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MULTIVARIATE STUDIES OF *SOLIDAGO* SUBSECT. *SQUARROSAE*. I. THE *SOLIDAGO SPECIOSA* COMPLEX (ASTERACEAE: ASTEREAE)

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ABSTRACT

Solidago speciosa complex includes four taxa in *Solidago* subsect. *Squarrosae*. The complex has been treated as a single species with for varieties and as four separate species. A multivariate morphometric analyses on 265 specimens of all 14 species of subsect. *Squarrosae* and 69 specimens of the *S. speciosa* complex were carried out to assess membership in different species complexes and to assess how statistically distinct *S. jejunifolia, S. pallida, S. rigidiuscula* and *S. speciosa* were from each other. *Solidago erecta* has also been included in the complex historically. A key to the five species of the *S. speciosa* complex is presented.

Solidago subsect. *Squarrosae* A. Gray (Asteraceae: Astereae) includes 9-14 species native primarily to central and eastern Canada and the midwestern and eastern portions of the USA. Semple and Cook (2006) recognized 9 species with multiple infraspecific taxa in several species, while Semple (2016 frequently updated) recognized 14 species: *S. bicolor* L., *S. erecta* Pursh, *S. hispida* Muhl., *S. jejunifolia* Steele, *S. pallida* (Porter) Rydb., *S. porteri* Small, *S. puberula* Nutt., *S. pulverulenta* Nutt., *S. rigidiuscula* (Torr. & A. Gray) Porter, *S. roanensis* Porter, *S. sciaphila* Steele, *S. speciosa* Nutt., *S. squarrosa* Muhl., and *S. villosicarpa* LeBlond. With 14 species subsect. *Squarrosae* is the second largest subsection in the genus; *S.* subsect. *Triplinerviae* (Torr. & A. Gray) G.L. Nesom is the largest with 16 species (Semple 2016 frequently updated).

All species of subsect. *Squarrosae* include plants with erect stems arising from woody short-branched rootstocks, the basal rosette and lower stem leaves are the largest and sometimes petiolate, usually serrate, and usually oblanceolate or lanceolate. Mid and upper stem leaves are usually reduced in size upward, sessile, and serrate or entire. Inflorescence arrays vary from narrow wand-shaped forms with short branches to broader club-shaped forms with more elongated branches. In some species, the lowest branches of large inflorescences elongate forming separate wand to club shapes arrays making the array essential compound. Involucres are generally narrowly to broadly cylindrical. Phyllaries are strongly imbricate in 3-6 series and mostly lanceolate or oblong with obtuse to rounded tips that are usually appressed, except for the spreading to recurved phyllaries of *S. squarrosa*. Cypselae body indument varies from absent to sparsely to densely strigose or strigulose. All species are diploid only with the exception of *S. speciosa*, including diploids and tetraploids (Beaudry 1963; Semple et al. 1981, 1984, 1993, 2015; unpublished counts), *S. sciaphila* being tetraploid only (unpublished counts), and *S. porteri* being hexaploid only (Semple & Estes 2015). A review of chromosome counts and the cytogeography of all species of subsect. *Squarrosae* is in preparation.

The *Solidago speciosa* complex includes four taxa that were treated in a single species in Flora North America (Semple & Cook 2006) or as four separate species historically and more recently (Semple 2016 frequently updated): *S. speciosa* (Fig. 1), *S. jejunifolia* (Fig. 2), *S. pallida* (Fig. 3), and *S. rigidiuscula* (Fig. 4). *Solidago erecta* (Fig. 5) is similar to smaller plants of *S. speciosa*, in which it has been included as a variety: *Solidago speciosa* var. *erecta* (Pursh) MacMillan. *Solidago erecta* was treated as a separate species by Cronquist (1980) and Semple and Cook (2006) and is distinguished by its narrower more spiciform inflorescences and narrow mid stem leaves from the broader showy paniculiform inflorescences and wider (>20 mm) leaves of *S. speciosa*. Thus, *S. erecta* is viewed as a peripheral member of the *S. speciosa* complex and also as part of the *S. bicolor* complex.

Figure 1. Morphology of *Solidago speciosa*: *Weatherby 7361* (NEBC) from Litchfield Co., Connecticut.

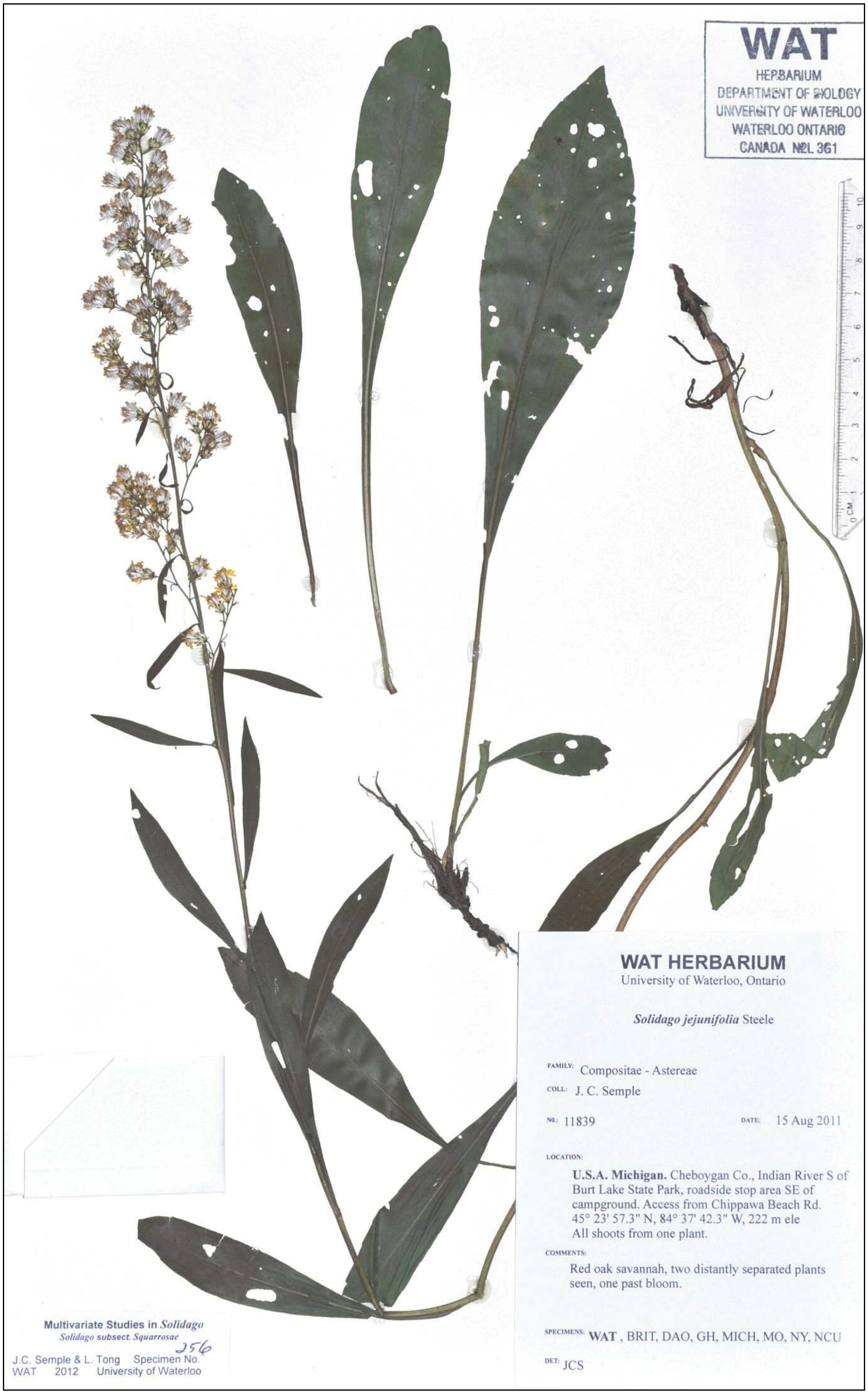

Figure 2. Morphology of *Solidago jejunifolia*: *Semple 11839* (WAT) from Cheboygan Co., Michigan.

