Cytogeography of the *Solidago rugosa* Mill. Complex (Asteraceae: Astereae) in Eastern North America

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**Abstract:** Chromosome numbers are reported here for the first time from 117 individuals of *Solidago rugosa* and *S. fistulosa*. Including 178 previously published reports for the two species plus *S. latissimifolia*, chromosome numbers have been determined from 295 individuals from 269 locations. Only diploids (2n = 18) were found throughout the range of *S. fistulosa* on the coastal plain in the eastern U.S.A. (44 counts). Diploids (2n = 18) were found in the northern portion of the range of *S. latissimifolia*, and tetraploids (2n = 36) and hexaploids (2n = 54) were found in the central and southern portions of the range (nine counts in total). Diploids (2n = 18) were found throughout the range of *S. rugosa* in much of eastern North America in four of the five varieties (northern var. *rugosa*, var. *sphagnophila*; southern var. *aspera* and var. *celtidifolia*). Tetraploids (2n = 36) were found in all four of these varieties and exclusively in var. *cronquistiana* in the southern high Appalachian Mountains. Hexaploids (2n = 54) were found in var. *sphagnophila* at scattered locations. One possible hexaploid in var. *rugosa* was found in the Allegheny Mountains. The diversity in ploidy levels was independent of the size of the range and the diversity of growing conditions among the three species of *S. subsect. Venosae*.

**Keywords:** cytotaxonomy; biogeography; goldenrods

1. Introduction

The *Solidago rugosa* Mill. complex in the broad sense occurs in eastern North America and is a taxonomically difficult group of goldenrods making up *Solidago* subg. *Pleiacitla* Raf. sect. *Venosae* (D. Don in Loudon) Nesom subsect. *Venosae* (G. Don in Loudon) Nesom (Semple and Beck 2021 [1]). The subsection includes three closely related species, *S. fistulosa* Mill., *S. latissimifolia* Mill., and *S. rugosa*, with four varieties recognized here and multiple basionyms: *Solidago aestivalis* Bicknell, *S. aspera* Ait., *S. celtidifolia* Small, *S. edissoniana* Mack., *S. elliottii* Torr. & A. Gray, *Solidago elliottii* Torr. & A. Gray var. *ascendens* Fern., *Solidago elliottii* Torr. & A. Gray var. *pedicellata* Fern., *Solidago elliptica* Ait., *S. elongata* Pépin, *S. fistulosa* Mill., *S. latissimifolia* Mill., *Solidago mirabilis* Small, *S. rugosa* Mill., *S. rugosa* var. *cronquistiana* Semple, *S. rugosa* var. *glabratra* Farwell, *S. rugosa* var. *sphagnophila* Graves, and *S. villosa* Pursh. The *Solidago rugosa* complex includes three to six species depending upon the classification scheme followed (Table 1). Fernald (1950 [2]) presented a treatment of members of the complex except for the much more recently described var. *cronquistiana*. He recognized three varieties in *S. elliottii*, no varieties in *S. fistulosa*, and five varieties in *S. rugosa*: var. *rugosa*, var. *villosa* (Pursh) Fern., var. *aspera* (Ait.) Fern., var. *celtidifolia* (Small) Fern., and var. *sphagnophila*. Earlier, Fernald (1936 [3]) dealt with the misapplication of the name *S. altissima* L. to members of the *S. rugosa* complex and acknowledged that var. *sphagnophila* might deserve species status as *S. aestivalis*. Cronquist (1947 [4], 1968 [5])
recognized three species in the complex and grouped the varieties of *S. rugosa* into two subspecies: a southern subsp. *aspera* and a northern subsp. *rugosa*. Cronquist (1980 [6]) referred to subsp. *villosa*, but this was likely a typographical error, since the taxon is clearly his subsp. *rugosa* of both Cronquist (1968 [5]) and Gleason and Cronquist (1991 [7]). Beaudry (1960 [8]) recognized four species based on limited cytological data that indicated normally a single ploidy level for each: *S. aestivalis*, *S. aspera*, *S. celtidifolia*, and *S. rugosa* (which included *f. villosa* (Pursh) Beaudry); *S. fistulosa* was not included in his study. Uttal and Porter (1988 [9]) determined that the older name *S. latissimifolia* was the same species as *S. elliottii* and should be used instead. This paper follows the classification presented in Semple and Cook (2006 [10]) and accepts the name *S. latissimifolia* and is most similar to Cronquist (1968 [5]) but includes var. *celtidifolia*, var. *cronquistiana* and does not recognize subspecies within *S. rugosa*.

**Table 1.** Comparison of some classification schemes of the *Solidago rugosa* complex and related species.

| Fernald (1950 [2])       | Cronquist (1947 [4], 1968 [5]) | Beaudry (1960 [8])       | Semple and Cook (2006 [9])       |
|--------------------------|--------------------------------|--------------------------|----------------------------------|
| *S. fistulosa*            | *S. fistulosa*                  |                          | *S. fistulosa*                   |
| *S. elliottii*           | *S. elliottii*                  | *S. elliottii*           | *S. latissimifolia*              |
| *S. rugosa*              | *S. rugosa*                     | *S. rugosa*              | *S. rugosa*                      |
| var. *rugosa*            | var. *rugosa*                   | f. *rugosa*              | var. *rugosa* (including var. *villosa*) |
| var. *villosa*           | var. *villosa*                  | f. *villosa*             |                                   |
| var. *sphagnophila*      | var. *sphagnophila*             | *S. aestivalis*          | var. *sphagnophila*              |
| subsp. *aspera*          | var. *aspera*                   | *S. aspera*              | subsp. *aspera*                  |
|                          | (including *S. celtidifolia*)   |                         | var. *aspera*                    |
| var. *celtidifolia*      | *S. celtidifolia*               | var. *celtidifolia*      | var. *cronquistiana*             |

Before the first author’s laboratory began working on the cytology of *Solidago* (Semple et al. 1981 [11]), 52 chromosome counts from 27 locations had been reported for all members of the *S. rugosa* complex (Table A1). The first report was by Goodwin (1937 [12]) for *S. rugosa* var. *rugosa*. Most of the early counts were published by Jean Beaudry of the Université de Montréal (Beaudry and Chabot 1959 [13]; Beaudry 1960 [8], 1963 [14], 1969 [15]). Beaudry’s contributions to our understanding of the genus are significant, but he adopted a “splitters” approach to recognizing species, which he apparently thought at the time should include little or no ploidy level variation. His very small sample sizes allowed him to maintain this position.

