solidago* species was insignificant in all cases, regardless of whether *Festuca* species were analysed together or separately. When *Festuca* species were analysed separately,

Table 1. Effects of *Solidago* species, *Festuca* as target species, leaf type and aqueous extract concentration on the natural-logarithm response ratio (LnRR) of percentage germination (PG) and seedling biomass (SB). df = degree of freedom, MS = mean sum of squares. Significant effects ($p < 0.05$) are given in bold.

Source of variation	df	LnRR (PG)			LnRR (SB)		
		MS	F	p	MS	F	P
Intercept	1	**2.669**	**232.44**	**< 0.001**	**6.057**	**586.55**	**< 0.001**
Solidago species (S)	3	0.006	0.50	0.681	0.009	0.84	0.475
Festuca species (F)	1	**0.067**	**5.81**	**0.019**	**0.961**	**93.07**	**< 0.001**
Leaf type (L)	1	**0.479**	**41.68**	**< 0.001**	**0.087**	**8.47**	**0.005**
Concentration (C)	1	**0.901**	**78.46**	**< 0.001**	**0.147**	**14.25**	**< 0.001**
S*F	3	0.031	2.68	0.054	0.016	1.56	0.209
S*L	3	0.010	0.86	0.467	0.001	0.09	0.965
F*L	1	**0.049**	**4.31**	**0.042**	**0.124**	**12.04**	**0.001**
S*C	3	0.003	0.22	0.880	0.015	1.48	0.228
F*C	1	**0.190**	**16.52**	**< 0.001**	0.020	1.93	0.170
L*C	1	**0.098**	**8.55**	**0.005**	0.000	0.05	0.831
S*F*L	3	0.010	0.88	0.456	0.022	2.17	0.100
S*F*C	3	0.004	0.37	0.777	0.005	0.47	0.705
S*L*C	3	0.005	0.40	0.757	**0.041**	**3.93**	**0.012**
F*L*C	1	0.003	0.28	0.601	0.005	0.50	0.481
Error	64	0.011					

Table 2. Effects of *Solidago* species, leaf type and aqueous extract concentration on the natural-logarithm response ratio (LnRR) of percentage germination (PG) and seedling biomass (SB) of *Festuca pratensis*. df = degree of freedom, MS = mean sum of squares. Significant effects ($p < 0.05$) are given in bold.

Source of variation	df	LnRR (PG)			LnRR (SB)		
		MS	F	p	MS	F	P
Intercept	1	**0.946**	**99.50**	**< 0.001**	**1.096**	**157.15**	**< 0.001**
Solidago species (S)	3	**0.031**	**3.24**	**0.035**	0.018	2.53	0.074
Leaf type (L)	1	**0.110**	**11.59**	**0.002**	**0.210**	**30.13**	**0.000**
Concentration (C)	1	**0.132**	**13.88**	**0.001**	**0.029**	**4.21**	**0.048**
S×L	3	0.015	1.62	0.204	0.016	2.23	0.104
S×C	3	0.001	0.16	0.925	0.007	1.05	0.384
L×C	1	0.033	3.47	0.072	0.001	0.18	0.673
S×L×C	3	0.009	0.92	0.441	0.005	0.78	0.515
Error	32	0.010			0.007		

Table 3. Effects of *Solidago* species, leaf type and aqueous extract concentration on the natural-logarithm response ratio (LnRR) of percentage germination (PG) and seedling biomass (SB) of *Festuca rubra*. df = degree of freedom, MS = mean sum of squares. Significant effects ($p < 0.05$) are given in bold.

Source of variation	df	LnRR (PG)			LnRR (SB)		
		MS	F	p	MS	F	P
Intercept	1	**1.790**	**132.98**	**< 0.001**	**5.922**	**432.97**	**< 0.001**
Solidago species (S)	3	0.006	0.43	0.732	0.007	0.52	0.672
Leaf type (L)	1	**0.418**	**31.05**	**< 0.001**	0.002	0.12	0.733
Concentration (C)	1	**0.959**	**71.23**	**< 0.001**	**0.138**	**10.07**	**0.003**
S×L	3	0.005	0.34	0.797	0.008	0.57	0.637
S×C	3	0.005	0.39	0.758	0.013	0.94	0.434
L×C	1	**0.068**	**5.07**	**0.031**	0.004	0.32	0.575
S×L×C	3	0.009	0.67	0.575	**0.049**	**3.57**	**0.025**
Error	32	0.013			0.014		

the effect of leaf type was significant for SB of *F. pratensis* (Table 2) and insignificant for SB of *F. rubra* (Table 3).

Withered leaf extracts had a stronger inhibitory effect on SB of *F. pratensis* than green leaf extracts (Fig. 3; $p < 0.001$, t-test). Green leaf extracts had no significant effect on SB of *F. pratensis*, while withered leaf extracts significantly reduced SB from 18.5 to 25.9% (extracts of *S. gigantea* and *S. canadensis*, respectively). Extracts of withered leaves of *S. gigantea* had a significantly stronger inhibitory effect on SB of *F. pratensis* than similar extracts of *S. virgaurea* ($Z = 2.81$, $p = 0.048$). Most extracts of both concentrations and both leaf types significantly lowered SB of *F. rubra* (Fig. 4) from 23.3 to 41.74% (green leaf extracts of *S. ×niederederi* and *S. canadensis*, respectively) and did not differ significantly between *Solidago* species.

