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Environmental changes caused by the clonal invasive plant *Solidago canadensis*

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Invasive plant species pose a threat to the diversity of natural habitats. The extent of the changes depends, among others, on soil properties, settlement time and the degree of coverage of sites by an invasive species. The objective of this study was to determine changes in the habitats of *Solidago canadensis* at two localities in Poland that differ in soil fertility and acidity. The content of organic carbon, nitrogen and phosphorus, as well as pH were analysed from soil samples collected from the sites invaded by *S. canadensis* and from the control sites. The composition and species richness of vascular plant communities at the same sites were also determined. The analyses revealed an increase in the soil organic carbon content and in the C/N ratio at the sites invaded by *S. canadensis*. The presence of *S. canadensis* also reduced the number of vascular plant species, mainly annuals and perennials. Thus, an increase in *S. canadensis* cover results in soil degradation and habitat homogenization.

Introduction

Invasions of alien plant species are a serious threat to biodiversity of natural habitats. Successful invasions of non-indigenous plants depend on their biological characteristics and interactions with native organisms, as well as the environmental properties of the invaded areas (Ehrenfeld 2010, Fukami *et al*. 2013, Torres *et al*. 2013, Lanta & Norrdahl 2018). Environmental impact of invasive plants is often greater within their non-native than native ranges (Simberloff *et al*. 2012, Ledger *et al*. 2015). Successful migrations of invasive plants are also determined by their life strategies. Such plants usually have diaspores that can be transported over long distances, while their individuals are characterised by rapid growth and intense reproduction (Cain *et al*. 2000, Myers *et al*. 2004, Moravcová *et al*. 2010). Compared with native species, they are characterised by a high net production. In new habitats, they usually reach high biomass of above-ground parts (Ledger *et al*. 2015), exceeding that of native plant species at comparable locations (Zhang *et al*. 2009).

High competitiveness of many invasive species reduces biodiversity (McGlone *et al*. 2012, Skálová *et al*. 2013, Gioria & Osborne 2014, Holeksa *et al*. 2015). Invasive plants can heavily modify properties of an ecosystem, including soil parameters (Dassonville *et al*. 2008, Zhang *et al*. 2009). The elemental composition of surface soil layers depends on the plant community composition (Sardans *et al*. 2017). Invasive plants have a particular effect on nutrients: they usually cause an increase in soil nitrogen (N) and phosphorus (P) concentrations (Dassonville *et al*. 2008, Sardans *et al.* 2017), both being important soil chemical components that may be involved in facilitating plant invasions (Sardans *et al.* 2017).

The extent of ecosystem modification by invasive plants depends on the species and location, hence invasions of the same species may have different effects, depending on local conditions (Dassonville *et al.* 2008). Also, the species composition of local communities changes over time due to species immigration and, consequently, the way species affect one another within a community also changes (Fukami *et al.* 2013).

Habitats vary greatly in terms of their sensitivity to invasions. In nutrient-poor environments, invasive plants tend to use soil nutrients with greater efficiency than in nutrient-rich environments (Sardans *et al.* 2017). Depending on their genotype, the uptake of nutrients by the same plant species may differ, thus affecting to a varying degree the C:N ratio in the soil (Eppinga & Molofsky 2013). Changes in soil C and N contents caused by invasive plants compared with those caused by native plants can be used to assess soil degradation resulting from invasion, the C:N ratio serving as an indicator. In Poland, the C:N ratios of 8–10, 11–17, 18–30 and 30–45 are typical for non-degraded, slightly degraded, moderately degraded and highly degraded soils, respectively (Baran & Turski 1996). An assessment of the effects of invasive species on invaded habitats should include detailed studies of soil physicochemical properties as well as species composition in a given area.

Solidago canadensis was introduced to Europe in the 18th century (Weber 2001). This species is one of the most aggressive clonal invaders in Europe and has also been introduced to some parts of Asia and Australia (Weber 2003, Dong *et al.* 2006a). The spread of *S. canadensis* is associated with its high production of seeds (Dong *et al*. 2006b). Individual shoots of this plant produce up to 10 000 seeds that are easily transported by wind over long distances (Gassman & Weber 2005). The seeds are characterised by very high germination capacity and high tolerance to chemical changes in the substrate (Lu *et al.* 2007, Priede 2008).

Being an invasive species, *S. canadensis* can also modify habitats. Its presence may cause an increase in organic carbon (C_{org}) (Lu *et al.* 2005, Vanderhoeven *et al.* 2006, Zhang *et al.* 2009) as well as N and P in the soil (Vanderhoeven *et al.* 2006). It can also reduce the amounts total N and P in the soil (Zhang *et al*. 2009). The species has an allelopathic effect on the co-occurring vegetation (Sun *et al.* 2006, Abhilasha *et al.* 2008, Yuan *et al.* 2013).

As *S. canadensis* is considered a threat in Poland, we explored its effects on the environment at two localities differing in soil chemical parameters such as C_{org}, N and pH. Our aim was to find out whether (1) the presence of *S. canadensis* contributes to changes in the chemical properties of soils and the taxonomic composition of vascular plant communities, (2) habitat fertility determines the extent of changes in the environment caused by the presence of *S. canadensis*, (3) there is a relationship between the percentage cover of *S. canadensis* and the changes in habitat characteristics, and (4) *S. canadensis* competes with all vascular species.

Material and methods

Study area

The study was carried out in Poland near and within the towns of Olkusz and Siedlce (Fig. 1 and Table 1). The choice of locality was determined by the time of invasion of each area by *S. canadensis*. In southern Poland (Olkusz), the species was recorded in the 1980s (Guzikowa & Maycock 1986). In eastern Poland (Siedlce), the species was still one of the very rare components of the segetal flora at the end of the 20th century (Skrzyczyńska & Marciniuk 2002).

