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First evidence for the presence of invasive *Solidago altissima* (Asteraceae) in Europe

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Abstract: The North American invasive species *Solidago altissima* L. (Asteraceae) is reliably recorded from a single locality in Belgium (Beveren, Waaslandhaven, Verrebroekse Plassen). Nuclear genome size, as measured by flow cytometry, showed this population to be distinct from the closely similar and widespread *S. canadensis* L. Plants were shown to be hexaploids, with an estimated chromosome number of $2n = 54$, while only diploids ($2n = 18$) of *S. canadensis* are known from Europe. These findings were further supported by morphological traits. *Solidago altissima* has repeatedly been claimed from Europe but all these records may be referable to *S. canadensis* var. *canadensis* and, more likely, *S. canadensis* var. *hageri* Fernald. To the best of our knowledge, the recently detected population in Belgium represents the first unequivocal record of *S. altissima* in Europe.

Key words: Asteraceae, Compositae, *Solidago*, *Solidago altissima*, *Solidago canadensis*, genome size, flow cytometry, Europe, Belgium, invasive

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Introduction

Solidago L. (Asteraceae) is a predominantly American genus. Of the c. 120 currently accepted species, only six to ten are native to Eurasia (Semple & Cook 2006; Semple 2016). Recent molecular phylogenetic studies considerably helped to resolve relationships within the genus, as well as to other genera within the tribe Astereae. For instance, the grass-leaved goldenrods [*Euthamia* (Nutt.) Cass.], traditionally included in *Solidago*, proved to be distinct. *Oligoneuron* Small, in turn, was shown to be part of *Solidago* (e.g. Beck & al. 2004; Schilling & al. 2008). Although goldenrod, as a genus, is readily recognized, identification to the species level is often difficult (Semple & al. 1999). This particularly holds true for *S.* subsect. *Triplinerviae* (Torr. & A. Gray) G. L. Nesom, also known

as the *S. canadensis* complex. This group is reputed for being one of the most taxonomically challenging species assemblages in North America (Melville & Morton 1982; Semple & Cook 2006). It includes several species that are widely grown as garden ornamentals (e.g. *S. canadensis* L. and *S. gigantea* Aiton; Yeo 2000). These species are vigorous perennial herbs with strong rhizomes. Wherever recorded in the wild (as escapes, from discarded garden waste or from transported rhizomes), they are readily considered noxious environmental weeds, also in Europe (e.g. Voser-Huber 1983; Guzikowa & Maycock 1986; Schlaepfer & al. 2010; etc.).

In Belgium, two species from this complex are more or less widely naturalized: *Solidago canadensis* and *S. gigantea* (Verloove 2016). The latter is by far the most frequent, although it long remained overlooked due to

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confusion with the former (Lawalrée & Vanden Berghen 1946). At present, however, both are rather easily separated based on characters such as stem indumentum (present or absent), involucre size and ray floret length (Lambinon & Verloove 2012). A third species from the complex, *S. altissima* L., has been claimed from other parts of Europe, although McNeill (1976) concluded that all claims appear to be referable to *S. canadensis* s.str. Further, he stated that *S. altissima* is cultivated and may also be naturalized. Yet, some authors disagree. Sell & Murrell (2006) suggested that the latter [as *S. canadensis* subsp. *altissima* (L.) O. Bolòs & Vigo] is the “common race” in the British Isles, and Weber (1997, 2000) even ascribed all European populations to *S. altissima*.

Solidago canadensis and *S. altissima* were both described by Linnaeus (1753). They were considered similar species that could be distinguished on features such as stature, flowering time and leaf serration: the latter was characterized as a taller plant with entire leaves that flowered later than *S. canadensis*. However, their separation has often been considered problematic, and some authors treated them as mere varieties or subspecies of a single variable species, *S. canadensis*: var. *canadensis*; and var. *scabra* (Muhl. ex Willd.) Torr. & A. Gray (= subsp. *altissima*) (e.g. Guzikowa & Maycock 1986; Weber 1997; Weber & Schmid 1998; Stace 2010). Multivariate morphometric analyses, however, showed them to be separate species (Semple & al. 2015). Both differ also in shoot growth and development, leaf morphology, and physiology, with *S. altissima* being in that respect more similar to *S. gigantea* than to *S. canadensis* (Schmid & al. 1988). Additional traits useful for their separation are length and width of involucre, as well as length of disc and ray florets (e.g. Beaudry & Chabot 1957; Weber 1997; Weber & Schmid 1998). Plants with differences in macro- and micro-morphological features of the leaf epidermis (Szymura & Wol-ski 2011) may point at *S. canadensis* var. *hargerii* Fernald rather than *S. altissima* (see below).

