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Morphological and cytological diversity of goldenrods (*Solidago* L. and *Euthamia* Nutt.) from south-western Poland

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Abstract: Correlations between the morphology and cytology of invasive species and the effectiveness of invasion are among the most interesting questions in invasion ecology. Amongst exceptionally successful worldwide plant invaders, species of goldenrod (*Solidago* and *Euthamia*) are considered. The main aim of the study was to compare the morphology (concerning life traits) and cytology of the selected goldenrods occurring in south-western Poland with the effectiveness of their invasion. The results of the study, conducted in south-western Poland, showed that life traits of invasive *Solidago* and *Euthamia* taxa were clearly not connected with the effectiveness of invasion. The most widespread species, *S. gigantea* and *S. altissima,* had the highest ramets and uncommon species such as *Euthamia graminifolia* and *S. virgaurea* had short ramets. However, *S. canadensis*, which is tall, is also uncommon. The most frequent species (*S. gigantea*) produced smaller inflorescence than less frequent species (*S. altissima*, *S. canadensis* and *Euthamia graminifolia*). The spread of particular taxa was also not connected with the ploidy level and DNA content.

Key words: biological invasions, chromosome number, DNA content, invasive plant species, life traits

1. Introduction

Biological invasions are considered as a permanent component of environmental changes connected with human activities. The spread of alien plant species results in a loss of economic value, biological diversity and function of the invaded ecosystems (Richardson & Pyšek 2006; Lambdon *et al.* 2008; Essl *et al.* 2011).

The effectiveness of invasion, characterised by the size of the occupied area and abundance of individuals, is determined by several factors connected with the environment in a new range of invasive species as well as plant biology (Essl *et al.* 2011; Pyšek & Richardson 2008). An important factor is the residence time that passes during species introduction (Rejmánek 2000). Following the introduction into a new range and time, when aliens occur in a few isolated areas, there is a period of slow or lack of proliferation (lag phase). Subsequently, a phase of rapid range expansion and filling-in takes place. The period of lag phase usually ranges from 80 to 150 years (Lockwood *et al.* 2007).

Invasive plants are defined as widespread, non-native species that produce reproductive offspring – often in huge numbers – which have the potential to spread over a large area (Pyšek & Richardson 2008). Several studies have focused on the reasons why plants, which are invasive, are more efficient in colonizing new areas than other plants (both native and alien species) which have no tendency to expand or invade. However, the biological mechanism of invasions still remains unclear (van Kleunen & Richardson 2007; Schlaepfer *et al.* 2010a). The process of colonisation in new areas is generally

controlled by two factors: competitiveness and dispersion ability (van Kleunen *et al.* 2010). Life traits such as plant height, inflorescence size and leaf number/size are frequently mentioned as factors ensuring effective invasion of alien species (Baker 1974; Szymura & Szymura 2015). Bigger inflorescences produce more seeds and higher stems ensure better dispersion of seeds. However, some drawbacks connected with higher stems such as increased exposure of the apex to damages (e.g. caused by wind) can disturb this pattern (Wise & Abrahamson 2010).

The spread of alien plants and their impact on the invaded vegetation is, in many cases, connected with the presence of polyploidy (Thompson 1991). Polyploidy allows plants to diversify their genome by its reorganization which increases adaptive plasticity (Mandák *et al.* 2003). Conversely, many naturalized alien plants have smaller genomes than their relatives which do not invade (Kubešova *et al.* 2010). Based on a variation in chromosome number, a variety in morphology is highly possible, including traits related to invasiveness such as stem height or inflorescence size (Stace 1989; Wise & Abrahamson 2010).

Exceptionally successful worldwide plant invaders are goldenrods (Pyšek 1998; Weber 2003). It is one of the most complex genera of higher plants and variability within this genus is increased due to hybridization, introgression and ecological factors (Beaudry & Chabot 1957; McNeil 1976; Semple *et al.* 1984).