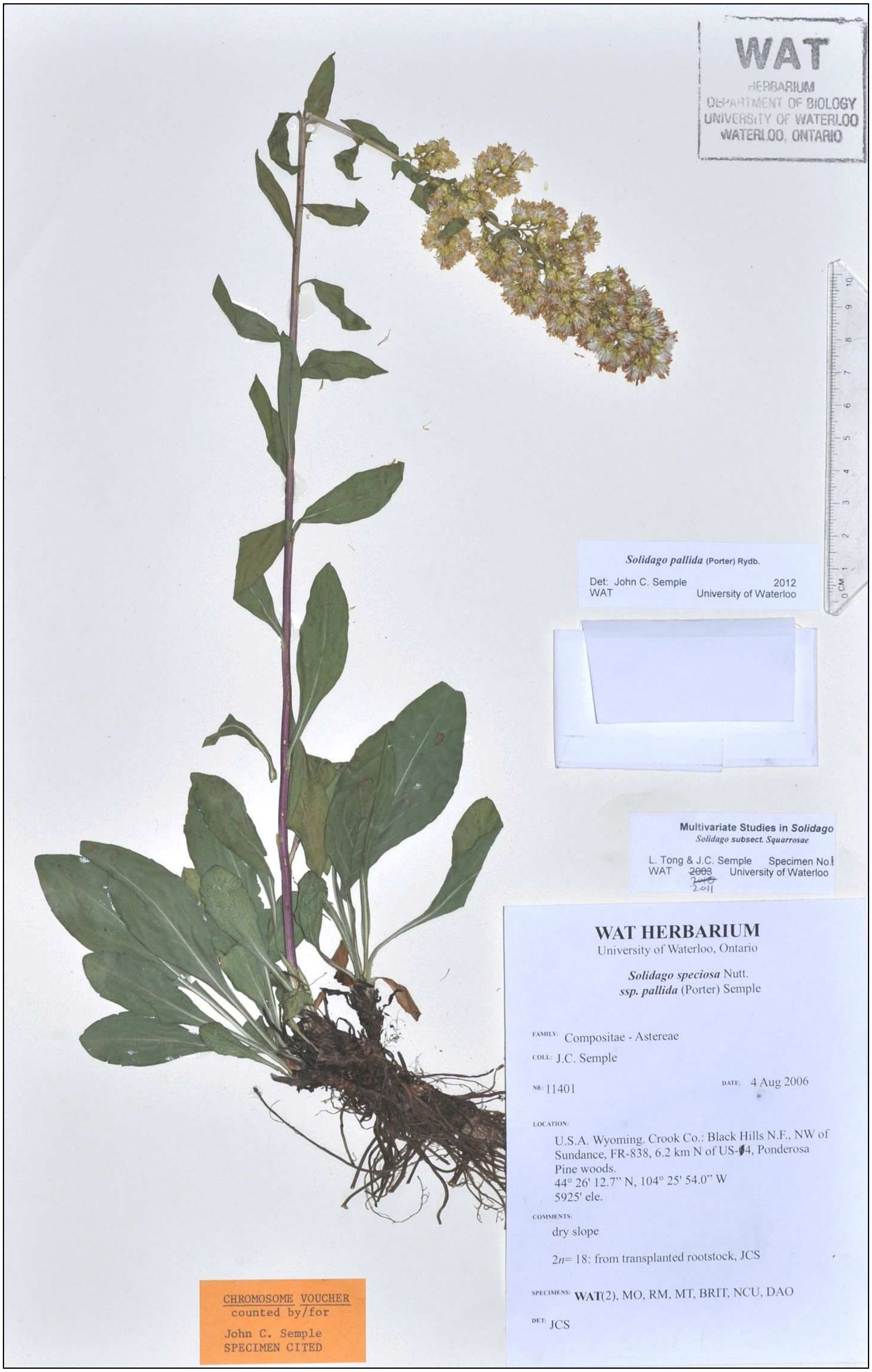

Figure 3. Morphology of *Solidago pallida*: Semple 11401 (WAT) from Crook Co., Wyoming.

Figure 4. Morphology of *Solidago rigidiuscula*: *Semple & Zhang 10602* (WAT) from Walpole Is., Ontario.

Figure 5. Morphology of *Solidago erecta*: *Semple & Suripto 9501* (WAT) from Atlantic Co., New Jersey.

There are a number of notable differences between species in the *Solidago speciosa* complex. *Solidago speciosa* produces the tallest stems (65-215 cm tall) and most robust shoots of the four species and has the largest lower stem leaves with some usually present at flowering. The inflorescence often has elongated branches and can be rather showy. The fruits are glabrous with the exception of the northeastern most population in southern Maine. Its heads vary in height, with diploids from east of the Appalachian Mts. having smaller heads than tetraploids occurring over most of the range and exclusively west of the Appalachians (Beaudry 1963; Semple et al. 1981, 1984, 1993; unpublished counts). *Solidago jejunifolia* was treated as a synonym under var. *speciosa* in Semple and Cook (2006), but field work in 2011 resulted in treating it as a separate diploid species defined by its long narrow petioles on the basal rosette and lower stem leaves which are usually present at flowering (Fig. 2). The fruits usually have some hairs on the body and generally more densely so distally. *Solidago pallida* has basal rosette and lower stem leaves like those of *S. speciosa* but usually smaller (Fig. 3) and diploid only (Semple et al. 1984; unpublished counts). Stems in general average 58 cm tall and have persistent lower stem leaves with tapering blade bases and short petioles. Upper leaves are reduced and lack serrations. Leaves are often a lighter green color than those of *S. rigidiuscula*. *Solidago rigidiuscula* includes diploids (Semple et al. 1984, 1989; unpublished counts) averaging 80 cm tall and nearly always drop the lower stem leaves by flowering (Fig. 4). Mid stem and upper leaves have few or no serrations and tend to be more congested than those of *S. jejunifolia* and *S. pallida*. Involucres of diploid *S. jejunifolia*, *S. pallida*, and *S. rigidiuscula* are smaller than those of tetraploid *S. speciosa* occurring in the ranges of the first three taxa.

The four species of the *Solidago speciosa* complex are allopatric over a significant portion of their ranges but are sympatric on the eastern prairies and in the Midwestern states. *Solidago speciosa* occurs in oak and pine woods, fields, open thickets, and along roadsides from southeastern Maine west to southeastern Minnesota and south to central Georgia, Alabama, and Mississippi in the east and northern Arkansas in the west (Fig. 6). *Solidago jejunifolia* occurs in dry sandy and gravelly soils on prairies, on sandy bluffs, and in dry open jack pine forests primarily in Minnesota, Wisconsin, and northern Michigan but extends into adjacent southeastern Manitoba (Semple et al.

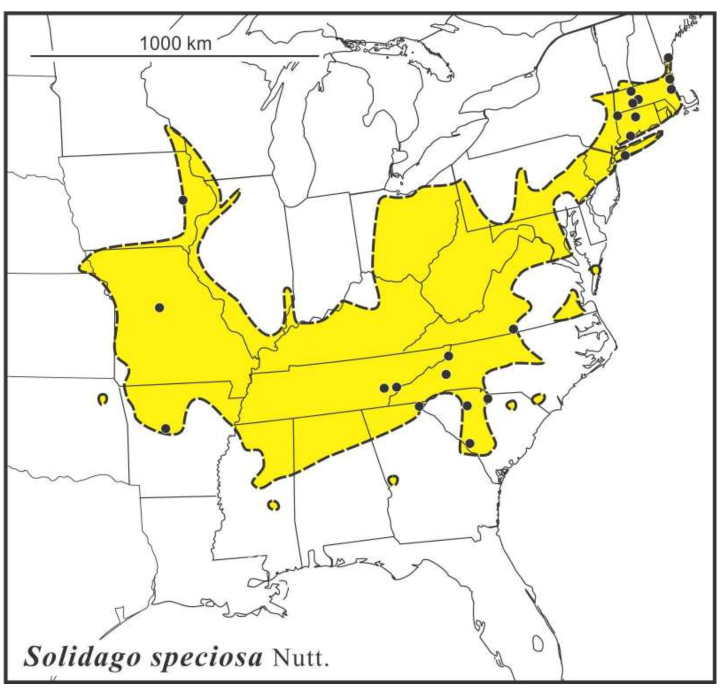

Figure 6. Range of distribution of *Solidago speciosa* and locations of specimens included in the analyses.

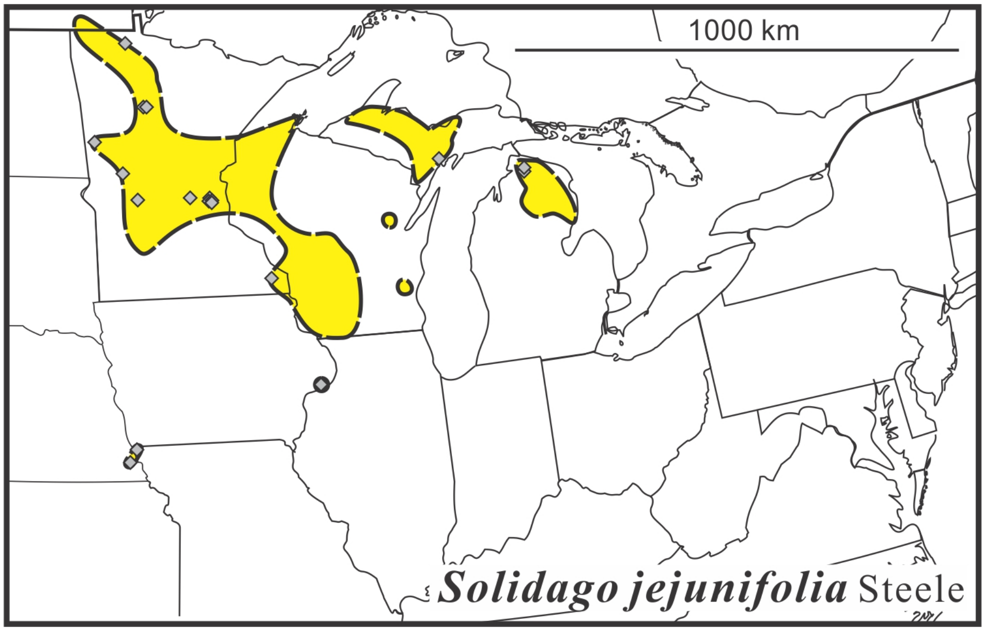

Figure 7. Range of distribution of *Solidago jejunifolia* and locations of specimens included in the analyses.