Collection and analysis of samples

Samples were collected during the flowering period of *S. canadensis*, i.e. in late August 2017. Twenty-five sites were randomly selected at each locality (Olkusz and Siedlce); at least 500 m^2 of

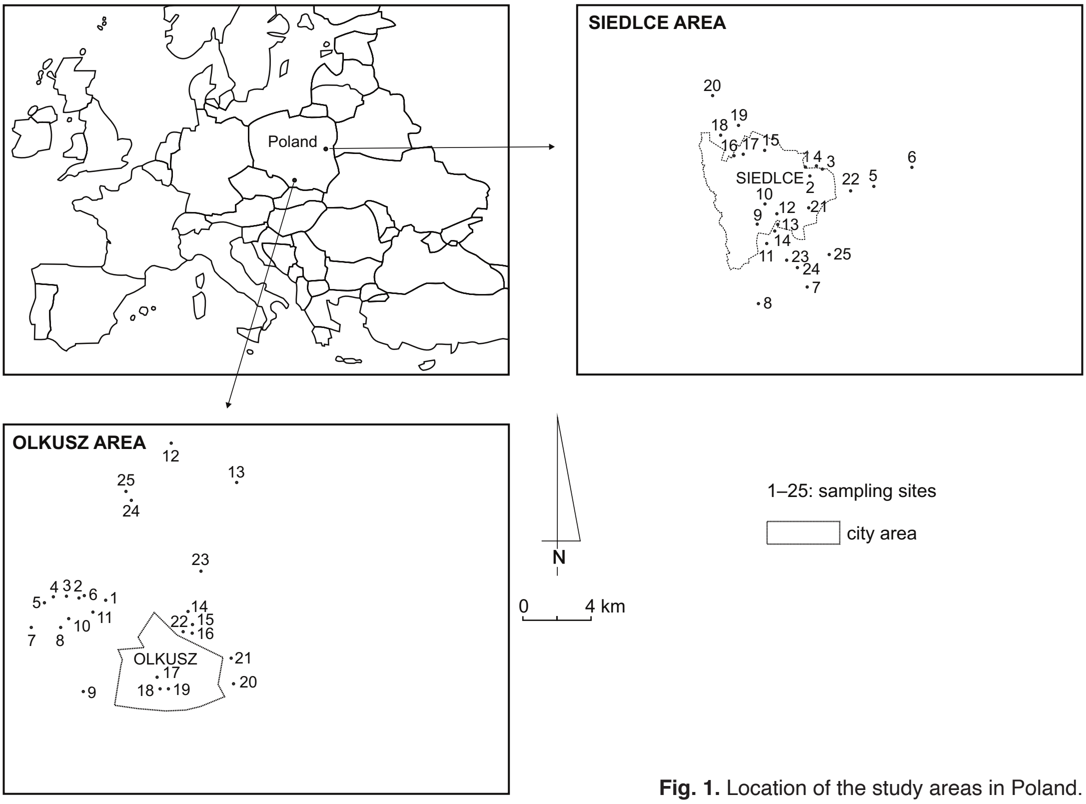

Fig. 1. Location of the study areas in Poland.

each site was covered by *S. canadensis*. Control sites (without *S. canadensis*), with an area similar to that of the invaded sites, were selected next to the sites invaded by the plant.

Three 3 × 3 m plots were randomly selected at each site. Using an Egner's sampling stick, from each plot we took four soil samples from a depth of 0–20 cm. All soil samples from each site were pooled. A total of 100 soil samples were collected for analysis (50 samples from the invaded and 50 samples from the control sites).

Soil samples were air-dried in a laboratory and sieved through a sieve with a mesh size of 2 mm. Soil pH was measured in reaction with 1 M KCl (1:2.5), organic carbon (C_{org}) was with Tiurin's method (Ostrowska *et al.* 1991), total

Table 1. Characteristics of the study areas.

	Olkusz[1]	Siedlce[2]
Location of the study area	southern Poland, on the boundary between Kraków and Częstochowa Upland and Silesian Upland	eastern Poland, South Podlasie Lowland
Geographic coordinates of sampling sites	50°15´83´´–50°23´39´´N, 19°26´50´´–19°36´46´´E	52°74´25´´–52°13´72´´N, 22°13´29´´–22°25´24´´E
Average annual precipitation (mm)	716	550
Growing season length (days)	200–210	200–220
Average annual temperature (°C)	7.6–7.7	6.9–7.1
Data on *S. canadensis* sites available since	early 1980s (Guzikowa & Maycook 1986)	late 1990s (Skrzyczyńska & Marciniuk 2002)

[1] Wach *et al.* (2014), [2] Anonymous (2011).

nitrogen (N) with the indophenol method, and total phosphorus (P) with the molybdate method (Marczenko 1979) were determined in the soil samples. To determine the soil content of N and P, the soil samples were mineralised in Kjeldahl flasks in 95% H_2SO_4 and 30% H_2O_2 (3:1, v/v). Subsequently, the contents of nitrogen and phosphorus were assessed using the indophenol and molybdenum-blue methods (Marczenko 1979). Concentrations of measured soil chemical parameters are expressed per 1 g dry weight of soil.

In each plot, the percentage cover of *S. canadensis* in the invaded plots and occurrence frequencies of all other vascular plants in the invaded and control plots were determined. The names of plant species follow Mirek *et al*. (2002). The list of vascular plant species occurring in control and invaded sites is provided in the Appendix.

Analysis of the results

Normality of the data was tested using the Shapiro-Wilk test. As all the variables were non-normally distributed, before the analyses they were transformed (Box-Cox method) to attain normality.

We used MANOVA with an interaction term to test whether the sites (control and invaded) and localities (Siedlce and Olkusz) differed in the studied factors. ANOVA was used to verify whether there were differences in (i) soil pH, (ii) carbon, (iii) phosphorus, (iv) nitrogen and (iv) carbon to nitrogen ratio as well as in the number of (1) annual plants, (2) biennials, (3) perennials, (4) trees and shrubs and (5) total number of plant species per site between the sites and localities. The analyses were performed using STATISTICA ver. 12.

We used Detrended Correspondence Analysis (DCA) to study the relationships among plant species whose frequency of occurrence was more than 30% and soil chemical parameters, as well the percentage cover of *S. canadensis* at invaded and control sites in both localities. As preliminary DCA results revealed a gradient (DCA1 axis length) of more than 3 SD units (5.33 SD units), DCA was deemed the most applicable method for exploring the compositional patterns at the sites studied. The DCA was carried out using the *metaphor* package in R.