***Solidago* germination experiment.** The germinability of *Solidago* seeds in the control treatment was rather low and differed between both target species significantly (50.0 ± 2.7% for *S. canadensis* and 32.5 ± 8.8% for *S. ×niederederi*, $p = 0.009$, t-test). Furthermore, target species had a significant effect on PG when *Solidago* leaf extracts were added (Table 4). The value of PG was also affected by extract concentration, while the effect of *Solidago* species used for extracts was insignificant.

Solidago leaf extracts had no significant effect on PG of *S. ×niederederi* (Fig. 5). However, more than half of extracts of the same concentration used in the *S. canadensis* germination treatment had a significant inhibitory effect on PG. Moreover, PG of *S. canadensis* in all other variants differed significantly from the control when extracts of higher concentrations (5 g L^{-1} and more) were added (Fig. 5). The PG values of *S. canadensis* treated with extracts of *S. gigantea* were significantly higher than of those treated with extracts of *S. ×niederederi* ($Z = 2.90$, $p = 0.023$) when the effects of extracts of all concentrations were analysed

Table 4. Effects of two *Solidago* species as target species, *Solidago* as allelopathic species and concentration of aqueous leaf extracts (0.5, 1, and 5 g L^{-1}) on the response ratio of percentage germination of *Solidago canadensis* and *S. ×niederederi*. df = degree of freedom, MS = mean sum of squares. Significant effects ($p < 0.05$) are given in bold.

Source of variation	df	MS	F	p
Intercept	1	**47.02**	**844.06**	**< 0.001**
Target species (T)	1	**3.84**	**68.85**	**< 0.001**
Solidago species (S)	3	0.08	1.40	0.251
Concentration (C)	2	**0.26**	**4.64**	**0.013**
T*S	3	0.11	2.00	0.122
T*C	2	0.03	0.55	0.579
S*C	6	**0.17**	**3.03**	**0.011**
T*S*C	6	0.04	0.68	0.663
Error	71	0.06		

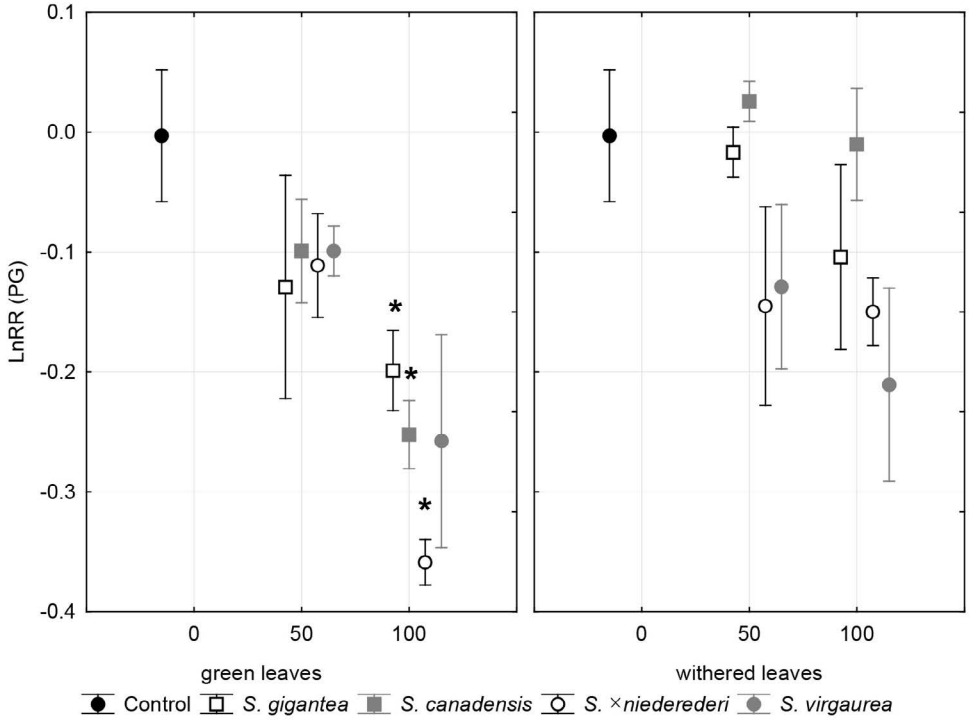

Fig. 1. Mean (± SE) natural-logarithm response ratio of percent germination of *Festuca pratensis* seeds for different treatments when distilled water (0) and two concentrations of aqueous extracts (50 and 100 g L^{-1}) of withered and green leaves of four *Solidago* species were used. Significance of difference is based on the t-test between each variant and the control. * $p < 0.05$.