An investigation of the cytogeography of the complex was undertaken by the Semple Astereae Lab in the 1980s and early 1990s in hopes of clarifying what role ploidy level might play in taxon delimitation. The field work to gather more data continued until 2012. Herbarium specimens, including nomenclatural types, were examined in order to more clearly understand how each of the above cited authors had applied names to their cytovouchers collected as part of the cytogeographic investigation. The overall objective was a better understanding of taxon limits within the complex, an assessment of the appropriate taxonomic ranks for these taxa, and a large cytological sampling of the entire ranges of all taxa in order to determine cytogeographic patterns in the taxa recognized.

**2. Materials and Methods**

Meiotic counts were made from pollen mother cells dissected from buds fixed in the field in Carnoy’s Fixative 3:1 (absolute EtOH: glacial acetic acid) and subsequently stored under refrigeration in 70% EtOH until examined. Anthers containing pollen mother cells were dissected out of florets and squashed in 1% acetic orcein stain. Counts were made from freshly prepared slides using either a Zeiss RA Standard Microscope or a Nikon Microscope with phase contrast optics. Mitotic counts were made from root tip cells taken
from transplanted wild rootstocks or from seedlings grown from fruits collected in the field. Root tips were pretreated in 0.01% colchicine or saturated paradichlorobenzene for 2–3 h, fixed in Acetic Alcohol Fixative (3:1/EtOH: glacial acetic acid), and hydrolyzed in 1 N HCl for 30 min at 60 °C before squashing. Counts were made from freshly prepared slides as above. Vouchers for all counts are deposited in WAT in MT (Thiers continuously updated [16]) with duplicates distributed to various other herbaria. Identifications were made by J.C.S.

3. Results

Cytovouchers for nearly all 178 previously published counts of *Solidago fistulosa*, *S. latissimifolia*, and *S. rugosa* were examined and identifications confirmed or corrected; these are listed in Appendix A Table A1, which includes a brief indication of geography, publication data, and indication of the name under which the counts were first published. Chromosome numbers were determined from an additional 117 individuals of the *Solidago rugosa* complex and are reported here for the first time in Appendix A Table A2. The distribution of all 41 diploid chromosome counts for *S. fistulosa* is shown in Figure 1. The distribution of the 9 diploid, tetraploid, and hexaploid chromosome counts for *S. latissimifolia* is shown in Figure 2. The distribution of all 242 diploid, tetraploid, and possible hexaploid counts for *S. rugosa* is shown in Figure 3 with ranges of each variety indicated.

![Cytogeography of Solidago fistulosa](image)

**Figure 1.** Cytogeography of *Solidago fistulosa* in eastern North America.
Figure 2. Cytogeography of Solidago latissimifolia in eastern North America; the identification of the northernmost diploid sample in Nova Scotia (red dot) was not confirmed.
Figure 3. Cytogeography of *Solidago rugosa* and its varieties in eastern North America.

A range of inflorescence branching patterns in *S. rugosa* were observed in the field. In one growth form, the inflorescence has very long arching lower branches. Type specimens and the majority of field collections of *S. rugosa* var. *aspera* and var. *rugosa* had large inflorescences with many long diverging branches with mostly secund branchlets with heads. Both varieties include some specimens with inflorescences with very short branches barely to slightly exceeding the subtending leaves. This is the supposedly diagnostic feature of var. *villosa*, but garden and greenhouse observations on transplanted individuals indicate that this trait is too unstable to be used as a diagnostic feature. It is common to find shoots of the same clone with the two extreme forms of inflorescence branching patterns. Plants with short-branched inflorescences are scattered through the range of var. *rugosa*. Thus, we treat var. *villosa* as a synonym of var. *rugosa*. 
The type specimens of *S. rugosa* var. *celtidifolia* have ovate upper stem leaves and inflorescences that have very short lateral branches. Throughout the range of the variety, plants often have large inflorescences with long lower branches like inflorescences in var. *rugosa* and var. *aspera*. Intermediate plants between obvious var. *aspera* and obvious var. *celtidifolia* plants were also encountered in the field.

During field work, a number of collections were found that had leaves typical of var. *aspera*, but an inflorescence form that was like the “var. *villosa*” inflorescence with short lateral branches. The indument was sparse for either of these morphs. Plants with these characteristics did not fit well into any of the five varieties recognized by Fernald and Cronquist (Table 1). All these populations were found in the Carolinas and northern Georgia at the southern end of the Appalachian Mountains. Additional herbarium sheet collections were seen subsequently. All collections counted were tetraploid $2n = 36$. These were placed in var. *cronquistiana*, named in honor of Art Cronquist.

