

**A MULTIVARIATE STUDY OF *SOLIDAGO* SUBSECT. *TRIPLINERVIVAE*
IN WESTERN NORTH AMERICA:
THE *SOLIDAGO LEPIDA* COMPLEX (ASTERACEAE: ASTEREAE)**

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ABSTRACT

Solidago subsect. *Triplinerviae* includes four species native to western North America: *S. altissima*, *S. elongata*, *S. gigantea*, and *S. lepida*. All of these except *S. gigantea* have been included at one time or another within *S. canadensis*. While rather similar among themselves, each species is distinguished by different sets of indument, leaf, and inflorescence traits. A series of multivariate morphometric analyses were performed on 244 specimens to discover additional technical traits useful in separating the species and to elucidate problems with identification in a group of species complicated by multiple ploidy levels and considerable infraspecific variation. Statistical support for recognizing *S. gigantea* var. *shinnersii* and *S. lepida* var. *salebrosa* was generated in comparisons of the varieties with the typical variety in each species.

Solidago subsect. *Triplinerviae* (Torrey & A. Gray) Nesom (Asteraceae: Astereae) includes 17 species native North and South America (Semple 2017 frequently updated). Semple and Cook (2006) recognized 11 species with infraspecific taxa in several species occurring in Canada and the USA: *S. altiplanities* Taylor & Taylor, *S. altissima* L., *S. canadensis* L., *S. elongata* Nutt., *S. gigantea* Ait., *S. juliae* Nesom, *S. leavenworthii* Torrey & A. Gray, *S. lepida* DC., *S. rupestris* Raf., *S. shortii* Torrey & A. Gray, and *S. tortifolia* Ell. Semple (2013) and Semple et al. (2013) added two additional species, *S. brendiae* Semple and *S. fallax* (Fern.) Semple, based on a multivariate study of the *S. canadensis*/*S. lepida* complex in eastern North America with *S. elongata* included for comparison. Data on type specimens of names critical in this study are presented in Table 1.

Semple et al. (2015) presented a multivariate morphometric analysis of *Solidago altissima*, *S. canadensis*, and similar species. Lopez Laphitz and Semple (2015) included some species native to the southern USA and Mexico in a study of the *S. chilensis* Meyen/*S. microglossa* DC. complex native to South America. Semple et al. (2016) and Semple and Lopez Laphitz (2016) included *S. durangensis* Nesom and *S. pringlei* Fern. native to Mexico in multivariate studies determining their morphological affinities within the genus *Solidago* and in subsect. *Triplinerviae*. Taxonomic problems involving species of subsect. *Triplinerviae* native to the western provinces in Canada and the western states of the USA were not fully addressed in these previous studies.

Over many years, Cronquist advocated lumping all western species of subsect. *Triplinerviae* except *Solidago gigantea* into *S. canadensis* (e.g., Cronquist 1955, 1994; Hitchcock & Cronquist 1973). In the Flora of British Columbia, Douglas (1998) lumped *S. altissima* var. *gilvocanescens* (Rydb.) Semple, *S. canadensis*, *S. elongata*, and *S. lepida* into a single very broadly defined *S. canadensis* but recognized *S. gigantea* as separate and left local botanists with keys insufficient to clarify which species of subsect. *Triplinerviae* were present in the province. Email exchanges between the first author and Frank Lomer regarding the identification of multiple *Solidago* collections in British Columbia indicated the need for additional work on the *Triplinerviae* problem in the Pacific Northwest by the Astereae Lab. Discussions with the late John K. Morton, who made numerous *Solidago* collections with Joan Venn (deposited in TRT, WAT, and other herbaria) over multiple

Table 1. Basionyms and types of taxa included in this study.

<i>Solidago canadensis</i> L., Sp. Pl. 878. 1753. TYPE: "Hab. Virginia, Canada", Herb. Linn. 998.2 (LINN!; Lectotype [A. Gray, 1882]). <i>Kalm s.n.</i> , Herb. Linn. 998.3 (LINN!) is pinned to 998.2; it is <i>S. rugosa</i> Mill. var. <i>rugosa</i> . Herb. Linn. 998.6 (LINN!) is <i>S. canadensis</i> var. <i>canadensis</i> .
<i>Solidago canadensis</i> L. var. <i>gilvocanescens</i> Rydb. Contr. U.S. Nat. Herb. 3: 162. 1895. TYPE: USA. Nebraska. Hooker Co.: Cody's Lakes at the head of the Dismal R, sandy soil, 10 Aug 1893, <i>Rydberg 1662</i> (holotype: US, photo!; isotype: GH!, NY2, photos!).
<i>Solidago elongata</i> Nutt., Trans. Amer. Philos. Soc., n. ser. 7: 327. 1840. Nom. cons., Semple (2007), non Pépin (1834), nec Hort. Par. ex A. Gray (1884). TYPE: {USA. Oregon. Sauvie Island W of Ft. Vancouver, Washington,} Wappatoo Island and Columbia Plains, [Sep 1834, or Aug-Sep 1835,] <i>Nuttall s.n.</i> (lectotype designated by (Semple 2007): BM!; isolectotype: PH!, S). "Wapp.", [Sep 1834, or Aug-Sep 1835] <i>Nuttall s.n.</i> (probable isolectotype: GH!).
<i>Solidago gigantea</i> Ait., Hort. Kew. 3: 211. 1789. TYPE: "Nat. North America. Cult. 1758, by Mr. Philip Miller." Hort. Kewensis 1778 {back of sheet} (holotype: BM!).
<i>Solidago lepida</i> DC., Prodr. 5: 339. 1836. TYPE: "ad Mullgrave seu Nootka," {USA. Alaska: Mulgrave, Nootka Sound, Yakutat Bay}, <i>Haenke s.n.</i> (holotype: G-DC!). The type has broadly oblanceolate coarsely serrate leaves.
<i>Solidago lepida</i> var. β <i>subserrata</i> DC., Prodr. 5: 339. 1836. TYPE: USA. Alaska. "Ad Mullgrave sen Nootka", {Mulgrave, Nootka Sound, Yakutat Bay}, <i>Haenke s.n.</i> (holotype: G-DC!). The type has oblanceolate finely serrate leaves.
<i>Solidago pruinosa</i> Greene, Pittonia 4: 70. 1899. SYNTYPES: CANADA. Saskatchewan. Moose Jaw, Assiniboia, 13 Aug 1895, <i>Macoun 10893</i> (holotype: ND-G digital image! marked at "type" by Greene; isotype: CAN!). <i>Macoun 10894</i> (ND-G digital image!, incorrectly designated in Semple et al. 2015 as lectotype).
<i>Solidago serotina</i> Ait., Hort. Kew. 3: 211. 1789. Non Retzius (1781), nec Hook. (1835). TYPE: "Nat. of North America. Cult. 1758, by Mr. Philip Miller" (holotype: BM!).
<i>Solidago serotina</i> Ait. var. <i>salebrosa</i> Piper in Piper & Beattie, Fl. Palouse Region, 185. 1901. TYPE: USA. Washington. Pullman, <i>Piper 1580</i> (holotype: WS!; isotype: GH!).

decades focusing on subsect. *Triplinerviae*, confirmed the first author's field observations that hexaploid plants of *S. gigantea* and *S. lepida*, and particularly var. *salebrosa* (Piper) Semple, could be very difficult to distinguish along the northern edge of the prairies from Alberta to Manitoba and along streams and rivers in eastern Washington and northern Idaho. Both *S. gigantea* and *S. lepida* var. *salebrosa* were left out of the multivariate analyses presented in Semple et al. (2013) in the paper on the *S. canadensis*/*S. lepida* complex in eastern North America.

Solidago altissima var. *gilvocanescens* is the only morph of the species present in western Canada and the western USA and is distinguished by being mostly diploid and tetraploid and having short canescent stems from base to apex and having upper strigose stem leaves that are sometimes more serrate than found in var. *altissima* and var. *pluricephala* M.C. Johnston (Semple et al. 2015). Variety *gilvocanescens* is common across the prairies west to the Rocky Mountains. In Montana, the mountains are broken up by broad valleys across much of the state where the Rocky Mts. cut northwest. In the first edition of the Flora of Alberta, Moss (1959) used the synonym *S. pruinosa* Greene with *S. canadensis* var. *gilvocanescens* Rydb. listed as a synonym. In the Flora of the Pacific Northwest, Hitchcock and Cronquist (1973) listed the taxon as *S. canadensis* var. *gilvocanescens*, as did Scoggan (1979) in the Flora of Canada, Moss revised by Packer (1983) in the second edition of the Flora of Alberta, and Douglas et al. (1998), who noted the variety as being present in the interior of British Columbia, but Douglas et al. (2002) did not map the distribution. The variety was illustrated in Semple et al. (2015). *Solidago canadensis* is not native to western Canada and the western USA as the species was defined in Semple and Cook (2006) and Semple et al. (2013), although var. *canadensis* has been listed as present in some floras, e.g., Moss revised by Packer (1983).

Solidago elongata is distinguished by being mostly diploid, having stems that are usually very sparsely hairy proximally and more so distally, having club shaped rather than secund conical inflorescences, and having very few small stipitate glands on the bracts, peduncles, and phyllaries in the inflorescence (Figs. 1-3). Every species of *Solidago* can have some small stipitate glands in the inflorescence, but only a few are obviously densely glandular. *Solidago elongata* was treated as *Solidago lepida* var. *elongata* (Nutt.) Fern., but Fernald (1915) applied the combination to plants in both western and eastern North America. Hitchcock and Cronquist (1973) treated *S. elongata* as a synonym of *S. canadensis* var. *salebrosa* (Piper) M.E. Jones as did Scoggan (1979) and Cronquist (1994). *Solidago elongata* was treated as *S. canadensis* subsp. *elongata* (Nutt.) D.D. Keck by Semple (1993), who later (Semple 2012) treated it as *S. elongata* in the second edition of the Jepson Manual.

