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# A MULTIVARIATE STUDY OF *SOLIDAGO* SUBSECT. *SQUARROSAE*. IV. THE *SOLIDAGO PUBERULA* COMPLEX (ASTERACEAE: ASTEREAE)

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## ABSTRACT

The *Solidago puberula* complex is considered to include four species in *Solidago* subsect. *Squarrosae*. **Solidago puberula** and **Solidago pulverulenta** have sometimes been treated as conspecific (at varietal or subspecific rank) but here are separated. **Solidago roanensis** has very short hairs on the upper stems similar to those of the first two, but is glabrous to very sparsely hairy proximally. **Solidago sciaphila** has been considered closely similar to *S. speciosa* and *S. hispida* or possibly to *S. roanensis*. Among these four, multivariate analyses indicate that *S. sciaphila* is the most distinct and *S. puberula* and *S. pulverulenta* are the most similar.

*Solidago* subsect. *Squarrosae* A. Gray (Asteraceae: Astereae) includes 14 species native primarily to eastern Canada and the midwestern and eastern portions of the USA (Semple et al. 2017a). Semple and Cook (2006) recognized 9 species with multiple infraspecific taxa in several species, while Semple (2020 frequently updated) has recognized 15 species: *S. bicolor* L., *S. erecta* Pursh, *S. georgiana* Semple, *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. Semple et al. (2017a) included a multivariate analysis of 14 species of subsect. *Squarrosae* emphasizing members of the *S. speciosa* complex; in their first analysis *S. puberula*, *S. pulverulenta*, *S. roanensis* and *S. sciaphila* formed a peninsula of taxa on the third canonical axis. Semple et al. (2017b) reported the results of the multivariate study of the *S. bicolor*-*S. hispida* complex. Semple et al. (2017c) described *S. georgiana* and reported the results of a multivariate analysis of the larger-headed species of the subsection plus *S. roanensis*.

The *Solidago puberula* complex consists of four species — *S. puberula* (Figs. 1-2) and *S. pulverulenta* (Figs. 3-4) and more distantly *S. roanensis* (Figs 5-6 in Semple et al. 2017b) and *S. sciaphila* (Figs 7-8 in Semple et al. 2017b). Both *S. puberula* and *S. pulverulenta* have stems that are covered in a dense indument of very short curved hairs (Figs. 2C-D, 4C) and phyllaries that are always linear lanceolate with acute elongated tips in *S. puberula* (Fig. 2G) and similarly so (Figs. 4E-F) or sometimes less so in *S. pulverulenta*. Both are known only at the diploid level (2*n*=18; Beaudry & Chabot 1959; Beaudry 1969; Kapoor 1970; Morton 1981; Semple et al. 1984, 1993; Semple & Chmielewski 1987; Semple & Cook 2004; unpublished data). *Solidago roanensis* is also known only at the diploid level (2*n*=18; Beaudry 1963; Semple et al. 1984; Semple et al. 2015; Semple et al. 2019), while *S. sciaphila* is known only at the tetraploid level (2*n*=36; Semple et al. 2015; unpublished data).

The ranges of distribution and the locations of specimens included in the analyses are shown for *Solidago puberula* and *S. pulverulenta* in Figure 5. The ranges of distribution and the locations of specimens included in the multivariate analyses for *S. roanensis* and *S. sciaphila* were shown in Figures 13-14 of Semple et al. (2017b), respectively. The range of *S. sciaphila* is near the driftless area of the Mississippi River drainage and surrounding areas and does not overlap with any of the other three, while the ranges of the other three are variously sympatric in the central and the southern


Figure 1. Morphology of *Solidago puberula*. *Semple & B. Semple 11456* (WAT) from New Brunswick.


Figure 2. Details of the morphology of *Solidago puberula*. **A-D, F-G.** Morton & Venn NA12493 (JKM in ROM). **A-B.** Basal rosette leaves and leaf margin. **C-D.** Lower stem. **E.** Upper stem leaf, Morton & Venn NA12622 (JKM in ROM). Figure 2. Details of the morphology of Solidago puberula. A-D, F-G. Morton & Venn NA12493 (JKM in ROM). A-B. Basal rosette leaves and leaf margin. C-D. Lower stem. E. Upper stem leaf, Morton & Venn NA12622 (JKM in ROM). F-G. Portion of Inflorescence and heads. Scale bars = 1 cm in A-B and E; = 1 mm in C-D and F-G. Portion of Inflorescence and heads. Scale bars = 1 cm in A-B and E; = 1 mm in C-D and F-G.


Figure 3. Morphology of *Solidago pulverulenta*. *Kral 33682* (MO) from Covington Co., Alabama.


Figure 4. Details of the morphology of *Solidago pulverulenta*. **A.** Small shoot, cropped from *Rodgers 340* LSU00137215_L.JPG, Florida; used with permission. **B.** Basal rosette leaves, *Kral 33682* (MO), Alabama. **C.** Lower stem, *Semple 11635* (WAT), North Carolina. **D.** Mid stem leaves, *Kral 44276* (WAT), Alabama. **E.** Upper stem leaves, *Kral 33682* (MO). **F.** Heads, *Semple 11597* (WAT), North Carolina. **G.** Heads, *Kral 41621* (MO), Alabama. **H.** Cypselae with old corollas, *Ahles 37731* (NCU), South Carolina. Scale bars = 1 dm in A, 1 cm in B, D-E; = 1 mm in C, E-G.