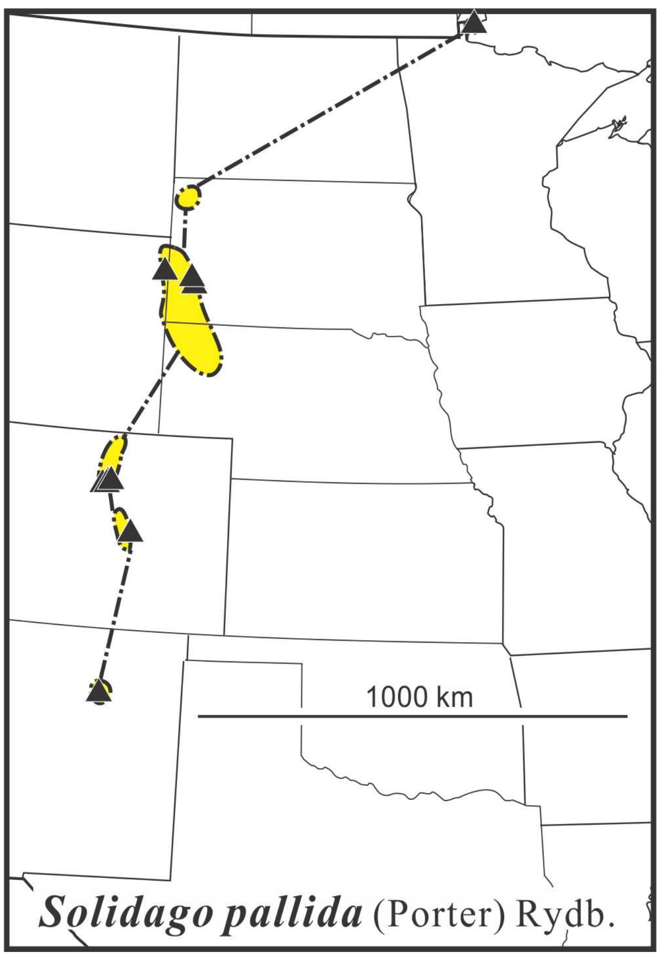

Figure 8. Range of distribution of *Solidago pallida* and locations of specimens included in the multivariate analyses.

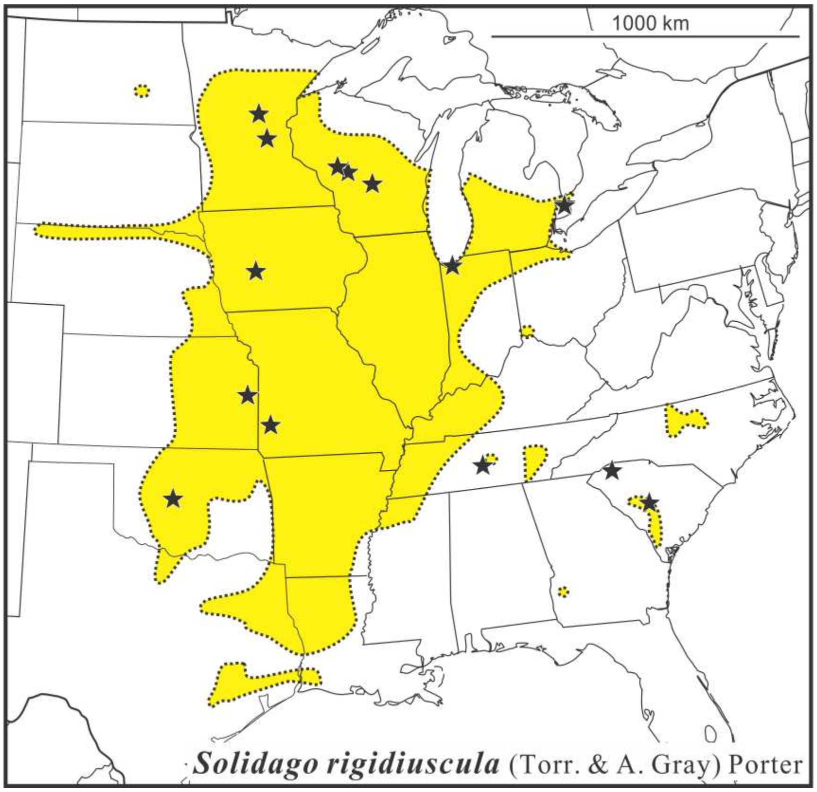

Figure 9. Range of distribution of *Solidago rigidiuscula* and locations of specimens included in the analyses.

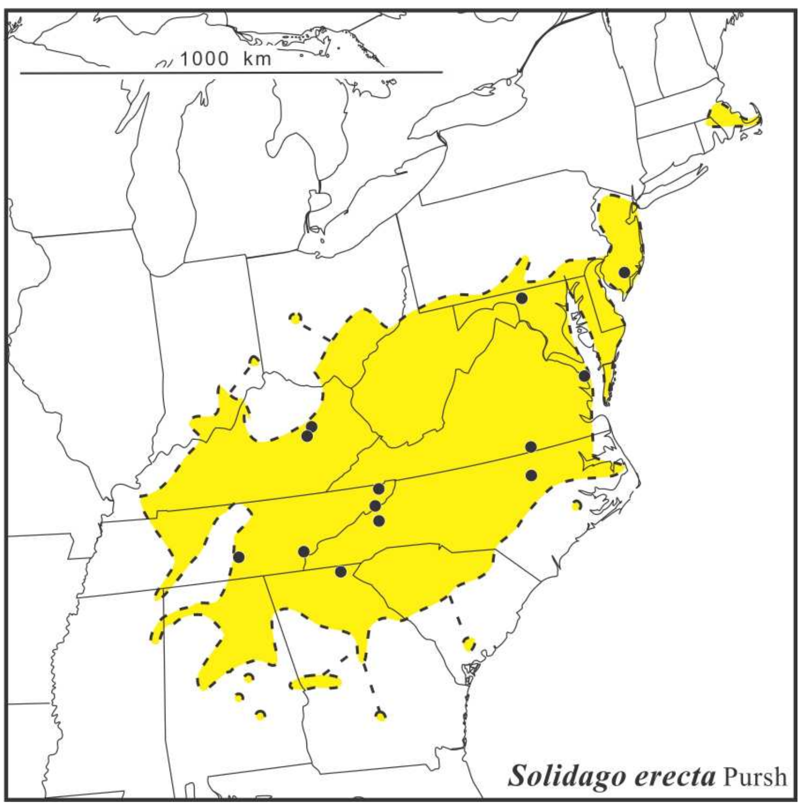

Figure 10. Range of distribution of *Solidago erecta* and locations of specimens included in the analyses.

2012) and scattered locations further to the south and west in Iowa, northwestern Missouri and adjacent Nebraska (Semple 2017; Fig. 7). *Solidago pallida* occurs in open Ponderosa pine forests in the Black Hills of eastern Wyoming and western South Dakota and along the foot hills of the Front Range of the Rocky Mountains in Wyoming, Colorado, and northern New Mexico (Fig. 8). It is also disjunct in Rainy River Dist., Ontario (Semple et al. 2012). *Solidago rigidiuscula* occurs in drier habitats in the forest prairie ecotone of the midwestern USA and scattered prairie-like habitats further east (Fig. 9). It is generally taller than *S. jejunifolia* and *S. pallida* but drops its lower stems leaves by flowering. *Solidago erecta* occurs in sandy and clay soils in open mixed oak and pine woods and along roadsides in partial to full sun. It occurs in eastern Massachusetts and adjacent Rhode Island in a disjunct area separated from the main distribution from New Jersey south to Georgia and west to southern Indiana and eastern Mississippi on in the Piedmont, central and southern Appalachians and the Cumberland and Mississippian Plateaus.

MATERIALS AND METHODS

In total, 281 specimens from A, BALT, GA, LSU, MO, the J.K. Morton personal herbarium now deposited in ROM, MT, NCU, NEBC, NY, TAWES, UNB, WAT in MT (Thiers, continuously updated) were scored and included in the analysis: *S. bicolor* (16 specimens), *S. erecta* (19 specimens), *S. hispida* (77 specimens representing 5 varieties), *S. jejunifolia* (18 specimens), *S. pallida* (12 specimens), *S. porteri* (11 specimens), *S. puberula* (16 specimens), *S. pulverulenta* (13 specimens), *S. rigidiuscula* (15 specimens), *S. roanensis* (20 specimens), *S. sciaphila* (20 specimens), *S. speciosa* (24 specimens), *S. squarrosa* (11 specimens), and *S. villosicarpa* (9 specimens). These were selected from more than 1700 specimens of *S.* subsect. *Squarrosae* examined. For each specimen, 18 vegetative and 19 floral traits were scored when possible: 1-5 replicates per character depending upon availability of material and whether or not the trait was meristic (Table 1). Basal rosette leaves were often not present. Lower stem leaves were sometimes not present. Mean values were used in the analyses, while raw values were used to generate means and ranges of variation for each trait. All traits scored are listed in Table 1.