Solidago gigantea is usually the least glandular and least pubescent species of subsect. *Triplinerviae* in North America (Figs 4-7). Stems can be glaucous and or often anthocyanotic. The stem leaves are usually sharply serrate from lower stem to the inflorescence. The inflorescence is secund conical and the longer lower branches are usually strongly arching; overall the inflorescence is less densely branched than *S. altissima*, *S. canadensis*, and *S. elongata*. Moss (1959), Hitchcock and Cronquist (1973), and Douglas et al. (1983) recognized the species as present in Alberta, the Pacific Northwest, and British Columbia, respectively. Semple (1993) listed *S. gigantea* as present in California but rejected this identification in Semple (2012) and treated the California plants as *S. lepida* var. *salebrosa*. *Solidago gigantea* is diploid and tetraploid in eastern North America but is exclusively hexaploid on the prairies. The latter cytotype has been treated as *S. gigantea* var. *shinersii* Beaudry and *Solidago shinersii* (Beaudry) Beaudry, but these names were treated as synonyms of *S. gigantea* in Semple and Cook (2006) following G. Morton (1984). As a consequence of the results presented below, Semple (2017, frequently updated) added var. *shinersii* to the list of taxa that should be recognized in *Solidago*.

Solidago lepida is the most morphologically varied of the western species of subsect. *Triplinerviae* (Figs. 8-13). Stem height is highly variable depending upon latitude and growing conditions. Stems vary from glabrous from base to apex to glabrous below to moderately densely short-woolly canescent distally to sparsely to moderately short-woolly canescent proximally to distally. Leaves can be narrowly lanceolate to broadly lanceolate and entire or finely to coarsely serrate; leaves vary from glabrous to sparsely strigose to moderately strigose. Upper stem leaves are usually much less reduced in size into the inflorescence in var. *lepida*, while upper stem leaves of var. *salebrosa* tend to be reduced below the inflorescence. Inflorescences vary from narrowly club-shaped to leafy secund conical forms with short spreading lower branches in var. *lepida* to broadly secund conical in var. *salebrosa* with intermediate forms common. In his flora of the Rocky Mountains, Rydberg (1922) treated var. *salebrosa* as *S. salebrosa* (Piper) Rydb. Moss (1959) recognized *S. lepida* and briefly discussed var. *fallax* Fern. and var. *elongata*. Hitchcock and Cronquist (1973) treated *S. lepida* as a synonym of *S. canadensis* var. *subserrata* (DC.) Cronquist. Moss revised by Packer (1983) included *S. lepida* in *S. canadensis* in a broadly defined var. *canadensis*. Douglas et al. (1998) noted that *S. lepida* equaled *S. canadensis* var. *subserrata* in their treatment and had outer phyllaries about half the length of the inner, while in *S. canadensis* var. *salebrosa* the phyllaries more graduated. Cronquist (1994) proposed the combination *S. canadensis* var. *lepida* (DC.) Cronquist in the list of synonyms under *S. canadensis*, noting that “the holotype at G! approaches the *elongata* phase of var. *salebrosa* in its inflorescences.” The species includes diploids, tetraploids, and hexaploids, which results in considerable variation in head size; phyllaries are generally graduated but sometimes the outer phyllaries are closer to half the length of the inner. Stipitate glands are often difficult to see on diploids but are larger and more obvious on hexaploids, which are the most stipitate glandular in subsect. *Triplinerviae*. Glands are can be found on upper stem leaves, leaves in the inflorescence, bracts, peduncles, and phyllary margins or outer faces, and sometimes on all these structures or only some of them.



Figure 1. Morphology of *Solidago elongata*: Semple & Brouillet 7114 (WAT) from Clatsop Co., Oregon.



Figure 2. Morphology of *Solidago elongata*: Semple & Heard 8550 (WAT) from Mendocino Co., California.



Figure 3. Details of *Solidago elongata*. **A-B.** Lower and mid stems; *Semple & Heard 8786* (WAT); California. **C.** Mid stem and leaf base; *Semple & Heard 8537* (WAT); California. **D.** Mid stem leaf; *Semple & Brouillet 7132* (WAT), Oregon. **E.** Small inflorescence; *Semple & Heard 8786* (WAT). **F.** Heads; *F. Lomer 6361* (WAT), British Columbia. Scale bars = 1 mm in A-C, F; = 1 cm in D-E.



Figure 4. Morphology of *Solidago gigantea*: Semple & Brouillet 3387 (WAT), Farnham, Québec, 2n=18.

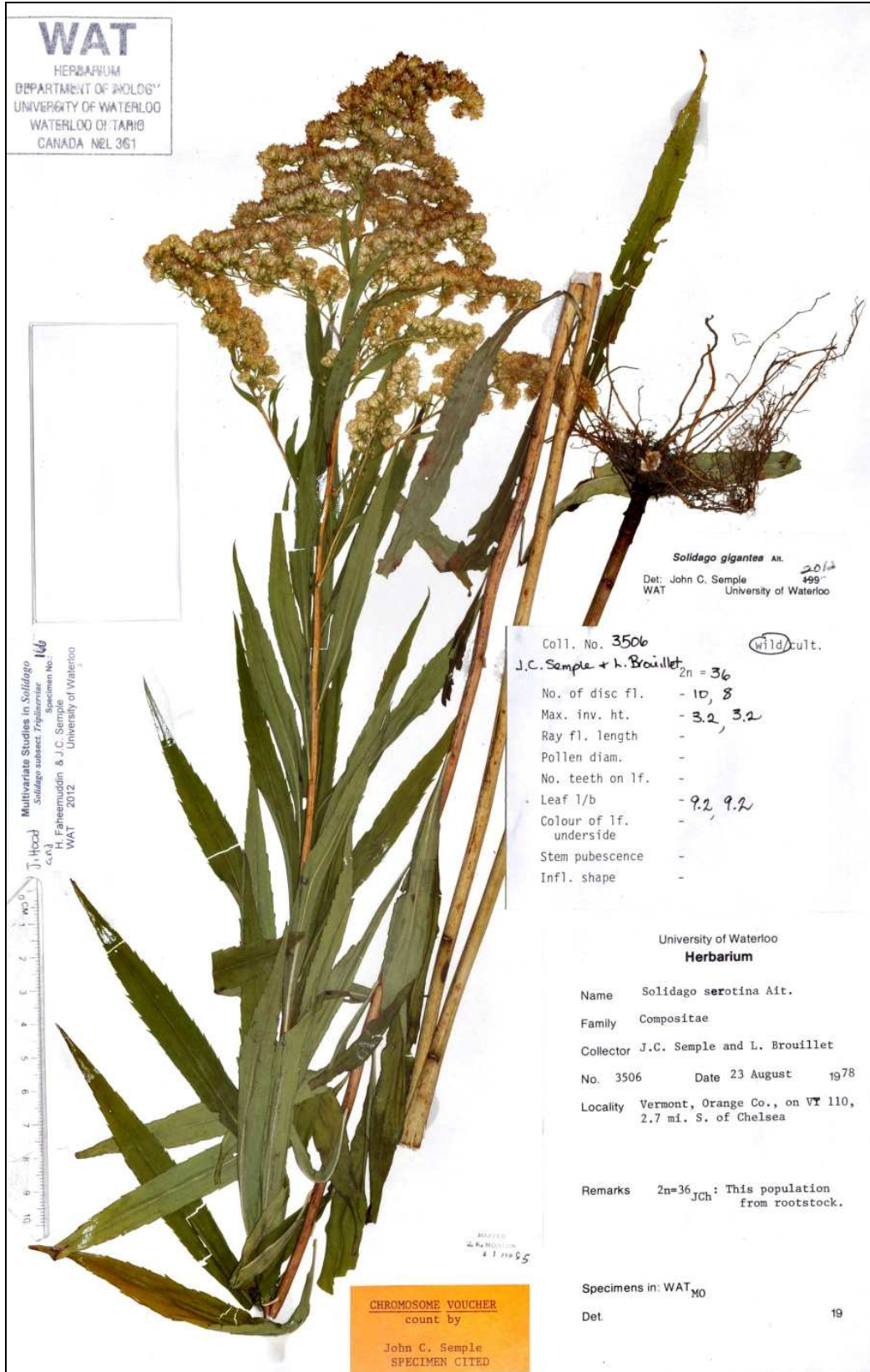


Figure 5. Morphology of *Solidago gigantea*: Semple & Brouillet 3506 (WAT), Chelsea, Vermont, 2n=36.