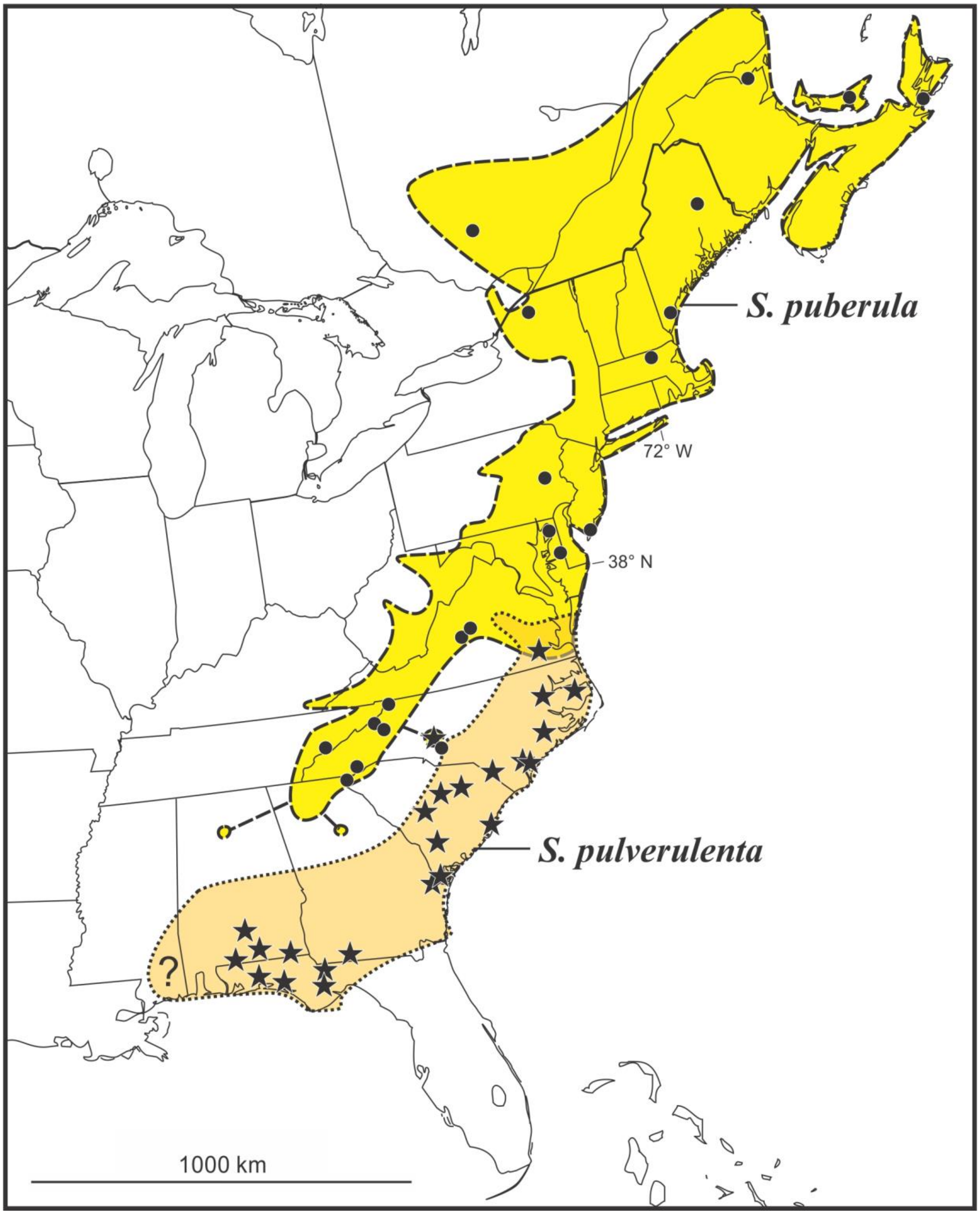


Figure 5. Ranges of distribution of *Solidago puberula* and *S. pulverulenta* and locations of specimens included in the multivariate analyses (no vouchers seen to confirm presence of *S. pulverulenta* in Mississippi or Louisiana; vouchers seen were misidentified specimens of *S. nemoralis*).

Appalachian Mountains (*S. roanensis* and *S. puberula*), along the edge of the Piedmont in North Carolina (*S. puberula* and *S. pulverulenta*), and where the Atlantic and Southern Coastal Plains come together in southeastern Virginia (*S. puberula* and *S. pulverulenta*). Most of the ranges of *S. puberula* and *S. pulverulenta* are allopatric.

*Solidago pulverulenta* has been treated as *S. puberula* var. *pulverulenta* (Nutt.) Chapm. and as *S. puberula* subsp. *pulverulenta* (Nutt.) Semple. Torrey and A. Gray (1942) treated the taxon at the species rank in the first Flora North America, while Semple and Cook (2006) treated the taxon as a subspecies in the second Flora North America. Fernald (1950) treated the taxon as a variety of *S. puberula* as did Cronquist (1968, 1980) and Radford et al. (1968). Weakley (2015) treated the taxon at species rank. Small (1903) treated *S. puberula* and *S. pulverulenta* as species distinguished by involucres being turbinate-campanulate, 2.5 mm thick for *S. pulverulenta* versus involucres being narrowly campanulate, 3 mm thick for *S. puberula*. Mackenzie in Small (1933) keyed out the two species as follows: "blades of the leaves about the middle of the stem oblong-obovate, hispidulous above all over: inner involucral bracts gradually narrowed, oblanceolate nearly 1 mm wide" in *S. puberula* and "blades of the leaves about the middle of the stem oblanceolate, strongly hispidulous above on mid rib, slightly so elsewhere; inner involucral bracts rather abruptly narrowed above middle, very narrowly lanceolate, about 0.5 mm wide" in *S. pulverulenta*. Mackenzie in Small (1933) listed *S. puberula* as occurring from Florida to Mississippi north to Québec and Prince Edward Island and noted in the description that the phyllaries veins were obsolete in *S. puberula* and obscure in *S. pulverulenta*. Semple and Cook (2006) keyed out subsp. *puberula* as having "leaves 20–50(–60), mid cauline usually 40–50 mm; phyllaries attenuate; Nova Scotia to Ontario, s to piedmont and mountains in Georgia", while subsp. *pulverulenta* had "leaves (20–)50–110+, mid cauline 10–40 mm; phyllaries acute to barely attenuate; coastal plain, se Virginia to n Florida, w to e Louisiana." Weakley (2015) separated the two species as follows: *S. puberula* had leaves 20-50 (-60) per stem, midstem leaves usually 4-5 cm long, and phyllaries attenuate; and *S. pulverulenta* had leaves (20-) 50-120 per stem, midstem leaves usually 1-4 cm long, and phyllaries acute to acuminate.

The objectives of this study were to determine which morphological traits best separate the taxa of the *Solidago puberula* complex and to determine the most appropriate nomenclatural rank for the taxa. No detailed multivariate analysis of the complex has been previously published, although specimens of *S. puberula*, *S. pulverulenta*, *S. roanensis*, and *S. sciaphila* were included in the overall analysis of subsect. *Squarrosae* in Semple al. (2017a).

## MATERIALS AND METHODS

In total, 87 specimens from BOON, GA, LSU, MIN, MO, NCU, NY, TAWES, J.K. Morton personal herbarium now in TRT, and WAT in MT (Thiers, continuously updated) were scored and included in the analysis: *Solidago puberula* (25 specimens), *S. pulverulenta* (24 specimens), *S. roanensis* (20 specimens), and *S. sciaphila* (18 specimens). These were selected from more than 400 hundred specimens examined. For each specimen, 18 vegetative and 15 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 ranges of variation for each trait. All traits scored are listed in Table 1. In addition, stem hair densities were rated for the lower, mid, and upper stem and used for identification purposes.

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 <u>first analysis</u>, four species of subsect. *Squarrosae* were included in a STEPWISE discriminant analysis. In the <u>second and third analyses</u>, three species of subsect. *Squarrosae* were included in STEPWISE discriminant analyses. In the <u>fourth analysis</u>, the two core species of the *Solidago puberula* complex were included in a STEPWISE discriminant analysis.

Table 1. Traits scored for the multivariate analyses of 261 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) |
| LONGBRLN | Length of the longest lower inflorescence branches (cm) |
| INVOLHT | Involucre height (mm) |
| OPHYLN | Outer phyllary length (mm) |
| IPHYLN | Inner phyllary length (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) |

## RESULTS

### Four Species Level Groups Analysis

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

In the STEPWISE discriminant analysis of 87 specimens of four species level a priori groups (*Solidago puberula*, *S. pulverulenta*, *S. roanensis*, and *S. sciaphila*), the following six traits were selected and are listed in order of decreasing F-to-remove values: mid leaf length (13.36), disc floret ovary/fruit body length at anthesis (13.28), mid leaf width (11.84), number of upper leaf margin serrations (8.06), ray floret lamina length (4.91), and disc floret corolla length (4.73). Wilks's lambda, Pillai's trace, and Lawley-Hotelling trace tests of the null hypothesis that all groups were 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 separation was between *S. pulverulenta* and *S. roanensis* (30.531); the smallest separation was between *S. puberula* and *S. pulverulenta* (5.386).