In central Europe, five representatives of goldenrods (*Solidago* and *Euthamia*) were found. Only one taxon, *S. virgaurea* L. agg., is native. This taxon is considered as an aggregate species and divided into growing on lowlands *Solidago virgaurea* L. and growing in the mountains *S. minuta* L. (*S. alpestris* Waldst. et Kit.) (Kiełtyk & Mirek 2014). The other four taxa are of American origin: *S. gigantea* Aiton, *S. canadensis* L., *S. altissima* L. (*S. canadensis* var. *scabra* (Muhl.) Torr. and Gray) and *Euthamia graminifolia* (L.) Nutt. The name commonly used for the last species in Europe is *Solidago graminifolia* (L.) Elliot. However, on the basis of anatomical and DNA studies (Semple *et al.* 1981, 1984) conducted in America, the taxon should be classified to *Euthamia* Nutt. genus and its taxonomical correct name is *Euthamia graminifolia* (L.) Nutt.

Three of the introduced taxa (*S. gigantea, S. canadensis* and *S. altissima*) are invasive and morphologically similar to each other. Up to now, the range of *Euthamia graminifolia* is limited to a few locations in Europe (Guzikowa & Maycock 1986; Weber 1997). However, in recent years, a few new localities of this species were reported in Poland (Dajdok & Nowak 2006; Kompała-Bąba & Bąba 2006; Urbisz & Urbisz 2006). Moreover, the pattern of biomass allocation in the case of *E. graminifolia* suggests its strong invasive potential (Szymura & Szymura 2015).

In close proximity to the aforementioned *Solidago,* a hybrid species of alien *Solidago canadensis* s.l. with native *S. virgaurea*, called *Solidago ×niederederi* was found in north-eastern Poland (Pliszko 2013; Migdałek *et al.* 2014). Moreover, numerous ornamental goldenrods e.g. *Solidago hybrida*, *S. caesia*, *S. sphacelata* and hybrid of *Aster ptarmicoides* × *Solidago*, called *×Solidaster ×luteus* are cultivated in Europe.

Goldenrods are clonal perennial herbs with an extensive rhizome system. Stems of these species are single up to the inflorescence and non-flowering leaf rosettes are often present. In the stands of this modular organism, particular stems and/or rosettes are called ramets and considered as individual. The height of the ramets in the native range varies from 50 to 200 cm in the case of *Solidago altissima* and *S. gigantea*, and from 30 to 150 cm in *S. candensis* and *Euthamia graminifolia* (Semple & Cook 2006). Inflorescences are fasciculate, thyrsoid (*S. altissima, S. canadensis*, *S. gigantea*, *S. virgaurea*) or form corymbose panicles (*Euthamia graminifolia*). Capitula are usually small and abundant and the florets are yellow. Seeds are multi-veined achenes with pappus-hair (McNeil 1976).

The taxonomical status of goldenrods which occur in Europe is still under discussion (Beaudry & Chabot 1957; Guzikowa & Maycock 1986; Weber 1997; Weber & Schmid 1998). The taxonomical status of *S. canadensis* and *S. altissima,* in particular, is unclear. These species are difficult to differentiate (Rothmaler 2007; Rutkowski 2013) and in many papers are reported as two varieties of *S. canadensis* s.l.: var. *canadensis* and var. *scabra* (Guzikowa & Maycock 1986; Weber 1997; Weber & Schmid 1998). Semple (personal information), suggests that *Solidago canadensis* var. *hargeri* Fern., which occurs in Central Europe, has more hairy, lower stems than *S. canadensis* var. *canadensis* and, for this reason, is identified as *S. altissima*. However, the taxa differ in rhizome systems (Schmid *et al.* 1988) as well as in the morphological and micro-morphological features of the leaf epidermis (Szymura & Wolski 2011). Unfortunately, these traits are difficult for instant application during field works. Other traits useful for distinguishing between the problematic taxa length and width of capitulum, as well as length of disc and ray florets, are suggested (Beaudry & Chabot 1957; Weber 1997; Weber & Schmid 1998; Rothmaler 2007; Rutkowski 2013). Previous studies revealed that particular *Solidago* species differ in morphological traits with the exception of *S. altissima* and *S. canadensis*. It was suggested that a morphological trait analysis which involves a higher number of indi-

viduals and locations is needed (Szymura & Szymura 2013).

The basic chromosome number in species of goldenrods is x=9. *Solidago virgaurea* and *Euthamia graminifolia* are diploids (2n=18). *S. canadensis* consists of diploid (2n=18) and tetraploid plants (2n=36), while *S. altissima* consists of hexaploid (2n=54), triploid (2n=27) and tetraploid (2n=36) cytotypes in the native range, whereas *Solidago canadensis* var. *hargeri* is diploid (2n=18) (Semple *et al.* 1981, 1984, 2015). *Solidago gigantea* occurs in three different cytotypes: diploid (2n=18), tetraploid (2n=36) and hexaploid (2n=54) (Weber & Jabobs 2005; Schlaepfer *et al.* 2010b).