Results

Soil properties

The soil samples collected at the localities in Olkusz and Siedlce differed from each other in pH, organic carbon content (C_{org}), nitrogen (N) and carbon-to-nitrogen ratio (C/N) all being higher in Olkusz. Soil pH, phosphorus (P) and N content were similar at the invaded and control (uninvaded) sites, whereas C content and C/N ratio were higher than at the control sites. Site and locality together (site × locality) had no effect on the studied soil chemistry factors (Fig. 2 and Table 2).

Vegetation

The cover of *S. canadensis* at the study sites was 30%–100% (mean ≈ 70%). In both localities, the identified species belonged to 47 families, of which Asteraceae, Fabaceae, Poaceae and Rosaceae were most common (Table 3 and Appendix).

The average number of plant species was lower in the invaded than control (uninvaded) sites by about 30% in Olkusz and 20% in Siedlce (Fig. 3), the differences being significant (*see* Table 4).

Among the identified plant species, biennial and shrubs/trees occurred at a low frequency (below 30%), while perennials were the most frequent. Also, the numbers of perennial and annual species were significantly lower at the invaded than at control (uninvaded) sites at both localities (Tables 3 and 4). Site and locality together (site × locality) had no effect on the numbers of taxonomic groups (Table 4).

In both localities, the presence of *S. canadensis* had no effect on the frequencies of *Achillea millefolium*, *Artemisia vulgaris* or *Agrostis capillaris*, while it negatively affected the frequency occurrences of *Arrhenatherum elatius*, *Cirsium arvense*, *Convolvulus arvensis*, *Daucus carota*,

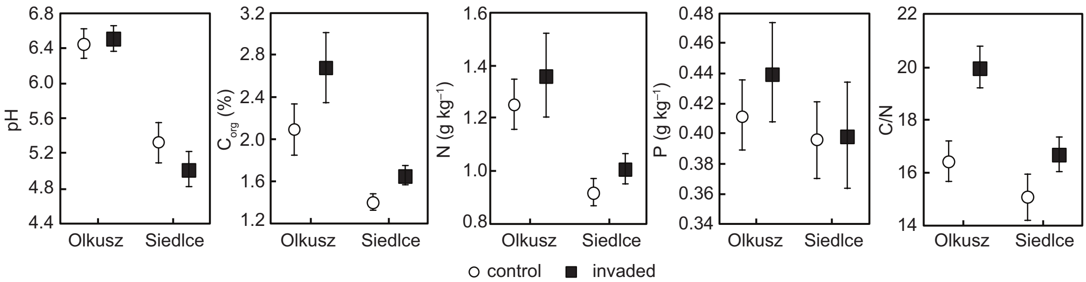

Fig. 2. pH, organic carbon, nitrogen, phosphorus and organic carbon/nitrogen ratio in soil at the control and invaded sites in Olkusz and Siedlce. Error bars are standard errors.

Elymus repens and *Festuca pratensis*. The frequencies of *Tanacetum vulgare* and *Calamagrostis epigejos* clearly increased at the sites with *S. canadensis* in Siedlce and Olkusz, respectively (Table 5 and Appendix).

Relationship between soil properties and vegetation

According to DCA, the sites invaded by *S. canadensis* were more similar in terms of species composition while the control sites in terms of species diversity which was higher than in the invaded sites (Fig. 4). The species composition and the C/N ratio in the invaded sites correlated with the percentage cover of *S. canadensis*. Other variables were irrelevant in explaining differences in the species composition between sites and localities (Table 6).

The species grouped in the right-hand side of Fig. 4 were most common in the control (uninvaded) sites. Species such as *Daucus carota*, *Cirsium arvense*, *Convolvulus arvensis*, *Phleum pratense*, *Dactylis glomerata* and *Elymus repens* avoid *S. canadensis*, while *Crepis biennis*, *Calamagrostis epigejos* and *Tanacetum vulgare* can coexist with it. The species able to compete

Table 2. Differences in soil parameters between two localities (Olkusz *vs*. Siedlce) and sites (control *vs*. invaded) as revealed by MANOVA and ANOVA. Results were considered significant at $p < 0.05$.

		Predictor	*F*	*p*
MANOVA		Locality: Olkusz *vs*. Siedlce	11.40	< 0.001
		Site: control *vs*. invaded	2.96	0.01
		Site × locality	0.67	0.64
ANOVA	Response variable			
	Soil pH	Locality: Olkusz *vs*. Siedlce	45.93	< 0.001
		Site: control *vs*. invaded	0.38	0.53
		Site × locality	0.67	0.64
	C_{org}	Locality: Olkusz *vs*. Siedlce	18.37	< 0.001
		Site: control *vs*. invaded	4.56	0.04
		Site × locality	0.63	0.42
	P	Locality: Olkusz *vs*. Siedlce	0.92	0.33
		Site: control *vs*. invaded	0.27	0.60
		Site × locality	0.18	0.66
	N	Locality: Olkusz *vs*. Siedlce	11.74	< 0.001
		Site: control *vs*. invaded	0.91	0.32
		Site × locality	0.09	0.92
	C/N	Locality: Olkusz *vs*. Siedlce	9.09	0.003
		Site: control *vs*. invaded	11.60	< 0.001
		Site × locality	1.67	0.19

Table 3. Number of species of vascular plants arranged by family at the control and invaded sites in Olkusz and Siedlce.