Taxa of *Solidago* subsect. *Triplinerviae* are reputed for their high diversity in chromosome number within the native range (e.g. Semple & al. 1981, 1984; Semple 2016). In Europe, however, only diploids ($2n = 18$, *S. canadensis* s.l.) and tetraploids ($2n = 36$, *S. gigantea*) have been encountered (e.g. Weber 1997, 2000; Schlaepfer & al. 2008). This seriously undermines the theory of genuine *S. altissima* (var. *altissima*) being present in Europe given that the latter is always hexaploid ($2n = 54$) in its introduced range and hexaploid or very rarely tetraploid ($2n = 36$) in its native range. The diploid status of “*S. altissima*” in Europe could be explained by confusion between *S. altissima* and *S. canadensis* var. *hargerii*, which is a diploid (Semple & al. 1981, 1984, 2015). *Solidago canadensis* var. *hargerii* is reminiscent of *S. altissima*, especially in stem indumentum characters: both have stems that are moderately hairy in the proximal to middle part, whereas in var. *canadensis* the stems are glabrous in the proximal half. The presence of var. *hargerii* has been con-

firmed from Europe by one of us (J.C.S.), and it is highly probable that previous European claims of *S. altissima* in fact belong to that taxon (Semple & al. 2013, 2015; Szymura & al. 2015). Also on macro-morphological grounds it is rather unlikely that *S. altissima* is the common species in Europe, as assumed by Weber (1997). Plants are described by him as having stems that are glabrous at the base, with leaf margins mostly serrate and peak flowering times between mid-August and the end of September; moreover, they are diploids ($2n = 18$). All these traits suggest that the widespread taxon in Europe is *S. canadensis* (var. *canadensis*), not *S. altissima*.

In July 2016 a small population of an odd-looking species of *Solidago* was discovered in a sand-raised site in the nature area Verrebroekse Plassen in the Waasland port area in Beveren (Belgium, province of East Flanders). Morphologically, these plants were clearly more similar to *S. canadensis* than to *S. gigantea*, especially with regard to the short-hairy stems. However, compared with *S. canadensis*, these plants were unusually tall (c. 200 cm), with stiff stems, and leaves that were markedly scabrous and hairy throughout. Moreover, flowering started very late in the season (late October to early November), several weeks after *S. canadensis*. These traits are characteristic of *S. altissima*. In order to confirm this identification based on morphological grounds, genome size was measured and compared with that of *S. canadensis*. Genome size as well as chromosome number demonstrated that this population indeed belongs to *S. altissima* (var. *altissima*).

In this paper the distinguishing features of *Solidago altissima* and *S. canadensis* are discussed and the former is illustrated.

Material and methods

Plant material

Leaf material of *Solidago canadensis* and *S. gigantea* was obtained from living plants cultivated at Leiden, the Netherlands, and that of the putative *S. altissima* from Verrebroekse Plassen in the Waasland port area in Beveren, Belgium, with voucher material deposited in the herbarium of the Botanic Garden of Meise (*F. Verloove 12620*, BR).

Flow-cytometric measurement of nuclear DNA content

For the isolation of nuclei, c. 0.5 cm² of a young leaf was chopped together with a piece of *Agave americana* ‘Aureomarginata’ as an internal standard (Galbraith & al. 1983). The nuclear DNA content (2C-value) of *A. americana* was measured as 15.9 picograms (pg) per nucleus with human leukocytes (2C = 7 pg; Tiersch & al. 1989) as the standard. Based on published male human genome size of 6.294×10^9 base pairs, the nucleus was calculated to contain 6.436 pg (Doležel & al. 2003). However, this is based on a human sequence for which the size of the very large repeat sequences could not be accurately

Table 1. Main distinguishing features of *Solidago altissima* var. *altissima* and *S. canadensis* var. *canadensis* in W Europe; *S. canadensis* var. *hargeri* differs from the latter only in stem indumentum characters (see text).