The main aim of this study was to compare the morphology (concerning life traits) and cytology of *Solidago* species which occur in Central Europe. We discuss the hypothesis that the effectiveness of invasion of particular *Solidago* species is correlated with life traits as well as ploidy level. That is to say, species with higher ramets, larger inflorescences and a higher ploidy level are more frequent. As a measure of the effectiveness of invasion, the number of stands invaded by particular species is considered.

2. Material and methods

2.1. Study site and studied taxa

The study was conducted in Lower Silesia between 2010 and 2012. The distribution of *Solidago* taxa was surveyed on the basis of a sampling design arranged in 10 x 10 km regular grid covering ca. 32,000 km^2 (Fig. 1). The grid was established in accordance with the ATPOL grid and the sampled plots were placed in the centre of the ATPOL square (Zając 1978).

The individual sampling plot was a circle of 25 ha in size. All sampling plots were visited and species of goldenrods were searched for. If these species were present in this area, the stands of goldenrods located nearest to the center of the plot were analysed. If two or more species of goldenrods were found within an area of one plot, they were examined separately. In all, 309 plots were inspected.

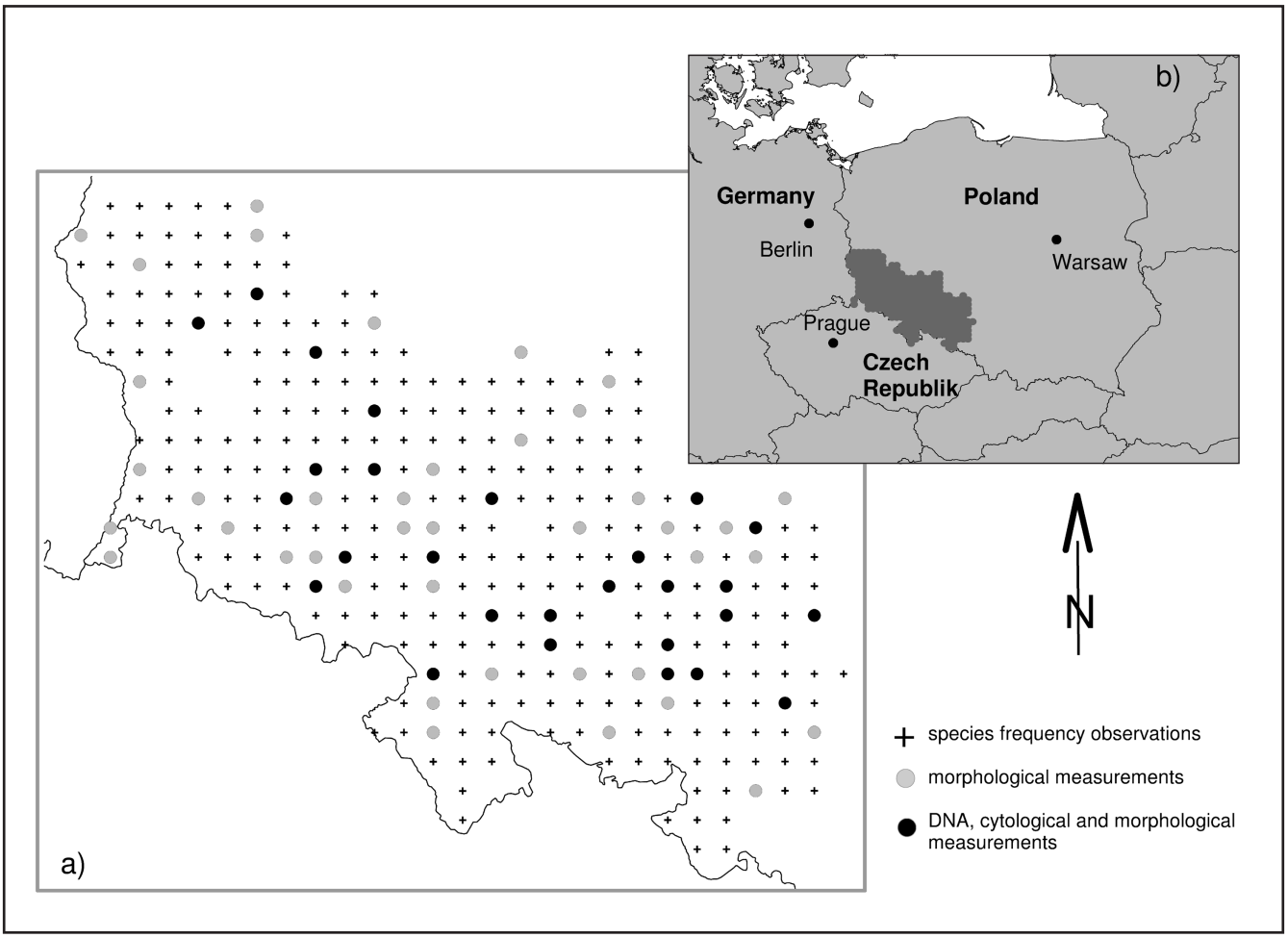

Fig. 1. Map of sampling plots arrangement (crosses, panel a) and location of the study area (panel b). The number of plots shown in the figure, selected to analyse, differs from the number of stands presented in the text (84 for morphological measurements, including 42 for DNA and cytological analysis) because, on some plots, stands of 2 or 3 taxa were presented

2.2. Morphological, cytological and molecular traits

From 241 stands where goldenrods occurred, 84 stands were randomly selected for a detailed study (Fig. 1). The taxa were used as strata to provide a similar number of samples for each taxon. On the stands with 10 ramets per plot, the height of ramets, length and width of inflorescences and the number/size of leaves were measured. All morphological measurements were made in September 2011.