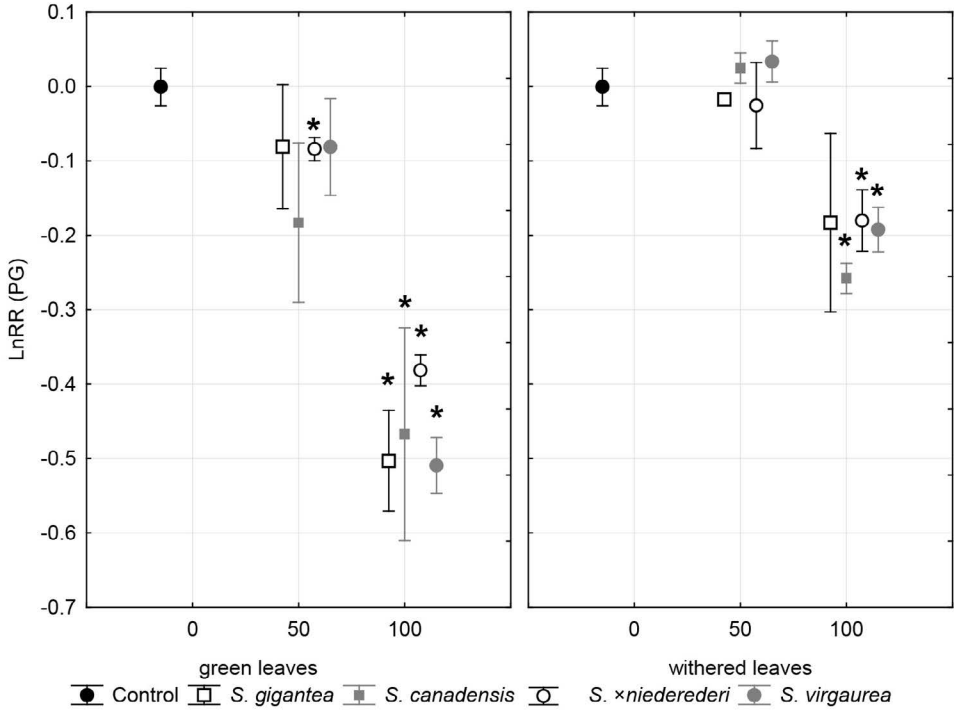

Fig. 2. Mean (± SE) natural-logarithm response ratio of percent germination of *Festuca rubra* seeds for different treatments when distilled water (0) and two concentrations of aqueous extracts (50 and 100 g L^{-1}) of withered and green leaves of four *Solidago* species were used. Significance of difference is based on the t-test between each variant and the control. * $p < 0.05$.

together. The highest concentration (100 g L^{-1}) of leaf extracts of all *Solidago* species except *S. gigantea* totally inhibited the germination of seeds of *S. canadensis*.

The mean length of radicles (RL) in control treatment was 1.2 ± 0.1 mm for *S. canadensis* and 2.0 ± 0.3 mm for *S. ×niedererderi*, and it differed significantly between species ($p = 0.04$, t-test). Only leaf extracts of *S. virgaurea* in a concentration of 5 g L^{-1} significantly reduced RL of *S. ×niedererderi* (Fig. 6), while RL of *S. canadensis* was more susceptible to extract addition. However, the extract con-

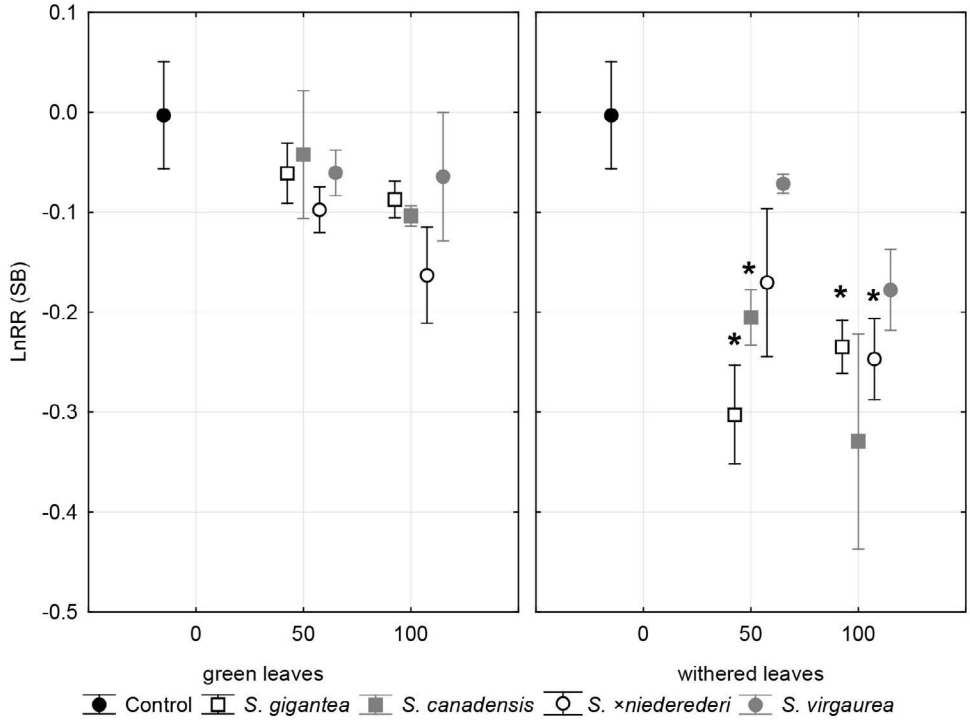

Fig. 3. Mean (± SE) natural-logarithm response ratio of seedling biomass of *Festuca pratensis* seeds for different treatments when distilled water (0) and two concentrations of aqueous extracts (50 and 100 g L^{-1}) of withered and green leaves of four *Solidago* species were used. Significance of difference is based on the t-test between each variant and the control. * $p < 0.05$.