Table 1. Traits scored for the multivariate analyses of 281 specimens of *Solidago* subsect. *Squarrosae*.

Abbreviation	Description of trait scored
STEMHT	Stem height measured from the stem base to tip (cm)
BLFLN	Basal rosette leaf length including petiole (mm)
BLFPETLN	Basal rosette leaf petiole length (not scored if winged margins broad)
BLFWD	Basal rosette leaf width measured at the widest point (mm)
BLFWTOE	Basal rosette leaf measured from the widest point to the end (mm)
BLFSER	Basal rosette leaf-number of serrations on 1 side of margin
LLFLN	Lower leaf length measured from the leaf base to tip (mm)
LLFWD	Lower leaf width measured at the widest point (mm)
LLFWTOE	Lower leaf measured from the widest point to the end (mm)
LLFSER	Lower leaf dentation-number of serrations of lower leaf
MLFLN	Mid leaf length measured from the leaf base to tip (mm)
MLFWD	Mid leaf width measured at the widest point (mm)
MLFWTOE	Mid leaf measured from the widest point to the end (mm)
MLFSER	Mid leaf dentation-number of serrations of mid leaf
ULFLN	Upper leaf length measured form the leaf base to tip (mm)
ULFWD	Upper leaf width measured at the widest point (mm)

ULFWTOE	Upper leaf measured from the widest point to the end (mm)
ULFSER	Upper leaf dentation-number of serrations of upper leaf
CAPL	Length of inflorescence (cm)
CAPW	Width of inflorescence (cm)
INVOLHT	Involucre height (mm)
OPHYLN	Outer phyllary length (mm)
OPHYLW	Outer phyllary width (mm)
IPHYLN	Inner phyllary length (mm)
IPHYLW	Inner phyllary width (mm)
RAYNUM	Number of ray florets per head
RSTRAPLN	Ray strap length top of the corolla tube to the tip of the strap (mm)
RSTRAPWD	Ray strap width measured at the widest point (mm)
RACHLN	Ray floret cypsela body length at anthesis (mm)
RPAPLN	Ray floret pappus length at anthesis (mm)
DCORLN	Disc floret corolla length from the base to tip of the corolla lobes (mm)
DLOBLN	Disc floret corolla lobe length lobe (mm)
DACHLN	Disc floret achene length at anthesis (mm)
DPAPLN	Disc floret pappus length at anthesis (mm)

All analyses were performed using SYSTAT v.10 (SPSS 2000). Details on the methodology are presented in Semple et al. (2016) and are not repeated here. Four analyses were performed. In the first analysis, all fourteen species of subsect. *Squarrosae* were included in a STEPWISE discriminant analysis. In the second analysis, eight traits with the highest F-to-remove values were used in COMPLETE discriminant analysis of all fourteen species of subsect. *Squarrosae*. In the third analysis, the four species of the *Solidago speciosa* complex were included in a STEPWISE discriminant analysis. In the fourth analysis, only specimens of *S. erecta*, *S. rigidiuscula* and *S. speciosa* were included in STEPWISE discriminant analysis. The number of specimens of each species included depended upon the traits selected.

RESULTS

The Pearson correlation matrix yielded r > |0.7| for most pairs of leaf traits reducing the number of traits to be used to either mid leaf length, mid leaf width, and mid leaf serrations. Basal rosette leaves were often absent and were not included in the discriminant analyses: basal leaf length, petiole length, and basal leaf length from widest point to tip were all highly correlated. Lower leaves were sometimes absent and lower leaf traits were excluded from discriminant analyses. Ray floret achene body length at anthesis correlated highly with disc floret achene body length and only the latter trait was included in discriminant analyses. Inflorescence length and width traits were generally used in defining a priori groups and were not included in the analyses.

Fourteen species groups analysis of subsect. *Squarrosae*

In the STEPWISE discriminant analysis of 276 specimens of fourteen species level a priori groups (*Solidago bicolor*, *S. erecta*, *S. hispida*, *S. jejunifolia*, *S. pallida*, *S. porteri*, *S. puberula*, *S. pulverulenta*, *S. rigidiuscula*, *S. roanensis*, *S. sciaphila*, *S. speciosa*, *S. squarrosa*, and *S. villosicarpa*), 13 traits selected in a STEPWISE analysis. Because there were only 9 specimens of *S. villosicarpa*, the following 8 traits were used in a COMPLETE analysis and are listed in decreasing order of F-to-remove values: ray floret lamina length (18.14), ray floret pappus length at anthesis

(16.25), number of mid stem leaf margin serrations (11.05), mid leaf length (9.70), number of ray florets (8.41), disc floret achene body length at anthesis (7.14), outer phyllary length (7.14), and (length of disc floret corolla at anthesis (5.23). Wilks's lambda, Pillai's trace, and Lawley-Hotelling trace tests of the null hypothesis that all groups were the samples of one group had probabilities of p = 0.000 that the null hypothesis was true. The F-matrix for the discriminant analysis is presented in Table 2. F-values based on Mahalanobis distances of the between group centroids indicated the largest separations were between *S. hispida* and *S. squarrosa* (43.266), *S. rigidiuscula* and *S. squarrosa* (42.322), and *S. hispida* and *S. villosicarpa* (40.407); the smallest separations were between *S. jejunifolia* and *S. rigidiuscula* (1.795), *S. pallida* and *S. rigidiuscula* (2.552), *S. roanensis* and *S. sciaphila* (2.688), *S. puberula* and *S. pulverulenta* (3.142), *S. jejunifolia* and *S. pallida* (3.655), *S. pallida* and *S. erecta* (4.039), and *S. erecta* and *S. speciosa* (4.668). The highest average F-values were between *S. squarrosa* (33.416) and all other species and *S. villosicarpa* (27.025) and all other species.

In the Classificatory Discriminant Analysis of the fourteen putative species level a priori groups, a posteriori assignments of specimens ranged from 44-91% to their own group. The Classification matrix and Jackknife classification matrix are presented in Table 3. Only six species had percents of correct assignment in the 70-91% range: *Solidago squarrosa* with 91%, *S. pulverulenta* with 85%, *S. villosicarpa* with 78%, *S. pallida* and *S. porteri* with 73%, and *S. sciaphila* with 70%. The details are not discussed further.

Two dimensional plots of CAN1 versus CAN 3 and CAN1 versus CAN2 canonical scores for 276 specimens of all fourteen species of subsect. *Squarrosae* showed strong separate of only a few species and were not very informative due to considerable overlap in group distributions on the diagrams (Fig. 11). Eigenvalues on the first three axes were 2.913, 1.662 and 0.962. Only the symbols of *Solidago villosicarpa* and *S. squarrosa* are fairly well separated from other taxa on CAN1 versus CAN2. Symbols for the hexaploid *S. porteri* are less well separated from other species but the 95% confidence limits ellipse overlaps only slightly with the ellipse for *S. speciosa*. Symbols for *S. villosicarpa*, *S. squarrosa*, *S. porteri*, and S. speciosa are the only one on the right half of the CAN1 versus CAN2 diagram. Symbols for the four species of the *S. speciosa* complex (*S. jejunifolia*, *S. pallida*, *S. rigidiuscula* and *S. speciosa*) occupy the upper left quarter of the CAN1 versus CAN2 plot, but are not separated from majority of taxa on the CAN1 versus CAN3 plot. Symbols for *S. puberula* and *S. pulverulenta* and their 95% confidence ellipses overlap considerable on the CAN1 versus CAN3 plot but are mostly separated from other species in the upper left portion of the diagram. Symbols for *S. bicolor*, *S. erecta*, *S. hispida*, and *S. roanensis*, *S. sciaphila* are not well separated in the center left portion of the CAN1 versus CAN2 plot, but with symbols of *S. bicolor* and *S. hispida* being partially separated from the other three species in the lower left portion of the CAN1 versus CAN3 plot.

Four species groups analysis of the *S. speciosa* complex

In the STEPWISE discriminant analysis of 69 specimens of four species level a priori groups (*Solidago jejunifolia*, *S. pallida*, *S. rigidiuscula*, and *S. speciosa*), the following nine traits selected in a STEPWISE analysis are listed in order of decreasing F-to-remove values: number of mid leaf serrations (8.97), mid leaf width (8.93), number of disc florets (6.15), ray floret lamina length (5.95), involucre height at anthesis (5.32), inner phyllary length (4.97), mid leaf length (4.61), disc achene body length at anthesis (4.13), and disc corolla length (4.04). Wilks's lambda, Pillai's trace, and Lawley-Hotelling trace tests of the null hypothesis that all groups were the samples of one group had probabilities of p = 0.000 that the null hypothesis was true. The F-matrix for the discriminant analysis

Table 2. Between groups F-matrix for the fourteen a priori group analysis of *S.* subsect. *Squarrosae* (df = 8 255).