Family	Number of species	Olkusz		Siedlce	
		control	invaded	control	invaded
Amaranthaceae	1	0	0	1	1
Amaryllidaceae	1	1	1	0	0
Apiaceae	12	11	8	9	5
Asteraceae	40	30	18	29	19
Betulaceae	2	2	0	1	1
Boraginaceae	2	2	1	0	0
Brassicaceae	4	3	1	3	2
Campanulaceae	1	1	0	1	1
Cannabaceae	1	0	1	0	1
Caryophyllaceae	8	5	2	4	3
Cornaceae	3	1	2	0	1
Convolvulaceae	1	0	0	1	1
Cucurbitaceae	1	1	0	0	0
Cupressaceae	1	1	0	0	0
Cyperaceae	3	1	3	2	2
Dipsacaceae	2	2	2	1	1
Euphorbiaceae	2	1	1	1	0
Fabaceae	18	17	10	7	6
Geraniaceae	2	2	1	0	0
Grossulariaceae	2	0	0	1	2
Hypericaceae	1	1	1	1	1
Juglandaceae	1	1	0	1	1
Juncaceae	2	0	1	2	2
Lamiaceae	9	7	3	3	3
Linaceae	1	1	0	0	0
Malvaceae	1	0	1	1	1
Oleaceae	2	2	1	0	2
Onagraceae	4	3	1	3	2
Orchidaceae	1	0	0	1	0
Orobanchaceae	2	1	1	1	0
Pinaceae	1	1	1	1	1
Plantaginaceae	6	6	2	0	0
Poaceae	27	20	13	24	17
Polygonaceae	8	5	2	7	5
Primulaceae	1	1	1	0	0
Ranunculaceae	2	1	2	1	1
Resedaceae	1	1	1	0	0
Rhamnaceae	1	0	0	0	1
Rosaceae	23	11	12	15	16
Rubiaceae	3	2	2	2	2
Salicaceae	1	1	0	0	0
Sapindaceae	2	1	0	1	2
Scrophulariaceae	2	1	1	0	0
Urticaceae	1	1	1	1	1
Valerianaceae	1	1	1	0	0
Violaceae	2	2	0	0	1
Vitaceae	1	0	1	0	1
Number of species in functional groups					
Annual	44	33	12	22	13
Biennial	14	11	8	6	5
Perennial	124	92	69	81	64
Shrub/tree	32	16	11	17	24

with *S. canadensis* have similar functional features as *S. canadensis*.

Discussion

The results of our study indicated that the presence of *S. canadensis* does not cause significant changes in the soil chemistry. There is however no agreement on whether or not *S. canadensis* invasion affects soil N or P content. Vanderhoeven *et al.* (2006) found that the presence of *S. gigantea* caused a slight increase in the soil N content. Also according to Lu *et al*. (2005), the presence of *S. canadensis* increased the N content in soil in China. On the other hand, Zhang *et al*. (2009) reported that the presence of *S. canadensis* reduced the soil total nitrogen and total phosphorus and increased soil pH. Contrary to Zhang *et al*. (2009), Vanderhoeven *et al*. (2006), noted a significant positive effect of *S. canadensis* on soil phosphorus.

In our study, the C_{org} content was higher at the sites invaded by *S. canadensis*, and similar was reported by e.g. Lu *et al*. (2005), Vanderhoeven *et al*. (2006) and Zhang *et al*. (2009).

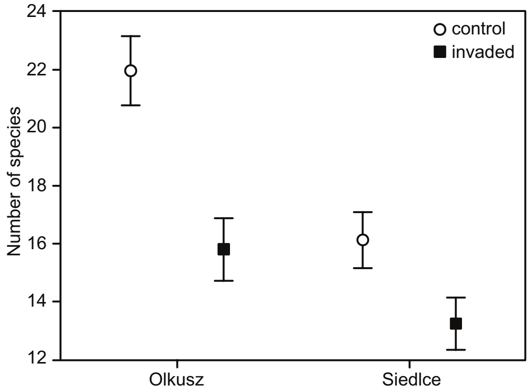

Fig. 3. The mean ± SE number of plant species at the control and invaded sites in Olkusz and Siedlce.

Eppinga and Molofsky (2013) found that invasive species caused an increase in soil total C_{org} increasing the C/N ratio.

Zhang *et al*. (2009) showed that changes in some chemical soil properties (e.g. an increase in C_{org} and C/N ratio) can be used as an indicator of *S. canadensis* invasion. In our study, the C_{org} content and C/N ratio were significantly higher at the invaded sites, more so in Olkusz than in Siedlce. The C/N ratios in around 10%

Table 4. Differences in taxonomic groups between localities (Olkusz *vs*. Siedlce) and sites (control *vs*. invaded) as revealed by MANOVA and ANOVA. Results were considered significant at $p < 0.05$.

		Predictor	*F*	*p*
MANOVA		Locality: Olkusz *vs*. Siedlce	5.91	< 0.001
		Site: control *vs*. invaded	9.97	< 0.001
		Site × locality	0.57	0.71
ANOVA	Response variable			
	Number of annual plants	Locality: Olkusz *vs*. Siedlce	0.07	0.78
		Site: control *vs*. invaded	5.48	0.02
		Site × locality	0.39	0.53
	Number of biennials	Locality: Olkusz *vs*. Siedlce	21.19	< 0.001
		Site: control/invaded	1.44	0.23
		Site × locality	1.00	0.31
	Number of perennials	Locality: Olkusz *vs*. Siedlce	18.34	< 0.001
		Site: control *vs*. invaded	19.63	< 0.001
		Site × locality	1.96	0.53
	Number of shrubs and trees	Locality: Olkusz *vs*. Siedlce	2.03	0.15
		Site: control *vs*. invaded	2.03	0.15
		Site × locality	1.69	0.19
	Number of total species	Locality: Olkusz *vs*. Siedlce	14.05	< 0.001
		Site: control *vs*. invaded	16.67	< 0.001
		Site × locality	2.79	0.09

and 90% of the soil samples taken from the sites in the Olkusz area (southern Poland) were typical for slightly and moderately degraded soils, respectively, while in the Siedlce area (eastern Poland) the respective percentages were approx. 60% and 40%. Our results do not support the findings of Sardans *et al*. (2017) who found that a more severe degradation of soils by invasive plants occured in habitats with a low rather than high nutrient contents (e.g. nitrogen). We found a positive correlation between percentage cover of *S. canadensis* and the C/N ratio in both localities.

High soil C_{org} content and C/N ratio immobilize inorganic nitrogen available to plants (Lehmam & Rondon 2005, Blumenthal *et al*. 2003). In order to use sites invaded by *S. canadensis* (fallow lands, agricultural lands), e.g., for agricultural purposes, it seems advantageous to use organic fertilizers with low C/N ratios on soils that are slow to release inorganic forms of nitrogen (Dias *et al*. 2010, Tiquia & Tam 2000).

The localities selected for our study differed in the total number of plant species at all sites. As evidenced by the results, the greater number of plant species at the control sites is likely associated with the more fertile soils in the Olkusz area. The soils in Olkusz are richer in C_{org} and N and have higher pH. Furthermore, precipitation in Olkusz (Wach *et al*. 2014) is higher than that

Table 5. Numbers of control and invaded sites in Olkusz and Siedlce where frequencies of occurrences of listed vascular plant species exceeded 30%.