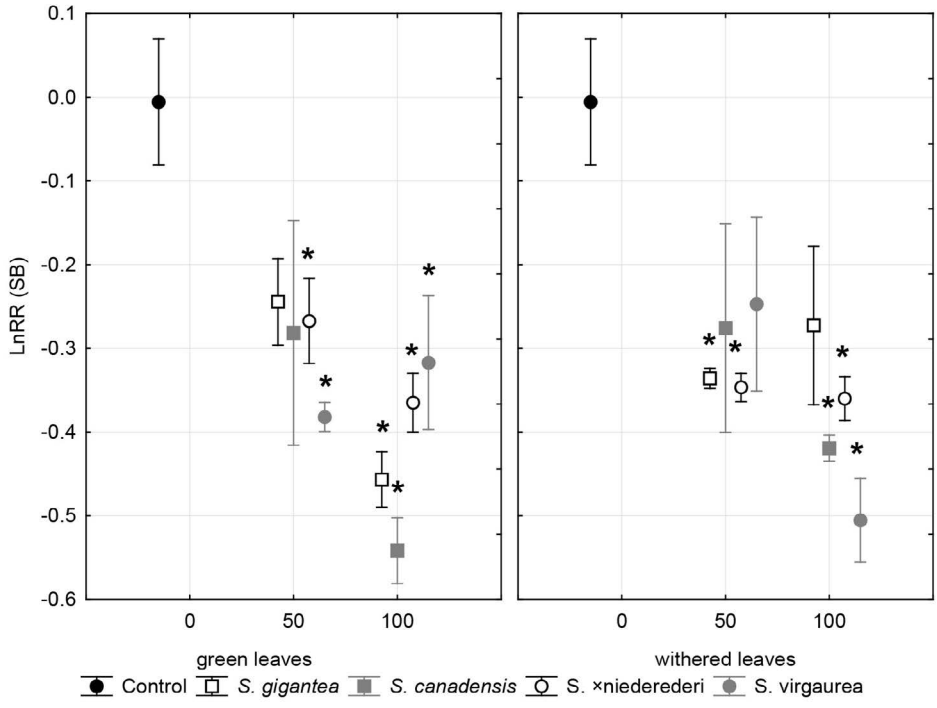

Fig. 4. Mean (± SE) natural-logarithm response ratio of seedling biomass of *Festuca rubra* seeds for different treatments when distilled water (0) and two concentrations of aqueous extracts (50 and 100 g L^{-1}) of withered and green leaves of four *Solidago* species were used. Significance of difference is based on the t-test between each variant and the control. * $p < 0.05$.

centration had no significant effect on RL, while only extracts of *S. virgaurea* sdiffered significantly among all *Solidago* species in having the weakest inhibitory effect on RL.

Mean length of the hypocotyl (HL) in the control treatment was 2.1 ± 0.4 mm for *S. canadensis* and 2.2 ± 0.2 mm for *S. ×niedererderi* and did not differ between species ($p = 0.89$, t-test). Moreover, neither the *Solidago* species used for extracts nor the concentration of extracts had any significant effect on HL in either target species (Fig. 7).