For 42 selected stands (Fig. 1), mature achenes were collected in September 2012 in order to study the chromosome numbers. The chromosome numbers were calculated in root tip meristems with 3 seedlings per plant. The achenes were left to germinate on wet filter paper in Petri dishes (in light conditions) and at room temperature. The seedlings were pre-treated with a 0,004 M aqueous solution of 8-hydroxyquinoline for 4h at 19-21°C in darkness. Afterwards, they were fixed in a 3:1 mixture of absolute ethanol:glacial acetic acid for at least 24h at 4°C. Before staining, the root tips were hydrolysed with 5 M HCl for 1h at room temperature (Kreitschitz & Vallès 2003). The stained meristems were squashed in a drop of 45% acetic acid.

Young leaves, for the purpose of measuring DNA content, were collected from the same stands as seeds for the chromosome studies (Fig. 1). Five ramets per stand were studied, i.e. 200 samples in all. Measurements were made using flow cytometric analysis in the Laboratory of Molecular Biology and Cytometry of the University of Technology and Life Sciences in Bydgoszcz. For measurements, a Partec CCA (Münster, Germany) flow cytometer equipped with an argon laser was used. Leaves of particular *Solidago* taxa and of an internal standard (*Zea mays* (2C=5.43 pg)) were chopped simultaneously with a sharp razor blade in a plastic Petri dish with Galbraith buffer, supplemented with propidium iodide and ribonuclease A. After chopping, the suspension was passed through a 50 µm mesh nylon filter. Analyses were replicated 10 times for each plant material.

2.3. Statistical methods

To check the significance of the differences between the studied groups, a Kruskal-Wallis nonparametric ANOVA rank was used. As a post-hoc test, a multiple comparison of median was conducted. All computations were made using Statistica 10 software.

3. Results

Species of goldenrods were present in 195 plots, i.e. in 63% of the inspected ones. Smooth goldenrod (*Solidago gigantea*) was the most numerous and was found in 125 stands. Late goldenrod (*S. altissima*) and Canadian goldenrod (*S. canadensis*) were found in 116 and 21 stands, respectively. Grass-leaved goldenrod (*Euthamia graminifolia*) was found in only 8 stands. Common goldenrod (*S. virgaurea*) was present in 11 stands, which were placed on lowlands or uplands, but not in the mountains, thus only *S. virgaurea sensu stricto* was analysed. The studied plants were found mostly on abandoned arable fields/meadows, road verges and habitat margins (e.g. forest margins, along fences, field margins).