4. Discussion

Including previously published reports (Goodwin 1937 [12]; Beaudry and Chabot 1959 [15]; Beaudry 1960 [8]; Beaudry 1963 [14]; Jones 1968 [17]; Beaudry 1969 [14]; Kapoor 1970 [18]; Anderson et al. 1974 [19]; Kapoor 1977 [20]; Semple et al. 1981 [11]; Morton 1981 [21]; Løve and Løve 1982 [22]; Semple et al. 1984 [23]; Semple 1985 [24]; Semple and Chmielewski 1987 [25]; Semple et al. 1989 [26]; Semple et al. 1992 [27]; Semple et al. 1993 [28]; Semple and Cook 2004 [29]; Semple et al. 2015 [30]; Morton et al. 2018 [31]; and Semple et al. 2019 [32]), 295 individuals have had chromosome numbers determined from 270 locations in total for *S. fistulosa*, *S. latissimifolia*, and *S. rugosa* (Figures 1–3). Morphologically, *S. fistulosa* is the most distinct of the three species and has the smallest range of variation in leaf shape, leaf venation, and inflorescence branching pattern. *Solidago fistulosa* is strictly diploid with 45 counts from 33 locations throughout its range on the inner and outer coastal plains from New Jersey south to southern Florida and west along the Gulf Coast to eastern Louisiana (Figure 1). Habitats include “mostly wetter sandy soils, seepage areas, boggy grounds, edges of marshes and thickets, open pine woodlands, roadside ditches” at 0–100 m elevation (Semple and Cook 2006 [10]). *Solidago latissimifolia* includes diploids, tetraploids, and hexaploids encountered in the small sample of nine counts from nine locations from southern Nova Scotia to South Carolina; no counts have been reported from disjunct populations in peninsular Florida (Figure 2). *Solidago latissimifolia* has the smallest range of the three species and occurs in “fresh and brackish swamps, thickets on the outer coastal plain” at 0–80 m (Semple and Cook 2006 [10]). Morphologically, *S. latissimifolia* might be confused with some individuals of *S. rugosa* var. *sphagnophila* due to convergence in leaf size, but the former has leaves that are glabrous and usually larger and less or not rugose (Semple and Cook 2006 [10]). *Solidago rugosa* includes diploids, tetraploids, and possibly hexaploids with counts for 242 individuals from 228 locations from much of eastern North America from Newfoundland west to Wisconsin and south to northern Florida and eastern Texas (Figure 3).

The four varieties of *S. rugosa* recognized here occur in overlapping ranges and include many individuals that can be difficult to assign definitively to a single variety. *Solidago rugosa* var. *sphagnophila* is the most morphologically distinct with its absence of hairs on at least the lower stems and often glabrous or glabrate leaves; upper stems can be glabrous/glabrate to moderately hairy in the inflorescence. Only diploids were found and reported here, while only hexaploids were reported by Beaudry (1960 [8], 1969 [15]); tetraploids were not found in the sample of 13 individuals from eight locations in outer coastal plain cedar swamps and bogs from Massachusetts to New Jersey, and no chromosome counts from disjunct populations in Virginia and North Carolina have been reported (Figure 3).

Although Cronquist (1947 [4], 1968 [5], 1980 [6]) grouped the more northern varieties into subsp. *rugosa* and the southern varieties into subsp. *aspera*, var. *rugosa* and var. *aspera* are often difficult to distinguish, with many specimens being only somewhat to
moderately rugose, that is, the intervening leaf surface is elevated slightly above the plain of the supporting venation which itself is prominent on the undersurface. The difference may correlate with growing conditions more than with geographic location, with more plants in southern populations growing in seasonally drier habitats during longer growing seasons than the more northern populations. In fact, only some of the plants assigned here to var. *aspera* were considered to have very pronounced rugose leaves and these came from the drier open woods and full sun habitats encountered in the southeastern states of the U.S.A. Plants assigned to var. *aspera* that grew in shaded thickets with wetter soils sometimes had less rugose leaves and were close in appearance to more northern plants of var. *rugosa*. Beck et al. (2021 [33]) included 15 samples of *S. rugosa* in their phylogenomic investigation of *S. ulmifolia*, but did not assign the *S. rugosa* samples to varieties. Seven of the collections were made by J.C. Semple and were cytovouchers for diploids cited in this paper; eight were for collections by other researchers and were not cytovouchers but varieties could be assigned to five based on online images. All specimens of *S. rugosa* were placed in a single branch of the tree with 74% support. The single collection of var. *sphagnophila* from Massachusets along with a single diploid collection of var. *rugosa* from New York were placed in the clade sister of the remainder of *S. rugosa*. The most derived branch of the *S. rugosa* samples included three diploid collections of var. *celtidifolia* from Louisiana, although two of these were biological duplicates. The remainder of the samples included a sample of var. *rugosa* from Ontario, samples of var. *aspera* from Arkansas and Mississippi, a diploid sample of var. *celtidifolia* from Mississippi, and samples of either var. *rugosa* or var. *aspera* from Arkansas, Missouri, and Louisiana. Thus, there was phylogenetic limited distinction among samples of vars. *aspera*, *rugosa*, *sphagnophila* and *celtidifolia* nor complete separation of northern and southern samples. Clearly, a much larger sampling of specimens of all varieties of *S. rugosa* from across the entire range of each variety must be undertaken before strong conclusions can be drawn about the phylogenetic separation of varieties in *S. rugosa*. Certainly, the limited data available do not support the recognition of northern and southern subspecies but do hint at some separation of varieties and raise the question of whether or not var. *aspera* really is distinct from var. *rugosa*.