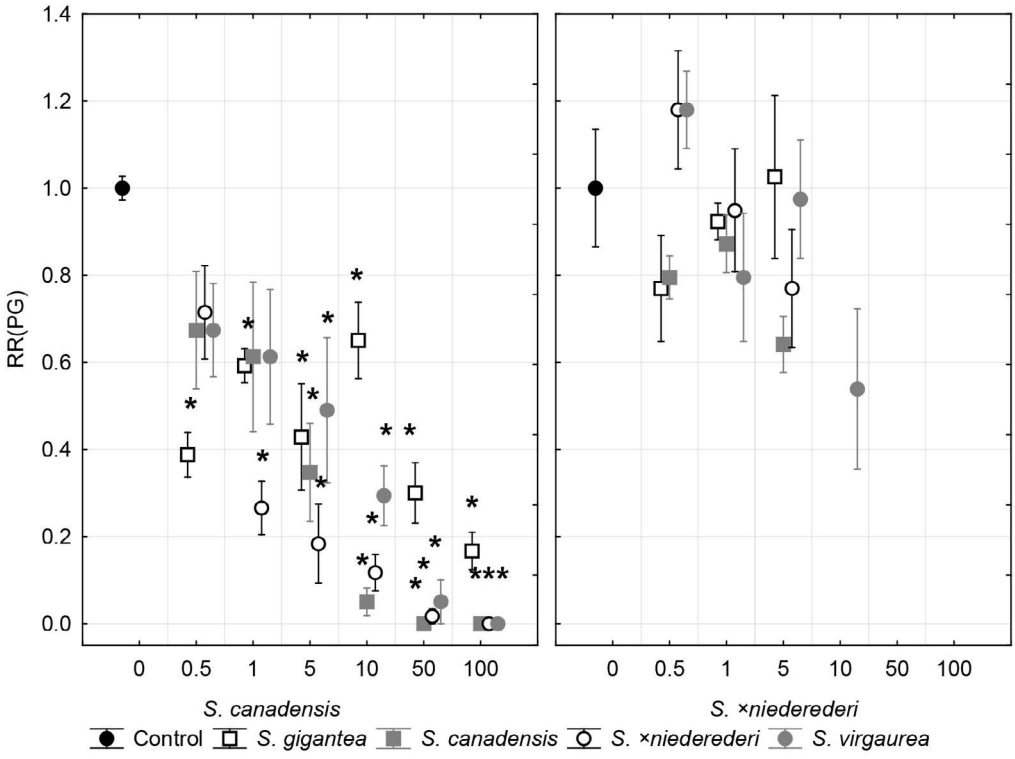

Fig. 5. Mean (± SE) response ratio of percent germination of *Solidago canadensis* and *S. ×niedererderi* seeds for different treatments when distilled water (0) and six concentrations of aqueous extracts (from 0.5 to 100 g L^{-1}) of green leaves of four *Solidago* species were used. Significance of difference is based on the t-test between each variant and the control.
* $p < 0.05$.

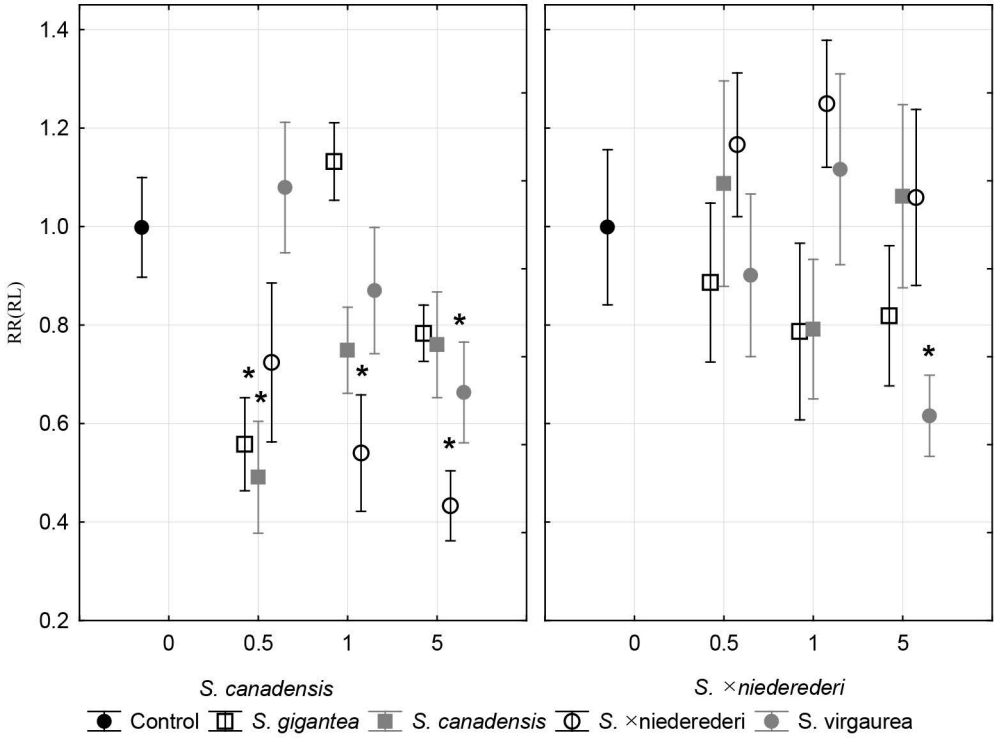

Fig. 6. Mean (± SE) response ratio of radicle length of *Solidago canadensis* and *S. ×niedererderi* seedlings for different treatments when distilled water (0) and three concentrations of aqueous extracts (from 0.5 to 5 g L^{-1}) of green leaves of four *Solidago* species were used. Significance of difference is based on the t-test between each variant and the control.
* $p < 0.05$.