3.1. Morphological traits

The studied species differed significantly in ramet height (H=303.9, p =0.000). The post-hoc test revealed that they formed two groups. *S. altissima, S. gigantea* and *S. canadensis* belonged to the group of high plants, whereas *Euthamia graminifolia* and *S. virgaurea* belonged to the group of short plants (Fig. 2a). Generally, the two most frequent species (*S. altissima, S. gigantea*) had tall ramets, whereas the uncommon species (*Euthamia graminifolia* and *S. virgaurea*) were short. However, the third tall species (*S. canadensis*) was also uncommon.

The species differed in leaf number (H=157.2, p =0.000). Post-hoc test revealed that the *Euthamia graminifolia* had the highest number of leaves and *S. virgaurea* – the lowest. The number of leaves of *S. altissima* and *S. canadensis* did not differ significantly (Fig. 2b).

S. gigantea and *S. altissima* had the longest leaves, whereby they did not differ to *S. canadensis* (H = 6.253, p =0.000), (Fig. 2c). *S. virgaurea* and *S. gigantea* had the widest leaves. In the case of this trait, the differences between *S. altissima* and *S. canadensis* were also not significant (H=131.3, p =0.000), (Fig. 2d).

The size of inflorescences was the biggest in the case of *S. altissima*. This species had the longest (Fig. 2e) and widest (Fig. 2f) inflorescences. Smaller inflorescences were observed in *S. gigantea*, the most frequent species. The differences between *S. altissima* and *S. canadensis* in the case of inflorescence sizes were not significant.

3.2. Chromosomes number and DNA content

For most of the species (*Solidago altissima, S. canadensis, S. virgaurea* and *Euthamia graminifolia*), the diploid number (2n=2x=18) was exclusively determined. All *S. gigantea* plants were tetraploid (2n=4x=36).

The results of the DNA content analysis showed significant differences among species. The highest DNA content was observed in tetraploid *S. gigantea* and the lowest - in *Euthamia graminifolia* (H=169.3, p =0.000), (Fig. 3, Table 1).

Intraspecies variability, which is variability among particular stands of a given taxa in DNA content, was