There were some patterns to the distribution of diploids and tetraploids in *S. rugosa* with differences in the patterns between varieties. All 55 samples of var. *rugosa* from Canada were diploid. Tetraploid samples of var. *rugosa* were scattered among diploid samples in New England and further south with the two ploidy levels occurring in approximately equal numbers of samples in the southern portion of the range of var. *rugosa*. For var. *rugosa*, 90% of the 106 samples were diploid. No unquestioned hexaploid samples were found in var. *rugosa*; one possible sample reported here (Table A2) is shown in Figure 3 with a question mark because of uncertainty that the voucher and the plant counted came from the same wild plant. A second hexaploid count by Löve and Löve (1982 [22]) was reported under the name *S. altissima* L., but the CAN voucher of the collection number is a specimen of *S. rugosa* var. *rugosa*. Therefore, the count cannot be assigned to either species with certainty as the voucher in CAN may not be the source plant of the count. In contrast, 91% of the 66 samples of var. *aspera* were tetraploid with diploids scattered in the central and northern portions of the range of var. *aspera* from eastern Kentucky to Mississippi. In var. *celtidifolia*, 51% of the 37 samples were tetraploids with diploids and tetraploids occurring throughout most of the range of var. *celtidifolia*. Only tetraploids were found in the southern high Appalachian Mountains in var. *cronquistiana*. In var. *sphagnophila*, diploids were sampled at five locations in the middle portion of the range and hexaploids were sampled in four locations over the range, but no tetraploids were sampled, perhaps due to limited sampling of populations.

The diversity in ploidy levels in the three species of *S. subsect. Venosae* was independent of the size of the range and the diversity of growing conditions. *Solidago latissimifolia* had the narrowest and smallest range, which included diploids, tetraploids, and hexaploids, even though the sample size was small and included only acidic soils mostly in Eastern White Cedar swamps along the Atlantic coast. *Solidago fistuosa* included only diploids
throughout its less narrow range from the sandy Atlantic Coastal plain of southern New Jersey to southern Florida and west to eastern Louisiana on the coastal plain in a mixture of wetter soil habitats. *Solidago rugosa* included diploids, tetraploids, and possibly hexaploids in a diversity of habitats across much of eastern North America with the ranges of the varieties being smaller and overlapping with at least one other variety. While the strictly tetraploid *S. rugosa* var. *cronquistiana* came from only higher elevation habitats in the southern Appalachian Mountains, these were not very different from the higher elevation habitats of some tetraploid samples of var. *aspera*. While each taxon in subsect. *Venosae* has a different range of distribution, the ranges of all taxa overlap with one or more other taxa. Ploidy level is thus neither correlated with a specific habitat nor associated with any particular taxon in subsect. *Venosae*.

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**Appendix A**

**Table A1.** Previously published chromosome number determinations in *Solidago rugosa* complex from Canada and the United States, arranged alphabetically by species and variety. **B** = Beaudry; **C** = R.E. Cook; **Ch** = Chmielewski; **T** = K. Tereszchuk; **M** & **V** = J.K. Morton and J. Venn; **S** = J. Semple; **&** = J. and B. Semple; **Su** = Bambang Agus Suripto. Herbarium abbreviations from Thiers continuously updated [13].

**Solidago fistulosa** Mill.—**2n = 9t** U.S.A. **Florida:** Hillsborough Co., *S & Wunderlin* 2527 (WAT; Semple et al. 1981 [11]); Osceola Co., *S* et al., 5356 (WAT; Semple 1985 [24]); count cannot be definitively assigned to species because voucher specimens include both *S. fistulosa* and *S. leavenworthii*); St. Johns Co., *G. Morton* 4553 NY; Semple et al. 2018 [23]. **North Carolina:** Brunswick Co., *G. Morton* GPNC21 (not seen; Semple et al. 1984 [23]); Martin Co., *S & Su* 9739 (WAT; Semple et al. 1993 [28]).—**2n = 9t + 1-3 supernumeraries. U.S.A. Florida:** St. Johns Co., *G. Morton* 4550 (not seen; Semple et al. 1984 [23]), *G. Morton* 4551 (NY; Semple et al. 1984 [23]), *G. Morton* 4552 (not seen; Semple et al. 1984 [23]).—**2n = 18U.S.A. Alabama:** Mobile Co., *S & Su* 10128 (WAT; Semple et al. 1993 [28]). **Delaware:** Sussex Co., *S & Ringius* 7649 (WAT; Semple 1985 [23]). **Florida:** Calhoun Co., *M & V* NA16484 (TRT; Morton et al. 2018 [30]); Lafayette Co., *S* et al., 7447 (WAT; Semple et al. 1984 [23]); Okeechobee Co., *M & V* NA16531 (TRT; Morton et al. 2018 [30]); St. Johns Co., *S* et al., 7542 (WAT; Semple et al. 1984 [23]); St. Lucie Co., *S* 11734 (WAT; Semple et al. 2019 [31]); Washington Co., *S* 10852 (WAT; Semple and Cook 2004 [28]). **Georgia:** Coffee Co., *S* et al., 7416 (WAT; Semple et al. 1984 [23]);ECHoLS Co., *S* 10879 (WAT; Semple and Cook 2004 [28]); Wilcox Co., *S & B. Semple* 11211 (WAT; Semple et al. 2015 [29]). **Mississippi:** Harrison Co., *S & Su* 10125 (WAT; Semple et al. 1993 [28]). **New Jersey:** Atlantic Co., *S & Su* 9506 (WAT; Semple et al. 1993 [28]); Cape May Co., *B* 57-221, 57-222, 57-223 (MT; Beaudry 1963 [14]); Ocean Co., *B* 57-222 (MT; Beaudry 1963 [14]), *S* 11812 (WAT; Semple et al. 2019 [31]). **North Carolina:** Carteret Co., *M & V* NA16561 (TRT; Morton et al. 2018 [30]); Jones Co., *S & Su* 9751 (WAT; Semple et al. 1993), New Hanover Co., *B and Beal* 57-408, 57-409, 57-410 (MT; Beaudry 1963 [14]). **South Carolina:** Clarendon Co., *S & Su* 9785 (WAT; Semple et al. 1993 [28]); Florence Co., *S & Ch* 6107 (WAT; Semple et al. 1984 [23]). **Virginia:** Southampton Co., *S* 11624 (WAT; Semple et al. 2019 [31]).—**2n = 18 + 1 supernumerary. U.S.A. Florida:** Osceola Co., *S* 7477 (WAT; Semple et al. 1984 [23]). **2n = 18 + 4 supernumeraries. U.S.A. South Carolina:** Beaufort Co., *EMH* 57-704 (MT; Beaudry 1963 [14])—**2n = 18 + 7, 8, 9, 10 supernumeraries. U.S.A. Georgia:** Ware Co., *B* 57-739 (MT; Beaudry 1963 [14]).
### Table A1. Cont.