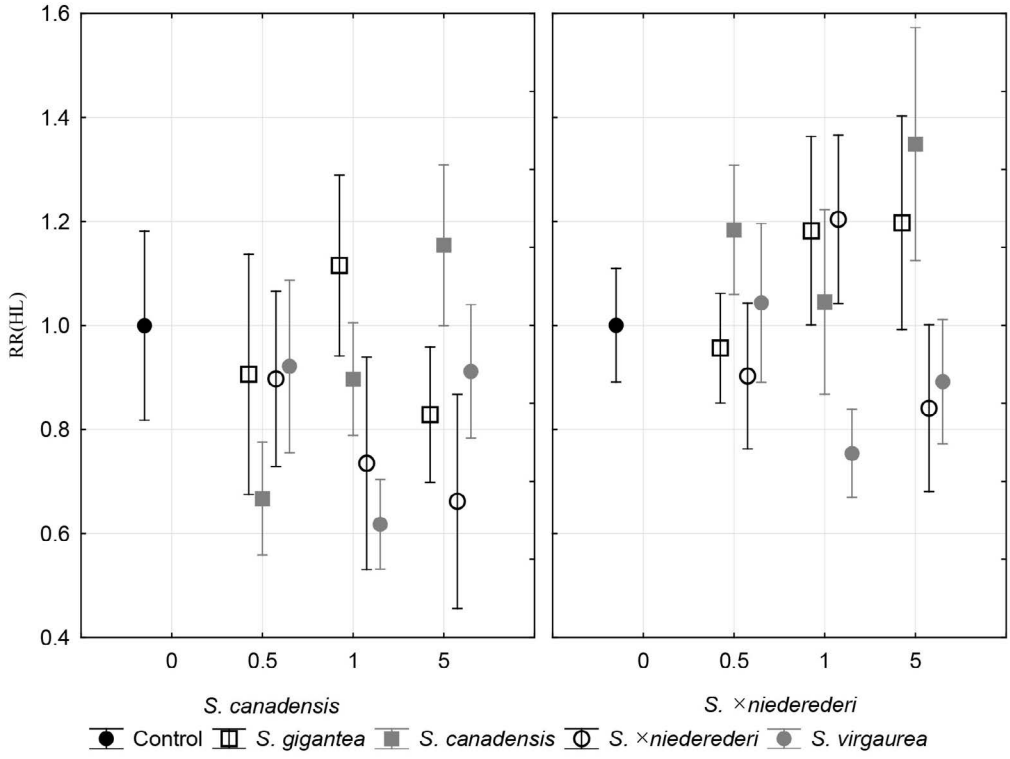

Fig. 7. Mean (± SE) response ratio of hypocotyl length of *Solidago canadensis* and *S. ×niederederi* seedlings for different treatments when distilled water (0) and three concentrations of aqueous extracts (from 0.5 to 5 g L^{-1}) of green leaves of four *Solidago* species were used. All differences are insignificant ($p > 0.05$) according to the t-test between each variant and the control.

DISCUSSION

The inhibitory effect of *Solidago* leaf extracts was target species-specific in both the *Festuca* and the *Solidago* germination experiments. The germination and initial seedling growth of *F. rubra* was more inhibited by all *Solidago* extracts than were those characteristics of *F. pratensis*. Similarly, germination and initial seedling growth of *S. canadensis* was more sensitive to all *Solidago* extracts than the same characteristics of *S. ×niederederi*. In both experiments, the species with lighter seeds were more suppressed. Decrease of target species susceptibility with increase of seed mass has been confirmed in extensive germination experiments (Liebman & Sundberg 2006; Kruidhof *et al.* 2011), but it is not always apparent when a small number of target species is used (e.g., Pisula & Meiners 2010).

The qualitative and quantitative composition of secondary metabolites, acting as allelochemicals, changes during leaf senescence and decomposition (Wilt *et al.* 1993). In many instances, leaf litter contains more phytotoxin than fresh tissue, suggesting that decomposition has initiated the conversion of some inactive secondary compounds to toxic ones (Orcutt & Nilsen 2000). According to Hashoum *et al.* (2017), extracts of senescent leaves have stronger negative effects on germination velocity compared to litter and green leaf extracts of the same species. However, in the *Festuca* germination experiment, seed germination was more suppressed by green leaf extracts, while the effect of leaf type on seedling growth was target species-specific. Similarly, Orr *et al.* (2005) found a weaker inhibitory effect of senescent leaf extracts on seed germination, while leaf litter had a significant inhibitory effect on leaf biomass of one target species. It is possible that germination and seedling growth are inhibited by different allelochemical compounds. Furthermore, interaction of the allelopathic effect of secondary metabolites is sometimes detected, with predominance of antagonism (Dias *et al.* 2018).

The difference in the inhibitory effect between the tested *Solidago* species was not general and was evident only on germination and seedling biomass of *Festuca pratensis* treated with withered leaf extracts, as well on germination and radicle length of *S. canadensis*. However, in some cases, when a difference between *Solidago* species was found, the weakest effect belonged to invasive species, *S. canadensis* or *S. gigantea*, whereas in most cases *S. ×niederederi* had the strongest inhibitory effect. The inhibitory effect of the native species *S. virgaurea* was weaker than the effect of *S. ×niederederi* or *S. gigantea* only in two variants. Consequently, our results do not support the hypothesis that invasive plant species have stronger persistent allelopathic effects on native plants compared to their native congeners. Zhang *et al.* (2010) compared the allelopathic effects of invasive and native *Solidago* species. They found that the difference

between species depends on the plant part used for extraction: invasive *S. canadensis* shows stronger allelopathic activity when root and rhizome extracts are used, while native *S. decurrens* shows a stronger inhibitory effect when extracts from the aboveground part are used.

The significant effect of *S. canadensis* leaf extracts on its own seed germination and seedling growth indicated an autotoxic effect. On the contrary, the interspecific hybrid *S. ×niederederi* was insensitive to extracts of both intraspecific and intrageneric origin. The role of autotoxicity cannot be rejected in attempting to explain the fact that no new genet recruitment occurs in denser populations of *S. canadensis* (Hartnett & Bazzaz 1985).

In conclusion, the results of this study do not support the hypothesis that invasive plant species have stronger persistent allelopathic effects on native plants compared to their native congeners. The stronger allelopathic effect of invasive *Solidago* species could be achieved only by higher biomass in dominant stands and consequent higher concentrations of biologically active compounds in dense stands. Considering only the allelopathic and autotoxic effect of *S. canadensis*, we can conclude that there is greater probability for establishment of *S. ×niederederi* than *S. canadensis* in existing *S. canadensis* stands.