Group	***bicolor***	***erecta***	***hispida***	***jejunifolia***	***pallida***	***porteri***	***puberula***	***pulverulenta***	***rigidiuscula***	***roanensis***	***sciaphila***
erecta	6.749										
hispida	5.036	10.293									
jejunifolia	9.656	9.380	19.041								
pallida	4.917	4.619	8.851	3.655							
porteri	12.281	7.270	24.111	10.304	9.541						
puberula	16.180	13.451	16.886	9.592	9.884	23.937					
pulverulenta	15.306	12.744	11.737	13.272	12.243	25.699	3.142				
rigidiuscula	7.103	7.284	11.845	1.795	2.552	14.218	7.363	9.016			
roanensis	6.231	12.114	9.442	14.536	8.239	22.049	9.774	12.275	9.64		
sciaphila	8.001	7.936	8.385	14.427	6.400	21.071	6.786	8.823	9.307	2.688	
speciosa	11.356	4.668	30.770	6.533	5.559	5.060	20.713	22.080	8.151	20.890	17.836
squarrosa	31.735	24.767	43.266	38.384	30.724	17.106	36.430	32.921	42.322	38.640	32.430
villosicarpa	30.507	16.307	40.407	33.653	26.092	15.355	32.963	29.861	33.800	34.051	26.968

Group (cont.)	***speciosa***	***squarrosa***
squarrosa	32.268	
villosicarpa	20.005	11.352

Wilks' lambda = 0.0187 df = 8 13 262; Approx. F= 13.2859 df = 104 1766 prob = 0.0000

is presented in Table 4. F-values based on Mahalanobis distances of the between group centroids indicated the largest separation was between *S. jejunifolia* and *S. speciosa* (18.609); the smallest separation was between *S. jejunifolia* and *S. rigidiuscula* (5.523).

In the Classificatory Discriminant Analysis of the four species level a priori groups, percents of correct a posterori assignment to the same a priori group ranged from 83-100%. The Classification matrix and Jackknife classification matrix are presented in Table 5. Results are presented in order of decreasing percents of correct placement. All 15 specimens of the *Solidago rigidiuscula* a priori group (100%) were assigned a posteriori into the *S. rigidiuscula* group; 7 specimens with 90-100% probability, 4 specimens with 80-89% probability, 2 specimens with 68% and 62% probabilities, and 2 specimen with 57% and 53% probabilities (42% and 46% probabilities to *S. jejunifolia*). Twenty-two of the 24 specimens of *S. speciosa* a priori group (92%) were assigned a posteriori to the *S. speciosa* group; 19 specimens with 91-100% probability, 1 specimen with 82% probability, 1 specimen with 73% probability, and 1 specimen with 68% probability. Two specimens of the *S. speciosa* a priori group were assigned to other species: 1 specimen to *S. pallida* with 96% probability (*Potsubay 69009*, NEBC from Holyoke, Massachusetts; 2 stem 67 cm tall, missing all but the upper most lower stem leaves); 1 specimen to *S. rigidiuscula* with 87% probability (*Eames s.n.*, NEBC from "dry field along the coast," Bridgeport, Connecticut; a small plant 67 cm tall with a small

Table 3. Linear and jackknife classification matrices from the Classificatory Discriminant Analysis of four a priori groups; a posteriori placements to groups in rows.

Group	***bicolor***	***erecta***	***hispida***	***jejunifolia***	***pallida***	***porteri***	***puberula***	***pulverulenta***	***rigidiuscula***	***roanensis***	***sciaphila***	***speciosa***	***squarrosa***	***villosicarpa***	**% correct**
bicolor	10	0	2	1	1	0	0	0	0	2	0	0	0	0	63
erecta	0	12	1	0	1	1	0	0	2	1	0	1	0	0	63
hispida	13	4	45	0	2	0	0	2	2	3	6	0	0	0	58
jejunifolia	0	0	0	7	0	0	0	0	6	0	0	1	0	0	50
pallida	0	1	0	1	8	0	1	0	0	0	0	0	0	0	73
porteri	0	0	0	0	1	8	1	0	0	0	0	1	0	0	73
puberula	0	0	0	0	0	0	7	7	2	0	0	0	0	0	44
pulverulenta	0	1	0	0	0	0	1	11	0	0	0	0	0	0	85
rigidiuscula	0	0	0	3	2	0	0	1	8	0	0	1	0	0	53
roanensis	2	0	2	0	0	0	1	0	0	13	2	0	0	0	65
sciaphila	0	0	0	0	1	0	0	0	1	4	14	0	0	0	70
speciosa	0	4	0	3	1	3	0	0	0	0	1	12	0	0	50
squarrosa	0	0	0	0	0	0	0	0	0	0	0	0	10	1	91
villosicarpa	0	2	0	0	0	0	0	0	0	0	0	0	0	7	78
Totals	25	24	50	15	17	12	11	21	21	23	23	16	10	8	62

Jackknifed classification matrix

Group	***bicolor***	***erecta***	***hispida***	***jejunifolia***	***pallida***	***porteri***	***puberula***	***pulverulenta***	***rigidiuscula***	***roanensis***	***sciaphila***	***speciosa***	***squarrosa***	***villosicarpa***	**% correct**
bicolor	8	0	3	1	2	0	0	0	0	2	0	0	0	0	50
erecta	0	10	1	0	1	1	0	0	2	1	0	3	0	0	53
hispida	13	4	45	0	2	0	0	2	2	3	6	0	0	0	58
jejunifolia	0	0	0	5	1	0	0	0	6	0	0	2	0	0	36
pallida	0	1	0	2	7	0	1	0	0	0	0	0	0	0	64
porteri	0	0	0	0	1	8	1	0	0	0	0	1	0	0	73
puberula	0	0	0	0	0	0	6	7	3	0	0	0	0	0	38
pulverulenta	0	1	0	0	0	0	1	11	0	0	0	0	0	0	85
rigidiuscula	0	0	0	3	3	0	0	0	7	0	0	1	0	0	47
roanensis	2	0	2	0	0	0	2	0	0	12	2	0	0	0	60
sciaphila	0	0	1	0	1	0	0	0	1	6	11	0	0	0	55
speciosa	0	5	0	3	1	4	0	0	0	0	1	10	0	0	42
squarrosa	0	0	0	0	0	0	0	0	0	0	0	0	10	1	91
villosicarpa	0	2	0	0	0	0	0	0	0	0	0	0	0	7	78
Totals	23	23	52	14	19	13	11	21	24	24	20	17	10	8	57

