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Chromosome numbers in hybrids between invasive and native *Solidago* (Asteraceae) species in Europe

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Abstract

In Europe, two North American species, *Solidago canadensis* and *S. gigantea* hybridize with native *S. virgaurea* producing the hybrids: *S.* ×*niederederi*, a hybrid between *S. canadensis* and *S. virgaurea*, and *S.* ×*snarskisii*, a hybrid between *S. gigantea* and *S. virgaurea*. The morphological description of both hybrids has been well established in contrast to the data on chromosome numbers which were insufficiently recorded or missing. The diploids of *S.* ×*niederederi* have been recently reported from a few localities in Austria and Lithuania. In this study, we evidenced a triploid of *S.* ×*snarskisii* from one locality in Lithuania, as well as confirmed diploids in the progenies of *S.* ×*niederederi* collected in 23 new localities in Austria, Poland, Lithuania, and Latvia, based on chromosome counting.

Keywords: alien species, plant hybridization, ploidy level, *Solidago* sect. *Solidago* nothosubsect. *Triplidago*

Introduction

Hybridization and polyploidization are active processes recognized as the most important evolutionary mechanisms affecting diversification, adaptation, and speciation in flowering plants (Leitch & Bennett 1997, Soltis *at al*. 2009, Wood *et al*. 2009, Sattler *et al*. 2016, Alix *et al*. 2017, Pelé *et al*. 2018). Cytogenetic and phylogenetic data show that all angiosperms have at least one, and often multiple, whole-genome duplication (WGD) in their ancestry (Weiss-Schneeweiss *et al.* 2013 and references therein). Determination of ploidy level is an integral part of taxonomic studies on describing new taxa of plants, especially in the case of taxonomically complicated agamic complexes, where ploidy is an important diagnostic feature for apomictic microspecies that are extremely difficult to distinguish based on morphological characteristics (e.g., Vašut *et al*. 2005, Marciniuk *et al*. 2012, 2018, Wolanin *et al*. 2016, 2018, Sochor *et al*. 2019). The analysis of chromosome numbers is also recommended in the proper identification of plant hybrids (Stace 1989, López-Caamal & Tovar-Sánchez 2014, Prančl *et al.* 2018). The number of chromosomes in the hybrids is usually intermediate between their parental species if parental species differ from each other by the number of chromosomes (e.g., James *et al*. 2000). However, sometimes due to introgressive hybridization the number of chromosomes in introgressants can be different from that evidenced in the intermediate F_1 hybrids (e.g., Krahulcová *et al*. 1996, Tu *et al*. 2009).