REFERENCES

Abhilasha D, Quintana N, Vivanco J & Joshi J. 2008. Do allelopathic compounds in invasive *Solidago canadensis* s.l. restrain the native European flora? *Journal of Ecology* **96**: 993–1001.

Baličević R, Ravlić M & Živković T. 2015. Allelopathic effect of invasive species giant goldenrod (*Solidago gigantea* Ait.) on crops and weeds. *Herbologia* **15**: 19–29.

Butcko V & Jensen R. 2002. Evidence of tissue-specific allelopathic activity in *Euthamia graminifolia* and *Solidago canadensis* (Asteraceae). *The American Midland Naturalist* **148**: 253–262.

Daehler CC. 2003. Performance's comparisons of co-occurring native and alien invasive plants: implications for conservation and restoration. *Annual Review of Ecology and Systematics* **34**: 183–211.

Dias AS, Dias LS & Pereira IP. 2018. Defensive role of allelopathic secondary compounds in plants: a review of data on two independent general hypotheses. *Journal of Allelochemical Interactions* **4**: 9–22.

Eppstein MJ & Molofsky J. 2007. Invasiveness in plant communities with feedbacks. *Ecology Letters* **10**: 253–263.

Goldberg DE & Scheiner SM. 2001. ANOVA and ANCOVA: field competition experiments. In: Scheiner SM & Gurevitch J (eds.), *Design and analysis of ecological experiments*, 2nd ed., pp. 77–98, Oxford University Press, Oxford.

Gruľová D, Baranová B, Ivanova V, De Martino L, Mancini E & De Feo V. 2016. Composition and bioactivity of essential oils of *Solidago* spp. and their impact on radish and garden cress. *Allelopathy Journal* **39**: 129–142.

Hartnett DC & Bazzaz FA. 1985. The genet and ramet population dynamics of *Solidago candensis* in an abandoned field. *Journal of Ecology* **73**: 407–413.

Hashoum H, Santonja M, Gauquelin T, Saatkamp A, Gavinet J, Greff S, Lecareux C, Fernandez C & Bousquet-Mélou A. 2017. Biotic interactions in a Mediterranean oak forest: role of allelopathy along phenological development of woody species. *European Journal of Forest Research* **136**: 699–710.

Hierro JL & Callaway RM. 2003. Allelopathy and exotic plant invasion. *Plant and Soil* **256**: 29–39.

Inderjit, Seastedt TR, Callaway RM, Pollock JL & Kaur J. 2008. Allelopathy and plant invasions: traditional, congeneric and bio-geographical approaches. *Biological Invasions* **10**: 875–890.

Kaczmarek S, Matysiak K & Kardasz P. 2012. Assessment of allelopathic potential of *Solidago virgaurea* L. on some selected crops. *Zeszyty Naukowe Uniwersytetu Przyrodniczego we Wrocławiu Rolnictwo* **100**: 53–62.

Kolar CS & Lodge DM. 2001. Progress in invasion biology: predicting invaders. *Trends in Ecology & Evolution* **16**: 199–204.

Kruidhof HM, Gallandt ER, Haramoto ER & Bastiaans L. 2011. Selective weed suppression by cover crop residues: effects of seed mass and timing of species' sensitivity. *Weed Research* **51**: 177–186.

Kruse M, Strandberg M & Strandberg B. 2000. *Ecological effects of allelopathic plants – a review. NERI Technical Report* **315**. National Environmental Research Institute, Silkeborg.

Lambdon P, Pyšek P & Basnou C. 2008. Alien flora of Europe: species diversity, temporal trends, geographical patterns and research needs. *Preslia* **80**: 101–149.

Li S, Wang P, Yuan W, Su Z & Bullard SH. 2016. Endocidal regulation of secondary metabolites in the producing organisms. *Scientific Reports* **6**: 29315.

Liebman M & Sundberg DN. 2006. Seed mass affects the susceptibility of weed and crop species to phytotoxins extracted from red clover shoots. *Weed Science* **54**: 340–345.

Migdałek G, Kolczyk J, Pliszko A, Kościńska-Pająk M & Słomka A. 2014. Reduced pollen viability and achene development in *Solidago ×niederederi* Khek from Poland. *Acta Societatis Botanicorum Poloniae* **83**: 251–255.

Orcutt DM & Nilsen ET. 2000. *The physiology of plants under stress: soil and biotic factors*. John Wiley & Sons, New York.

Orr SP, Rudgers JA & Clay K. 2005. Invasive plants can inhibit native tree seedlings: Testing potential al-

lelopathic mechanisms. *Plant Ecology* **181**: 153–165.

Pal RW, Chen S, Nagy DU & Callaway RM. 2015. Impacts of *Solidago gigantea* on other species at home and away. *Biological Invasions* **17**: 3317–3325.

Pisula NL & Meiners SJ. 2010. Allelopathic effects of goldenrod species on turnover in successional communities. *The American Midland Naturalist* **163**: 161–172.

Pyšek P, Richardson DM, Rejmánek M, Webster GL, Williamson M & Kirschner J. 2004. Alien plants in checklists and floras: towards better communication between taxonomists and ecologists. *Taxon* **53**: 131–143.