| Taxonomy | Mill. —2n = 9\textsubscript{II} U.S.A. | Connecticuto: New London Co., S & Su 9538 (WAT; Semple et al. 2019 [31]). —2n = 18 CANADA. Nova Scotia: Halifax Reg. Mun., Kapoor 69-109-1 (SMUH; Kapoor’72, as S. elliotti var. ascendens). U.S.A. North Carolina: Harnett Co., B & Beal 57-378 (MT; Beaudry 1963 [14] as S. elliotti var. ascendens). Rhode Island: Washington Co., B & Palmer 57-171 (MT; Beaudry 1963 [14] as S. elliotti var. ascendens). B & Palmer 57-171 (MT; Beaudry 1963 [14] as S. elliotti var. ascendens). —2n = 18 U.S.A. South Carolina: Chesterfield Co., S & Su 9778 (WAT; Semple et al. 1993 [28]). —2n = 36 U.S.A. Massachussetts: Plymouth Co., S & Brouillet 3553 (WAT; Semple et al. 1993 [28]). New Jersey: Ocean Co., S 11815 (WAT; Semple et al. 2019 [31]). —2n = 27\textsubscript{II} U.S.A. Rhode Island: Washington Co., S & Su 9544 (WAT; Semple et al. 1993 [28]). —2n = 54 U.S.A. Massachussetts: Plymouth Co., S & Su 9568 (WAT; Semple et al. 1993 [28]). |
| Solidago latissimifolia | Mill. —2n = 9\textsubscript{II} U.S.A. Minnesota: Jasper Co., S, Jones 15167 (MSS; S. Jones 1968 [17] as var. rugosa). —2n = 18 U.S.A West Virginia: Monongalia Co., B 57-265 (MT; Beaudry 1969 [15] as S. aspera); Monongalia Co., B, 57-265 (MT; Beaudry 1969 [15] as S. aspera). —2n = 36 U.S.A. Arkansas: Fayetteville Co., B & Fautrier 62-109 (MT; Beaudry 1969 [15] as S. aspera); Yell Co., M & V NA16268 (TRT; Morton et al. 2018 [30] as var. aspera). Delaware: Sussex Co., S & R. Ringus 7641 (WAT; Semple et al. 1992; to sp.). New Jersey: Ocean Co., B 57-215, 57-216, 57-217 (MT; Beaudry 1960 [8], as S. aspera). North Carolina: Henderson Co., B & Fautrier 62-109 (MT; Beaudry 1969 [15] as S. aspera); Richard Co., S, Brammall & Hart 3045 (WAT; Semple et al. 1981 [25]; as var. aspera); Transylvania Co., S 10843 (WAT; Semple and Cook 2004 [28]; as var. aspera). Oklahoma: Pushmataha Co., Semple & Heard 8264 (WAT; Semple and Chmielewski 1987 [25] to sp.). South Carolina: Beaufort Co., Horlbeck 7-57-709 (MT; Beaudry 1960 [8], as S. aspera). Virginia: Allegheny Co., Cook & Treschuck 357 (WAT; Semple et al. 2015 [29] as var. aspera); Prince William Co., Semple, Bramball & Hart 3069 (WAT; Semple et al. 1981 [11] as var. aspera). |
| Solidago rugosa | Mill. —2n = 36 U.S.A. North Carolina: Averky, B & Fautrier (MT; Beaudry 1969 [15], as S. aspera). —2n = 36 + 1 supernumerary. U.S.A. Rhode Island: Washington Co., B & Palmer 57-172 (MT; Beaudry 1960 [8]). |
| Solidago rugosa | var. aspera —2n = 36 U.S.A. North Carolina: Averky, B & Fautrier (MT; Beaudry 1969 [15], as S. aspera). —2n = 36 + 1 supernumerary. U.S.A. Rhode Island: Washington Co., B & Palmer 57-172 (MT; Beaudry 1960 [8]). |
| Solidago rugosa | var. aff. aspera —2n = 36 U.S.A. North Carolina: Averky, B & Fautrier (MT; Beaudry 1969 [15], as S. aspera). —2n = 36 + 1 supernumerary. U.S.A. Rhode Island: Washington Co., B & Palmer 57-172 (MT; Beaudry 1960 [8]). |
| Solidago rugosa | var. cronquistiana Semple—2n = 18\textsubscript{II} U.S.A. North Carolina: Averky, S 11131 (WAT; Semple et al. 2015 [29] as var. cronquistiana). |
| State   | Counties/locations                                                                 |
|---------|-----------------------------------------------------------------------------------|
| New York | Delaware Co., S & Keir 4942 (WAT; Semple et al. 1984 [23] to sp.).               |
| Pennsylvania | Butler Co., R. Cook & D. Cook 55 (WAT; Semple and Cook 2004 [28]).             |
| Vermont | Addison Co., S 6898 (WAT; Semple et al. 1984 [23] to sp.).                    |
| Virginia | Bland Co., S, 10735 (WAT; Semple and Cook 2004 [28]).                           |
| West Virginia | Marion Co., S 10687 (WAT; Semple and Cook 2004 [28]).                 |
| Michigan | Crawford Co., S, 8052 (WAT; Semple et al. 1989 [26] to sp.).                   |
| Rhode Island | Franklin Co., S & Keir 4631 (WAT; Semple et al. 1984 [23] to sp.).         |
| Wisconsin | New Castle Co., S & Ringius 4928 (WAT; Semple et al. 1989 [26] to sp.).       |
| Ohio | Ashland Co., R. Cook & D. Cook 36 (WAT; Semple and Cook 2004 [28]).          |
| Maryland | Washington Co., S & Ringius 7665 (WAT; Semple et al. 1992 [27] to sp.).       |
| Massachusetts | Nantucket Co., McKeever 64-1, -2, -3, -4, -5, -6, -7, -8 (MT; Beaudry 1969 [15], as S. aspera). |
| New Jersey | Ocean Co., S end of Parkertown, by US-9,                                      |
| New York | Chattaragus Co., S & Ringius 7571 (WAT; Semple et al. 1992 [27] to sp.).    |
| South Carolina | Centre Co., S & Ringius 7603 (WAT; Semple et al. 1989 [26] to sp.). |
| Rhode Island | Washington Co., S & Palmatier 57-177 (MT; Beaudry 1969 [8]).               |
| New Jersey | Ocean Co., cult. Montréal, B 57-220 (MT; Beaudry 1960 [8] as S. aestivalis). |
| Florida | US-287 just W of Farm Rd.-321,                                                 |
| Florida | US-250 ca. 0.2 km E of Calf Pasture Creek, Cook & Terezchuck 383; Bath Co., US-220 ca. 1 km S of VA-39, Cook & Terezchuck 370. |