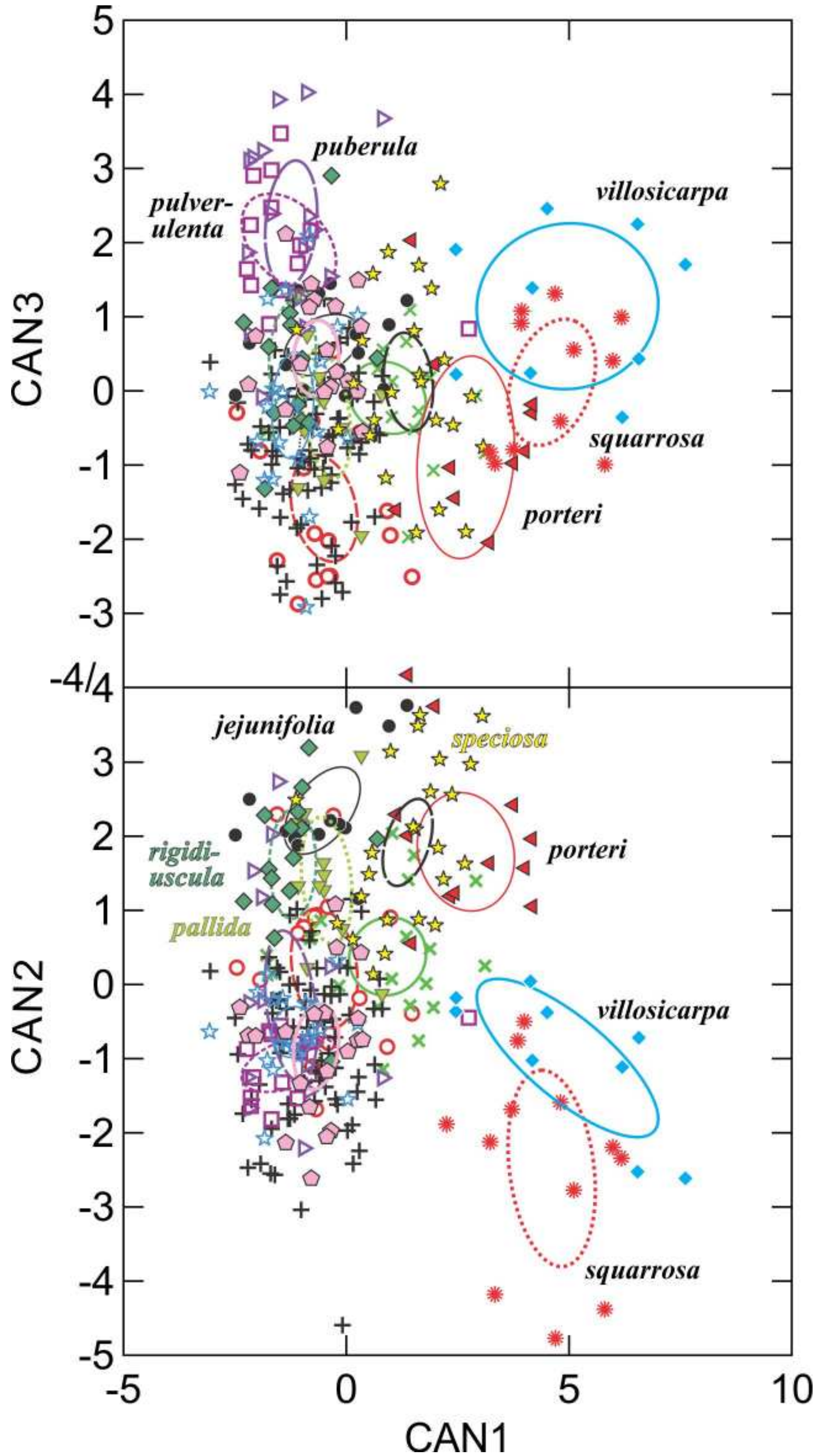

Figure 11. Plot of canonical scores (CAN1 vs CAN3 and CAN1 vs CAN2) for 276 specimens of *Solidago* subsect. *Squarrosae*: *S. bicolor* (red circles), *S. erecta* (green ×s, *S. hispida* (black +s), *S. jejunifolia* (black dots), *S. pallida* (light green triangles), *S. porteri* (red triangles), *S. puberula* (open purple triangles), *S. pulverulenta* (magenta squares), *S. rigidiuscula* (green diamonds), *S. roanensis* (open blue stars), *S. sciaphila* (pink pentagons), *S. speciosa* (yellow stars), *S. squarrosa* (red star bursts), and *S. villosicarpa* (light blue diamonds).

Table 4. Between groups F-matrix for the four a priori group analysis (df = 9 89).

Group	*jejunifolia*	*pallida*	*rigidiuscula*
pallida	10.099		
rigidiuscula	5.523	7.173	
speciosa	18.609	8.262	12.420

Wilks' lambda = 0.0631 df = 9 3 65; Approx. F= 9.7471 df = 27 167 prob = 0.0000

Table 5. Linear and jackknife classification matrices from the Classificatory Discriminant Analysis of four a priori groups; a posteriori placements to groups in rows.

Group	*jejunifolia*	*pallida*	*rigidiuscula*	*speciosa*	% correct
jejunifolia	15	0	3	0	83
pallida	1	10	1	0	83
rigidiuscula	0	0	15	0	100
speciosa	0	1	1	22	92
Totals	16	11	20	22	90

Jackknifed classification matrix

Group	*jejunifolia*	*pallida*	*rigidiuscula*	*speciosa*	% correct
jejunifolia	14	0	3	1	78
pallida	2	9	1	0	75
rigidiuscula	2	0	12	1	80
speciosa	0	2	1	21	88
Totals	18	11	17	23	81

inflorescence 6.2 cm tall). Fifteen of the 18 specimens of the *S. jejunifolia* a priori group (83%) were assigned a posteriori to the *S. jejunifolia* group: 11 specimens with 97-100% probability, 2 specimens with 82-83% probability, 1 specimen with 77% probability; and 1 specimen with 68% probability (15% to *S. speciosa*, and 9% each to *S. pallida* and *S. rigidiuscula*). Three specimens of the *S. jejunifolia* a priori group were assigned a posteriori to the *S. rigidiuscula* group: 2 with 83-84% (*Smith 14946* MIN from Houston Co., Minnesota, a 47 cm tall shoot with few leaves and one long petioled lower stem leaf; *Heitlinger 790* MIN from Anoka Co., Minnesota, a 55 cm tall shoot with few leaves along the entire stem and basal rosette and lower stem leaves with long petioles grading into the long tapering blade bases), and 1specimen with 58% to *S. rigidiuscula* (42% to *S. jejunifolia*; *Converse 1906* MIN from Pope Co., Minnesota; a 48 cm tall plant with basal rosette and lower stem leaves with long thin petioles typical of *S. jejunifolia*). Ten of the 12 specimens of the *S. pallida* a priori group (83%) were assigned a posteriori to the *S. pallida* group: 9 with 97-100% probability and 1 with 80% probability. Two specimens of the *S. pallida* a priori group were assigned a posteriori to other groups: 1 specimen was assigned to *S. jejunifolia* with 50% probability (38% to *S. pallida* and 9% to *S. rigidiuscula*; *Semple 11304* WAT from Pennington Co., South Dakota, a 68 cm tall shoot with large lower stem leaves and a 23 cm tall inflorescence; a smaller second shoot with much smaller lower stem leaves from the same population and collection was assigned to *S. pallida* with 98% probability); and 1 specimen was assigned to *S. rigidiuscula* with 65% probability (18% to *S. jejunifolia* and 17% to *S. pallida*; *Semple 11304*, WAT from Pennington Co., South Dakota, a third sample from the same population and collection as above, a 43 cm tall shoot with large lower stem leaves, the lowest with a short petiole).

Two dimensional plots of CAN1 versus CAN3 and CAN1 versus CAN2 canonical scores for 69 specimens of *Solidago jejunifolia*, *S. pallida*, *S. rigidiuscula*, and *S. speciosa* are presented in Figure 12. Eigenvalues on the first three axes were 3.259, 1.099 and 0.774.

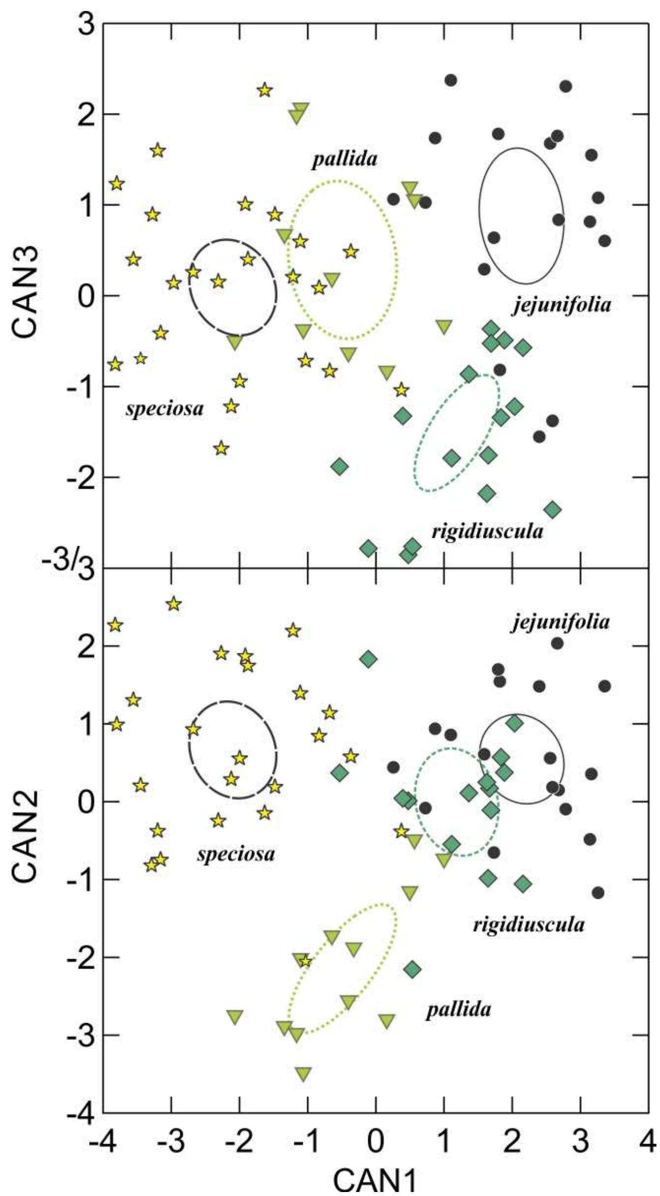

Figure 12. Plot of canonical scores (CAN1 vs CAN3 and CAN1 vs CAN2) for 69 specimens of subsect. *Squarrosae*: *S. jejunifolia* (black dots), *S. pallida* (light green triangles), *S. rigidiuscula* (green diamonds), and *S. speciosa* (yellow stars).

Three species groups analysis of the *S. speciosa* complex

In the STEPWISE discriminant analysis of 56 specimens of three species level a priori groups (*Solidago erecta*, *S. rigidiuscula*, and *S. speciosa*), the following eight traits selected in a STEP-WISE analysis are listed in order of decreasing F-to-remove values: disc corolla lobe length (9.72), number of disc florets (9.17), ray floret lamina length (6.09), mid leaf width (5.55), disc floret pappus length at anthesis (4.63), upper leaf width (4.30), inner phyllary length (4.01), and number of mid leaf serrations (4.00). Wilks's lambda, Pillai's trace, and Lawley-Hotelling trace tests of the null hypothesis that all groups were the samples of one group had probabilities of p = 0.000 that the null hypothesis was true. The F-matrix for the discriminant analysis is presented in Table 6. F-values based on Mahalanobis distances of the between group centroids indicated the largest separation was between *S. erecta* and *S. rigidiuscula* (15.915); the smallest separation was between *S. erecta* and *S. speciosa* (10.010).