Ravlić M, Baličević R & Peharda A. 2015. Allelopathic effect of invasive species giant goldenrod (*Solidago gigantea* Ait.) on wheat and scentless mayweed. In: Baban M & Rašić S (eds.), *Proceedings & abstracts of the 8th International Scientific/Professional Conference Agriculture in Nature and Environment Protection*, pp. 186–190, Glas Slavonije, Osijek.

Rice EL. 2012. *Allelopathy* 2nd ed. Academic Press, Florida.

Sekutowski TR, Bortniak M & Domaradzki K. 2012. Assessment of allelopathic potential of invasive plants – goldenrod (*Solidago gigantea*) on buckwheat (*Fagopyrum sagittatum*) and sunflower (*Helianthus annuus*). *Journal of Research and Applications in Agricultural Engineering* **57**: 86–91.

Singh HP, Batish DR & Kohli RK. 2010. Autotoxicity: concept, organisms, and ecological significance. *Critical Reviews in Plant Sciences* **18**: 757–772.

Szymura M & Szymura TH. 2013. Soil preferences and morphological diversity of goldenrods (*Solidago* L.) from south-western Poland. *Acta Societatis Botanicorum Poloniae* **82**: 107–115.

Theoharides KA & Dukes JS. 2007. Plant invasion across space and time: factors affecting nonindigenous species success during four stages of invasion. *New Phytologist* **176**: 256–273.

van Kleunen M, Weber E & Fischer M. 2010. A meta-analysis of trait differences between invasive and non-invasive plant species. *Ecology Letters* **13**: 235–245.

Wang C, Xiao H, Zhao L, Liu J, Wang L, Zhang F, Shi Y & Du D. 2016. The allelopathic effects of invasive plant *Solidago canadensis* on seed germination and growth of *Lactuca sativa* enhanced by different types of acid deposition. *Ecotoxicology* **25**: 555–562.

Weber E. 1998. The dynamics of plant invasions: a case study of three exotic goldenrod species (*Solidago* L.) in Europe. *Journal of Biogeography* **25**: 147–154.

Weber E. 2000. Biological flora of Central Europe: *Solidago altissima* L. *Flora* **195**: 123–134.

Weber E. 2011. Strong regeneration ability from rhizome fragments in two invasive clonal plants (*Solidago canadensis* and *S. gigantea*). *Biological Invasions* **13**: 2947–2955.

Weber E & Jakobs G. 2005. Biological flora of Central Europe: *Solidago gigantea* Aiton. *Flora* **200**: 109–118.

Wilt FM, Miller GC, Everett RL & Hackett M. 1993. Monoterpene concentrations in fresh, senescent, and decaying foliage of single-leaf pinyon (*Pinus monophylla* Torr. & Frem.: Pinaceae) from the western Great Basin. *Journal of Chemical Ecology* **19**: 185–194.

Yuan Y, Wang B, Zhang S, Tang J, Tu C, Hu S, Yong JW & Chen X. 2013. Enhanced allelopathy and competitive ability of invasive plant *Solidago canadensis* in its introduced range. *Journal of Plant Ecology* **6**: 253–263.

Zedler JB & Kercher S. 2004. Causes and consequences of invasive plants in wetlands: opportunities, opportunists, and outcomes. *Critical Reviews in Plant Sciences* **23**: 431–452.

Zhang ZX, Zhang XP, Liu HJ & Shao JW. 2010. Comparative study on the allelopathy of invasive species *Solidago canadensis* L. and native species *Solidago decurrens* Lour. *Journal of Wuhan Botanical Research* **28**: 191–198.

Botanica SERBICA

REZIME

Srodničko poređenje alelopatskih i autotoksičnih efekata četiri vrste roda *Solidago*

Birutė Karpavičienė, Julija Danilovienė i Roberta Vykertaitė

Za vrste *Solidago canadensis* i *S. gigantea* je poznato da deluju inhibirajuće na okolne vrste kroz alelopatiju. Međutim, ne postoje podaci o alelopatskim svojstvima prirodnog interspecijskog hibrida *S.* ×*niederederi* i poređenje alelopatskog potencijala autohtonih i invazivnih *Solidago* vrsta. Otuda je istraživan alelopatski efekat vodenog ekstrakta lista *S. virgaurea*, *S. canadensis*, *S. gigantea* i *S.* ×*niederederi* na dva srodna para vrsta (*Festuca* i *Solidago*), koje se spontano javljaju u zajednicama sa istraživanim vrstama roda *Solidago*. Klijanje i rast klijanaca vrste *Festuca rubra* je inhibirano svim *Solidago* ekstraktima više nego u slučaju *F. pratensis*, dok je *S. canadensis* osetljiviji na svoje i kongenerične ekstrakte nego *S.* ×*niederederi*. Učinak listova (zeleni ili osušeni) na rast sadnice *Festuca* bio je specifičan za ciljne vrste, dok je klijanje semena bilo suzbijenije ekstraktima zelenih listova. Rezultati ove studije ne podržavaju hipotezu da invazivne biljne vrste imaju jači postojani alelopatski uticaj na autohtone biljke u poređenju sa njihovim srodnim vrstama.

Ključne reči: alelopatija, klijanje, inhibicija, invazivne vrste, *Solidago*