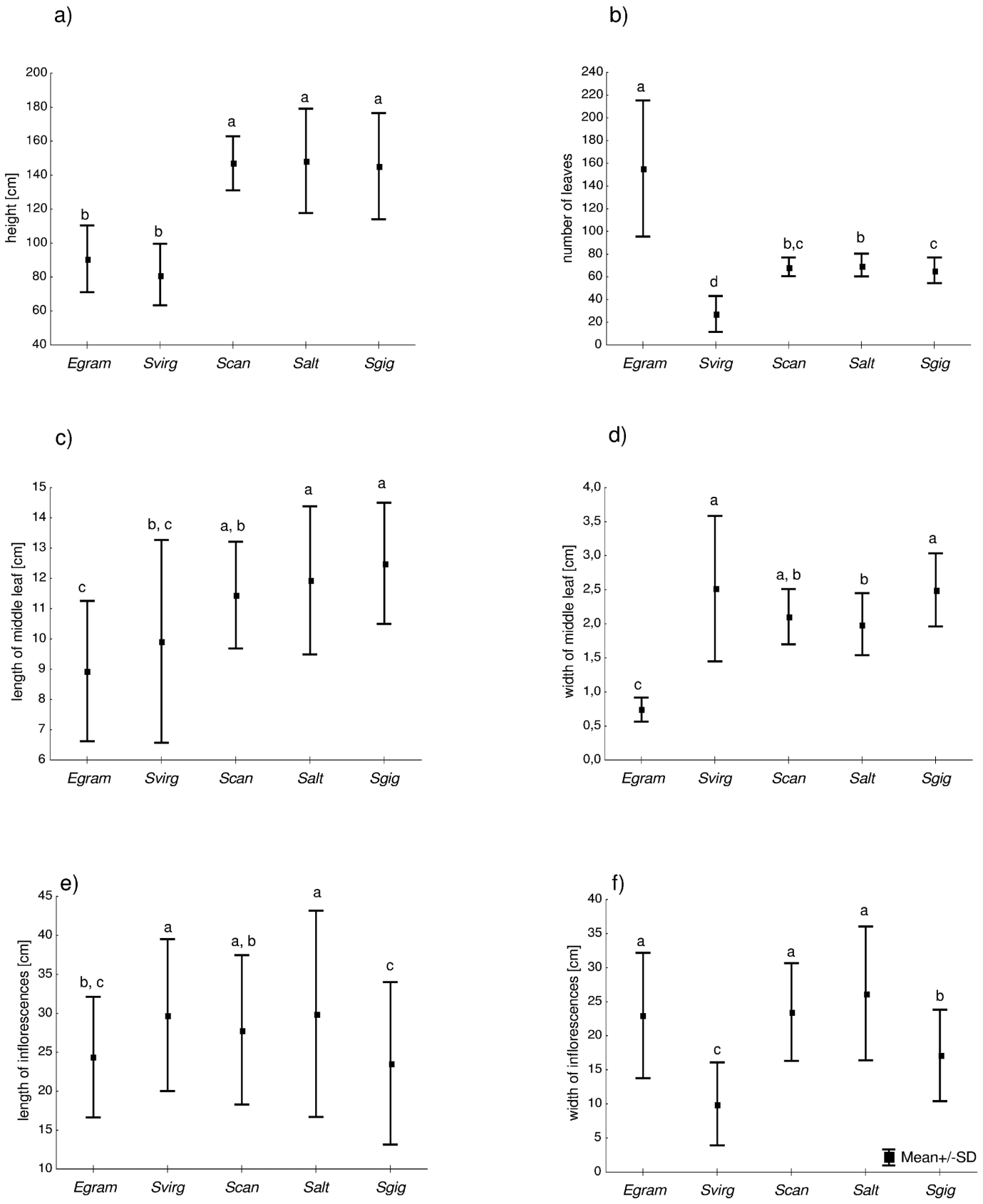

Fig. 2. Morphological traits of goldenrod taxa: a – height of ramets, b – number of leaves, c – length of leaves, d – width of leaves, e – length of inflorescences, f – width of inflorescences

Explanations: significant differences were marked by different letters; mean value (points) and standard deviation (whiskers) are shown; *Egram – Euthamia graminifolia*, *Svirg – Solidago virgaurea*, *Salt – S. altissima*, *Scan – S. canadensis*, *Sgig – S. gigantea*

Table 1. Chromosome number and DNA content in goldenrods taxa

Sample	Taxon	DNA content [pg]		Chromosome number (2n)
		mean	S.D.	
1	*Salt*	2.01	0.028	18
2	*Salt*	2.05	0.022	18
3	*Salt*	2.05	0.021	18
4	*Salt*	2.04	0.021	18
5	*Salt*	2.02	0.012	18
6	*Salt*	2.05	0.007	18
7	*Salt*	2.12	0.049	18
8	*Salt*	2.07	0.017	18
9	*Scan*	2.05	0.020	18
10	*Scan*	2.03	0.033	18
11	*Scan*	2.06	0.027	18
12	*Scan*	2.03	0.035	18
13	*Scan*	2.04	0.037	18
14	*Scan*	2.21	0.097	18
15	*Scan*	2.06	0.015	18
16	*Scan*	2.04	0.017	18
17	*Scan*	2.08	0.025	18
18	*Sgig*	3.80	0.014	36
19	*Sgig*	3.70	0.017	36
20	*Sgig*	3.73	0.039	36
21	*Sgig*	3.71	0.060	36
22	*Sgig*	3.74	0.030	36
23	*Sgig*	3.72	0.024	36
24	*Sgig*	3.75	0.023	36
25	*Sgig*	3.74	0.023	36
26	*Sgig*	3.74	0.029	36
27	*Sgig*	3.73	0.023	36
28	*Sgig*	3.78	0.028	36
29	*Sgig*	3.74	0.016	36
30	*Sgig*	3.80	0.023	36
31	*Sgig*	3.70	0.017	36
32	*Egram*	1.92	0.031	18
33	*Egram*	1.91	0.077	18
34	*Egram*	1.92	0.033	18
35	*Egram*	1.90	0.026	18
36	*Egram*	1.95	0.027	18
37	*Egram*	1.94	0.020	18
38	*Egram*	1.95	0.017	18
39	*Svirg*	2.36	0.036	18
40	*Svirg*	2.34	0.015	18
41	*Svirg*	2.36	0.018	18
42	*Svirg*	2.34	0.023	18

Explanations: *Salt* – *Solidago altissima*, *Scan* – *S. canadensis*, *Scan/Salt* – plants with intermediate traits between *S. canadensis* and *S. altissima*, *Sgig* – *S. gigantea*, *Egram* – *Euthamia graminifolia*, *Svirg* – *S. virgaurea*

also checked. There were significant differences among stands in *S. altissima* (H=15.089, p =0.020), *S. canadensis* (H =17.093, p =0.009). A significant difference was observed also in *S. gigantea* (H=38.63, p =0.000). Stands of the remaining two species did not differ in DNA content (detailed results not shown).