Table 6. Between groups F-matrix for the four a priori group analysis (df = 6 46).

Group	***erecta***	***rigidiuscula***
rigidiuscula	15.915	
speciosa	10.010	14.895

Wilks' lambda = 0.0933 df = 8 2 53; Approx. F= 13.0797 df = 16 92 prob = 0.0000

In the Classificatory Discriminant Analysis of the three species level a priori groups, percents of correct a posterori assignment to the same a priori group ranged from 78-100%. The Classification matrix and Jackknife classification matrix are presented in Table 7. Results are presented in order of decreasing percents of correct placement. All 15 specimens of the *S. rigidiuscula* a priori group (100%) were assigned a posteriori into the *S. rigidiuscula* group; 12 specimens with 100% probability, 2 specimens with 98-99% probability, and 1 specimen with 95%. Twenty of the 23 specimens of *S. speciosa* a priori group (87%) were assigned a posteriori to the *S. speciosa* group; 17 specimens with 91-100% probability, 2 specimens with 89% and 82% probabilities, and 1 specimen with 57% probability (39% to *S. erecta* and 4% to *S. rigidiuscula*). Three specimens of the *S. speciosa* a priori group were assigned to *S. erecta*: 1 specimen with 80% probability (*Semple & Chmielewski 6103*, WAT from Lancaster Co., South Carolina; 177 cm tall shoot with 39 × 8 cm inflorescence and wilted or dropped lower stem leaves; this was placed into *S. speciosa* with 98% probability in the four species analysis above); 1 specimen with 74% probability (26% to *S. speciosa*; *Semple 11675*, WAT from Union Co., South Carolina; 135 cm tall shoot with petiolate 172 × 35 mm lower stem leaves and a 49 × 5 cm inflorescence), and 1 specimen with 42% (42% to *S. speciosa* and 16% to *S. rigidiuscula*; *Eames s.n.*, NEBC from Bridgeport Connecticut; a 65 cm tall shoot with a small 6 × 2 cm inflorescence and a second upper stem with a 34 × 8 cm inflorescence and an upper stem thicker than the basal stem of the small shoot). Fourteen of the 18 specimens of the *S. erecta* a priori group (78%) were assigned a posteriori to the *S. erecta* group: 13 with 97-100% probability and 1 with 50% probability (49% to *S. rigidiuscula*). Four specimens of the *S. erecta* a priori group were assigned a posteriori to the other groups: 1 specimen was assigned to *S. rigidiuscula* with 86% probability (13% to *S. erecta* and 1% to *S. speciosa*; *Semple & Ringius 7659*, WAT from Washington Co., Maryland; a 54 cm tall shoot with small narrow upper leaves and a 15 × 2 cm inflorescence); 1

specimen was assigned to *S. rigidiuscula* with 71% probability (15% to *S. erecta* and 15% to *S. speciosa*; *Cook et al. C-589,* WAT from Monroe Co., Tennessee; a 69.5 cm tall shoot with greatly reduced upper stem leaves and 8.5 × 3 cm inflorescence); 1 specimen assigned to *S. speciosa* with 70% probability (30% to *S. erecta*; *Semple & Suripto 9688,* WAT from Mt. Mitchell, Yancy Co., North Carolina; a 53 cm tall shoot with 12 × 2 cm inflorescence); and 1 specimen assigned to *S. speciosa* with 53% probability (47% to *S. erecta*; *Semple & Chmielewski, 5984* WAT from Northumberland Co., Virginia; a 89 cm tall shoot with 28-39 mm wide lower stem leaves, greatly reduced upper stem leaves, and a 36 × 2.5 cm inflorescence).

Table 7. Linear and jackknife classification matrices from the Classificatory Discriminant Analysis of three a priori groups; a posteriori placements to groups in rows.

Group	*erecta*	*rigidiuscula*	*speciosa*	% correct
erecta	14	2	2	78
rigidiuscula	0	15	0	100
speciosa	3	0	20	87
Totals	17	17	22	88

Jackknifed classification matrix

Group	*erecta*	*rigidiuscula*	*speciosa*	% correct
erecta	13	3	2	72
rigidiuscula	0	15	0	100
speciosa	6	0	17	74
Totals	19	18	19	80

Two dimensional plots of CAN1 versus CAN2 canonical scores for 56 specimens of *Solidago erecta*, *S. rigidiuscula*, and *S. speciosa* are presented in Fig. 13. Eigenvalues on the first two axes were 2.946 and 1.717.

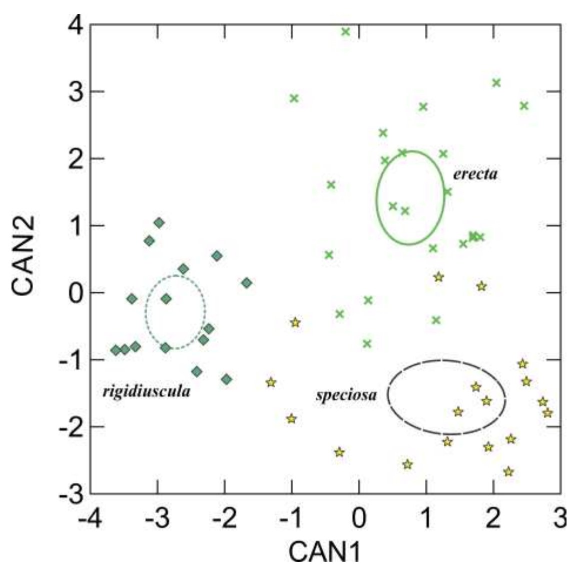

Figure 13. Plot of canonical scores (CAN1 vs CAN2) for 56 specimens of Solidago subsect. Squarrosae: *S. erecta* (green ×s), *S. rigidiuscula* (green diamonds), and *S. speciosa* (yellow stars).

DISCUSSION

The results of the first two multivariate analyses indicate that *Solidago villosicarpa, S. squarrosa,* and *S. porteri* are the most distinct species of the 14 species in subsect. *Squarrosae.* Ray floret lamina length had the highest F-to-remove value and ranged from a low of 1.83 (*S. bicolor*) to a high of 4.46 mm (*S. villosicarpa*): *S. squarrosa* had a mean of 3.99 mm and *S. porteri* had the next longest mean of 2.86 mm. Mean involucre height was 6.30 mm for *S. porteri*, 6.29 mm for *S. squarrosa,* and 6.13 mm for *S. villosicarpa* and ranged from 3.7-4.4 mm for all other species. However, although involucre height was selected in the STEPWISE analysis, it had a lower F-to-remove value than the eight traits that were included in the COMPLETE analysis and thus this trait was not used in generating canonical scores plotted in Fig. 11. The large involucres of the very rare *S. porteri* make it an easy species to recognize when encountered. The large involucres of *S. squarrosa* are the most distinct in subsect. *Squarrosae* due to the spreading to recurved phyllaries. The large involucres and long rays of the rare coastal southern North Carolina *S. villosicarpa* make the heads of the species the most showy in the subsection.

The results of the COMPLETE multivariate analysis indicate that other species fall into several groups. The *Solidago speciosa* complex includes *S. jejunifolia, S. pallida, S. rigidiuscula,* and *S. speciosa,* and less so *S. erecta*. The small *S. puberula* complex includes *S. puberula* and *S. pulverulenta*, which both have stems densely covered with very short hairs and are the only two species that include individuals with long narrow attenuate phyllaries. All other species are part of the *S. bicolor* complex that also includes *S. erecta, S. hispida, S. roanensis,* and *S. sciaphila,* and these species will be examined further in a manuscript on subsect. *Squarrosae* (in prep.). The *S. puberula* complex will be the subject of a third manuscript in preparation on subsect. *Squarrosae*.

The results of the second analysis strongly support the recognition of *Solidago jejunifola, S. pallida, S. rigidiuscula,* and *S. speciosa* as separate species. Each species has a range of distribution allopatric over all or part of the range. It is likely that the four species evolved as a result of vicariant biogeography events from an ancestral diploid species having moderately hairy ovaries and occurring in an interglacial period in the past that had a broad range that was reduced to four distinct refugial populations during a subsequent glacial advance in eastern North America. The locations of the refugial populations is unknown, but it seems likely that *S. pallida* evolved from the westernmost populations, while *S. speciosa* evolved from populations east of the Appalachian Mountains and *S. jejunifolia* and *S. rigidiuscula* evolved in refugial populations west of the Appalachians in the midwest or southern USA. Loss of ovary hairs occurred several times, with *S. speciosa* being the only species consistently lacking fruit hairs, except for the Maine population, which likely regained them as occurs in marginal populations. The range of *S. speciosa* west of the Appalachians is the result of the evolution of tetraploids with the ability to tolerate drier conditions of the midwestern prairies and dry open oak woods. The range of *S. rigidiuscula* from the midwest into the Carolinas likely occurred in a postglacial, drier period when prairie-adapted species expanded into the southeastern USA. Today, diploid *S. rigidiuscula* occurs in drier more prairie-like habits than *S. speciosa* in the Carolinas.