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The genus *Solidago* Linnaeus (1753: 878) (Asteraceae) is native to North America, South America, Europe, the Azores, and Asia and comprises about 133 species (Semple 2020). In *Solidago*, the basic chromosome number is x=9 and different ploidy levels have been documented within the genus, namely 2x, 3x, 4x, 5x, 6x, 8x, 10x, 12x, and 14x (Semple *et al*. 1981, 1984, Morton *et al*. 2017, Semple 2020). Most taxa are diploids, but tetraploids are also quite common, while triploid, pentaploid and higher ploidy levels have been so far found only in a few *Solidago* species (Semple 2016). Available data confirm the occurrence of infraspecific cytotype variation in *Solidago*; however, taxa with a single ploidy level are more frequent than taxa with multiple cytotypes (Peirson *et al*. 2012, Semple 2016, 2020). In Europe, two North American invasive species, *S. canadensis* Linnaeus (1753: 878) and *S. gigantea* Aiton (1789: 211) hybridize with native *S. virgaurea* Linnaeus (1753: 880) giving the hybrids: *S.* ×*niederederi* Khek (1905: 22), a hybrid between *S. canadensis* and *S. virgaurea* (Pliszko & Zalewska-Gałosz 2016, Skokanová *et al.* 2020a), and *S.* ×*snarskisii* Gudžinskas & Žalneravičius (2016: 148), a hybrid between *S. gigantea* and *S. virgaurea* (Gudžinskas & Žalneravičius 2016). Both hybrids belong to *Solidago* sect. *Solidago* nothosubsect. *Triplidago* Gudžinskas and Žalneravičius (2016: 152) which is characterized by the formation of pseudorosettes on the apices of vegetative shoots (Gudžinskas & Žalneravičius 2016). Taxonomic treatment of *S.* ×*niederederi* and *S.* ×*snarskisii* was presented by Pliszko (2015), Skokanová *et al.* (2020a), and Gudžinskas & Žalneravičius (2016), respectively. *Solidago* ×*niederederi* has been recorded in Austria, Italy, France, Germany, the United Kingdom, Denmark, Sweden, Norway, Finland, Czechia, Poland, Hungary, Slovakia, Romania, Lithuania, Latvia, and European part of Russia (Jaźwa *et al.* 2018, Skokanová *et al.* 2020b and references therein) whereas *S.* ×*snarskisii* has been evidenced only in Lithuania, Poland, European part of Russia, and Sweden, so far (Gudžinskas & Žalneravičius 2016, Pliszko 2018, Vinogradova & Galkina 2019, 2020). Moreover, *S.* ×*niederederi* is treated as an established alien whereas *S.* ×*snarskisii* is currently treated as a casual alien. *Solidago* ×*niederederi* is found in anthropogenic habitats such as abandoned fields, disused quarries, roadsides, railway embankments, forest clearings, and tree plantations, usually with both parental species (Pagitz & Lechner-Pagitz 2015, Gudžinskas & Petrulaitis 2016, Pagitz 2016, Pliszko & Kostrakiewicz-Gierałt 2017, 2019, Pliszko *et al*. 2017, 2019). *Solidago* ×*snarskisii* also inhabits abandoned fields (Gudžinskas & Žalneravičius 2016, Pliszko 2018). Despite its reduced pollen viability, *S.* ×*niederederi* can produce a low number of fruits (cypselas) with viable seeds (Migdałek *et al*. 2014, Karpavičienė & Radušienė 2016, Pliszko & Kostrakiewicz-Gierałt 2017). Moreover, the seeds of *S.* ×*niederederi* germinate easily with no involvement of cold stratification (Pliszko & Kostrakiewicz-Gierałt 2018) and even if their pappus is removed from the fruit (Pliszko & Kostrakiewicz-Gierałt 2020). In contrast, the development of fruits in *S.* ×*snarskisii* has not been observed so far suggesting its sterility (Gudžinskas & Žalneravičius 2016, Pliszko 2018). Nevertheless, *S.* ×*snarskisii* produces long underground rhizomes similar to those found in *S. gigantea* allowing vegetative propagation (Gudžinskas & Žalneravičius 2016, Pliszko 2018).

In Europe, it is known that *S. canadensis* and *S. virgaurea* s. str. are diploids whereas *S. gigantea* is a tetraploid or rarely a diploid (Schlaepfer *et al.* 2008, Hull-Sanders *et al.* 2009, Szymura *et al.* 2015, Karpavičienė & Radušienė 2016, Verloove *et al.* 2017, Morton *et al.* 2019). Given this, the expected ploidy level of *S.* ×*niederederi* is 2x (2n=18) whereas in *S.* ×*snarskisii* it should be 3x (2n=27) or 2x (2n=18). The diploids of *S.* ×*niederederi* and its parental species have been recently confirmed in specimens collected in one population in Austria (Pagitz 2016) and six populations in Lithuania (Karpavičienė & Radušienė 2016) using flow cytometry and chromosome counting, respectively. Unfortunately, the data on chromosome numbers in *S.* ×*snarskisii* are missing. In 2018, an interesting specimen of *Solidago* was discovered in Kotuń near Siedlce, central-eastern Poland. The specimen grew on a pond levee, among *S. canadensis*, *S. gigantea*, and *S. virgaurea*, and resembled *S.* ×*snarskisii* by having large capitula, almost naked stems and leaves and forming long underground rhizomes. Surprisingly, the specimen had numerous well-developed fruits with viable seeds what is not expected from *S.* ×*snarskisii* which is considered sterile (Gudžinskas & Žalneravičius 2016). Recognizing the number of chromosomes in hybrids between alien and native *Solidago* species in Europe can help to resolve their parentage and can be also useful in predicting their potential of generative reproduction. In this research, therefore, we aimed to establish chromosome numbers in the specimens of *S.* ×*snarskisii* from its *locus classicus* in Lithuania as well as in the progenies of *S.* ×*niederederi* from Austria, Poland, Lithuania, and Latvia. We also included the ambiguous specimen which resembled *S.* ×*snarskisii* and was collected in Poland.