In the Classificatory Discriminant Analysis of the four species level a priori groups (*Solidago puberula*, *S. pulverulenta*, *S. roanensis*, and *S. sciaphila*), percents of correct a posterori assignment to the same a priori group ranged from 70-83%. The Classification matrix and Jackknife classification matrix are presented in Table 3. Results are presented in order of decreasing percents of correct placement. Fifteen of the 18 specimens of the *S. sciaphila* a priori group (83%) were assigned a posteriori into the *S. sciaphila* group; 11 specimens with 90-100% probability, 1 specimen with 86% probability, 1 specimen with 77% probability, and 1 specimen with 65% probability. Three specimens of the *S. sciaphila* a priori group were assigned a posteriori to other species: 2 specimens to *S. roanensis* with 66% probability (19% to *S. sciaphila* and 12% to *S. puberula*; *Smith 14978* MIN from Houston Co, Minnesota: and 1 specimen with 34% probability to S. *roanensis*; *Smith 14982A* MIN from Houston Co., Minnesota); 1 specimen to *S. pulverulenta* with 51% probability (26% to *S. puberula*, 14% to *S. roanensis* and 9% to *S. sciaphila*). Nineteen of the 24 specimens of *S. pulverulenta* a priori group (79%) were assigned a posteriori to the *S. pulverulenta* group; 6 specimens with 90-97% probability, 6 specimens with 85-89% probability, 4 specimens with 73-79% probability, and 7 specimens with 60-65% probability. Five specimens of the *S. pulverulenta* a priori group were assigned a posteriori to *S. puberula*: 64% probability (33% to *S. pulverulenta*; *Semple 11635* WAT from Pender Co., North Carolina; 108 cm tall shoot with 77 stem leaves), 58% probability (42% to *S. pulverulenta*; *Massey 3129* NCU from Sussex Co., Virginia; a 100+ cm tall shoot with many stem nodes and a large long branches inflorescence and a flowering branch arising ca. 50 cm below the apex), 55% probability (44% to *S. pulverulenta*; *Semple 11597* WAT from Rowan Co., North Carolina; 117 cm tall shoot with more than 75 stem leaves), 52% probability (48% to *S. pulverulenta*; *Bell 10884* NCU from Florence Co., South Carolina; a 77 cm tall shoot with 58 nodes below the inflorescence), and 52% probability (47% to *S. pulverulenta*; *Radford 42490* NCU from Tyrrell Co., North Carolina; 57 cm tall shoot with ca. 45 nodes below the inflorescence). Nineteen of 25 specimens of the *S. puberula* a priori group (76%) were assigned a posteriori to the *S. puberula* group: 61 specimens with 93-100% probability, 3 specimens with 81-84% probability, 4 specimens with 70-76% probability; 2 specimens with 68-69% probability, 3 specimens with 55% probability (45% to *S. pulverulenta*; *Semple & Ringius 7638* WAT from Caroline Co., Virginia; 82

cm tall shoot ca. 51 leaves below the inflorescence), 54% probability (44% to *S. pulverulenta*; *Duncan 10356* GA from Rabun Co., Georgia; 70 cm tall shoot with ca. 24 stem leaves below the inflorescence), and 54% probability (46% to *S. pulverulenta*; *Freye 8037* TAWES from Cecil Co., Maryland; 47 cm tall shoot with ca. 23 stem leaves below the inflorescence), and 1 specimen with 38% probability (*Cook et al. C-561* WAT from Transylvania Co., North Carolina; 42.6 cm tall shoot with ca. 22 leaves below the inflorescence). Six specimens of the *S. puberula* a priori group were assigned a posteriori to the other species: 5 specimens to *S. pulverulenta* with 70% probability (30% to *S. puberula*; *Freer 12280* NC from Amherst Co., Virginia; 56.5 cm tall shoot with ca. 50 stem leaves below the inflorescence), 68% probability (32% to *S. puberula*; *Semple & B. Semple 11479* WAT from Queens Co., Prince Edward Island; 67 cm tall shoot with 22 stem leaves below the inflorescence), 63% probability (33% to *S. puberula*; *Cook & Seiden C-124* WAT from Reserve la Verendrye, Québec; 73.6 cm tall shoot with ca. 28 stem leaves below the inflorescence), and 50% probability (49% to *S. puberula*; *Freer 12280* NC from Amherst Co., Virginia; 56.5 cm tall shoot with ca. 50 stem leaves below the inflorescence), and; and 1 specimen to *S. roanensis* with 57% probability (26% to *S. puberula and 13% to S. sciaphila*; *Semple & Suripto 9586* WAT from York Co., Maine; lower stem finely puberulent). Fourteen of the 20 specimens of the *S. roanensis* a priori group (70%) were assigned a posteriori to the *S. roanensis* group: 10 specimens with 91-100% probability, 2 specimens with 64-65% probability, and 2 specimen with 56% probability (31% to *S. sciaphila* and 9% to *S. puberula*; *Morton & Venn NA6471* WAT from Swain Co., North Carolina) and 51% probability (43% to *S. sciaphila* and 5% to *S. puberula*; *Williams s.n.* NY from Clay Co., North Carolina). Six specimens of the *S. roanensis* a priori group were assigned a posteriori to the other species, all had glabrous/glabrate lower stems and mid and inner phyllaries with multiple veins: 4 specimens to *S. sciaphila* with 93% probability (*Biltmore Herb. 4622* NY from Buncombe Co., North Carolina), 74% probability (*Cannon 213* NY from Avery Co., North Carolina), 68% probability (*Kral 62768* NY from Polk Co., Tennessee), and 57% probability (31% to *S. roanensis*; Cook *et al. C-557* WAT from Haywood Co., North Carolina); and 2 specimens to *S. puberula* with 86% probability (*Poindexter 05-1580* BOON from Ashe Co., North Carolina) and 52% probability (18% to *S.* sciaphila, 15% to *S. roanensis*, and 15% to *S. pulverulenta*; Cook *et al. C-557* WAT from Haywood Co., North Carolina).

Table 2. Between groups F-matrix for the three a priori group analysis (df = 5 56).

| Group | *puberula* | *pulverulenta* | *roanensis* |
|---|---|---|---|
| ***pulverulenta*** | 5.386 | | |
| ***roanensis*** | 23.030 | 30.531 | |
| ***sciaphila*** | 20.505 | 20.885 | 8.395 |

Wilks' lambda = 0.1098 df = 6 3 83; Approx. F= 18.5333 df = 18 221 prob = 0.0000

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 | *puberula* | *pulverulenta* | *roanensis* | *sciaphila* | % correct |
|---|---|---|---|---|---|
| ***puberula*** | 19 | 5 | 1 | 0 | 76 |
| ***pulverulenta*** | 5 | 19 | 0 | 0 | 79 |
| ***roanensis*** | 2 | 0 | 14 | 4 | 70 |
| ***sciaphila*** | 0 | 1 | 2 | 15 | 83 |
| **Totals** | 26 | 25 | 17 | 19 | 77 |

Jackknifed classification matrix

| Group | *puberula* | *pulverulenta* | *roanensis* | *sciaphila* | % correct |
|---|---|---|---|---|---|
| ***puberula*** | 19 | 5 | 1 | 0 | 76 |
| ***pulverulenta*** | 5 | 19 | 0 | 0 | 79 |
| ***roanensis*** | 2 | 1 | 12 | 5 | 60 |
| ***sciaphila*** | 1 | 1 | 2 | 14 | 78 |
| **Totals** | 27 | 26 | 15 | 19 | 74 |

Two dimensional plots of CAN1 versus CAN3 and CAN1 versus CAN2 canonical scores for 87 specimens of *Solidago puberula*, *S. pulverulenta*, *S. roanensis*, and *S. sciaphila* are presented in Figure 6. Eigenvalues on the first three axes were 3.171, 0.770, and 0.233.

**Three Species Level Groups Analysis I: *Solidago puberula*, *S. pulverulenta*, and *S. sciaphila***

The Pearson correlation matrix yielded r > |0.7| for most pairs of leaf traits reducing the number to be used to mid leaf length, width, and serrations and sometimes upper leaf width and serrations. Basal rosette and lower stem leaves were often/sometimes absent and were not included in the discriminant analyses. The numbers of ray florets and disc florets were highly correlated and only former trait was used in the analyses. Ray floret ovary/ cypsela body length at anthesis correlated highly with disc floret ovary/ cypsela body length at anthesis and only the latter trait was included in the discriminant analyses.

In the STEPWISE discriminant analysis of 63 specimens of three species level a priori groups in (*Solidago puberula*, *S. pulverulenta*, and *S. sciaphila*), the following five traits were selected and are listed in order of decreasing F-to-remove values: disc floret ovary/fruit body length at anthesis (31.25), upper leaf width (29.78), upper leaf length from widest point to apex (23.17), mid stem leaf length (15.78), and number of ray florets (6.32). 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 4. F-values based on Mahalanobis distances of the between group centroids indicated the largest separation was between *S. pulverulenta* and *S. sciaphila* (54.235); the smallest separation was between *S. puberula* and *S. pulverulenta* (9.204).