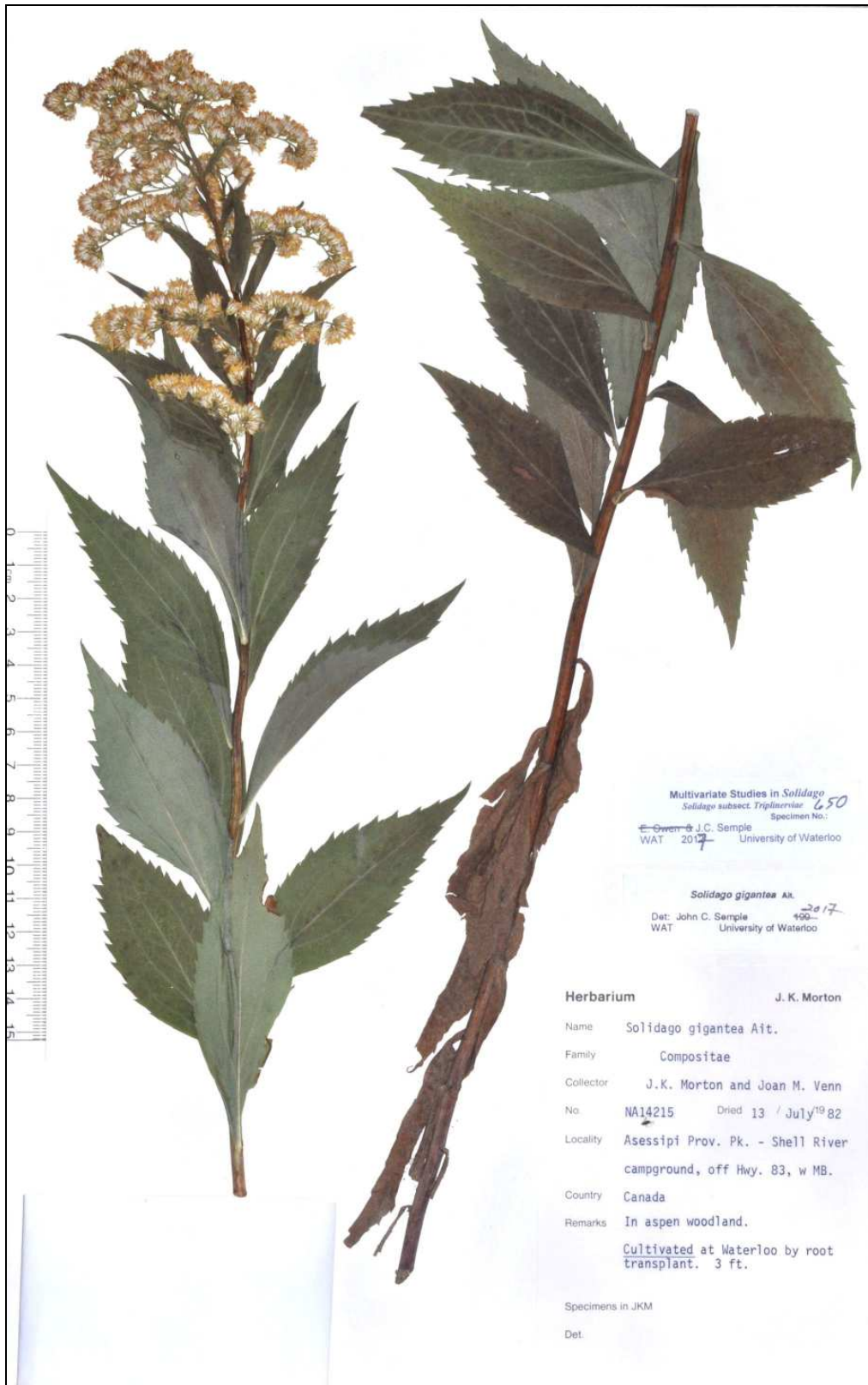


Figure 6. Morphology of *Solidago gigantea*, broader leaf morph: Morton & Venn NA14215 (TRT), Assinipi Provincial Park, Manitoba, $2n=54$.



Figure 7. Details of *Solidago gigantea*. **A.** Lower stem; *Semple & B. Semple 11489* (WAT); New Brunswick. **B.** Mid stem; *Semple & Brouillet 4507* (WAT); Iowa. **C-D.** Upper and lower stem in inflorescence; *J.K. Morton NA18725* (TRT); Illinois. **E.** Lower stem leaf; *J.K. Morton NA18688* (TRT), cult. greenhouse, transplanted from Pennsylvania. **F.** Mid stem leaf; *J.K. Morton NA18764* (TRT), North Carolina. **G.** Mid stem leaf; *J.K. Morton NA18772* (TRT), North Carolina. **H.** Heads; *J.K. Morton NA18764* (TRT), $2n=36$. Scale bars = 1 mm in A-D, H; = 1 cm in E-G.

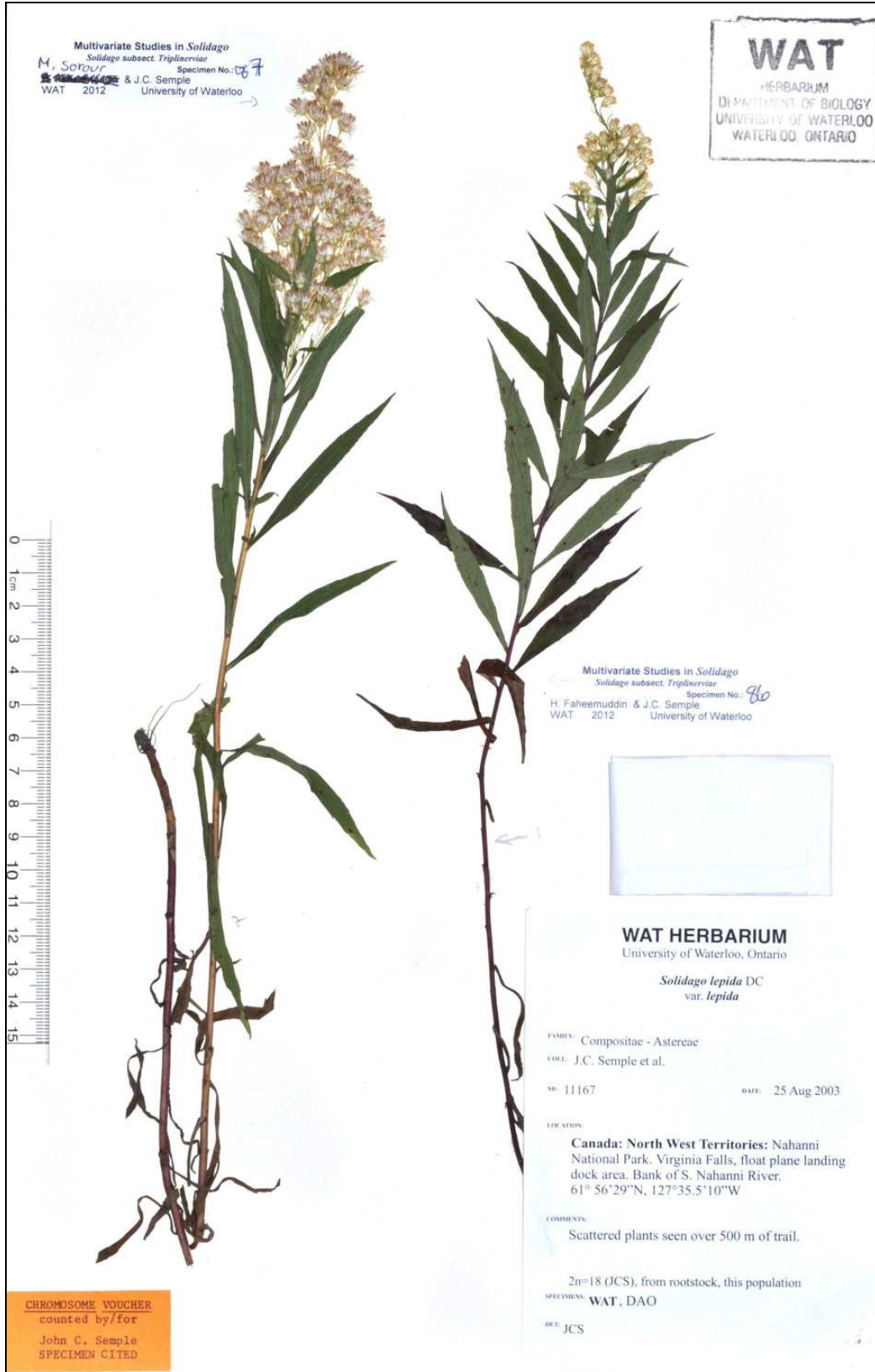


Figure 8. Morphology of *Solidago lepida* var. *lepida*: Semple et al. 11167 (WAT), Nahanni Nat. Park. Reserve, Northwest Territories, 2n=18.



Figure 9. Morphology of *Solidago lepida* var. *lepida*: Chmielewski et al. CC4736 (WAT), S of Dease Lake, British Columbia, $2n=36$; shoot on right side has damaged inflorescence with elongated branches.

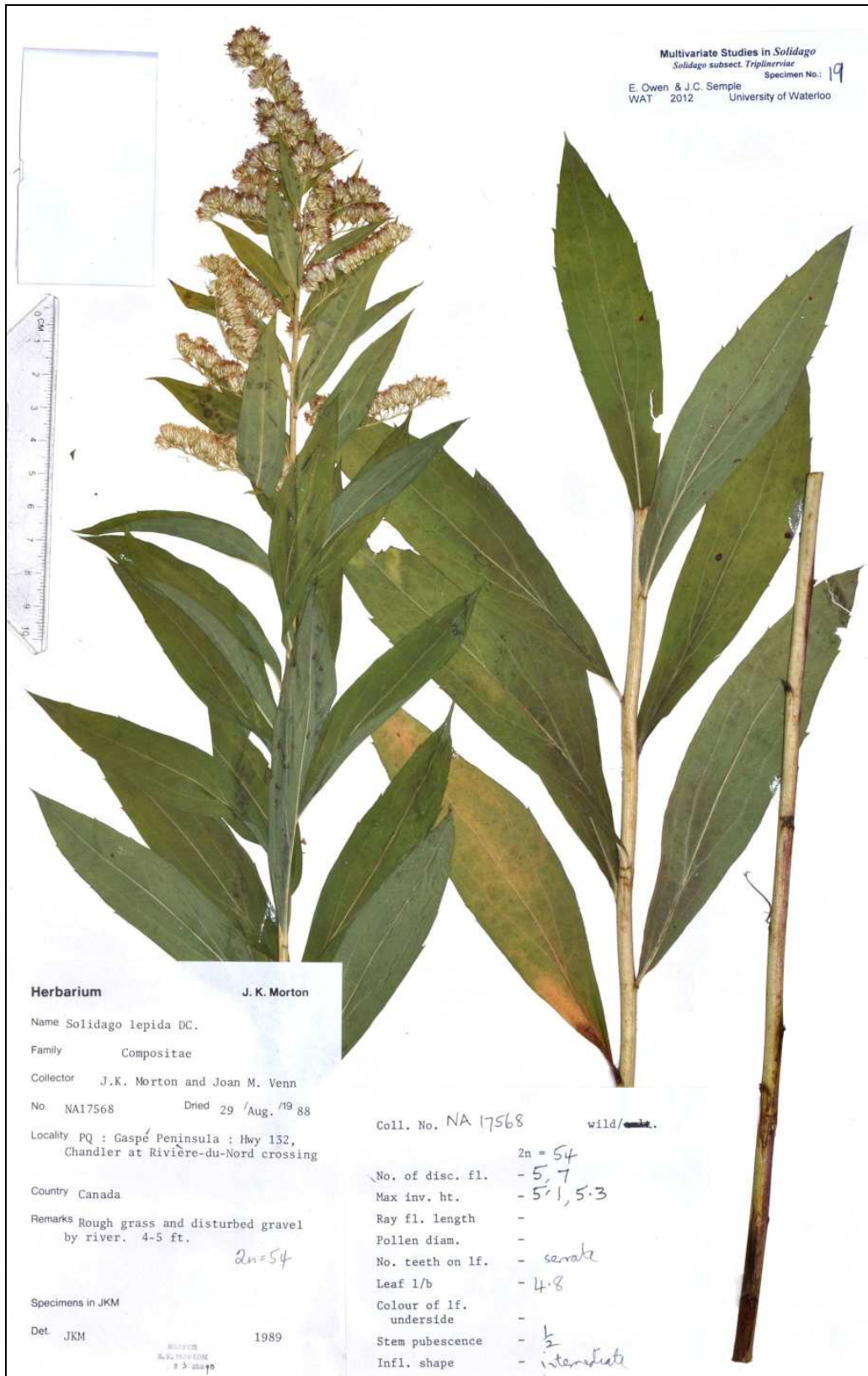


Figure 10. Morphology of *Solidago lepida* var. *lepida*: Morton & Venn NA17568 (TRT), Gaspé Peninsula, Québec, $2n=54$.