Material and methods

Plant material

Fruits (cypselas) of *Solidago ×niederederi* were collected from 26 localities in Austria (10), Poland (10), Lithuania (5), and Latvia (1), in 2018. Fruits of specimen resembling *S. ×snarskisii*, as well as fruits of *S. gigantea*, *S. virgaurea*, and *S. canadensis*, were collected from one locality in Poland, in 2018. The fruits of the above-mentioned taxa were sampled from 10 shoots (panicles) per locality (population), except the *S. ×snarskisii*-like specimen from which only two shoots with mature fruits were sampled. Each shoot (panicle) was taken from separate cluster of shoots, except the *S. ×snarskisii*-like specimen. Three live specimens of *S. ×snarskisii* were collected from its *locus classicus* in Lithuania, in September 2019. Flowering shoots with roots and rhizomes from three separate clumps of *S. ×snarskisii* were dug, aerial part was cut and the roots with rhizomes planted into a pot. Aerial parts of the sampled plants were dried as herbarium specimens (deposited in BILAS). The list of localities from which the samples were taken for chromosome counts is presented in Appendix 1. Most of the presented localities are new for the *Solidago* chromosome study, except three localities of *S. ×niederederi* (Unterperfuss in Austria and Anykščiai and Rokiškis in Lithuania). However, the individuals of *S. ×niederederi* were not the same as those previously studied (Pagitz 2016, Karpavičienė & Radušienė 2016). The identification of hybrids was based on morphological features provided by Nilsson (1976) and Gudžinskas and Žalneravičius (2016). The specimens of *S. ×niederederi,* from which the seeds were collected, most likely represented F_1 generation by their intermediate morphology. However, the progenies of these specimens could be represented by F_2 generation or backcrosses with parental species, since the hybrids and parental species occurred together in the studied localities.

Chromosome number determination

Sets of 50 fruits per taxon from each locality were placed on moist filter paper in Petri dishes and kept in light at room temperature for a few days until seed germination occurred and in the case of *S. ×snarskisii*, 25 fresh roots about 1 cm long were excised from rooted plant cuttings. The karyological analysis was performed according to the procedure previously applied to the taxa of *Hieracium* and *Taraxacum* (Musiał & Szeląg 2015, Wolanin & Musiał 2017). Young seedlings or roots were immersed in a saturated aqueous solution of 8-hydroxychinoline for 4 h at room temperature and then fixed in absolute ethanol/glacial acetic acid (3:1, v/v) for 24 h. After fixation, the plant material was stained in 2% acetic orcein for 4 days at room temperature. Stained samples were transferred to 45% acetic acid, heated to boiling, and then under stereoscopic microscope tips of roots were cut from them. Preparations were made by squashing the root meristems in a drop of 45% acetic acid. Coverslips were removed after freezing in liquid nitrogen and the slides were air-dried and mounted in Entellan. For each species, the somatic number of chromosomes was determined by analyzing at least 20 well-spaced metaphase plates that were documented using a Nikon Eclipse E400 microscope equipped with a CCD camera.

Results and discussion

The analysis of the samples collected in Kotuń confirmed the diploid chromosome number (2n=18) in *Solidago virgaurea* and *S. canadensis* (Fig. 1a, b), and the tetraploid chromosome number (2n=36) in *S. gigantea* (Fig.1c). The results of our research also confirmed that the progenies obtained from the seeds of *S. ×niederederi* collected in Austria, Poland, Lithuania, and Latvia were diploids (2n=18) (Fig. 1d). Unexpectedly, the progenies of the specimen resembling *S. ×snarskisii* turned out to be diploids (2n=18) (Fig. 1e); however, in the samples of *S. ×snarskisii* from its *locus classicus*, we recorded a triploid chromosome number (2n=27) (Fig. 1f). The occurrence of supernumerary chromosomes or aneuploid cytotypes has not been found in *Solidago* individuals studied in the current work, although supernumerary chromosomes and aneuploidy were previously recorded in specimens of various *Solidago* species, including *S. canadensis* and *S. gigantea* (Kapoor 1978, Semple *et al*. 1984, 2019, Szymura & Wolski 2011). Data on chromosome numbers of the investigated taxa are summarized in Table 1. Interestingly, Gudžinskas & Žalneravičius (2016) did not check the chromosome numbers in specimens of *S. ×snarskisii*; however, they assumed that the hybrid is triploid because of its sterility. Considering the co-occurrence of *S. ×niederederi* with the parental species, the progenies obtained from the seeds of *S. ×niederederi* could be represented by the F_2 generation of the hybrids as well as the backcrosses with the parental species. Regardless of their origin, a lack of chromosome aberrations in the progenies of *S.* ×*niederederi* suggests that they may have a potential for further sexual reproduction.