**Table A2.** Previously unpublished chromosome counts for *Solidago fistulosa* and *S. rugosa*. S = J.C. Semple; Su = B.A. Surirpto. All cytovouchers in WAT in MT (Thiers continuously updated) [13].

**Solidago rugosa** Mill. var. rugosa—2n = 54 CANADA. Quebeck; Lëve, Lëve et Lëve 1982; voucher is not for 6x count). U.S.A. New York: Chaataragus Co., S & Ringius 5751 (WAT; Semple et al. 1992 [27] to sp.; identity of greenhouse collection sample could not be confirmed to be same as voucher; may be a field numbering error).

**Solidago rugosa** aff. var. rugosa—2n = 18 CANADA. Ontario: Hastings Co., S & Brammall 2925 (WAT; Semple et al. 1981 [11] as var. rugosa). U.S.A. Virginia: Flood Co., B & Fautrier 62-25 (MT; Beaudry 1969 [15], as S. aspera; leaves weakly rugose); West Virginia: Preston Co., B 57-268 (MT; Beaudry 1969 [15]).

**Solidago rugosa** Mill. var. sphagnophila—2n = 54 CANADA. Nova Scotia: Shelburne Co., Kapoor 69-130-1 (SMUH not seen; Kapoor 1970 as S. aestivalis), Kapoor 69-130-4 (SMUH not seen; Kapoor 1977). U.S.A. Massachusetts: Nantucket Co., McKeever 64-1, -2, -3, -4, -5, -6, -7, -8 (MT; Beaudry 1969 [15], as S. aestivalis). New Jersey: Ocean Co., B 57-219 (MT; Beaudry 1960 [8]), B 57-220 (MT; Beaudry 1960 [8]).

**Solidago rugosa** aff. var. sphagnophila—2n = 54 U.S.A. New Jersey: Ocean Co., cult. Montréal, B 57-220 (MT; Beaudry 1960 [8] as S. aestivalis); stem glabrous proximally, becoming moderately strigose by mid stem, to strigose in inflorescence).

**Solidago fistulosa** Ait.—2n = 18 U.S.A. North Carolina: Bladen Co., NC-242 N of Elizabethtown, 0.8 km N of US-701, S 11792.