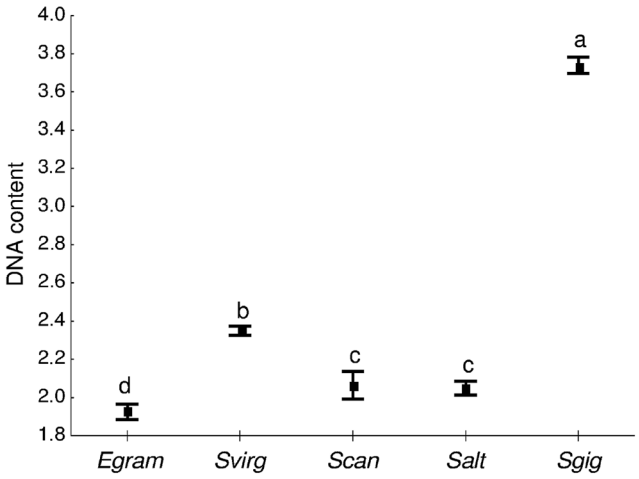

Fig. 3. DNA content of goldenrod taxa
Explanations: significant differences were marked by different letters; mean value (points) and standard deviation (whiskers) are shown; *Egram* – *Euthamia graminifolia*, *Svirg* – *Solidago virgaurea*, *Salt* – *S. altissima*, *Scan* – *S. canadensis*, *Sgig* – *S. gigantea*

4. Discussion

The studied taxa of goldenrods were introduced as ornamental plants from North America to London in the second part of the 17th century. They were then distributed to gardens in different parts of Europe (Hitchmough *et al.* 2004). After a short time, the goldenrods "escaped" from cultivation and spread across Europe widely. The occurrence of *Solidago gigantea* in Poland was referred to earlier (in 1853) than *S. canadensis* s.l. (1872), and its spread had also been observed twenty years earlier – in 1940s (Tokarska-Guzik 2003). The results of this study suggest that *S. gigantea* is currently the most common species of goldenrods in south-western Poland. *Euthamia graminifolia* was introduced and naturalized at a similar time (1885); however, it only occurs in restricted areas with a low number of stands. It is considered as a species which is still in the lag phase of the invasion process (Weber 2001). However, recently a sudden spread of this species in different natural habitats has been observed (Dajdok & Nowak 2006; Szymura & Szymura 2011). It suggests that this species now reaches a phase of rapid range expansion during the invasion process. The native goldenrod, *S. virgaurea*, occurred sparsely in the studied area. This species exploits environmental resources less effectively and produces a few times less biomass than alien goldenrods (Szymura & Szymura 2015).

Life traits of invasive goldenrods are not evident indicators of invasion effectiveness. The most widespread species, *S. gigantea* and *S. altissima*, have the highest ramets, while the uncommon species, *Euthamia graminifolia* and *S. virgaurea*, are short. However, *S.*

canadensis, which belongs to the group of tall taxa, was also uncommon. With regards to inflorescence size, the most frequent species (*S. gigantea*) produced smaller inflorescences than the less frequent species (*S. altissima*, *S. canadensis* and *Euthamia graminifolia*). These results are in accordance with previous assessments but included a larger area (Szymura & Szymura 2013). However, it should be mentioned that *S. gigantea* and *Euthamia graminifolia* invest more biomass in the below-ground parts (including rhizomes) than the remaining species (Schlaepfer *et al.* 2010a; Szymura & Szymura 2015). Therefore, the observed above-ground traits indicating the invasiveness were not able to fully reflect the invasive potential of the species.