Figure 11. Morphology of *Solidago lepida* var. *salebrosa* diploid from west slope of Rocky Mts.: Semple & Brouillet 4376 (WAT), Moyie, British Columbia; an *S. elongata*-like morphotype.



Figure 12. Morphology of *Solidago lepida* var. *salebrosa*: Semple & Xiang 10324 (WAT), Edith Lake, Belt Mts., Montana, $2n=54$; *S. gigantea*-like but moderately to densely stipitate glandular in inflorescence.

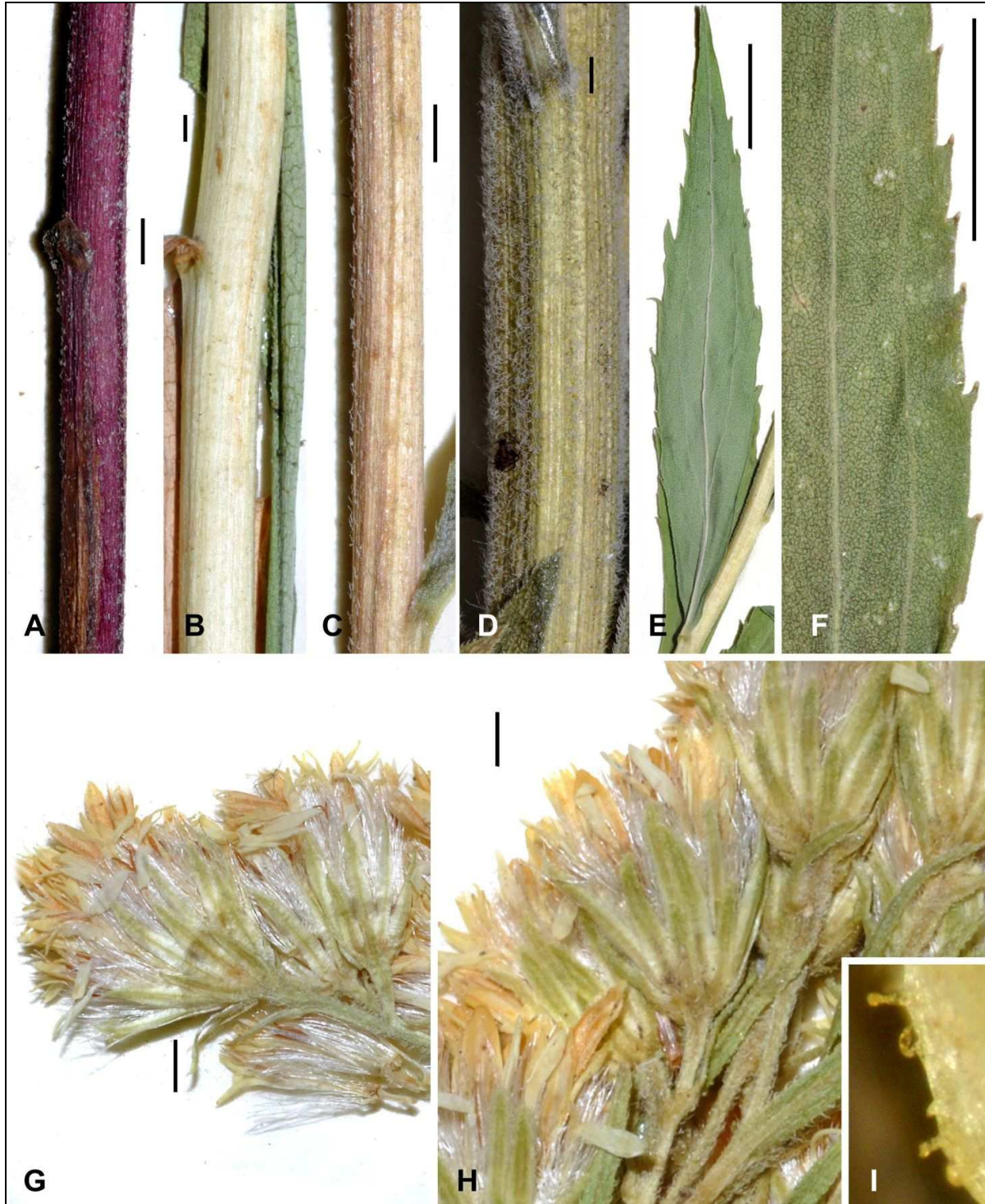


Figure 13. Details of *Solidago lepida*. **A-B.** Lower stems. **A.** *Semple 11167* (WAT); Northwest Territories. **B.** *Semple et al. 9207* (WAT), Wyoming. **C.** Mid stem; *Semple 11376* (WAT), Idaho. **D.** Upper stem; *Oldham 30688* (WAT), Ontario. **E.** Mid stem leaf; *Semple et al. 9209* (WAT), Wyoming. **F.** Mid stem leaf margin; *Semple & Cli-Marchaud 11173* (WAT), Northwest Territories. **G.** Heads; *Semple 11167* (WAT); $2n=18$. **H.** Heads; *Semple et al.* (WAT), Utah; $2n=54$. **I.** Glands on phyllary; *Morton & Venn NA17568* (TRT); Québec. Scale bars = 1 mm in A-D, G-H; = 1 cm in E-F. A, C, D, F, H-I = var. *lepida*; B, E, G = var. *salebrosa*.

Each species has a significant portion of its range allopatric from the other species, but ranges overlap on the margins. *Solidago altissima* var. *gilvocanescens* is common on the prairies from central Alberta to New Mexico and extends east to Manitoba south to northern Texas. The range extends eastward in the Prairie Peninsula in Illinois and Indiana. It also occurs in a few valleys west of the front range of the Rocky Mts. in southeastern and southcentral British Columbia. *Solidago elongata* is confined to the coastal ranges and the Cascade Mts. from southwestern British Columbia to the coastal ranges and the Sierra Nevadas in California (Fig. 14). Diploid and tetraploid *Solidago gigantea* occur in moist soils along streams and rivers and in thickets from Nova Scotia to eastern Manitoba south to Panhandle Florida and eastern Texas (Fig. 15). Hexaploids occur in similar habitats on the prairies from Manitoba to Alberta and south to Colorado and Texas. *Solidago lepida* occurs on tundra and in boreal and pine forests from Central Alaska and the eastern Aleutian Islands south to Arizona and northeastern Mexico and east in the boreal forests and aspen parklands to Ontario with scattered and possibly introduced populations in eastern Québec and New Brunswick (Fig. 16). Diploids, tetraploids and hexaploids occur in the western part of the range, while only hexaploids are known in Ontario and eastward. The var. *lepida* occurs throughout the range of the species though less common in the southern part of the Rocky Mts., while var. *salebrosa* occurs throughout the mountainous parts of the range. Some var. *salebrosa* like plants occur in the southern edge of the aspen parkland/boreal forest in Alberta, Saskatchewan, and Manitoba but these may be hybrids between hexaploid var. *lepida* and hexaploid *S. gigantea*.

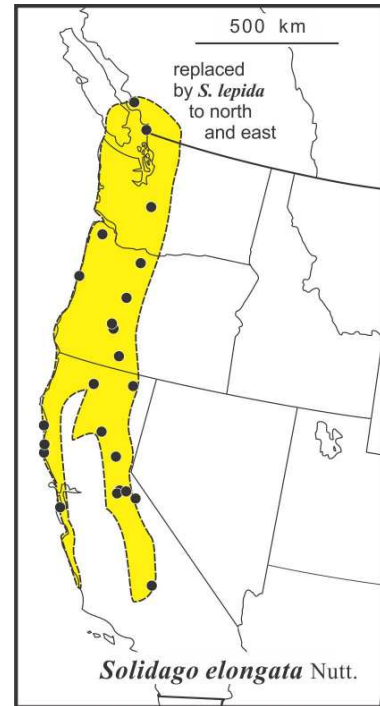


Figure 14. Range of distribution of *Solidago elongata* and locations of specimens included in the analyses; British Columbia south to California.

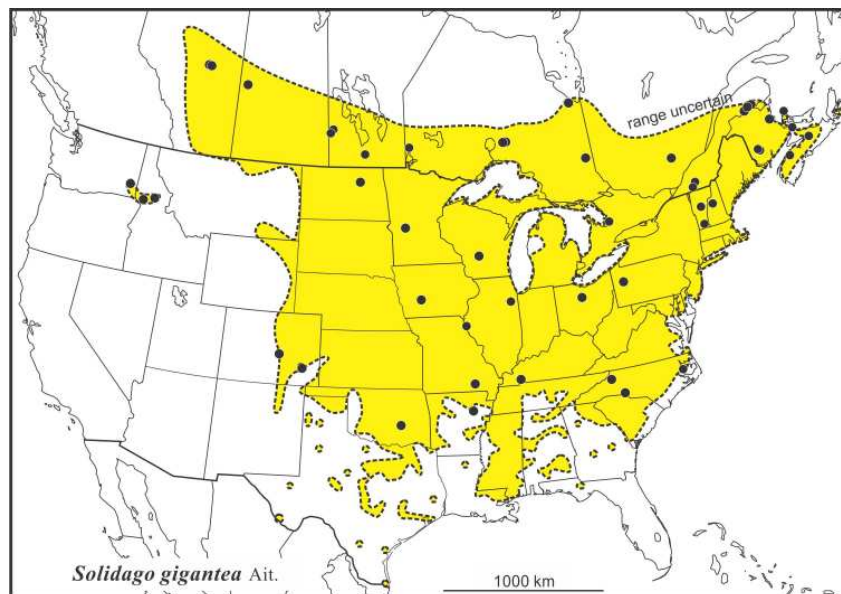


Figure 15. Range of distribution of *Solidago gigantea* and locations of specimens included in the analyses.