Family	Species	Olkusz		Siedlce	
		control	invaded	control	invaded
Apiaceae	*Daucus carota*	60	28	0	0
Asteraceae	*Achillea millefolium*	64	84	44	56
	Artemisia vulgaris	60	68	44	44
	Cirsium arvense	64	44	52	48
	Tanacetum vulgare	0	0	28	40
	Crepis biennis	48	48	0	0
	Taraxacum spp.	32	24	0	0
Fabaceae	*Vicia sepium*	56	30	0	0
Poaceae	*Agrostis capillaris*	68	68	72	86
	Arrhenatherum elatius	60	28	28	32
	Calamagrostis epigejos	24	60	0	0
	Dactylis glomerata	80	52	56	40
	Elymus repens	48	32	72	52
	Festuca pratensis	40	16	0	0
	Phleum pratense	52	56	32	24
Convolvulaceae	*Convolvulus arvensis*	0	0	32	16
Polygonaceae	*Rumex acetosa*	40	20	40	36
Urticaceae	*Urtica dioica*	16	32	16	32
Valerianaceae	*Valeriana officinalis*	44	24	0	0

Table 6. Parameters of passively fitted environmental variables with DCA axes. Determination coefficients (R^2) and p values were estimated using permutation tests with 999 iterations. Results are considered significant at $p < 0.05$.

Parameter	DCA1	DCA2	R^2	p
Soil pH	–0.515	0.856	0.05	0.11
Carbon (C)	–0.979	0.201	0.06	0.07
Phosphorus (P)	–0.550	0.834	0.01	0.72
Nitrogen (N)	–0.764	0.644	0.06	0.09
Carbon to nitrogen ratio (C/N)	–0.346	–0.938	0.11	0.01
Percentage cover of *S. canadensis*	–0.769	–0.639	0.42	< 0.01

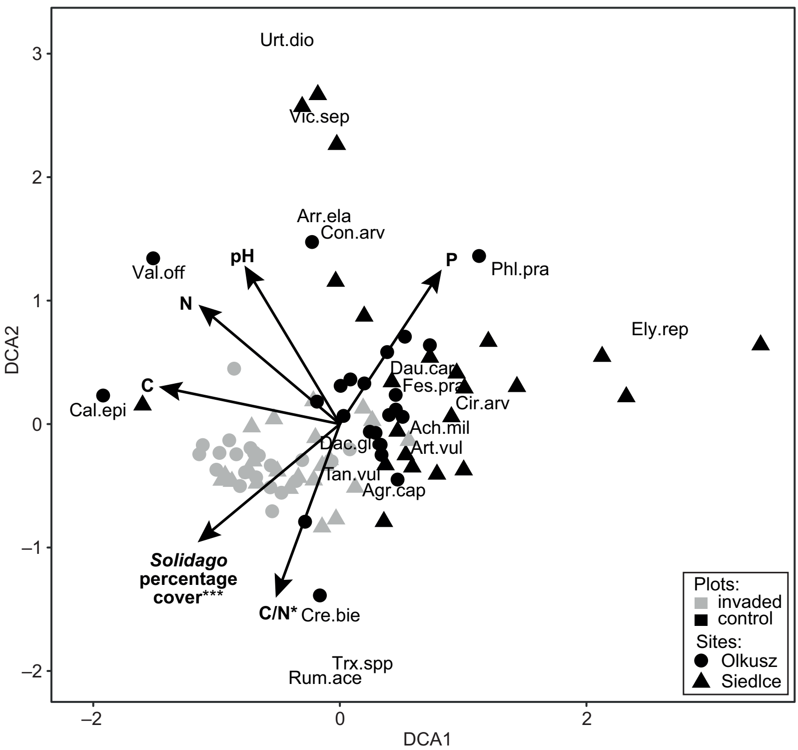

Fig. 4. DCA ordination on control and invaded sites in Olkusz and Siedlce with passively fitted soil chemical parameters (soil pH, C = carbon (C), phosphorus (P), nitrogen (N), C/N ratio) and *S. canadensis* percentage cover. Coordinates of species more frequent than 30 occurrences are also shown: Ach.mil = *Achillea millefolium*, Agr.cap = *Agrostis capillaris*, Arr.ela = *Arrhenatherum elatius*, Art.vul = *Artemisia vulgaris*, Cal.epi = *Calamagrostis epigejos*, Cir.arv = *Cirsium arvense*, Con.arv = *Convolvulus arvensis*, Cre.bie = *Crepis biennis*, Dac.glo = *Dactylis glomerata*, Dau.car = *Daucus carota*, Ely.rep = *Elymus repens*, Fes.pra = *Festuca pratensis*, Phl.pra = *Phleum pratense*, Rum.ace = *Rumex acetosa*, Tan.vul = *Tanacetum vulgare*, Trx.spp = *Taraxacum* spp., Urt.dio = *Urtica dioica*, Val.off = *Valeriana officinalis*, Vic.sep = *Vicia sepium*.

Siedlce (Anonymous 2011). It should also be noted that in Olkusz the decline in the number of species under the influence of *S. canadensis* was greater.

Invasive species are a serious threat to native ecosystems and their biodiversity (Dong *et al*. 2006a). Greater competitiveness leads to their dominance in plant communities, which results in the reduction in species numbers and the formation of nearly monospecific phytocoenoses (McGlone *et al*. 2012, Bottollier-Curtet *et al*. 2013, Skálová *et al*. 2013, Gioria & Osborne 2014, Holeksa *et al*. 2015). In this study we found compositional homogeneity in invaded habitats. Guo (2005) and Fenesi *et al*. (2015) emphasised that the species diversity of plant communities decreases with the expansion of *S. canadensis*. At sites dominated by this species, the decline in plant species richness can reach up to 60% (de Groot *et al*. 2007). In our study, the greatest decline in the number of species (about 40%–65%; mainly annuals and perennials) was recorded at the sites with 90%–100% cover of *S. canadensis*.

Many occurrences of *S. canadensis* in southern Poland were recorded already in the early 1980s, and it occasionally occurred also in other parts of the country (Guzikowa & Maycock 1986). According to the most recent data, in the first decade of the 21st century, the species was spreading at an increasing rate in northeastern Poland (Korniak *et al*. 2012) but also in eastern Poland (Siedlce) (Rzymowska 2015). Greater differences in the plant species composition at the control and invaded sites were more apparent in Olkusz than in Siedlce. We can assume that the longer the period of *S. canadensis* invasion, the greater the elimination of plant species.