Table 5. Between groups F-matrix for the three a priori group analysis (df = 5 56).

| Group | *puberula* | *pulverulenta* |
|---|---|---|
| ***pulverulenta*** | 0.924 | |
| ***sciaphila*** | 46.123 | 54.235 |

Wilks' lambda = 0.0880 df = 5 6 60; Approx. F= 26.5489 df = 10 112 prob = 0.0000

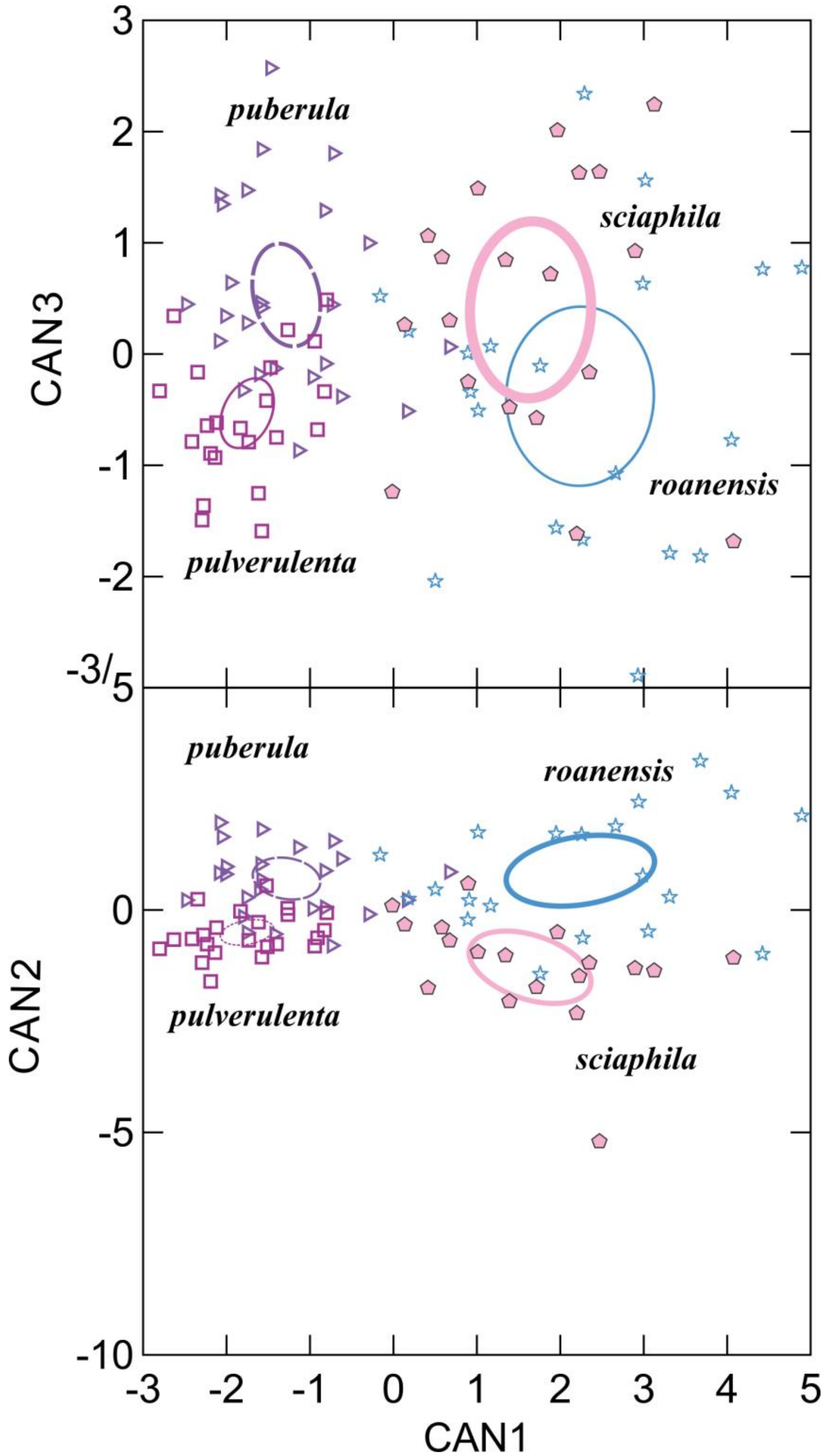


Figure 6. Plot of canonical scores (CAN1 vs CAN3 and CAN1 vs CAN2) for 876 specimens of *Solidago* subsect. *Squarrosae*: *S. puberula* (open purple right oriented triangles), *S. pulverulenta* (magenta squares), *S. roanensis* (open blue stars), and *S. sciaphila* (pink pentagons); symbols match those in Fig 11 in Semple et al. 2017a.

In the Classificatory Discriminant Analysis of the three species level a priori groups (*Solidago puberula*, *S. pulverulenta*, and *S. sciaphila*), percents of correct a posterori assignment to the same a priori group ranged from 76-83%. The Classification matrix and Jackknife classification matrix are presented in Table 6. Results are presented in order of decreasing percents of correct placement. Fifteen of the 15 specimens of the *S. sciaphila* a priori group (100%) plus two specimens only included a posteriori were assigned a posteriori into the *S. sciaphila* group; 16 specimens with 100% probability and 1 specimen with 84% probability. One specimen of the *S. sciaphila* not included in the *S. sciaphila* a priori group in this analysis was assigned a posteriori to *S. pulverulenta* with 65% probability (35% to *S. puberula*; *Semple 11854* WAT from Carroll Co., Illinois; 16 cm tall shoot with ovate mid stem leaves with many obvious margin serrations; tetraploid). Twenty-one of the 24 specimens of the *S. pulverulenta* a priori group (88%) were assigned a posteriori to the *S. pulverulenta* group: 16 specimens with 90-98% probability and 5 specimens with 80-86% probability. Three specimens of the *S. pulverulenta* a priori group were assigned a posteriori to *S. puberula* with 90% probability (10% to *S. pulverulenta*; *Massey 3129* NCU; from Sussex Co., Virginia; a 100+ cm tall shoot with many stem nodes and a large long branches inflorescence and a flowering branch arising ca. 50 cm below the apex), 82% probability (*Semple 11597* WAT from Rowan Co., North Carolina; 117 cm tall shoot with more than 75 stem leaves), and 66% probability (34% to *S. pulverulenta*; *Semple 11635* WAT from Pender Co., North Carolina; 108 cm tall shoot with 77 stem leaves). Twenty of the 24 specimens of the *S. puberula* a priori group were assigned a posteriori to the *S. puberula* group: 11 specimens with 90-100%, 5 specimens with 82-88% probability, 1 specimen with 72% probability, 1 specimen with 62% probability, and two specimens with 57% probability (43% to *S. pulverulenta*; *Bell 15176* NCU from Burke Co., North Carolina; 63 cm tall shoot with ca. 40 stem leaves below the inflorescence) and 53% probability (47% to *S. pulverulenta*; *Ahles & Leisner 19614* NCU from Cabarrus Co., North Carolina; 50 cm tall shoot with ca. 33 stem leaves below the inflorescence). Four specimens of the *S. puberula* a priori group were assigned a posteriori to *S. pulverulenta* with 86% probability (*Semple & Ringius 7638* WAT from Caroline Co., Virginia; 82 cm tall shoot ca. 51 leaves below the inflorescence), 84% probability (*Semple & B. Semple 11479* WAT from Queens Co., Prince Edward Island; 67 cm tall shoot with 22 stem leaves below the inflorescence), 84% probability (*Freye 8037* TAWES from Cecil Co., Maryland; 47 cm tall shoot with ca. 23 stem leaves below the inflorescence), and 70% probability (*Freer 12280* NCU from from Amherst Co., Virginia; 56.5 cm tall shoot with ca. 50 stem leaves below the inflorescence).