**Solidago fistulosa** Mill. var. aspera—2n = 18 U.S.A. Alabama: Bibb Co., NW of Lawley, US-82 5.2 km N of county line, S & Su 10161. Kentucky: Leslie Co., S of Stinettt, US-421 just S of bridge across river, S & Su 9616. Oklahoma: McCurtain Co., US-259 S 60.2 km N of county line, 5.0 km E of OK-144, S & Su 9898. South Carolina: Kershaw Co., S of Camden, US-521 4.4 km NW of Swift Creek, S & Su 9781-2. —2n = 18 U.S.A. Nebraska: Hunt Co., S end of Parkertown, by US-9, S & Su 9523.—2n = 36 U.S.A. Arkansas: Logan Co., AR-23 5.5 km E of US-77, 1.1 km E of Scott Co. line, S & Su 9979, SE of Booneville, AR-23 2.2 km E of Carrollon Cemetery, S & Su 9978; Polk Co., US-270, NW of Mena, Cook & Terezchuck 225, AR-88, unmarked unpaved rest area (1st on AR side), Cook & Terezchuck 234; Sebastian Co., AR-28 14 km W of US-71, 4.6 km E of Canthron, S & Su 9982. Kentucky: Christian Co., SE of Dawson Springs, KY-109 0.8 km from KY-398, S & Su 10334; Laurel Co., Daniel Boone St. For., For-Rd-056 ca. 2 km W of KY-192, S & Su 9610, Rockcastle R., gravel bar at Pine Is. Branch, S & Su 9857. Louisiana: Rapides Par., SE of Gardner, LA-121 5.1 km N of LA-1199, 1.8 km SE of LA-28, S & Su 10094; Red River Par.: NE of Edgefield, LA-7 11.2 km S of county line, S & Su 10037. Missouri: Wayne Co., Co.Rd.-A 10.9 km SW of US-67, N of Williamsville, S & Su 9898, Co.Rd.-F 0.1 km E of US-67 7.8 km S of Greenvilie, S & Su 9896. Mississippi: Franklin Co., NW of Roxie, US-84 8 km NE of county line, 1.5 km W of MS-33, S & Su 10099; Itawamba Co., MS-23 10.1 km N of Trenton, S & Su 10777, MS-23 7.4 km N of county line, S & Su 10717; Monroe Co., S of Becker, MS-25 0.9 km N of MS-8, S & Su 10168. North Carolina: Alamance Co., NC-62 1.5 km N of Alamance, by Gunn Creek, S & Su 9717; Buncombe Co., US-19 at S city limits of Weaverville, S & Su 9695; Yadkin Co., WSW of Yadkinville, US-421 ca. 1 km E of US-21, S & Su 9710; Yancey Co., Spruce Pine, US-191 by-pass, S & Su 9697. Oklahoma: Flore Co., US-59 just N of Ouchita Nat'l For., S & Su 9988; McCurtain Co., S of Broken Bow, US-259 20.9 km N of US-71, S & Su 9992, W of Millerton, US-70 3.6 km E of Valient, S & Su 9986. Texas: Anderson Co., ca. 20 km NW of Palestine, US-287 just W of Farm Rd.-321, S & Su 10015, E of Palestine, US-84 17.6 km E of Loop Rd.-56, S & Su 10018; Cherokee Co., US-84 4.9 km E of Neches River, W of Maydelle, S & Su 10020; Harrison Co., NE of Marshall, TX-43 7.2 km NE of US-59, S & Su 10027; Newton Co., NE of Burkeville, TX-63 2.5 km W of Sabine R., S & Su 10051-B. Virginia: Augusta Co., George Washington N.F, US-250 ca. 0.2 km E of Calf Pasture Creek, Cook & Terezchuck 383; Bath Co., US-220 ca. 1 km S of VA-39, Cook & Terezchuck 370.
Solidago rugosa var. aspera aff. var. rugosa—2n = 18 U.S.A. Virginia: Lee Co., US-421 just outside Duffield, S & Su 9622.—2n = 36 U.S.A. Arkansas: Logan Co., Magazine Mt., For.Rd.-1606 1.5 km W of AR-309, S & Su 9974; Sebastian Co., AR-28 14 km W of US-71, 4.6 km E of Cauthorn, S & Su 9983; Washington Co., N of Brentwood, US-71 at rest area, bank of creek, S & Su 9961. Kentucky: Menifee Co., Red R. Gore, KY-715 1.2 km E of Tower Rock Trail No. 206, deeply shaded woods, S & Su 9861. Louisiana: East Feliciana Par.: S of Felps, S of LA-422, S & Su 10110; Webster Par.: Co., LA-159 8.4 km S of Leton (LA-2), S & Su 10035. Mississippi: Itawamba Co., MS-23 10.1 km N of Trenton, S & Su 10176. Oklahoma: Flore Co.: US-59 just N of Ouchita Nat’l For. boundary, S & Su 9986. Texas: Rusko Co., US-84 6.4 km E of Reklaw, E of TX-204, S & Su 10024.

Solidago rugosa var. cruciata—2n = 36 U.S.A. Georgia: Habersham Co., GA-15 2.0 km N of Tallulah Falls, S & Su 9828 (population a mixture of var. cruciata and var. aspera. X cruciata plants).

Solidago rugosa Mill. var. celtidifolia Fernald—2n = 91 U.S.A. Alabama: Mobile Co., N of Theodore, Co.Rd.-59 ca. 2 km S of I-10, S & Su 10127. Mississippi: Harrison Co., US-46 12 km N of Lyman, just N of Nat’l For. boundary, S & Su 10122. North Carolina: Richmond Co., NC-177 just S of Hamlet, S & Su 9775. South Carolina: Chesterfield Co., US-1 just SE of US-52, S & Su 9779; Kershaw Co., S of Camden, US-521 4.4 km NW of Swift Creek, S & Su 9781. —2n = 18 U.S.A. Alabama: Autauga Co., just W of Prattville, AL-206 at US-82, S & Su 10157; Dale Co., US-84 near Choctawhatchee, near Choctawhatchee R., S & Su 10153. Florida: Walton Co., FL-20 4.8 km E of Freeport, S & Su 10135. Louisiana: Calcasieu Par.; E of DeQuincy, LA-12 0.5 km E of county line, S & Su 10086; Rapides Par., N of Forest Hill, LA-112 2.1 km W of US-165, S & Su 10093; Taugipahoa Par.; LA-22 8 km E of centre of Ponchatoula, S & Su 10117. North Carolina: Granville Co., NE of Butner, W of I-85 on county rd., S & Su 9723.—2n = 181 U.S.A. North Carolina: Brunswick Co., NC-133 W of Wilmington, S & Su 9764; Jones Co., US-17 ca. 5 km N of Maysville, S & Su 9754; Pender Co., Hampstead, NC-210 ca. 4.1 km W of US-17, S & Su 9759.—2n = 36 U.S.A. Florida: Jackson Co., Co.Rd.-286 1.5 km N of Calhoun Co. (SE corner) line, S & Su 10143. Georgia: Thomas Co., W of Thomasville, US-84 just W of US-84 bus.-W, S & Su 10149. Louisiana: Beauregard Par.: LA-12 SE of DeQuincy, S & Su 10084; Caddo Par., S of junction of LA-2 and LA-1, S & Su 10029. Mississippi: Loundes Co., Columbus, N end of town, US-45 just S of Chapman Rd., S & Su 10166. North Carolina: Martin Co., US-64 just W of Parmele, S & Su 9738-A. Oklahoma: Flore Co., US-59 just N of Ouachita Nat’l For., S & Su 9987. South Carolina: Colleton Co., NW of Jacksonboro, NC-64 ca. 2.5 km from US-17, S & Su 9797. Texas: Newton Co., TX-63 2.5 km W of Sabine River, NE of Burkeville, S & Su 10051-A; Orange Co., NE of Vidor, TX-12 ca. 3 km NE of I-10, S & Su 10081; Polk Co., E of Livingston, US-190 1.8 km E of Soda, 16.4 km E of TX-146, S & Su 10060.