	<i>Solidago altissima</i> var. <i>altissima</i>	<i>Solidago canadensis</i> var. <i>canadensis</i>
Stem height	up to 200 cm	rarely exceeding 150 cm
Stem indumentum	short-hairy throughout	glabrous in proximal half
Start of flowering	end of October to early November	end of August to early September
Leaf margin (leaves on distal half of stem)	nearly entire (finely and remotely serrate)	usually sharply serrate or serrulate
Leaf texture	thick, ± leathery	thin, not leathery
Involucre length	3–4 mm	1.7–2.5(–3) mm
Chromosome number	2n = 54	2n = 18

Table 2. Genome size, number of measurements and origin of *Solidago* species.

	2C-value (pg per nucleus)	Number of measurements	Origin
<i>Solidago altissima</i>	5.61	2	Belgium: Waasland port area
<i>Solidago canadensis</i>	2.14	4	Netherlands: Leiden Schubertlaan
<i>Solidago gigantea</i>	3.81	6	Netherlands: Leiden Schubertlaan

determined, so the genome size could be closer to 7 pg than now envisioned. The Animal Genome Size Database (<http://www.genomesize.com>, release 2.0) too gives a haploid size (C-value) of 3.5 pg.

Chopping of leaflets was done at room temperature with a new razor blade in a Petri dish in 0.25 ml nuclei-isolation buffer [per litre: MgCl₂ × 6H₂O 9.15 g, tri-sodium citrate 8.8 g, MOPS 4.15 g, Triton X-100 1 ml, polyvinylpyrrolidone 10 000 25 g, dithiothreitol 1.55 g, 0.01 % RNase, pH 7 (c. 1.12 g KOH)] (changed after Bharathan & al. 1994). After adding 1.75 ml propidium iodide solution (50 mg PI/l) in isolation buffer, the suspension with nuclei was filtered through a 20 µm nylon filter. Fluorescence of the nuclei was measured 30 and 60 minutes after addition of PI using a BDA Accuri flow cytometer. The more DNA present in a nucleus, the higher is the intensity of the fluorescence. The 2C DNA content of the sample was calculated as the sample peak mean, divided by the *Agave* peak mean, and multiplied by the amount of DNA of the *Agave* standard. For each clone, two to four different runs (determinations with around 3000–5000 nuclei) were measured.

Macro-morphological identification

All relevant taxonomic literature on *Solidago* subsect. *Triplinerviae* was investigated (e.g. Semple & al. 1999, 2013, 2015; Semple & Cook 2006; etc.). Identification was based on macro-morphological characters of the available herbarium specimens.

Results and Discussion

A small population recently discovered in Belgium exhibits morphological features that fully correspond with *Solidago altissima*. Plants were unusually tall with stems up to 200 cm long (“verge d’or haute”) and short-hairy throughout. Their leaves were nearly entire, more or less leathery and stiff in texture, and rough and large up into the inflorescence (typical for *S. altissima* var. *altissima*). Flowering commenced very late in the season (end of October to early November; “late goldenrod”). Moreover, involucres were markedly longer than in *S. canadensis*. The main distinguishing features of both species are summarized in Table 1 and illustrated in Fig. 1–4. A detailed description of *S. altissima* var. *altissima* is presented below in order to prevent further confusion with *S. canadensis* var. *hargeri* in Europe.

Solidago altissima L., Sp. Pl. 2: 878. 1753
≡ *Solidago canadensis* subsp. *altissima* (L.)
O. Bolòs & Vigo in Collect. Bot. (Barcelona) 14: 102. 1983.

= *Solidago canadensis* var. *scabra* (Muhl. ex Willd.)
Torr. & A. Gray, Fl. N. Amer. 2: 224. 1842 ≡ *Solidago*
scabra Muhl. ex Willd., Sp. Pl. 3: 2059. 1803.

The following description refers to *Solidago altissima* var. *altissima*; values given in **boldface** are means.