A two dimensional plots of CAN1 versus CAN2 canonical scores for 63 specimens of *Solidago puberula*, *S. pulverulenta*, and *S. sciaphila* are presented in Fig. 7. Eigenvalues on the first two axes were 5.397 and 0.776.

Table 6. Linear and jackknife classification matrices from the Classificatory Discriminant Analysis of three a priori groups; a posteriori placements to groups in rows.

| **Group** | ***puberula*** | ***pulverulenta*** | ***sciaphila*** | **% correct** |
|---|---|---|---|---|
| ***puberula*** | 20 | 4 | 0 | 83 |
| ***pulverulenta*** | 3 | 21 | 0 | 88 |
| ***sciaphila*** | 0 | 0 | 15 | 100 |
| **Totals** | 23 | 25 | 15 | 89 |

Jackknifed classification matrix

| Group | *puberula* | *pulverulenta* | *sciaphila* | % correct |
|---|---|---|---|---|
| ***puberula*** | 20 | 4 | 0 | 83 |
| ***pulverulenta*** | 3 | 21 | 0 | 88 |
| ***sciaphila*** | 0 | 0 | 15 | 100 |
| **Totals** | 23 | 25 | 25 | 89 |

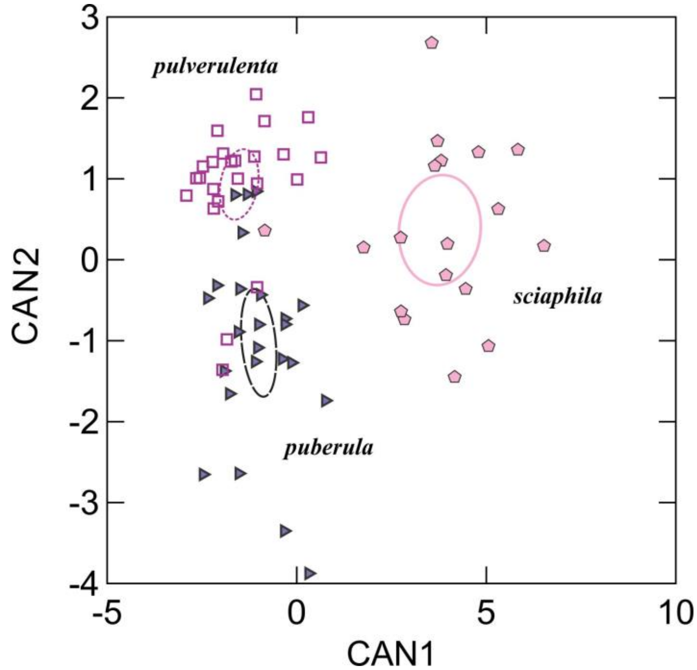


Figure 7. Plot of canonical scores (CAN1 vs CAN2) for 63 specimens of *Solidago puberula* (right-oriented purple triangles), *S. pulverulenta* (magenta squares), and *S. sciaphila* (pink pentagons).

**Three Species Level Groups Analysis II: *Solidago puberula, S. pulverulenta*, and *S. roanensis***

The Pearson correlation matrix yielded r > |0.7| for most pairs of leaf traits reducing the number to be used to upper leaf width and serrations. Basal rosette and lower stem leaves were often/sometimes absent and were not included in the discriminant analyses. The numbers of ray florets and disc florets were highly correlated and only former trait was used in the analyses. Ray floret ovary/ cypsela body length at anthesis correlated highly with disc floret ovary/ cypsela body length at anthesis and only the latter trait was included in the discriminant analyses.

In the STEPWISE discriminant analysis of 67 specimens of three species level a priori groups in (*Solidago puberula*, *S. pulverulenta*, and *S. roanensis*), the following four traits were selected and are listed in order of decreasing F-to-remove values: number of upper leaf margin serrations mid leaf length (11.94), disc floret ovary/fruit body length at anthesis (11.33), disc floret corolla length (6.93), and ray floret lamina length (5.71). 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 7. F-values based on Mahalanobis distances of the between group centroids indicated the largest separation was between *S. pulverulenta* and *S. roanensis* (32.441); the smallest separation was between *S. puberula* and *S. pulverulenta* (3.863).

Table 7. Between groups F-matrix for the three a priori group analysis (df = 5 56).

| **Group** | ***puberula*** | ***pulverulenta*** |
|---|---|---|
| ***pulverulenta*** | 3.863 | |
| ***roanensis*** | 30.180 | 32.441 |