Solidago canadensis eliminates selected species of the Poaceae (e.g. *Dactylis glomerata*, *Elymus repens*) but also *Cirsium arvense*, *Convolvulus arvensis* and *Daucus carota*. These species have a different growth strategy than *S. canadensis*. In addition, they occur in cultivated areas and meadows. These habitats are very similar to habitats occupied by them within their native ranges, and they can be quite aggressive in these habitats in North America as well.

Our results also show that *S. canadensis* did not compete with e.g., *Tanacetum vulgare* (sites in Siedlce) and *Calamagrostis epigejos* (sites in Olkusz). *Tanacetum vulgare* is a stronger competitor than *S. canadensis* on infertile soils (Rebele 2000) and the presence of *S. canadensis* affects *T. vulgare* growth and biomass via species-specific effects on soil fungal communities and unique plant–soil effects, respectively (Schittko & Wurst 2014). *Calamagrostis epigejos* co-dominates with *S. canadensis* on long-term fallows. This species occurs at brownfield sites, as well as on dumping grounds of strip mines where it forms clusters (Rebele & Lehmann 2001). Szymura and Szymura (2016) indicated that the most frequent species co-occurring with *S. canadensis* are *Artemisia vulgaris*, *Achillea millefolium*, *Cirsium arvense* and *Dactylis glomerata*. Also in our study, those species co-existed with *S. canadensis* and their frequency at the study sites was over 30%. Just like *S. canadensis*, these species are not limited by soil quality (Stachon & Zimdahl 1980, Warwick & Black 1982, Barney & DiTommaso 2003, Abhilasha *et al*. 2008).

Conclusions

Solidago canadensis does not cause significant changes in soil N, P and pH, while it increases C and C/N ratio. It reduces species diversity of vascular plants, especially annuals and perennials regardless of the site location. Soil degradation and homogenization of habitats increases with the increase of the *S. canadensis* cover.

The presence of *S. canadensis* does not adversely affect the occurrence of *Achillea millefolium*, *Artemisia vulgaris*, *Cirsium arvense*, *Dactylis glomerata*, *Tanacetum vulgare* or *Calamagrostis epigejos*.

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Appendix. Frequency occurrences (%) of vascular plant species in the control and invaded sites at the two localities (Olkusz and Siedlce).

Species	Family	Functional group	Olkusz		Siedlce	
			control	invaded	control	invaded
Acer negundo	Sapindaceae	shrubs/trees	4	0	8	20
Acer platanoides	Sapindaceae	shrubs/trees	0	0	0	4
Achillea millefolium	Asteraceae	perennials	64	84	44	56
Aegopodium podagraria	Apiaceae	perennials	0	4	4	0
Agrimonia eupatoria	Rosaceae	perennials	4	4	4	4
Agrimonia procera	Rosaceae	perennials	12	0	0	0
Agrostis capillaris	Poaceae	perennials	68	68	72	86
Allium oleraceum	Amaryllidaceae	annuals	4	4	0	0
Angelica sylvestris	Apiaceae	biennials	4	8	4	4
Anthemis cotula	Asteraceae	annuals	4	0	0	0
Anthriscus sylvestris	Apiaceae	perennials	8	0	8	4
Apera spica-venti	Poaceae	annuals	0	0	4	4
Armoracia rusticana	Brassicaceae	perennials	4	4	12	8
Aronia melanocarpa	Rosaceae	shrubs/trees	0	0	4	4
Arrhenatherum elatius	Poaceae	perennials	60	28	28	32
Artemisia campestris	Asteraceae	perennials	4	0	12	4
Artemisia vulgaris	Asteraceae	perennials	60	68	44	44
Avena fatua	Poaceae	annuals	4	0	4	0
Berteroa incana	Brassicaceae	perennials	4	0	8	4
Betula pendula	Betulaceae	shrubs/trees	4	0	4	4
Briza media	Poaceae	perennials	4	0	0	4
Bromus inermis	Poaceae	perennials	0	4	8	4
Bromus secalinus	Poaceae	perennials	0	0	4	0

continued

Appendix. Continued.

Species	Family	Functional group	Olkusz		Siedlce	
			control	invaded	control	invaded
Calamagrostis canescens	Poaceae	perennials	0	0	4	4
Calamagrostis epigejos	Poaceae	perennials	24	60	0	0
Capsella bursa-pastoris	Brassicaceae	annuals	4	0	0	0
Carduus acanthoides	Asteraceae	perennials	4	12	0	0
Carduus crispus	Asteraceae	biennials	4	0	4	4
Carex echinata	Cyperaceae	perennials	0	4	4	4
Carex hirta	Cyperaceae	perennials	20	20	24	12
Carex ovalis	Cyperaceae	perennials	0	4	0	0
Carlina vulgaris	Asteraceae	biennials	16	4	0	0
Centaurea cyanus	Asteraceae	annuals	4	0	8	0
Centaurea jacea	Asteraceae	perennials	4	0	4	0
Centaurea scabiosa	Asteraceae	perennials	24	16	0	0
Centaurea stoebe	Asteraceae	biennials	0	0	4	4
Cerastium holosteoides	Caryophyllaceae	perennials	8	0	0	0
Cerastium semidecandrum	Caryophyllaceae	perennials	0	4	4	0
Cerasus sp.	Rosaceae	shrubs/trees	0	0	0	4
Chaerophyllum hirsutum	Apiaceae	perennials	20	16	4	0
Chenopodium album	Amaranthaceae	annuals	0	0	4	4
Cichorium intybus	Asteraceae	perennials	4	4	8	4
Cirsium arvense	Asteraceae	perennials	64	44	52	48
Convolvulus arvensis	Convolvulaceae	perennials	0	0	32	16
Cornus alba	Cornaceae	shrubs/trees	0	0	0	4
Cornus mas	Cornaceae	shrubs/trees	8	12	0	0
Cornus sanguinea	Cornaceae	shrubs/trees	0	8	0	0
Corylus avellana	Betulaceae	shrubs/trees	4	0	0	0
Crataegus sp.	Rosaceae	shrubs/trees	0	0	4	8
Crepis biennis	Asteraceae	biennials	48	48	0	0
Dactylis glomerata	Poaceae	perennials	80	52	56	40
Dactylorhiza sp.	Orchidaceae	perennials	0	0	4	0
Danthonia decumbens	Poaceae	perennials	0	0	4	0
Daucus carota	Apiaceae	biennials	60	28	0	0
Deschampsia caespitosa	Poaceae	perennials	20	16	4	4
Echinochloa crus-galli	Poaceae	annuals	8	0	4	0
Echinocystis lobata	Cucurbitaceae	annuals	4	0	0	0
Echium vulgare	Boraginaceae	perennials	4	4	0	0
Elymus repens	Poaceae	perennials	48	32	72	52
Epilobium hirsutum	Onagraceae	perennials	4	0	4	4
Epilobium palustre	Onagraceae	perennials	4	0	16	0
Epilobium roseum	Onagraceae	perennials	16	8	0	16
Erigeron acris	Asteraceae	perennials	4	0	4	4
Erigeron annuus	Asteraceae	biennials	20	24	4	12
Erigeron canadensis	Asteraceae	annuals	12	4	24	0
Euphorbia cyparissias	Euphorbiaceae	perennials	12	4	0	0
Euphorbia esula	Euphorbiaceae	perennials	0	0	4	0
Falcaria vulgaris	Apiaceae	biennials	4	0	0	0
Fallopia convolvulus	Polygonaceae	annuals	4	0	8	12
Fallopia dumetorum	Polygonaceae	annuals	0	0	0	4
Festuca arundinacea	Poaceae	perennials	12	0	4	0
Festuca ovina	Poaceae	perennials	4	0	4	4
Festuca pratensis	Poaceae	perennials	40	16	0	0
Festuca rubra	Poaceae	perennials	24	4	12	8
Filago minima	Asteraceae	annuals	0	0	4	0
Fragaria × ananassa	Rosaceae	perennials	0	0	12	4