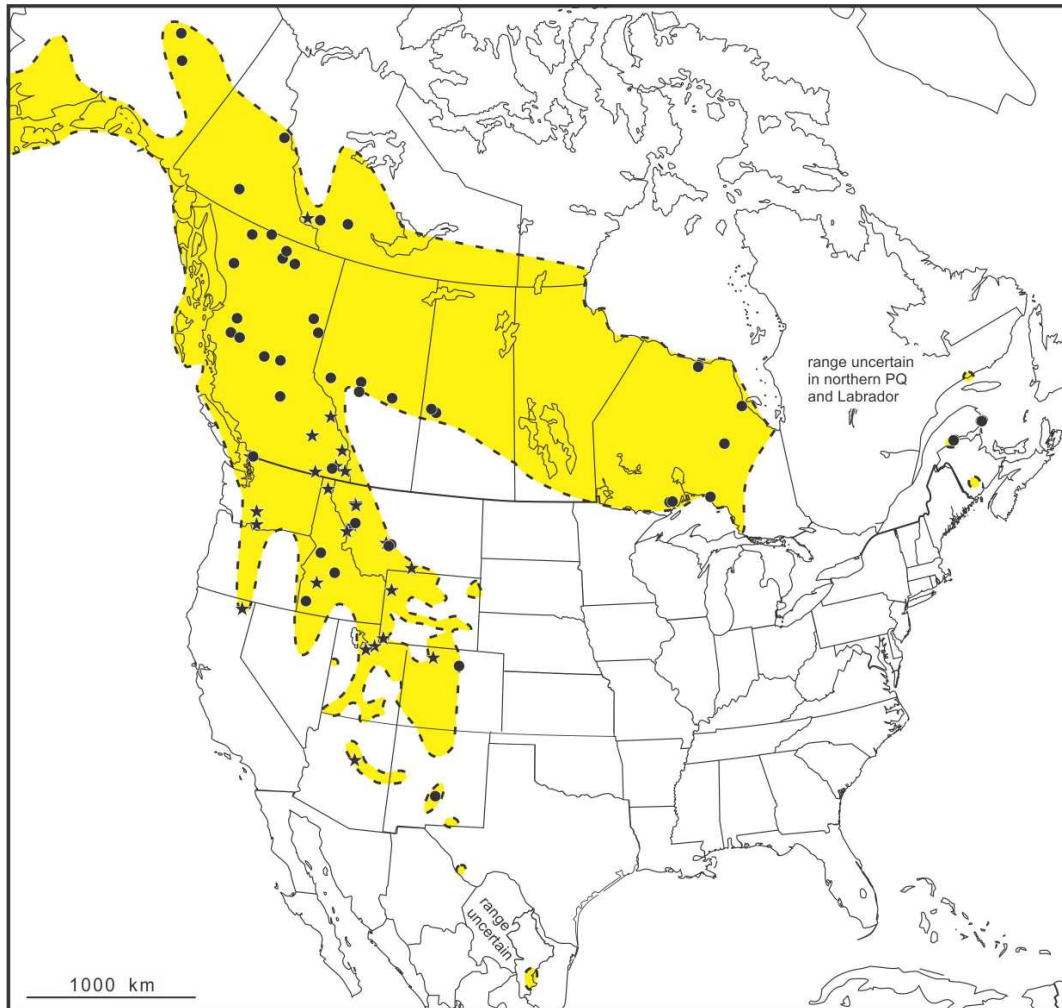


Figure 16. Range of distribution of *Solidago lepida* and locations of specimens included in the analyses; var. *lepida* (dots), var. *salebrosa* (stars).

A multivariate analysis focusing on western North American *Solidago* subsect. *Triplinerviae* has not been previously published. A number of problems need exploration. Does typical *S. canadensis* occur in the Pacific Northwest? How distinct are *S. elongata* and *S. lepida*? Is *S. gigantea* always easily distinguished from *S. lepida*? Should *S. lepida* be divided into var. *lepida* and var. *salebrosa* based on differences in inflorescence branching pattern? Are the diploid plants on the western slope of the Rocky Mts. members of *S. elongata* or *S. lepida*? Are the western hexaploid prairie individuals of *S. gigantea* sufficiently distinct from the diploid/tetraploid eastern individuals to warrant recognition as var. *shinersii*? The following analyses and results were undertaken to answer these questions.

MATERIALS AND METHODS

In total, 244 specimens from the J.K. Morton personal herbarium now deposited in TRT, NH, UBC, and WAT in MT (Thiers, continuously updated) were scored and included in the analyses: *S. altissima* var. *gilvocanescens* (33 specimens, most were included in Semple et al. 2015), *S. canadensis* (53 specimens; included in Semple et al. 2015; all from eastern North America), *S. elongata* (28 specimens, most included in Semple et al. 2013), *S. gigantea* (49 specimens), and *S.*

lepida (81 specimens; 50 specimens of var. *lepida* with most included in Semple et al. 2013 and 31 specimens of var. *salebrosa*). These were selected from more than 3500 specimens examined in many herbaria. For each specimen, 13 vegetative and 16 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 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 2. Leaf size in the inflorescence, orientation and density of the lower inflorescence branches, and density of stipitate glands were used in assigning specimens to a priori groups and were not included in the multivariate analyses.

Table 2. Traits scored for the multivariate analyses of 244 specimens of *Solidago* subsect. *Triplinerviae*.

Abbreviation	Description of trait scored
STEMHT	Stem height measured from the stem base to tip (cm)
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 from 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)
CAPBRLN	Length of longest inflorescence branches (cm)
INVOLHT	Involucre height (mm)
OPHYLN	Outer phyllary length (mm)
IPHYLN	Inner phyllary length (mm)
IPHYLW	Inner phyllary width (mm; not measures on the majority of specimens)
RAYNUM	Number of ray florets per head
RLAMLN	Ray strap length top of the corolla tube to the tip of the strap (mm)
RLAMPWD	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 were presented in Semple et al. (2015) and are not repeated here. Six STEPWISE discriminant analyses were performed. In the first analysis, *S. altissima* var. *gilvocanescens*, *S. canadensis*, *S. elongata*, *S. gigantea*, and *S. lepida* were included. In the second analysis, *S. elongata*, *S. gigantea*, and *S. lepida* were included. In the third analysis, *S. elongata* and *S. lepida* were included. In the fourth analysis, *S. gigantea* and *S. lepida* were included. In the fifth analysis, *S. lepida* var. *lepida* and var. *salebrosa* were included. In the sixth analysis, *S. gigantea* var. *gigantea* and var. *shinnersii* were included.

Many of the specimens included in the analyses had their chromosome number determined, but only some have been published, often under incorrect names. These will all be published or corrected in a set of manuscripts now in preparation reporting chromosome numbers and the cytogeography of *S. altissima*, *S. canadensis*, *S. elongata*, *S. gigantea* and *S. lepida* by the Astereae lab or in collaboration with the J.K. Morton lab. Only ploidy levels are referred to below; details of locations will be included in these manuscripts in preparation.

RESULTS

Five species level a priori groups analysis

The Pearson correlation matrix yielded $r > |0.7|$ for the following pairs of leaf traits reducing the number to be used: 1) mid stem leaf length and upper stem leaf length, 2) mid stem leaf width and upper stem leaf width, 3) number of mid stem leaf margin serrations and number of upper stem leaf margin serrations, 4) ray floret ovary body length at anthesis and disc floret ovary body length at anthesis, 5) ray floret pappus length and disc floret corolla length, 6) ray floret pappus length and disc floret pappus length, and 7) disc floret corolla length and disc floret pappus length. Lower leaves were usually absent and lower leaf traits were excluded from discriminant analyses. Inflorescence length and width traits were highly variable in all species and were not included in the analyses. Length of leaves in the inflorescence and the degree of arching of the lower branches of an inflorescence and the branch density of the inflorescence were used in assigning specimens to an a priori group. For example, specimens of *S. gigantea* typically had broad inflorescences with arching lower branches and overall had the least densely branched inflorescences. The density of stipitate glands were used in assigning specimens to an a priori group. Usually glands were obvious and abundant on either bracts, peduncles and/or phyllaries of specimens of *S. lepida*. Such glands were usually obscure or present in very low numbers in other species. Less glandular specimens of *S. lepida* were sometimes difficult to assign to the *S. lepida* a priori group; these were usually diploid when the ploidy level was known. The size of leaf serrations varied considerably even within a species and on a single shoot. In all species, lower mid stem leaves usually had the largest serrations in the greatest numbers, while upper stem leaves usually had serrations reduced in size and number.

In the STEPWISE discriminant analysis 244 specimens of five species level a priori groups (*Solidago altissima*, *S. canadensis*, *S. elongata*, *S. gigantea*, and *S. lepida*), the following six traits were selected as best separating the groups and are listed in order of decreasing F-to-remove values: ray floret pappus length at anthesis (31.44), number of mid stem leaf serrations (20.26), mid stem leaf width (13.29), number of disc florets (9.82), number of ray florets (6.41), and disc corolla lobe length (5.95). 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 3. F-values based on Mahalanobis distances between group centroids indicated the largest separations were between *S. canadensis* and *S. lepida* (56.513), *S. canadensis* and *S. gigantea* (42.847), and *S. canadensis* and *S. elongata* (33.979), and the least separations were *S. elongata* and *S. lepida* (11.267) and *S. altissima* (var. *gilvocanescens*) and *S. elongata* (11.840).

Table 3. Between groups F-matrix for the five a priori group analysis (df = 6 225).