Wilks' lambda = 0.2243 df = 4 2 64; Approx. F= 16.9496 df = 8 122 prob = 0.0000

In the Classificatory Discriminant Analysis of the three species level a priori groups (*Solidago puberula*, *S. pulverulenta*, and *S. roanensis*), percents of correct a posterori assignment to the same a priori group ranged from 70-83%. The Classification matrix and Jackknife classification matrix are presented in Table 8. Results are presented in order of decreasing percents of correct placement. Sixteen of the 19 specimens of the *S. roanensis* a priori group (84%) plus 1 additional specimen included a posteriori were assigned a posteriori into the *S. roanensis* group; 12 specimens with 98-100% probability, 2 specimens with 89% and 81% probabilities, 1 specimen with 72% probability, 1 specimen with 67% probability, and 1 specimen with 55% probability (23% to *S. puberula* and 22% to *S. pulverulenta*; *Morton & Venn NA6471* WAT from Swain Co., North Carolina). Three specimens of the *S. roanensis* a priori group were assigned to other species, all had glabrous/glabrate lower stems and oligoneurate mid and inner series phyllaries: 2 specimens to *S. pulverulenta* with 77% probability (15% to *S. puberula* and 8% to *S. roanensis*; 227) and 72% (26% to *S. puberula*; 108); and 1 specimen to *S. puberula* with 57% probability (40% to *S. pulverulenta*; *Williams s.n.* NY from Clay Co., North Carolina). Nineteen of the 24 specimens of the *S. pulverulenta* a priori group (79%) were assigned a posteriori into the *S. pulverulenta* group; 1 specimen with 90% probability, 3 specimens with 87-89% probability, 7 specimen with 70-79% probability, 4 specimens with 63-67% probability, and 4 specimens with 57% probability (42% to *S. puberula*; *Nelson & Desportes 9973* USCH from Georgetown Co., South Carolina; 69 cm tall shoot with damaged stem), 54% probability (46% to *S. puberula*; *Bell 10884* NCU from Florence Co., South Carolina; a 77 cm tall shoot with 58 nodes below the inflorescence), 54% probability (46% to *S. puberula*; *Bell 5327* NCU from Jasper Co., South Carolina; 81 cm tall shoot with ca. 74 stem leaves below the inflorescence), and 51% probability (49% to *S. puberula*; *Radford 41825* NCU from Martin Co., North Carolina; 78 cm tall shoot with more than 55 stem leaves below the inflorescence). Five specimens of the *S. pulverulenta* a priori group were assigned to *S. puberula* with 75% probability (25% to *S. pulverulenta*; *Rodgers 338* LSU from Okaloosa Co., Florida; 78 cm tall shoot with ca. 80 stem leaves below the inflorescence), 71% probability (27% to *S. pulverulenta*; *Semple 11635* WAT from Pender Co., North Carolina; 108 cm tall shoot with 77 stem leaves), 59% probability (41% to *S. pulverulenta*; *Radford 42490* NCU from Tyrrell Co., North Carolina; 57 cm tall shoot with ca. 45 nodes below the inflorescence), 57% probability (43% to *S. pulverulenta*; *Semple 11597* WAT from Rowan Co., North Carolina; 117 cm tall shoot with more than 75 stem leaves), 54% probability (45% to *S. pulverulenta*; *Kral 41668* WAT from Geneve Co., Alabama; 108 cm tall shoot with ca. 66 stem leaves below the inflorescence). Thirteen of the 24 specimens of the *S. puberula* a priori group (54%) were assigned a posteriori into the *S. puberula* group; 4 specimens with 91-95% probability, 2 specimens with 89% and 86% probabilities, 2 specimens with 77% probability each, 2 specimens with 61% probability each, and 3 specimens with 56% probability (44% to *S. pulverulenta*; *Bell 15176* NCU from Burke Co., North Carolina; 63 cm tall shoot with ca. 40 stem leaves below the inflorescence), 56% probability (43% to *S. pulverulenta*; *Freer 12280* NCU from from Amherst Co., Virginia; 56.5 cm tall shoot with ca. 50 stem leaves below the inflorescence), and 54% probability (46% to S. pulverulenta; *Semple & B. Semple 11479* WAT from Queens Co., Prince Edward Island; 67 cm tall shoot with 22 stem leaves below the inflorescence). Eleven specimens of the *S. puberula* a priori group were assigned to other species: 9 specimens to *S. pulverulenta* with 72% probability (28% to *S. puberula*; *Freer 12297* NCU from Nelson Co., Virginia; 72 cm tall shoot with ca. 41 leaves below the inflorescence), 71% probability (29% to *S. puberula*; *Stewart s.n.* NCU from Transylvania Co., North Carolina; 52.5 cm tall shoot with ca. 37 leaves below the inflorescence), 70% probability (30% to *S. puberula*; *Semple & Ringius 7638* WAT from Caroline Co., Virginia; 82 cm tall shoot ca. 51 leaves below the inflorescence), 56% probability (42% to *S. puberula*; *Duncan 10356* GA from Rabun Co., Georgia; 70 cm tall shoot with ca. 24 stem leaves below the inflorescence), 55% probability (45% to *S. puberula*; *Morton & Venn NA17622* TRT from Piscataquis Co., Maine; 87 cm tall shoot with 38 leaves below the inflorescence), 55% probability (45% to *S. puberula*; *Cook & Seiden C-124* WAT from Reserve la Verendrye, Québec; 73.6 cm tall shoot with ca. 28 stem leaves below the inflorescence), 53% probability (47% to *S. puberula*; *Poindexter 09-1113* NCU from Alleghany Co., North Carolina; 87 cm tall shoot with ca. 46 leaves below the inflorescence), 52% probability (48% to *S. puberula*; *Morton & Venn NA16106* TRT from Cape May Co., New Jersey; 79 cm tall shoot with ca. 55 leaves below the inflorescence), and 50% probability (50% to *S. puberula*; *Ahles & Leisner 19614* NCU from Cabarrus Co., North Carolina; 50 cm tall shoot with ca. 33 stem leaves below the inflorescence); and 2 specimens to *S. roanensis* with 63% probability (27% to *S. puberula* and 10% to *S. pulverulenta*; *Cook et al. C-561* WAT from Transylvania Co., North Carolina; 42.6 cm tall shoot with ca. 22 leaves below the inflorescence) and 60% probability (20% to *S. puberula* and 19% to *S. pulverulenta*; *Semple & Suripto 9586* WAT from York Co., Maine; lower stem finely puberulent).

Table 8. Linear and jackknife classification matrices from the Classificatory Discriminant Analysis of three a priori groups; a posteriori placements to groups in rows.

| **Group** | ***puberula*** | ***pulverulenta*** | ***roanensis*** | **% correct** |
|---|---|---|---|---|
| ***puberula*** | 13 | 9 | 2 | 54 |
| ***pulverulenta*** | 5 | 19 | 0 | 79 |
| ***roanensis*** | 1 | 2 | 16 | 84 |
| **Totals** | 26 | 25 | 19 | 77 |

Jackknifed classification matrix

| **Group** | ***puberula*** | ***pulverulenta*** | ***roanensis*** | **% correct** |
|---|---|---|---|---|
| ***puberula*** | 13 | 9 | 2 | 54 |
| ***pulverulenta*** | 7 | 17 | 0 | 71 |
| ***roanensis*** | 2 | 2 | 15 | 79 |
| **Totals** | 27 | 26 | 19 | 74 |

A two dimensional plot of CAN1 versus CAN2 canonical scores for 63 specimens of *Solidago puberula*, *S. pulverulenta*, and *S. roanensis* are presented in Fig. 8. Eigenvalues on the first two axes were 5.397 and 0.776.

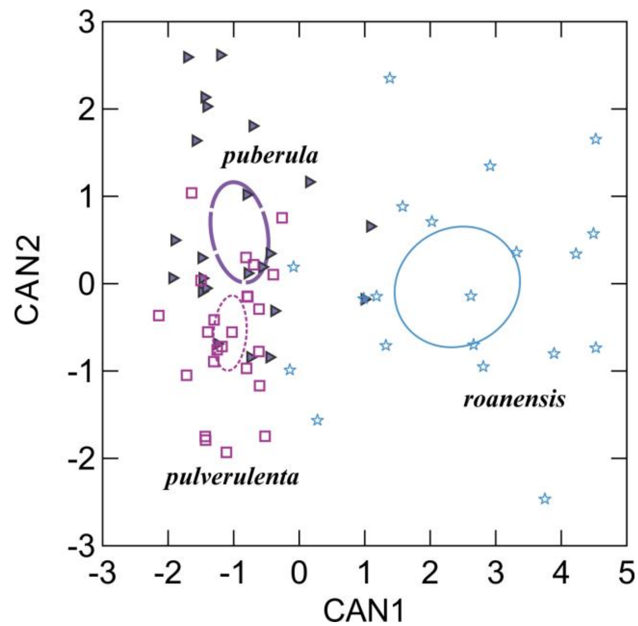


Figure 8. Plot of canonical scores (CAN1 vs CAN2) for 63 specimens of *Solidago puberula* (right-oriented purple triangles), *S. pulverulenta* (magenta squares), and *S. roanensis* (blue stars).

**Two Species Level Groups Analysis: *Solidago puberula* and *S. pulverulenta***

The Pearson correlation matrix yielded r > |0.7| for most pairs of leaf traits reducing the number to be used to mid stem leaf length and number of margin serrations and upper leaf width and number of margin serrations. Basal rosette and lower stem leaves were often/sometimes absent and were not included in the discriminant analyses. The numbers of ray florets and disc florets were highly correlated and only the former trait was used in the analyses. Ray floret ovary/ fruit body length at anthesis correlated highly with disc floret ovary/ fruit body length at anthesis and only the latter trait was included in the discriminant analyses.

In the STEPWISE discriminant analysis of 48 specimens of two species level a priori groups in (*Solidago puberula* and *S. pulverulenta*), the following three traits were selected and are listed in order of decreasing F-to-remove values: mid stem leaf length (23.30), involucre height (11.19), and disc floret corolla length (5.05). 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. *Solidago puberula* and *S. pulverulenta* had an F-to separate value of 13.618 (Wilks' lambda = 0.5185 df = 3 1 46; Approx. F= 13.6177 df = 3 44 prob = 0.0000).