The traits of the four species of the *Solidago speciosa* complex are summarized in Table 8. Minimum, mean, and maximum values for numbers, lengths, and width of parts are included for all traits scored for the specimens included in the multivariate analyses. It is likely that individuals will be encountered with more extreme values. The raw values were used to generate the data presented. Detailed descriptions of all the four species were not included in Flora North America (Semple & Cook 2006), while the species description of *S. speciosa* included data on all four taxa treated here as separate species. Therefore the description of *S. speciosa* in Flora North America is not accurate for the species limits followed here. Basal leaf data for *S. rigidiuscula* is not included because no basal leaves were observed on herbarium sheets. Lower stem leaves of *S. rigidiuscula* were present in limited numbers and some data is included in the table; such leaves are present on stems earlier in the season before blooming.

Table 8. Descriptive statistics on raw data on morphological traits of specimens used in the multivariate analysis *S. jejunifolia*, *S. pallida*, *S. rigidiuscula*, and *S. speciosa*: min-**mean**-max. No data for basal leaves of *S. rigidiuscula* at flowering. The lowest stem leaves are also generally absent by flowering. * traits selected in STEPDISC.

Trait	***S. jejunifolia***	***S. pallida***	***S. rigidiuscula***	***S. speciosa***
Stem height (cm)	44.5–**65.8**–82.8	32.5–**58.2**–85.8	34.3–**80.9**–120.4	65.3–**119**–215
Basal leaf length (mm)	44.5–**171**–298	55–**119.**8–240	–	65–**158**–210
Basal leaf petiole length (mm)	9–**88.7**–176	23–**45**–110	–	21–**43**–95
Basal leaf width (mm)	7–**23.5**–40	14–**22.3**–33	–	17–**37.3**–55
Basal leaf widest to tip (mm)	13–**33.5**–70	11–**31.1**–60	–	17–**36.4**–48
Basal leaf serrations (1 side)	0–**3.4**–17	0–**7.3**–20	–	7–**12.9**–27
Lower leaf length (mm)	58–**117**–205	60–**112**–215	61–**98**–153	65–**120**–181
Lower leaf petiole length (mm)	10–**47**–110	10–**23.4**–45	7–**20**–63	3–**23.8**–80
Lower leaf width (mm)	8–**18**–35	15–**27**–56	10–**18.8**–35	10–**34.4**–90
Lower leaf widest to tip (mm)	17–**30.4**–47	22–**40**–84	22–**39.0**–60	27–**52**–81
Lower leaf serrations (1 side)	0–**1.5**–7	0–**1.9**–7	0–**1.6**–9	0–**8**–21
Mid leaf length (mm)*	45–**78**–116	19–**62.5**–119	19–**62.6**–119	40–**78.8**–117
Mid leaf width (mm)*	5–**11.4**–28	3–**11.5**–19	3–**11.5**–19	5–**19.9**–38
Mid leaf widest to tip (mm)	12–**29.3**–53	10–**28.5**–40	10–**28.5**–40	17–**39.7**–67
Mid leaf serrations (1 side)*	0–**0.5**–5	0–**0.35**–5	0–**0.35**–5	0–**3.7**–13
Upper leaf length (mm)	13–**45.5**–88	14–**37.1**–57	14–**37.1**–57	17–**44.9**–79
Upper leaf width (mm)	3–**5.6**–12	2.8–**5.9**–10	2.8–**5.9**–10	2.8–**9.3**–24
Upper widest to tip (mm)	4–**19.9**–40	7–**18.6**–32	7–**18.6**–32	5–**23.8**–48
Upper serrations (1 side)	0–**0.03**–2	0	0	0–**1**–7
Inflorescence length (cm)	6.7–**18.7**–34.4	9.6–**14.8**–24.6	9.6–**14.8**–24.6	6.5–**25.3**–83
Inflorescence width (cm)	2.5–**5.4**–12.8	2.5–**4.8**–7.1	2.5–**4.8**–7.1	2–**9.9**–15
Inflor. long branch length (cm)	1.8–**4.7**–17	2–**3.9**–7	2—**3.9**–7	1.2–**5.4**–17.5
Involucre height (mm) at anethsis*	2.5–**3.7**–4.3	3–**4.2**–5.1	3–**4.2**–5.2	3–**4.7**–7
Outer phyllary length (mm)	0.8–**1.5**–2.1	0.8–**1.35**–2.6	0.8–**1.4**–2.2	0.85–**1.5**–2.5
Inner phyllary length (mm)	2.2–**3.5**–5	2.2–**3.6**–5	2.2–**3.6**–5	1.7–**3.9**–5.7
Number of ray florets	3–0–**6.3**–12	4–**6.6**–9	4–**6.6**–9	2–**5.8**–9
Ray floret lamina length (mm)*	1.1–**2.1**–3.4	1–**2.0**–3.8	1.2–**2.0**–3.8	1.5–**2.8**–4.4
Ray floret lamina width (mm)	0.3–**0.56**–1.1	0.2–**0.62**–1.2	0.2–**0.62**–1.2	0.3–**1.0**–2.0
Ray achene body length (mm) at anthesis	0.5–**1.0**–1.4	0.6–**1.1**–1.5	0.6–**1.1**–1.5	0.6–**1.5**–2
Ray achene pappus length (mm) at anthesis	1.8–**3.1**–4	2–**2.95**–4.3	2–**2.95**–4.3	2.4–**3.6**–4
Number of disc florets*	2–**8.4**–13	4–**6.5**–9	4–**6.5**–9	5–**7.7**–15
Disc corolla length (mm)*	2.6–**3.2**–4	2.6–**3.4**–5.4	2.6–**3.4**–4.8	2.2–**4.0**–6.2
Disc corolla lobe length (mm)	0.5–**9.6**–1.6	0.5–**1.3**–2	0.5–**1.3**–2	0.75–**1.3**–2
Disc achene body length (mm) at anthesis*	0.5–**1.0**–1.3	0.6–**1.1**–1.5	0.6–**1.1**–1.5	0.6–**1.6**–2.1
Disc achene pappus length (mm) at anthesis	2.1–**4.0**–4.4	2.6–**3.4**–4.2	2.6–**3.4**–4.2	3–**1.2**–5

Number of hairs disc achene body distal half	0–**4.2**–29	0–**0.1**–3	0–**0.1**–3	0–**0.7**–41
Number of hairs disc entire achene body	0–**4.2**–29	0–**0.1**–3	0–**0.1**–3	0–**0.9**–23

Cronquist (1947) discussed *Solidago jejunifolia* under the synonym *Solidago speciosa* Nutt. var. *jejunifolia* (Steele) Cronq. (Rhodora 49: 77. 1947). As he understood the variety, it was so similar to what he treated as *Solidago speciosa* var. *pallida* Porter (Bull. Torrey Bot. Club 19: 130. 1892.) that if the ranges were not disjunct (as known at the time) that the two varieties would not be separable. He noted that Dr. L.H. Shinners had told him that var. *jejunifolia* was "more or less strong sweet-scented in the field, a condition which so far as I {Cronquist} am aware, does not obtain in the other varieties." Cronquist also noted that the inflorescence was "more open than in the other varieties, with fewer heads on longer peduncles." He suggested that var. *jejunifolia* might have been derived from var. *rigidiuscula* during postglacial xerothemic times. The results of the analyses presented here clearly show that the two species *S. jejunifolia* and *S. pallida* are statistically distinct and that their ranges likely are potentially sympatric in Minnesota or the Dakotas or were at one time.

Key to the *Solidago speciosa* complex and *S. erecta*

1. Arrays of heads either narrowly thyrsiform and often interrupted or branches well-spaced; mid cauline leaves 5–20 mm wide; Massachusetts to southern Indiana, south to Georgia and Mississippi, mostly avoiding coastal plain southward .... **Solidago erecta**
1. Arrays of head broadly thyrsiform or if narrow then congested; mid cauline leaves 3-38 mm wide; Maine to Georgia west to northwestern Ontario and adjacent Manitoba, southwest to Wyoming to New Mexico and south to Georgia in the east and eastern Texas in the west

  2. Basal rosette and lower stem leaves with narrow petioles often making up half or more of the total leaf length, present at flowering; northern Michigan to southeastern Manitoba south to eastern Iowa and northwestern Missouri and adjacent Nebraska .... **Solidago jejunifolia**
  2. Basal rosette and lower stem leaves with narrow petioles making up less than a third of the total leaf length

    3. Lowest stem leaves absent at flowering, present early to mid growing season; middle and upper stem leaves relatively numerous and overlapping .... **Solidago rigidiuscula**
    3. Lower stem leaves usually present at flowering, blades tapering to short narrow petioles

      4. Fruit body with some short hairs occurring on the upper half or over much of the fruit; Northwestern Ontario, Black Hills of South Dakota and Wyoming, stems 32–86 cm averaging 58 cm; foot hills of the Rocky Mountains in southern Wyoming to northern New Mexico .... **Solidago pallida**
      4. Fruit body hairless (except for plants from southeastern Maine); stems 65.3–215 cm averaging > 100 cm; eastern US from southeastern Maine south to Georgia west to southeastern Minnesota south to Arkansas .... **Solidago speciosa**

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