Despite the high diversity in chromosome number within the native range (Semple *et al.* 1981, 1984; Weber & Jabobs 2005) in the studied area, only diploid plants of *Solidago altissima, S. canadensis, Euthamia graminifolia* were found and, in the case of *S. gigantea*, only tetraploid plants. This complies with data from Germany (Weber 1997, 2000) that in Europe only diploid plants of *S. canadensis* are noted. In *S. altissima*, the diploid chromosome level was also noted and the occurrence of additional B-chromosomes was observed (Małecka 1988; Musiał 1989). Only tetraploid populations of *S. gigantea* were found in Europe (Schlaepfer *et al.* 2008a, 2008b, 2010b). In the studied area, tetraploid taxon (*Solidago gigantea*) was the most numerous (present in 125 points) but, the second one (*S. altissima*) – which is a diploid – was present and plentiful (in 116 points). Tetraploid cytotypes of *S. gigantea* are more expansive than the diploid ones in the native range (Schlaepfer *et al.* 2008a), therefore, the polyploidy plays an important role in the invasion success of this taxon. *S. altissima* in its native range is most often hexaploid (2n=54), but triploid (2n=27) and tetraploid (2n=36) cytotypes also occur (Semple *et al.* 1981, 1984; Weber 2000). It has been suggested that *S. altissima* developed as an allohexaploid by doubling the chromosomes of a hybrid between an 18-chromosome *S. canadensis* and 36-chromosome cytotype of *S. gigantea* (Beaudry & Chabot 1957). In Europe, only diploid plants have been found (Weber 1997, 2000). It is likely that diploid races of *S. altissima* exist in North America. If such specimens are found, they may represent possible ancestors of the plants introduced in Europe (Weber 2000). The second explanation of the diploid status of *S. altissima* in Europe is that these plants belong actually to the taxon *S. canadensis* var. *hargeri* which is a diploid in America (Semple *et al.* 1981, 1984, 2015). Factors allowing the vast spread of this taxon in Europe are probably connected with its intensive reproduction system by generative and vegetative propagation, as well as wide tolerance for nutrient and soil moisture. *S. altissima* in Europe produces more than 10,000 seeds per shoot (Weber 2000). The small size of diaspores and the presence of pappus favours long-distance dispersal by wind. Established populations increase mainly by clonal growth. Individual clones have a long life span and can reach an age of 100 years (Weber 2000). However, a pattern could be found in the variation of DNA content and the frequency of occurrences of *Solidago* taxa. Significant differences in the DNA content of plants collected from different stands of *S. gigantea*, *S. altissima*, *S. canadensis* were observed in the studied area. Two of these taxa, namely *S. altissima* and *S. gigantea* are prevalent and common in the studied area. Numerous stands of these taxa in different environmental conditions occur which could both influence or be a result of variation in DNA content (Bennett *et al.* 2000; Śliwińska & Thiem 2007; Kubešova *et al.* 2010). The other plants, whose stands differ according to DNA content, belong to *Solidago canadensis*. On the contrary, plants of *Euthamia graminifolia* from different stands did not differ with respect to their DNA content. Differences between the genome of this species should be expected on the basis of the 'genotypic' hypothesis of lag phase. It suggests that the lag phase is a time necessary for the development of different genotypes with increased dispersal ability (Pyšek & Richardson 2008). However, in a recently observed situation of rapid spread of this taxon, differentiation in DNA content was not found. The lack of significant differences was also observed in native taxon (*S. virgaurea*). However, in the studied area, only plants which grew on lowland localities were observed. The results could change if stands of *S. minuta* were included in the analysis (Kiełtyk & Mirek 2014).

5. Conclusions

- Life traits of invasive goldenrods did not precisely indicate their effectiveness of invasion. The most widespread species, *S. gigantea* and *S. altissima*, had the highest ramets and the uncommon species, *S. virgaurea* and *Euthamia graminifolia*, were short. However, *S. canadensis*, which was tall, was also uncommon. Furthermore, the most frequent species, *S. gigantea*, produced smaller inflorescences than less frequent species such as *S. altissima*, *S. canadensis* and *Euthamia graminifolia*.
- Tetraploid taxon (*Solidago gigantea*) was the most numerous in the studied area (present in 125 stands), but the second one (*S. altissima*), which was a diploid, was present in 116 stands. The other taxa occurred in a much smaller number of stands. As a result, the spread of particular taxa was most likely connected not only to ploidy level.

- The pattern in variation of DNA content and frequency of occurrences of taxa of goldenrods could be defined. Stands of less frequent species (*Euthamia graminifolia* and *Solidago virgaurea*) did not differ with respect to DNA content.

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