In the Classificatory Discriminant Analysis of the two species level a priori groups (*Solidago puberula* and *S. pulverulenta*), percents of correct a posterori assignment to the same a priori group were 83% for both groups. The Classification matrix and Jackknife classification matrix are presented in Table 7. Twenty of the 24 specimens of the *S. puberula* a priori group (83%) were assigned a posteriori into the *S. puberula* group; 10 specimens with 90-100% probability, 1 specimen with 89% probability, 5 specimens with 74-78% probability, 3 specimens with 62-64% probability, and 1 specimen with 59% probability (*Semple & Chmielewski 6227* WAT from Blount Co., Tennessee; 96 cm tall shoot with ca. 59 stem leaves below the inflorescence). Four specimens of the *S. puberula* a priori group were assigned a posteriori to *S. pulverulenta* with 81% probability (*Freer 12280* NCU from from Amherst Co., Virginia; 56.5 cm tall shoot with ca. 50 stem leaves below the inflorescence), 61% probability (*Freye 8037* TAWES from Cecil Co., Maryland; 47 cm tall shoot with ca. 23 stem leaves below the inflorescence), 56% probability (*Cook et al. C-561* WAT from Transylvania Co., North Carolina; 42.6 cm tall shoot with ca. 22 leaves below the inflorescence), and

53% probability (*Semple & Ringius 7638* WAT from Caroline Co., Virginia; 82 cm tall shoot ca. 51 leaves below the inflorescence). Twenty of the 24 specimens of the *S. pulverulenta* a priori group (83%) were assigned a posteriori into the *S. pulverulenta* group; 13 specimens with 92-99% probability, 1 specimen with 88% probability, 3 specimens with 72-78% probability, 1 specimen with 61% probability, and 2 specimens with 55% probability (*Radford 42490* NCU from Tyrrell Co., North Carolina; 57 cm tall shoot with ca. 45 nodes below the inflorescence) and 51% probability (*Kral 61116* MO from Calhoun Co., Florida; 85 cm tall shoot with a damaged inflorescence apex and ca. 63 leaf nodes below the inflorescence). Four specimens of the *S. pulverulenta* a priori group were assigned a posteriori to *S. puberula* with 90% probability (*Massey 3129* NCU from Sussex Co., Virginia; a 100+ cm tall shoot with many stem nodes and a large long branches inflorescence and a flowering branch arising ca. 50 cm below the apex), 78% probability (*Semple 11597* WAT from Rowan Co., North Carolina; 117 cm tall shoot with more than 75 stem leaves), 78% probability (*Ahles 37308* NCU from Robeson Co., North Carolina; 98 cm tall shoot with ca. 65 stem leaves below the inflorescence), and 50% probability (*Kral 41668* WAT from Geneve Co., Alabama; 108 cm tall shoot with ca. 66 stem leaves below the inflorescence).

Histograms of CAN1 frequencies for 63 specimens of *Solidago puberula* and *S. pulverulenta* are presented in Fig. 9. The Eigenvalue on the first axis was 0.776.

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** | ***puberula*** | ***pulverulenta*** | **% correct** |
|---|---|---|---|
| ***puberula*** | 20 | 4 | 83 |
| ***pulverulenta*** | 4 | 20 | 83 |
| **Totals** | 24 | 24 | 83 |

Jackknifed classification matrix

| **Group** | ***puberula*** | ***pulverulenta*** | **% correct** |
|---|---|---|---|
| ***puberula*** | 20 | 4 | 83 |
| ***pulverulenta*** | 5 | 19 | 79 |
| **Totals** | 24 | 23 | 81 |

## DISCUSSION

The results of the multivariate analyses indicate that *Solidago puberula*, *S. pulverulenta*, and *S. roanensis* and *S. sciaphila* can be treated as separate species with *S. sciaphila* being the most distinct and *S. puberula* and *S. pulverulenta* being the most similar. The phylogenetic position of the tetraploid species *S. sciaphila* has not been determined by DNA sequence data but it is assumed to be either the basal member of the *S. puberula* complex clade or perhaps more closely related to *S. hispida* in the *S. bicolor/S. hispida* clade. Semple and Cook (2006) treated *S. puberula* and *S. pulverulenta* as conspecific subspecies within *S. puberula*. Weakley (2012) treated the two taxa as varieties within *S. puberula*. but as separate species in Weakley (2015).

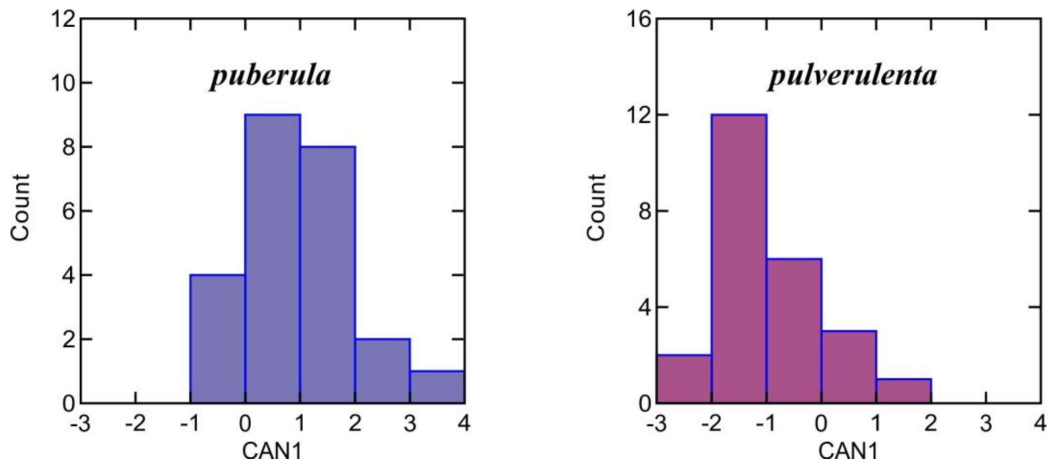


Figure. 9. Histograms of CAN1 canonical scores for 48 specimens of *S. puberula* (left) and *S. pulverulenta* (right).

The results of the third analysis indicate that *Solidago roanensis* is significantly different from *S. puberula* and *S. pulverulenta* on technical traits as well as the more obvious shift from glabrous/glabrate lower stem to increasing more densely short-canescent mid and upper stems. General leaf shape is similar in all three species being broadly to narrowly oblanceolate to lanceolate. There are obvious differences in the phyllaries with those of *S. roanensis* being less attenuate and with the mid and inner ones usually having 3 or more pronounced veins, while the phyllaries of *S. puberula* and *S. pulverulenta* are usually narrow and attenuate and single veined. The limited number of vegetative traits included in the analysis resulted in weak separate of *S. puberula* from *S. pulverulenta* with only 54% of the *S. puberula* specimens being assigned a posteriori to *S. puberula*.

The results of the first, second and fourth analysis indicate that there are significant differences between *Solidago puberula* and *S. pulverulenta* with the latter generally being more strongly supported. It can be argued that the two taxa do not differ sufficiently to warrant species status as was done by Semple and Cook (2006) in Flora North America where the two were treated as subspecies. The two taxa have also been treated as varieties within *S. puberula*, e.g., Cronquist (1980). The results of this study are not sufficiently strong to indicate that species level status is the only option.

Semple (1974) presented a discussion of subspecies, variety and form level ranks using *Xanthisma texanum* DC. as the example following the concepts of Ehrendorfer (1968). The subspecies concept was considered to have a strong allopatric element to its application and the ranges of *Solidago puberula* and *S. pulverulenta* are mostly allopatric and were thus treated as subspecies of *S. puberula* in Semple and Cook (2006). Varietal rank was for different races with mostly or completely sympatric ranges. During the intervening 46 years since 1974, the lack of consensus in North America on how to apply the subspecies rank has shifted with the school favoring subspecies as merely a grouping category gaining dominance over those who viewed it as like varietal rank but with a strong allopatric distribution. Asa Gray did not use subspecies and his varieties included both strongly allopatric races and much more or totally sympatric races. It is my observation that for many (likely the majority) of taxonomists in North America today, subspecies is just a grouping category and that this is significantly the result of proponents of the grouping category school having simply academically outbred the alternative group. Contributors to Flora North America and regional floras have been and are required to choose between using subspecies or varieties even when they would prefer to recognize both in a floristic treatment. Thus, continuing to treat *S. pulverulenta* as a subspecies within *S. puberula* has become much more problematic now because the two taxon are clearly closely related but at the same time have ranges of distribution that indicate significant differences in adaptations to different habitats. Varietal rank is not sufficient to indicate the extent of difference between *S. puberula* and *S. pulverulenta* in terms of morphology and ecology. Stem height and the associated number of nodes (and leaves) on a stem are highly variable within the two species. The taller the stem, the more reduced in size the upper most leaves are, but this is more pronounced in *S. pulverulenta*. However, very short plants of *S. pulverulenta* from Florida were examined as part of this study resulting in these plants having very few leaves of very small size; e.g. *Rodgers 340* LSU (Fig. 4A). Such plants will key out to *S. puberula* because they are short and have few stem leaves but are just dwarf morphs of *S. pulverulenta*.