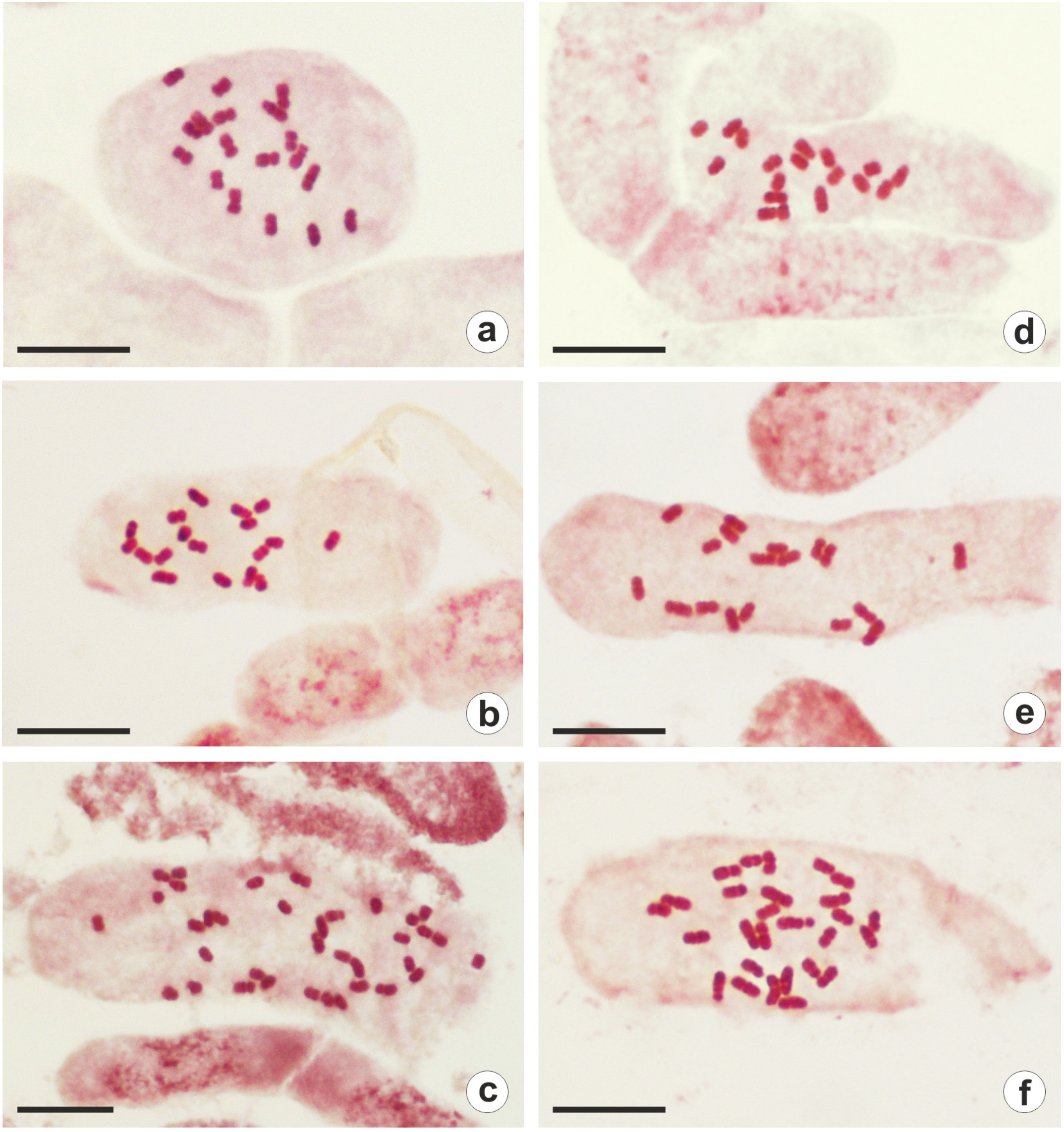

FIGURE 1. Metaphase plates in somatic cells of investigated specimens: diploid *Solidago virgaurea* (**a**), diploid *S. canadensis* (**b**) and tetraploid *S. gigantea* (**c**) (all taxa from Kotuń in Poland), diploid *S.* ×*niederederi* from Rokiškis in Lithuania (**d**), diploid *S.* ×*snarskisii*-like specimen from Kotuń in Poland (**e**), and triploid *S.* ×*snarskisii* from Zabarauskai in Lithuania (**f**). Scale bars = 10 µm.

In its native range, *S. gigantea* can be diploid, triploid, tetraploid, pentaploid (2n=45) and hexaploid (2n=54) (Semple *et al.* 1984, Schlaepfer *et al.* 2008, Hull-Sanders *et al.* 2009, Morton *et al.* 2019). On the other hand, in its secondary range in Europe, it is represented by diploids and tetraploids only (Schlaepfer *et al.* 2008, Hull-Sanders *et al.* 2009, Morton *et al.* 2019). However, tetraploid is considered the most frequent cytotype of this species in both native and invasive geographical ranges (Hull-Sanders *et al*. 2009). Although there is a probability that the hybrid between *S. gigantea* and *S. virgaurea* s. str. can be also diploid, it is hard to confirm that the fertile specimen resembling *S.* ×*snarskisii* collected in Kotuń is a true hybrid between *S. gigantea* and *S. virgaurea* since the progenies of *S. gigantea* collected in Kotuń were determined as tetraploids and there is no report on diploid *S. gigantea* in Poland (Schlaepfer *et al*. 2008, Szymura *et al*. 2015). It is possible that *S.* ×*snarskisii*-like specimen from Kotuń is a result of the repeated crossing of *S.