continued

Appendix. Continued.

Species	Family	Functional group	Olkusz		Siedlce	
			control	invaded	control	invaded
Fragaria vesca	Rosaceae	perennials	8	12	0	4
Fraxinus excelsior	Oleaceae	shrubs/trees	4	4	0	12
Galeopsis tetrahit	Lamiaceae	annuals	0	4	4	8
Galinsoga ciliata	Asteraceae	annuals	4	0	0	0
Galinsoga parviflora	Asteraceae	annuals	0	0	4	0
Galium aparine	Rubiaceae	annuals	0	4	8	20
Galium mollugo	Rubiaceae	perennials	48	56	4	8
Galium verum	Rubiaceae	perennials	4	0	0	0
Geranium pratense	Geraniaceae	perennials	4	4	0	0
Geranium pusillum	Geraniaceae	annuals	8	0	0	0
Geum urbanum	Rosaceae	perennials	4	4	4	12
Glechoma hederacea	Lamiaceae	perennials	4	0	0	4
Gnaphalium sylvaticum	Asteraceae	perennials	4	4	12	0
Gnaphalium uliginosum	Asteraceae	annuals	4	0	0	0
Helianthus tuberosus	Asteraceae	perennials	0	0	4	0
Helichrysum arenarium	Asteraceae	perennials	0	0	4	0
Heracleum sphondylium	Apiaceae	perennials	12	12	8	8
Hieracium pilosella	Asteraceae	perennials	0	0	20	4
Hieracium umbellatum	Asteraceae	perennials	0	0	8	16
Holcus lanatus	Poaceae	perennials	16	16	36	40
Humulus lupulus	Cannabaceae	perennials	0	4	0	4
Hypericum perforatum	Hypericaceae	perennials	20	16	36	28
Jacobaea vulgaris	Asteraceae	perennials	28	24	8	4
Jasione montana	Campanulaceae	perennials	4	0	12	4
Juglans regia	Juglandaceae	shrubs/trees	4	0	12	12
Juncus conglomeratus	Juncaceae	perennials	0	0	8	4
Juncus effusus	Juncaceae	perennials	0	4	4	4
Juniperus communis	Cupressaceae	shrubs/trees	4	0	0	0
Knautia arvensis	Dipsacaceae	perennials	8	12	28	8
Lactuca serriola	Asteraceae	annuals	4	0	0	0
Lamium amplexicaule	Lamiaceae	annuals	4	0	0	0
Lamium purpureum	Lamiaceae	perennials	4	0	0	0
Lapsana communis	Asteraceae	annuals	8	4	0	0
Lathyrus pratensis	Fabaceae	perennials	20	12	0	8
Leontodon autumnalis	Asteraceae	perennials	28	8	8	4
Ligustrum vulgare	Oleaceae	shrubs/trees	4	0	0	4
Linaria vulgaris	Plantaginaceae	perennials	4	0	0	0
Linum catharticum	Linaceae	biennials	4	0	0	0
Lolium perenne	Poaceae	perennials	12	0	8	4
Lotus corniculatus	Fabaceae	perennials	4	4	0	0
Lupinus polyphyllus	Fabaceae	perennials	4	0	4	4
Lysimachia vulgaris	Primulaceae	perennials	4	8	0	0
Malus sp.	Rosaceae	shrubs/trees	0	0	4	0
Medicago lupulina	Fabaceae	annuals	20	0	0	0
Medicago sativa L. ssp. *falcata* × ssp. *sativa*	Fabaceae	perennials	24	8	0	0
Melilotus albus	Fabaceae	annuals	8	12	0	0
Melilotus officinalis	Fabaceae	annuals	8	8	0	0
Mentha arvensis	Lamiaceae	perennials	4	0	8	0
Molinia caerulea	Poaceae	perennials	4	0	4	4
Myosotis arvensis	Boraginaceae	annuals	4	0	0	0
Odontites vernus ssp. *serotinus*	Orobanchaceae	perennials	0	0	4	0
Oenothera sp.	Onagraceae	biennials	0	0	16	0

continued

Appendix. Continued.