**Key to *Solidago puberula*, *S. pulverulenta*, *S. roanensis*, and *S. sciaphila*.**

1. Mid stem leaves lanceolate to ovate, usually with small and large serrations; native to bluffs of Mississippi R. and tributaries in SE Minnesota and adjacent Wisconsin, Illinois and Iowa ........................................................................................................................ **Solidago sciaphila**

1. Mid stem leaves lanceolate to oblanceolate, serrations few, small or none; Nova Scotia and Québec south to northern Georgia and Alabama in the mountains and Piedmont and to Florida on the coastal plain

    2. Lower stems glabrous or glabrate, mid to upper stems increasingly finely canescent; mid to inner phyllaries usually oligoneurate; mid to higher elevations in Piedmont and Applachian Mts. from Pennsylvania to northern Georgia eastern Tennessee, and northeastern Alabama ........................................................................................................................**Solidago roanensis**

    2. Lower to upper stems densely finely canescent; phyllaries single veined, usually attenuate

        3. Leaves 20–50(–60), mid cauline usually 40–50 mm long, upper leaves somewhat reduced; phyllaries attenuate; Nova Scotia to Ontario south to Piedmont and mountains in Georgia (adjacent Alabama?) ............................................................................ **Solidago puberula**

        3. Leaves (20–)50–110+, mid cauline 10–40 mm long, upper leaves much reduced; phyllaries attenuate to acute; coastal plain, southeastern Virginia to northern and western Florida (possibly southern Mississippi and eastern Louisiana) .................. **Solidago pulverulenta**

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## LITERATURE CITED

Beaudry, J.-R. 1969. Études sur les *Solidago* L. IX. Une troisième liste de nombres chromosomiques des taxons du genre *Solidago* et de certains genres voisins. Naturaliste Canad. 96: 103–122.

Beaudry, J.R. and D.L. Chabot. 1959. Studies on *Solidago* IV. The chromosome numbers of certain taxa of the genus. Canad. J. Bot. 37: 209–288.

Cronquist, A. 1968. *Solidago* L. Pp. 413–438, in H.A. Gleason (ed.). The New Britton and Brown Illustrated Flora of the Northeastern United States and Adjacent Canada. Hafner Pub. Co., New York.

Cronquist, A. 1980. Vascular Flora of the Southeastern United States. I. Asteraceae. Univ. North Carolina Press, Chapel Hill.

Ehrendorfer, F. 1968. Geographical and ecological aspects of infraspecific differentiation. In V.H. Heywood (ed.). Modern methods of plant taxonomy. Academic Press, New York.

Fernald, M.L. 1950. Gray's Manual of Botany, 8th ed. Van Nostrand, New York.

Kapoor, B.M. 1970. In IOPB chromosome number reports XXVII. Taxon 19: 438–439.

Mackensie, K.K. 1933. *Solidago* L. Pp. 1344–1360, in J.K. Small. Manual of the Southeastern Flora. Univ. of North Carolina Press, Chapel Hill.

Morton, J.K. 1981. Chromosome numbers in Compositae from Canada and the U.S.A. Bot. J. Linn. Soc. 82: 357–368.

Radford, A.E., H.E. Ahles, and C.R. Bell. 1968. Manual of the Vascular Flora of the Carolinas. Univ. of North Carolina Press, Chapel Hill.

Semple, J.C. 2020 (frequently updated). Classification and Illustrations of Goldenrods. <https://waterloo.ca/astereae-lab/research/goldenrods/classification-and-illustrations>

Semple, J.C. and J.G. Chmielewski. 1987. Chromosome numbers in Fam. Compositae, Tribe Astereae. II. Additional Counts. Rhodora 89: 319–325.

Semple, J.C. and R.E. Cook. 2004. Chromosome number determinations in fam. Compositae, Tribe Astereae. VII. Mostly eastern North American and some Eurasian taxa. Rhodora 106: 253–272.

Semple, J.C. and R.E. Cook. 2006. *Solidago* Linnaeus. Pp. 107–166, in Flora North America Editorial Committee (eds.). Flora of North America, Vol. 20. Asteraceae, Part 2. Astereae and Senecioneae. Oxford Univ. Press, New York and Oxford.

Semple, J.C., R.A. Brammall, and J. Chmielewski. 1981. Chromosome numbers of goldenrods, *Euthamia* and *Solidago*, (Compositae-Astereae). Canad. J. Bot. 59: 1167–1173.

Semple, J.C., R.E. Cook, and E. Owen. 2015. Chromosome numbers in Fam. Compositae, Tribe Astereae. VIII. Eastern North American taxa. II. Rhodora 117: 80–91.

Semple, J.C., L. Tong, and Y.A. Chong. 2017a. Multivariate studies of *Solidago* subsect. *Squarrosae*. I. The *Solidago speciosa* complex (Asteraceae: Astereae). Phytoneuron 2017-18: 1–23.

Semple, J.C., L. Tong, and Y.A. Chong. 2017b. Multivariate studies of *Solidago* subsect. *Squarrosae*. III. *S. georgiana*, *S. porteri*, *S. roanensis*, *S. squarrosa*, and *S. villosicarpa* (Asteraceae: Astereae). Phytoneuron 2017-55: 1–17.

Semple, J.C., L. Tong, Y.A. Chong, and M. Kaddoura. 2017c. Multivariate studies of *Solidago* subsect. *Squarrosae*. II. The *Solidago bicolor–S. hispida* complex (Asteraceae: Astereae). Phytoneuron 2017-33: 1–44.

Semple, J.C., Jie Zhang and ChunSheng Xiang. 1993. Chromosome numbers in Fam. Compositae, Tribe Astereae. V. Eastern North American taxa. Rhodora 95: 234–253.

Semple, J.C., G.S. Ringius, C. Leeder, and G. Morton. 1984. Chromosome numbers of goldenrods, *Euthamia* and *Solidago* (Compositae: Astereae). II. Additional counts with comments on cytogeography. Brittonia 36: 280-292. Erratum. Brintonia 37: 121. 1985.

Semple, J.C., R.E. Cook, G.H. Morton, J.B. Beck, and R.M. Lopez Laphitz. 2019. Chromosome number determinations in Fam. Compositae, Tribe Astereae. IX. North American taxa. II. Rhodora 121: 37–53.

Semple, J.C., T. Shea, H. Rahman, Y. Ma, and K. Kornobis. 2016. A multivariate study of the *Solidago sempervirens* complex (Asteraceae: Astereae: *S.* subsect. *Maritimae*). Phytoneuron 2016-73: 1–31.

Small, J.K. 1903. Flora of the Southeastern United States. Published by the author, New York.

Thiers, B. [continuously updated]. Index Herbariorum: A global directory of public herbaria and associated staff. Virtual Herbarium, New York Botanical Garden, Bronx. <http://sciweb.nybg.org/science2/IndexHerbariorum.asp>
Weakley, A. 2012. Flora of the Southern and Mid-Atlantic States. Working Draft of 30 Nov 2012. Univ. of North Carolina, Chapel Hill.
Weakley, A. 2015. Flora of the Southern and Mid-Atlantic States. Working Draft of 21 May 2015. Univ. of North Carolina, Chapel Hill.