Solidago rugosa Mill. var. celtidifolia aff. var. aspera—2n = 91 U.S.A. North Carolina: Chowan Co., NC-37 just N of Albermarle Sound Causeway, ca. 10 km S of Edenton, S & Su 9744.—2n = 18 U.S.A. Alabama: Coffee Co., NNNW of Enterprise, AL-167 13.3 km S of county line, S & Su 10154.—2n = 36 U.S.A. Louisiana: East Feliciana Par.: Co., E of Woodland, LA-432 1.5 km E of LA-67, S & Su 10112. Mississippi: Itawamba Co., MS-23 7.4 km N of county line, S & Su 10170. South Carolina: Berkeley Co., SC-45 ca. 5 km E of St. Stephen, Francis Marion Nat’l For., S & Su 9791; Jasper Co., NC-462 2.8 W of W of Cossawhatchie, S & Su 9860. Texas: San Jacinto Co., TX-150 3.6 km E of Shepherd, S & Su 10063.

Solidago rugosa Mill. var. cruciata Semple—2n = 36 U.S.A. NC: Avery Co., between Linville and Roseborough, E of Blue Ridge Parkway, Semple 11120, US-221 just S of Linville, S & Su 9698, E of Linville, Grandfather Mt., ca. 5000 ft el., S & Su 9675; Mitchell Co., top of Roan Mt., ca. 6260 ft el., Roan High Bluff Rd. (For.Rd.-130), S & Su 9667.

Solidago rugosa Mill. var. rugosa—2n = 91 U.S.A. Pennsylvania: Lycoming Co., SE of South Williamsport, vicinity of rest area by junction of US-15 and Skyline Drive, S & Su 9480; Tioga Co., Cowanesque Conservation Area Rd., W of US-15, S & Su 9476.—2n = 18 CANADA. Ontario: Parry Sound Co., Hwy-522 at junction of Stumpy Bay Rd, 27.4 km W of Loring, Semple & B. Semple 11072.—2n = 18 CANADA. Québec: Abitibi-Témiscamingue Co., 0.3 km from Hwy-117 on rd to la Mine Doyon, Cook & Seiden 105, Hwy-109 between Ames et Rivière-Héva, Cook & Seiden 104; Outaouais Co., Reserve la Verendrye, off Hwy-117, Park Rd-14, Cook & Seiden 122. U.S.A. Connecticut: New Haven Co., US-1 W of Branford, S & Su 9532; New London Co., Waterford, swamp by Cross Roads Mall, S & Su 9541-1, Waterford Conservation Area, Nevis Brook, S, 9190. Kentucky: Menifee Co., Boone Nat’l For., KY-715, S & Su 9463. Maine: Oxford Co., Hwy-2 5 m i West of West Bethel, Ringius 1597. Massachusetts: Barnstable Co., Scusset Beach St.Pk., along road to beach, S & B. Semple 11033, Cape Cod, W of Harwich, Great Western Rd. 2.0 km W of Clough Rd., just E of Lathop Ave, S & Su 9563, Orleans, S & Su 9557; Norfolk Co., Dover, Springdale Ave. N of town centre, Chennin Park, S & Su 9572, NW of Medfield, Farm St. WW of Centre St, by RR, Semple 11027. New Jersey: Burlington Co., SE of Chatworth on county rd., S & Su 9515; Ocean 10334Co., E of Cedar Run, cedar swamp just S of Cedar Run Dock Rd., S & Su 9521. New York: Livingston Co., Webster Crossing, NY-15, S & Su 9472; Suffolco Co., East Islip, Post Office Rd., S & Su 9529.—2n = 36 US. Connecticut: New London Co., NE of Voluntown, Pachaug State For., S 9188.

Solidago rugosa var. rugosa aff. var. aspera—2n = 36 U.S.A. Massachusetts: Plymouth Co., Marion, US-6, S & Su 9548. Pennsylvania: York Co., PA-372 woods below bridge over Susquehanna R., S & Ringius 7607.

Solidago rugosa Mill. var. sphagnophila Graves—2n = 91 U.S.A. Connecticut: New London Co., Waterford, swampy ground by Cross Roads Mall, S, 9192-A, S 9192-B. Massachusetts: Barnstable Co., Cape Cod, W of Harwich, Great Western Rd. just E of Lathop Ave., S & Su 9564; New Jersey: Atlantic Co., alongside rd. E of NJ-50 just S of US-40 and just N of Co.Rd.-669, S & Su 9505.—2n = 18 U.S.A. Massachusetts: Barnstable Co., Cape Cod, Orleans, S & Su 9556-3, NE of Orleans, junction of Mallard Lane and Skaket Beach Rd., S & Su 9554-2.
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