* ×*niederederi* with its parental species. Solitary individuals of putative backcross origin were recorded in Lithuania and they tend to be closer to *S. virgaurea* by characters of capitula and florets, but characters of stems and leaves are closer to *S.* ×*niederederi*. Also, we cannot exclude that this specimen represents abnormal *S. virgaurea*. To explain the morphological variation of *Solidago* hybrids in Europe, further molecular analyses should be undertaken.

TABLE 1. Chromosome numbers in *Solidago* hybrids and their parental species evidenced in the study.

Taxon	Country	Number of localities	Chromosome number	Additional remarks
Solidago ×niederederi	Austria	10	2n=18	Pagitz (2016) evidenced diploids in the hybrid occurring in one locality in Austria
	Latvia	1	2n=18	-
	Lithuania	5	2n=18	Karpavičienė & Radušienė (2016) found diploids in the hybrids occurring in six localities in Lithuania
	Poland	10	2n=18	-
Solidago ×snarskisii	Lithuania	1	2n=27	-
Solidago canadensis	Poland	1	2n=18	Szymura *et al*. (2015) found diploids in populations occurring in south-western Poland
Solidago gigantea	Poland	1	2n=36	Szymura *et al*. (2015) found tetraploids in populations occurring in south-western Poland
Solidago virgaurea	Poland	1	2n=18	Szymura *et al*. (2015) found diploids in populations occurring in south-western Poland

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APPENDIX 1. Origin of *Solidago* samples. Data provided in the list below: name of taxon, type of material sampled (f—fruits, l—living plants), country, locality with GPS coordinates and elevation (m a.s.l.), habitat, date of collection, collector. Countries and localities are given in alphabetical order.