Plants up to 200 cm tall; *rhizome* short- to long-creeping. *Stems* 1–40+, short-hairy throughout. *Leaves* all cauline, sessile or subpetiolate, tapering to bases, proximal leaves withering by flowering; *leaf blade* oblanceolate, 95–150 × 16–20 mm, relatively thick and firm, strongly 3-nerved, abaxial surface finely strigose, more so along nerves, adaxial surface ± scabrous, margin (nearly) entire, apex acute to acuminate; middle to distal cauline blades oblanceolate (proximally) to lanceolate (distally), middle blades (30–)45–**74**–120(–170) × (5–)6–**11**–16(–25) mm, much reduced on distal blades [20–**46**–83 × 3–**7.3**–13(–17) mm], abaxial surface moderately strigillose, densely villous-strigillose along nerves, sometimes minutely stipitate-glandular on distal blades, adaxial surface ± scabrous, margin finely serrate on middle blades (teeth 0–**6**–8) per side), usually becoming entire or remotely serrulate on distal blades. *Inflorescence* not flowering before September (later in Europe), a secund, conical, paniculiform array, 5–30 × 2–25 cm, with (15–)100–1200+ secund capitula; branches divergent and recurved, sometimes ascending-divergent, inflorescence sometimes merely club-shaped thyriform in small plants. *Peduncles* 1–3.5 mm, moderately densely shortly hispidulous-strigillose; *bracteoles*



Fig. 1. *Solidago altissima* in Verrebroekse Plassen nature area in Beveren, Belgium, photographed on 9 October 2016. The tall and stiff habit of the plants is very characteristic.



Fig. 2. *Solidago altissima*, emerging inflorescence. Note the leafy inflorescence and the late flowering time. – Belgium, Beveren, Verrebroekse Plassen nature area, 9 October 2016.



Fig. 3. *Solidago altissima*, cauline leaves. Leaves are thick and stiff and only remotely serrate. – Belgium, Beveren, Verrebroekse Plassen nature area, 9 October 2016.



Fig. 4. *Solidago altissima*, stem indumentum just above base. The stem is short-hairy throughout. – Scale bar = 1 mm. – Source: F. Verloove 12620 (BR).

linear. *Involucre*s narrowly campanulate, 3–3.5–4.5 mm. *Phyllaries* in c. 3 series, strongly unequal; outer phyllaries lanceolate, apex acute; inner phyllaries linear-lanceolate, apex acute to obtuse. *Ray florets* 5–10–16; laminae 0.7–1.3–2.5 × 0.1–0.27–0.6 mm. *Disc florets* 2–4.4–6(–13); corollas usually 2.9–3.8–4.3 mm, lobes 0.4–0.75–1.1 mm. *Cypselae* (not seen yet in Europe) narrowly obconic, 0.5–1.5 mm, sparsely to moderately strigillose; *pappus* 2.5–3.5 mm at maturity (disc floret pappus at anthesis 2–3 mm). $2n = 36$ (very rare in North America) or 54 (adapted from Semple & Cook 2006 and Semple & al. 2015).

In order to strengthen our identification on macro-morphological grounds, genome size and estimated chromosome number were assessed and compared with those of the two most widespread species of the complex in W Europe, *Solidago canadensis* and *S. gigantea*. The Belgian population of putative *S. altissima* had 2C-values (pg DNA) of 5.61 while those of *S. canadensis* were 2.14 (see Table 2). Previous measurements in the Czech Republic for the latter were 2.04 (Kubešová & al. 2010), while those in Poland ranged between 2.03 and 2.21 (Szymura & al. 2015). These findings correspond with an estimated chromosome number of $2n = 54$ and $2n = 18$ for *S. altissima* and *S. canadensis*, respectively, which is in agreement with earlier counts for these species (see also Halverson & al. 2008).

Our findings represent the first unequivocal record of *Solidago altissima* in Europe. Although this species is thought to have been introduced more or less worldwide (Semple & Cook 2006), its distribution outside of the New World is uncertain. Its presence was confirmed recently in South Africa (Cheek & Semple 2016), China (Chen & Semple 2011) and Japan (Sakata & al. 2015). However, it is unknown whether other Australasian claims (e.g. Porteners 1992) pertain to *S. altissima* or *S. canadensis*. Diploids ($2n = 18$) have been reported in *S. altissima* var. *gilvocanescens* (Rydb.) Semple (Semple &

al. 2015), but the Belgian collections do not match this taxon on multiple leaf traits and involucre size.

Several species of *Solidago* subsect. *Triplinerviae* are reputed environmental weeds and have naturalized far beyond their native ranges. *Solidago canadensis* and *S. gigantea* are well-known examples, as is *S. chilensis* Meyen (e.g. Gonçalves Silva & al. 2008). It has been shown that polyploidy plays an important role in the invasion success of taxa in this complex (Schaeffler & al. 2008, 2010). It can be expected that hexaploid *S. altissima* will turn out to be even more invasive than diploid *S. canadensis*. Therefore, eradication of the population recently detected in Belgium has been recommended.

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