Species	Family	Functional group	Olkusz		Siedlce	
			control	invaded	control	invaded
Origanum vulgare	Lamiaceae	perennials	16	12	0	0
Padus avium	Rosaceae	shrubs/trees	0	4	4	8
Parthenocissus quinquefolia	Vitaceae	perennials	0	4	0	4
Pastinaca sativa	Apiaceae	perennials	8	12	8	0
Peucedanum oreoselinum	Apiaceae	perennials	4	0	4	0
Phleum pratense	Poaceae	perennials	52	56	32	24
Phragmites australis	Poaceae	perennials	0	0	4	8
Pimpinella saxifraga	Apiaceae	perennials	8	0	8	0
Pinus sylvestris	Pinaceae	shrubs/trees	16	16	8	4
Plantago lanceolata	Plantaginaceae	perennials	24	4	0	0
Plantago major	Plantaginaceae	perennials	16	0	0	0
Plantago media	Plantaginaceae	perennials	4	0	0	0
Poa trivialis	Poaceae	perennials	0	4	8	0
Polygonum aviculare	Polygonaceae	perennials	8	0	4	0
Polygonum bistorta	Polygonaceae	perennials	0	0	4	0
Polygonum persicaria	Polygonaceae	annuals	8	0	8	0
Populus tremula	Salicaceae	shrubs/trees	4	0	0	0
Potentilla anserina	Rosaceae	perennials	8	4	12	8
Potentilla argentea	Rosaceae	perennials	0	0	4	0
Potentilla reptans	Rosaceae	perennials	4	8	0	0
Prunus domestica L. ssp. *syriaca*	Rosaceae	shrubs/trees	0	4	12	24
Prunus serotina	Rosaceae	shrubs/trees	4	12	8	0
Prunus spinosa	Rosaceae	shrubs/trees	4	0	0	4
Pyrus communis	Rosaceae	shrubs/trees	0	0	4	8
Ranunculus acris	Ranunculaceae	perennials	0	4	0	0
Ranunculus repens	Ranunculaceae	perennials	20	12	4	4
Raphanus raphanistrum	Brassicaceae	annuals	0	0	4	0
Reseda luteola	Resedaceae	biennials	4	4	0	0
Rhamnus cathartica	Rhamnaceae	shrubs/trees	0	0	0	8
Rhinanthus minor	Orobanchaceae	annuals	4	4	0	0
Ribes nigrum	Grossulariaceae	shrubs/trees	0	0	4	4
Ribes rubrum	Grossulariaceae	shrubs/trees	0	0	0	4
Robinia pseudacacia	Fabaceae	shrubs/trees	4	0	4	4
Rosa canina	Rosaceae	shrubs/trees	8	4	0	8
Rubus caesius	Rosaceae	shrubs/trees	0	24	0	8
Rubus idaeus	Rosaceae	shrubs/trees	4	0	4	4
Rubus sp.	Rosaceae	shrubs/trees	0	0	4	0
Rudbeckia laciniata	Asteraceae	perennials	0	0	0	4
Rumex acetosa	Polygonaceae	perennials	40	20	40	36
Rumex acetosella	Polygonaceae	perennials	0	0	4	8
Rumex obtusifolius	Polygonaceae	perennials	4	4	4	12
Salvia verticillata	Lamiaceae	perennials	8	0	0	0
Sanguisorba officinalis	Rosaceae	perennials	0	4	0	0
Scabiosa ochroleuca	Dipsacaceae	perennials	4	4	0	0
Scleranthus annuus	Caryophyllaceae	annuals	0	0	0	4
Secale cereale	Poaceae	annuals	4	0	4	0
Securigera varia	Fabaceae	perennials	16	4	0	0
Seseli annuum	Apiaceae	annuals	16	12	0	4
Setaria glauca	Poaceae	annuals	4	0	4	0
Setaria viridis	Poaceae	annuals	4	4	20	4
Silene latifolia	Caryophyllaceae	perennials	44	24	24	20
Silene vulgaris	Caryophyllaceae	perennials	16	0	0	0
Solidago canadensis	Asteraceae	perennials	52	100	60	100

continued

Appendix. Continued.

Species	Family	Functional group	Olkusz		Siedlce	
			control	invaded	control	invaded
Solidago gigantea	Asteraceae	perennials	0	12	12	16
Solidago virgaurea	Asteraceae	perennials	4	0	20	20
Sonchus arvensis	Asteraceae	perennials	4	0	4	0
Sorbus aucuparia	Rosaceae	shrubs/trees	4	4	4	12
Spergula arvensis	Caryophyllaceae	annuals	0	0	4	0
Stachys palustris	Lamiaceae	perennials	0	4	8	4
Stellaria graminea	Caryophyllaceae	perennials	4	0	20	4
Stellaria media	Caryophyllaceae	annuals	4	0	0	0
Tanacetum vulgare	Asteraceae	perennials	0	0	28	40
Taraxacum sp.	Asteraceae	perennials	32	24	0	0
Thymus pulegioides	Lamiaceae	perennials	12	0	0	0
Tilia cordata	Malvaceae	shrubs/trees	0	4	4	4
Torilis japonica	Apiaceae	annuals	4	4	4	8
Tragopogon pratensis	Asteraceae	biennials	8	8	12	4
Trifolium arvense	Fabaceae	annuals	8	0	16	0
Trifolium aureum	Fabaceae	annuals	0	0	4	4
Trifolium hybridum	Fabaceae	perennials	12	0	8	0
Trifolium medium	Fabaceae	perennials	8	0	0	0
Trifolium pratense	Fabaceae	perennials	12	0	4	0
Trifolium repens	Fabaceae	perennials	4	4	0	0
Tripleurospermum maritimum	Asteraceae	annuals	8	0	4	0
Tussilago farfara	Asteraceae	perennials	24	0	4	0
Urtica dioica	Urticaceae	perennials	16	32	16	32
Valeriana officinalis	Valerianaceae	perennials	44	24	0	0
Verbascum nigrum	Scrophulariaceae	biennials	0	4	0	0
Verbascum phlomoides	Scrophulariaceae	biennials	8	0	0	0
Veronica chamaedrys	Plantaginaceae	perennials	8	4	0	0
Veronica persica	Plantaginaceae	annuals	4	0	0	0
Vicia cracca	Fabaceae	perennials	20	16	0	4
Vicia hirsuta	Fabaceae	annuals	8	4	12	8
Vicia sepium	Fabaceae	perennials	56	30	0	0
Viola arvensis	Violaceae	annuals	4	0	0	0
Viola tricolor	Violaceae	annuals	4	0	0	4