Group	<i>altissima</i> <i>gilvocanescens</i>	<i>canadensis</i>	<i>elongata</i>	<i>gigantea</i>
<i>canadensis</i>	19.840			
<i>elongata</i>	11.840	33.979		
<i>gigantea</i>	22.931	42.847	20.087	
<i>lepida</i>	13.475	56.513	11.367	17.188

Wilks' lambda = 0.15003 df = 6 4 230; Approx. F= 23.6681 df = 24 786 prob = 0.0000

In the Classificatory Discriminant Analysis of the five species level a priori groups (*Solidago altissima*, *S. canadensis*, *S. elongata*, *S. gigantea*, and *S. lepida*), percents of correct a posteriori assignment to the same a priori group ranged from 89% down to 53%. The Classification matrix and Jackknife classification matrix are presented in Table 4. Results are presented in order of decreasing percents of correct placement. Forty-seven of the 53 specimens of the *S. canadensis* a priori group (89%) were assigned a posteriori to the *S. canadensis* group; 26 specimens with 91-100% probability, 7 specimens with 80-88%, 7 specimens with 70-79%, 3 specimens with 60-68%, 2 specimens with 56-57% probability, and 1 specimen with 47% probability (24% to *S. altissima*, 13% to *S. gigantea* and 11% to *S. lepida*). Six specimens of the *S. canadensis* a priori group were assigned a posteriori to other species: 3 specimens to *S. altissima* with 83% probability (*Semple & Brouillet 2786* WAT from Bruce Co., Ontario; var. *hargerii*), 63% probability (*Semple 9087* WAT from Winnebago Co., Wisconsin; var. *hargerii*), and 52% probability (37% to *S. canadensis*; *Morton & Venn NA10785* WAT from Bruce Co., Ontario; var. *canadensis*); 2 specimens to *S. elongata* with 78% probability (*Morton & Venn NA17617* TRT from Washington Co., Maine) and 44% probability (*Morton & Venn NA8219* WAT from Bruce Co., Ontario; var. *canadensis*); and 1 specimen to *S. gigantea* with 35% probability (26% to *S. altissima*, 25% to *S. canadensis*, and 9% to *S. elongata*; *Melville 401* WAT from Timiskaming Dist., Ontario). Twenty-two of 28 specimens of *S. elongata* (79%) were assigned a posteriori to the *S. elongata* group: 8 specimens with 90-96% probability, 4 specimens with 83-89% probability, 3 specimens with 74-76% probability, 4 specimens with 51-58% probability, and 2 specimens with 45% probability (44% to *S. lepida*; *Semple & Brouillet 7125* WAT from Lincoln Co., Oregon), and 44% probability (28% to *S. gigantea* and 26% to *S. lepida*; *Lomer 6466* WAT from Surrey, British Columbia). Six specimens of the *S. elongata* a priori group were assigned a posteriori to other species groups: 4 specimens to *S. altissima* with 66% probability (*Wells 699* UBC from Tsawwassen, British Columbia), 45% probability (35% *S. elongata* and 18% *S. lepida*; *Semple & Heard 8543* WAT from Medocino Co., California; glabrous lower stem, mid stem moderately short woolly), 39% probability (29% each to *S. elongata* and *S. lepida*; *Semple & Heard 8660* WAT from Tulare Co., California), and 35% probability (29% to *S. lepida*, 23% to *S. elongata* and 13% to *S. gigantea*; *Semple & Brouillet 7114* WAT from Clatsop Co., Oregon; lower stem glabrous, Fig. 1); 1 specimen to *S. canadensis* with 62% probability (19% to *S. altissima* and 17% to *S. elongata*; *Semple & Heard 8492* WAT from San Mateo Co., California); and 1 specimen to *S. lepida* with 56% probability (43% to *S. elongata*; *Semple & Brouillet 7170B* WAT from Lane Co., Oregon; small narrowly lanceolate entire leaves; 2x). Thirty-six of the 48 specimens of the *S. gigantea* a priori group (75%) were assigned a posteriori to the *S. gigantea* group: 13 specimens with 90-100% probability, 9 specimens with 80-88% probability, 4 specimens with 73-79% probability, 5 specimens with 61-69% probability, 2 specimens with 55% probability (16% to *S. altissima*, 15% to *S. elongata*, and 6% to *S. lepida*; *Semple & Keir 4693* WAT from Loggieville, New Brunswick), and 51%

Table 4. Linear and jackknife classification matrices from the Classificatory Discriminant Analysis of five a priori groups; a posteriori placements to groups in rows.

Group	<i>altissima</i>	<i>canadensis</i>	<i>elongata</i>	<i>gigantea</i>	<i>lepida</i>	% correct
<i>altissima</i>	23	3	4	1	1	72
<i>canadensis</i>	3	47	2	1	0	89
<i>elongata</i>	4	1	22	0	1	79
<i>gigantea</i>	2	2	3	36	5	75
<i>lepida</i>	13	0	13	9	39	53
Totals	45	53	44	47	46	71

Jackknifed classification matrix

Group	<i>altissima</i>	<i>canadensis</i>	<i>elongata</i>	<i>gigantea</i>	<i>lepida</i>	% correct
<i>altissima</i>	23	3	4	1	1	72
<i>canadensis</i>	3	47	2	1	0	89
<i>elongata</i>	4	1	21	0	2	75
<i>gigantea</i>	2	2	3	36	5	75
<i>lepida</i>	14	0	14	9	37	50
Totals	46	53	44	47	45	70

probability (40% to *S. lepida*; Melville 984 WAT from Thunder Bay Dist., Ontario; typical *S. gigantea* inflorescence), and 3 specimens with 43% (31% to *S. lepida* and 16% to *S. altissima*; Semple & B. Semple 6178 WAT from Ingolf, Kenora Dist., Ontario; 6x), 42% probability (33% to *S. lepida* and 19% to *S. elongata*; Semple 11517 WAT from Fredericton, New Brunswick; 4x), and 41% probability (23% to *S. altissima*, 16% to *S. lepida*, and 11% to *S. elongata*; Turner 3205 WAT from Fort Saskatchewan, Alberta). Twelve specimens of the *S. gigantea* a priori group plus for additional specimens included a posteriori were assigned a posteriori to other species: 8 specimens to *S. lepida* with 85-41% probability; 3 specimens to *S. elongata* with 90%, 68%, and 67% probabilities; 3 specimens to *S. altissima* with 49% probability (26% to *S. elongata* and 17% to *S. canadensis*; Semple & B. Semple 11489 WAT from Cape Jourmain, New Brunswick), 47% probability (40% to *S. lepida*; Semple 11523 WAT from York Co., New Brunswick), and 30% probability (25% to *S. gigantea*, 23% to *S. lepida* and 21% *S. elongata*; Melville 974 WAT from Thunder Bay Dist., Ontario; 4x); and 2 specimens to *S. canadensis* with 52% probability (33% to *S. gigantea*; Semple et al. 3422 WAT from Rougemont, Québec) and 42% probability (28% to *S. gigantea* and 20% to *S. lepida*; Semple & Brouillet 6984 WAT from Douglas Co., Minnesota; 6x). Twenty-three of 32 specimens of the *S. altissima* var. *gilvocanescens* a priori group (72%) were assigned a posteriori to the *S. altissima* group: 2 specimens with 92% and 96% probabilities, 7 specimens with 80-89% probability, 2 specimens with 76% and 78% probabilities, 1 specimen with 67% probability, and 4 specimens with 59% probability (16% to *S. canadensis* and 15% to *S. elongata*; Morton & Venn NA15663 TRT from Mower Co., Minnesota; 4x), 57% probability (41% to Morton & Venn NA16028 TRT from Scott Co., Iowa; 2x) 56% probability (41% to *S. canadensis*; Semple et al. 9210 WAT from Carbon Co., Wyoming; 4x), and 49% probability (31% to *S. elongata*; Morton & Venn NA15672 from Rock Co., Iowa; 4x). Nine specimens of the *S. altissima* var. *gilvocanescens* a priori group were assigned to other species: 4 specimens to *S. elongata* with 63% probability (19% to *S. altissima* and 11% to *S. lepida*; Semple & B. Semple 11389 WAT from Glacier Co., Montana; 4x), 48% probability (39% to *S. altissima*; Semple & B. Semple 10645 WAT from Ste. Agathe, Manitoba; 2x), 44% probability (34% to *S. altissima*; Morton & Venn NA16303 from Canadian Co., Oklahoma), and 37% probability (30% *S. altissima* and 32% *S. lepida*; Semple et al. 9208 WAT from Carbon Co.,

Wyoming; 4x); 3 specimens were assigned to *S. canadensis* with 82% probability (6% each to *S. bicolor*; 66), 79% probability (22% to *S. roanensis*; 77), and 76% probability (36% to *S. roanensis*; 66); 1 specimen to *S. gigantea* with 72% probability (20% to *S. lepida*; Cannings s.n. UBC from Penticton, British Columbia; 33 cm tall shoot with indument typical of var. *gilvocanescens* but large leaves for size of plant); and 1 specimen to *S. lepida* 53% probability (22% to *S. elongata* and 21% to *S. altissima*; Semple & K. Shea 1926 WAT from Balgonie, Saskatchewan; indument of var. *gilvocanescens*). Thirty-nine of 74 specimens of the *S. lepida* a priori group (53%) plus 5 additional specimens added a posteriori were assigned a posteriori to the *S. lepida* group: 6 specimens with 91-96% probability, 8 specimens with 80-89% probability, 4 specimens with 71-78% probability, 10 specimens with 61-69% probability, 6 specimens with 50-58% probability, and 4 specimens with 48% probability (32% to *S. gigantea* and 19% to *S. altissima*; Semple & B. Semple 5817 WAT from Boulder Co., Colorado; 6x), 48% probability (Semple & Brouillet 7209 WAT from Teton Co., Wyoming; 6x), 44% probability (38% to *S. altissima* and 14% to *S. canadensis*; Oldham & Sutherland 24798 WAT from Polar Bear Prov. Park, Ontario), and 36% probability (34% to *S. altissima* and 18% to *S. elongata*; Ringius et al. 940 WAT from Kapiskau R. near James Bay, Kenora Dist., Ontario). Thirty-four specimens of the *S. lepida* a priori group plus 1 specimen added a posteriori were assigned a posteriori to other species: 14 specimens were assigned to *S. altissima* var. *gilvocanescens* with 49-80% probability (none had the stem indument of var. *gilvocanescens*); 13 specimens were assigned to *S. elongata* with 40-80% probability; 9 specimens were assigned to *S. gigantea* with 40-91% probability.