Solidago* ×*niederederi (f)—**AUSTRIA:** Innsbruck, Allerheiligen north, 47°16.330' N, 11°21.237' E, 735 m, forest road, 26 Oct 2018, K. Pagitz; Innsbruck northeast, "Nordkette", 47°16.471' N, 11°21.097' E, 795 m, forest road, slope, 26 oct 2018, K. Pagitz; Inzing, 47°16.015' N, 11°11.589' E, 810 m, clearing, afforestation, 1 Nov 2018, K. Pagitz; Natters, 47°14.731' N, 11°22.475' E, 835 m, forest road, 15 Oct 2018, K. Pagitz; Pettnau east, 47°17.217' N, 11°11.093' E, 625 m, forest road, 14 Oct 2018, K. Pagitz; Terfens, above Neuterfens, 47°19.014' N, 11°37.691' E, 690 m, forest road, 16 Nov 2018, K. Pagitz; Terfens northwest, 47°18.810' N, 11°37.118' E, 695 m, forest road, slope, 16 Nov 2018, K. Pagitz; Terfens northwest, 47°18.923' N, 11°37.370' E, 720 m, forest road, clearing, slope, 16 Nov 2018, K. Pagitz; Terfens west, towards Fritzens, 47°18.881' N, 11°37.568' E, 635 m, forest road, 16 Nov 2018, K. Pagitz; Unterperfuss, 47°15.155' N, 11°15.049' E, 690 m, gravel pit, slopes, 28 Oct 2018, K. Pagitz; **LATVIA:** Daugavpils, 55°51.961' N, 26°29.354' E, 290 m, fallow land, 29 Sep 2018, Z. Gudžinskas; **LITHUANIA:** Anykščiai, 55°31.103' N, 25°07.597' E, 108 m, abandoned dry grassland, 27 Sep 2018, Z. Gudžinskas; Pagiriai, 54°34.265' N, 25°11.777' E, 147 m, abandoned mesic grassland, 25 Sep 2018, Z. Gudžinskas; Rokiškis, 55°34.227' N, 25°35.911' E, 135 m, fallow land, 27 Sep 2018, Z. Gudžinskas; Sausiai, 54°42.247' N, 25°00.024' E, 137 m, abandoned mesic grassland, 25 Sep 2018, Z. Gudžinskas; Vilnius, 54°48.027' N, 25°16.765' E, 154 m, abandoned dry grassland, 22 Sep 2018, Z. Gudžinskas; **POLAND:** Bakałarzewo, 54º05.943' N, 22º39.543' E, 168 m, fallow land, 20 Sep 2018, A. Pliszko; Czajowice, 50º11.431' N, 19º48.394' E, 458 m, fallow land, 29 Sep 2018, A. Pliszko; Gołdap, 54º17.884' N, 22º18.601' E, 173 m, fallow land, 21 Sep 2018, A. Pliszko; Harbutowice near Palcza, 49°48.731' N, 19°45.318' E, 545 m, fallow land, 27 Oct 2018, A. Pliszko; Kielce, 50º52.542' N, 20º34.951' E, 266 m, fallow land, 25 Sep 2018, A. Pliszko; Kraków, 50º05.433' N, 19º50.471' E, 229 m, disused limestone quarry, 29 Sep 2018, A. Pliszko; Olecko near Możne, 54º01.436' N; 22º31.462' E, 161 m, fallow land, 23 Sep 2018, A. Pliszko; Suwałki, 54º07.397' N, 22º57.131' E, 179 m, fallow land, 23 Sep 2018, A. Pliszko; Taciewo, 54º09.313' N, 22º48.410' E, 205 m, fallow land, 22 Sep 2018, A. Pliszko; near Wolbrom, 50º22.103' N, 19º44.719' E, 391 m, fallow land, 30 Sep 2018, A. Pliszko.

Solidago* ×*snarskisii (l)—**LITHUANIA:** Zabarauskai, 54º33.311' N, 24º30.779' E, 107 m, fallow land, 31 Aug 2019, Z. Gudžinskas. ***Solidago* ×*snarskisii*-like specimen** (f)—**POLAND:** Kotuń near Siedlce, 52°10.564' N, 22º05.879' E, 145 m, pond levee, 26 Sep 2018, G. Łazarski. ***Solidago canadensis*** (f)—**POLAND:** Kotuń near Siedlce, 52°10.641' N, 22°06.094' E, 145 m, pond levee, 29 Oct 2018, G. Łazarski. ***Solidago gigantea*** (f)—**POLAND:** Kotuń near Siedlce, 52º10.642' N, 22º06.187' E, 145 m, pond levee, 29 Oct 2018, G. Łazarski. ***Solidago virgaurea*** (f)—**POLAND:** Kotuń near Siedlce, 52º10.644' N, 22º06.008' E, 145 m, pond levee, 29 Oct 2018, G. Łazarski.