Two dimensional plots of CAN1 versus CAN3 and CAN1 versus CAN2 canonical scores for 244 specimens of *Solidago altissima* var. *gilvocanescens*, *S. canadensis*, *S. elongata*, *S. gigantea*, and *S. lepida* are presented in Fig. 17. Eigenvalues on the first three axes were 1.688, 0.682 and 0.284.

Three species level a priori groups analysis

The Pearson correlation matrix yielded $r > |0.7|$ for the following pairs of leaf traits reducing the number to be used: mid stem leaf length and upper stem leaf length, number of mid stem leaf margin serrations and number of upper stem leaf margin serrations, and ray floret ovary body length at anthesis and disc floret ovary body length at anthesis. Mid stem leaf length, number of upper stem leaf margin serrations, and disc floret ovary body length at anthesis were included in the analysis.

In the STEPWISE discriminant analysis of 150 specimens of three species level a priori groups (*Solidago elongata*, *S. gigantea*, and *S. lepida*), the following seven traits were selected as best separating the groups and are listed in order of decreasing F-to-remove values: number of upper stem leaf margin serrations (33.01), mid stem leaf length (22.15), disc corolla lobe length (10.26), involucre height (7.39), number of ray florets (5.57), disc corolla length (4.48), and ray floret lamina length (4.26). 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 5. F-values based on Mahalanobis distances between group centroids indicated the largest separation was between *S. elongata* and *S. gigantea* (21.892), and the least separations were between *S. gigantea* and *S. lepida* (12.862) and *S. elongata* and *S. lepida* (13.818).

In the Classificatory Discriminant Analysis of 150 specimens of the three species level a priori groups (*Solidago elongata*, *S. gigantea*, and *S. lepida*), percents of correct a posteriori assignment to the same a priori group ranged from 68-100%. The Classification matrix and Jackknife classification matrix are presented in Table 6. Results are presented in order of decreasing percents of correct placement. All 28 specimens of the *S. elongata* a priori group

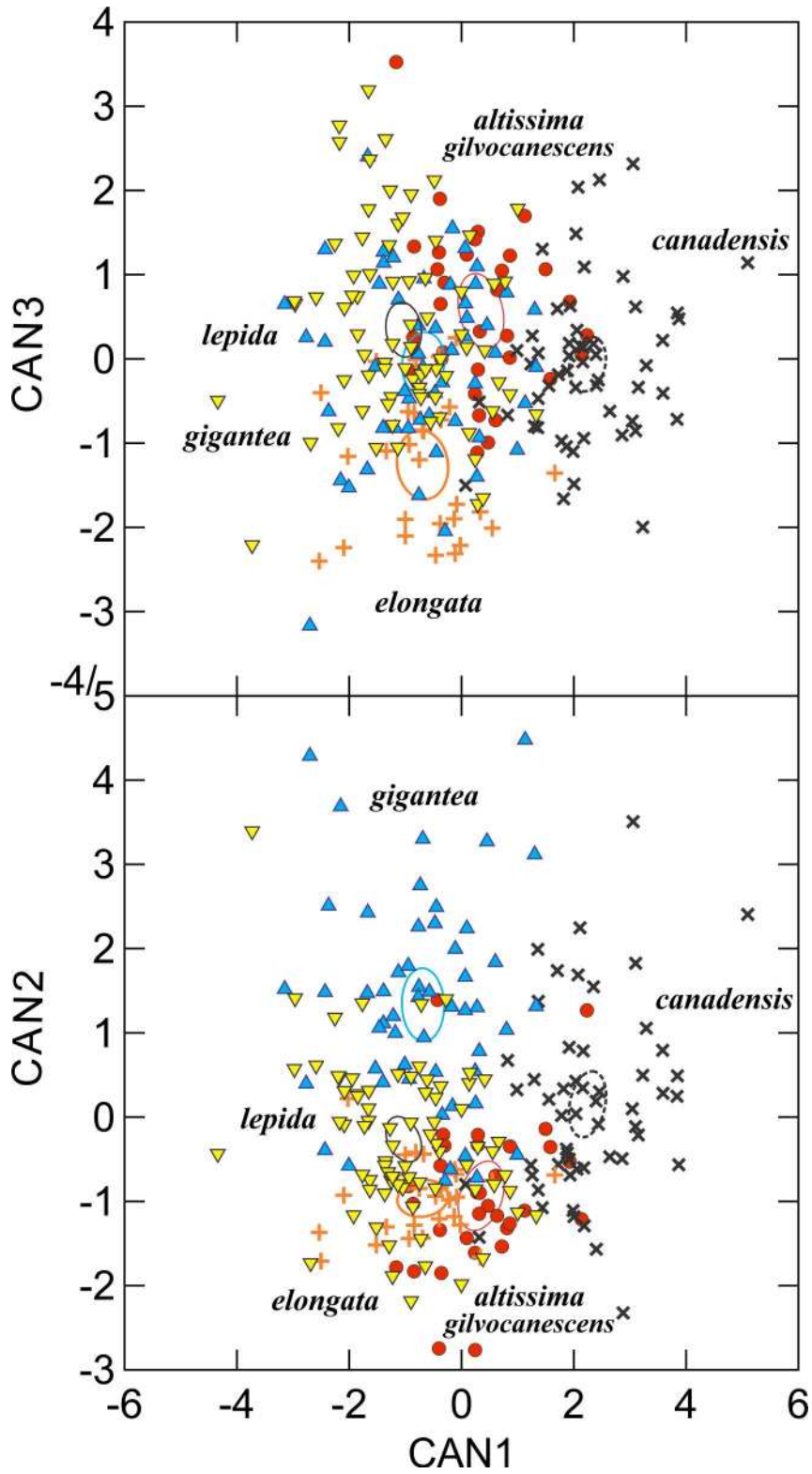


Figure 17. Two dimension plots of CAN1 versus CAN2 and CAN1 versus CAN3 scores generated by the Canonical Analysis of 244 specimens of *Solidago altissima* var. *gilvocanescens* (red dots), *S. canadensis* (Xs), *S. elongata* (+s), *S. gigantea* (blue triangles), and *S. lepida* (inverted yellow triangles); 95% confidence ellipses are shown for each taxon.

Table 5. Between groups F-matrix for the five a priori groups analysis (df = 7 141).

Group	<i>elongata</i>	<i>gigantea</i>
<i>gigantea</i>	21.892	
<i>lepida</i>	13.818	12.862

Wilks' lambda = 0.3309 df = 7 2 147; Approx. F= 14.8734 df = 14 282 prob = 0.0000

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	<i>elongata</i>	<i>gigantea</i>	<i>lepida</i>	% correct
<i>elongata</i>	28	0	0	100
<i>gigantea</i>	3	36	9	75
<i>lepida</i>	11	13	50	68
Totals	42	49	59	76

Jackknifed classification matrix

Group	<i>elongata</i>	<i>gigantea</i>	<i>lepida</i>	% correct
<i>elongata</i>	26	0	2	93
<i>gigantea</i>	4	36	8	75
<i>lepida</i>	12	14	48	65
Totals	42	50	58	73

(100%) were assigned a posteriori into the *S. elongata* group; 14 specimens with 92-99% probability, 4 specimen with 80-85% probability, 2specimens with 72% and 79% probabilities, 7 specimens with 60-68% probability (including *Semple & Brouillet 7114* WAT), and 1 specimen with 49% probability (49% to *S. lepida*; *Wells 699* UBC from Tsawwassen, British Columbia). Thirty-six of the 48 specimens of the *S. gigantea* a priori group (75%) plus 7 additional specimens included a posteriori were assigned a posteriori to the *S. gigantea* group; 21 specimens with 90-100% probability, 7 specimens with 81-89% probability, 6 specimens with 72-76% probability, 1 specimens with 67% probability, and 2 specimen with 59% probability (*Semple & Brouillet 4507* TRT from Adair Co., Iowa; tall shoot with glabrous stem, lanceolate leaves, and a large open secund conical inflorescence with long diverging lower branches; 6x) and 57% probability (195). Twelve specimens of the *S. gigantea* a priori group were assigned to other species: 12 specimens to *S. lepida* with 83% probability (*Morton & Venn NA17577* TRT from Gaspé Peninsula, Québec; open secund conical inflorescence with some glands; 4x), 81% probability (*Semple & B. Semple 11489* WAT from Cape Jourimain, New Brunswick; small leafy inflorescence with short diverging lower branches; 2x), 72% probability (*Morton & Venn NA14185* TRT from Maidstone, Saskatchewan; broadly oblanceolate mid stem leaves to lanceolate upper stem leaves; 6x), 63% probability (*Semple & B. Semple 6718* WAT from Ingolf, Kenora Dist., Ontario; leaves are lanceolate; 6x), 59% probability (*Cheek 1987* NH from KwalZulu-Natal South Africa; typical looking *S. gigantea*, not glandular), 56% probability (*Semple & Brouillet 7292* WAT from Bent Co., Colorado; leaves are lanceolate to narrowly lanceolate; 6x), 56% probability (*Morton NA18706* TRT from Crawford Co., Ohio; narrow lanceolate leaves with few small margin serrations, not glandular; 4x), 55% probability (*Morton & Venn NA17597* TRT Gaspé Peninsula, Québec; open elongated secund conical inflorescence with some glands; 4x), 53% probability (*Semple & Brammall 2743* WAT from Hughes Co., Oklahoma; narrow

lanceolate leaves, open leafy inflorescence with diverging lower branches, glands on peduncles, bracts and phyllaries; 6x), and 35% probability (*Semple & Brouillet 4173* WAT from Bagot, Manitoba; broad oblanceolate to lanceolate leaves, open secund conical inflorescence; 6x); and 3 specimens to *S. elongata* with 94% probability (*Semple & B. Semple 11489* WAT from Cape Jourimain, New Brunswick; small leafy inflorescence with short diverging lower branches; 2x; first of two shoots of this collection), 91% probability (*Semple & B. Semple 11489* WAT from Cape Jourimain, New Brunswick 2x; second of two shoots of this collection), and 88% probability (*Morton & Venn NA14213* TRT from Roblin, Manitoba; treated as *S. gigantea* but subsequently annotated as *S. lepida* aff. var. *lepida*; ascending diverging lower inflorescence branches, glandular; 6x). Fifty of the 74 specimens of the *S. lepida* a priori group (68%) plus 6 additional specimens added a posteriori were assigned a posteriori to the *S. lepida* group: 12 specimens with 92-100% probability, 7 specimens with 83-89% probability, 7 specimens with 70-79% probability, 12 specimen with 60-68% probability, and 7 specimens with 59% probability (*Bell & Davidson 27* UBC from Fernie, British Columbia; var. *salebrosa*; lanceolate leaves reduced distally, secund conical inflorescence, heads with small involucre with some glands), 59% probability (*Semple & B. Semple 5817* WAT from Boulder Co., Colorado; 6x), 57% probability (*Semple & B. Semple 11367* WAT from Custer Co., Idaho; var. *lepida*; 2x), 53% probability (*Semple & Brouillet 7066* WAT from Valley Co., Idaho; var. *lepida* with ascending branches in small glandular inflorescence; 6x), 52% probability (*Semple et al. 11157* WAT from Wildmint Hot Springs, Nahanni Nat. Park Reserve, Northwest Territories; var. *salerosa*; 2x), 50 % probability (*Chmielewski et al CC4714* WAT from N of Good Hope, British Columbia; var. *lepida* with very leafy inflorescence; 4x), and 50% probability (*Oldham & Sutherland 24798* WAT from Polar Bear Prov. Park, Ontario). Twenty-four specimens of the *S. lepida* a priori group plus one additional specimen added a posteriori were assigned a posteriori to the other groups: 13 specimens to *S. gigantea* with 88% probability (*Semple & Brouillet 7064* WAT from Boise Co., Idaho; var. *salebrosa* with sparsely pubescent mid and upper stem and glands in inflorescence; 6x), 83% probability (*Semple & Brouillet 7203* WAT; Teton Co., Wyoming; var. *salebrosa*; 6x), 74% probability (*Semple & Xiang 10329* WAT from Belt Mts., Broadwater Co., Montana; var. *lepida* with long ascending lower branches in leafy inflorescence; 6x), 68% probability (*Morton & Venn NA14185* TRT from Maidstone, Saskatchewan; var. *lepida* with glands on upper leaves, bracts and phyllaries), 67% probability (*Semple 10312* WAT from Powell Co., Montana; var. *lepida*; 6x), 61% probability (*Morton & Venn NA15876* TRT wild from Coconino Co., Arizona; var. *salebrosa*, a robust shoot with pubescent mid and upper stem and a narrow secund conical inflorescence; 6x), 60% probability (*Semple & Brouillet 4410* WAT from Lolo Pass, Idaho Co., Idaho; var. *salebrosa* with sparsely pubescent lower mid stem and densely so upper stem; 2x), 57% probability (*Morton & Venn NA14159* TRT from SE of Whitecourt, Alberta; var. *lepida* with leafy inflorescence with short ascending branches), 56% probability (*Semple & B. Semple 10622* WAT from NW of Jakey, Yukon Territory; var. *lepida*; 4x), 53% probability (*Morton & Venn NA13644* TRT from W of Vanderhoof, British Columbia; var. *lepida* with sparsely woolly stem and large inflorescence with long ascending branches; 6x), 43% probability (Rogers s.n. UBC from N of Trail, British Columbia; var. *salebrosa* with sparsely woolly proximally to densely woolly-strigose distally stem and a broadly spreading secund conical glandular inflorescence), 42% probability (*Morton & Venn NA14195* TRT from Battleford, Saskatchewan; *S. gigantea* like inflorescence but glandular; 6x), and 40% probability (*Semple & Brouillet 4381* WAT from Boundary Co., Idaho; var. *salebrosa*; lanceolate leaves with large serrations; 2x); and 11 specimens to *S. elongata* with 86% probability (*Eastham s.n.* UBC from between Kimberley and Fairmont, British Columbia; a small shoot with small heads; var. *salebrosa*), 82% probability (*Semple 11376* MONTU from Lake Co. Montana; var. *salebrosa*; 2x), 79% probability (Melville BC6 WAT from Surrey, British Columbia; var. *lepida*; 6x), 78% probability

(Semple & Xiang 10239 WAT from Carbon Co., Montana; var. *salebrosa*; 4x), 69% probability (Chmielewski et al CC4760 WAT from Kitwanga, British Columbia; var. *lepida*), 69% probability (Semple 11371 WAT from Lake Co., Montana; var. *salebrosa*; 2x), 65% probability (Semple & Brouillet 4305 WAT from Nojack, Alberta; var. *lepida* with sparsely villous-strigose mid stem and leafy inflorescence with ascending branches), 62% probability (Semple et al. 11169 WAT from Meilleur River Hotsprings, Nahanni Nat. Park Reserve, Northwest Territories; var. *lepida*; 2x), 56% probability (Semple & Semple & B. Semple 5817 WAT from Boulder Co., Colorado; var. *lepida* with small glandular inflorescence; 6x), and 55% probability (Morton & Venn NA14151 TRT from N of Wonowon, British Columbia; var. *lepida* with broadly lanceolate to narrowly ovate leaves and about average height involucre; 6x).

A two dimensional plot of CAN1 versus CAN2 canonical scores for 150 specimens of *Solidago elongata*, *S. gigantea*, and *S. lepida* is presented in Fig. 18. Eigenvalues on the first two axes were 1.092 and 0.445. Figure 19 is the same plot as Fig. 18 but with different symbols for the two varieties of *S. lepida*.

Two species level a priori groups analysis I

The Pearson correlation matrix of specimens of *Solidago elongata* and *S. lepida* yielded $r > |0.7|$ for the following pairs of leaf traits reducing the number to be used: mid stem leaf length and upper stem leaf length, mid stem leaf length and upper stem leaf width, mid stem leaf width and upper stem leaf width, and ray floret ovary body length at anthesis and disc floret ovary body length at anthesis. Midstem stem leaf length and disc floret ovary body length at anthesis were included in the analysis.

In the STEPWISE discriminant analysis of 93 specimens of *Solidago elongata* and *S. lepida*, the following five traits selected in a STEPWISE analysis are listed in order of decreasing F-to-remove values: mid leaf length (22.37), disc lobe length (20.74), number of upper leaf margin serrations (11.81), disc corolla length (6.42), and number of ray florets (4.08). 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 elongata* and *S. lepida* had an F-to separate value of 16.977 (Wilks' lambda = 0.5062 df = 5 1 91; Approx. F= 16.9770 df = 5 87 prob. 0.0000).

In the Classificatory Discriminant Analysis of the two species level a priori groups, percents of correct a posteriori assignment to the same a priori group were 96% for *Solidago elongata* and 82% for *S. lepida*. The Classification matrix and Jackknife classification matrix are presented in Table 7. Twenty-four of the 25 specimens of *S. elongata* were assigned a posteriori to *S. elongata*: 14 specimens with 93-99% probability, 4 specimens with 80-84% probability, 5 specimens with 70-77% probability (including Semple & Brouillet 7114 WAT), and 1 specimen with 55% probability (Semple & Brouillet 7132 WAT from Klamath Co., Oregon). One specimen of the *S. elongata* a priori group was assigned to *S. lepida* with 56% probability (Wells 699 UBC from Tsawwassen, British Columbia; 110 cm tall shoot, mid to upper stem densely short hairy, inflorescence small but broadly secund conical; growing in very moist soil). Fifty-six of the 68 specimens of *S. lepida* were assigned a posteriori to the *S. lepida* group: 38 specimens with 92-100% probability, 12 specimens with 80-89% probability, 5 specimens with 70-79% probability, 2 specimens with 65% and 69% probabilities, and 3 specimens with 59% probability (Morton & Venn NA15876 TRT cult. transplant from Coconino Co., Arizona; var. *salebrosa*; very robust lower and mid stem leaves; wild pressed shoot was assigned to *S. lepida* with 78% probability and was a robust shoot with a narrow secund conical inflorescence), 57% probability (Semple et al. 9238 WAT from Summit Co., Utah; var. *salebrosa*; 6x), and 54% probability (Morton & Venn NA14123 TRT from Liard Hot Springs, British Columbia; var. *lepida*; 6x).

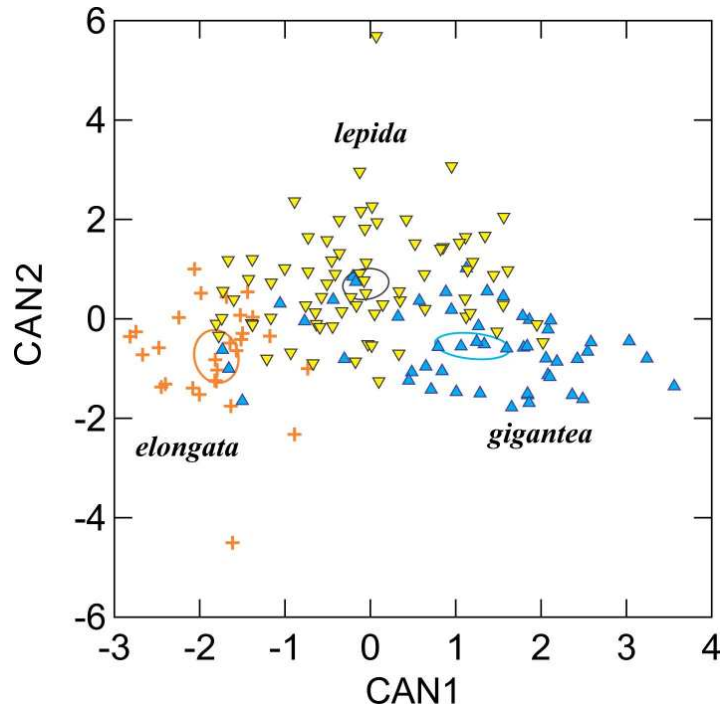


Figure 18. Two dimension plot of CAN1 versus CAN2 scores for 150 specimens of three priori groups of the *Solidago elongata* (orange +s), *S. gigantea* (blue triangles), and *S. lepida* (yellow inverted triangles); 95% confidence ellipses are shown for each taxon.

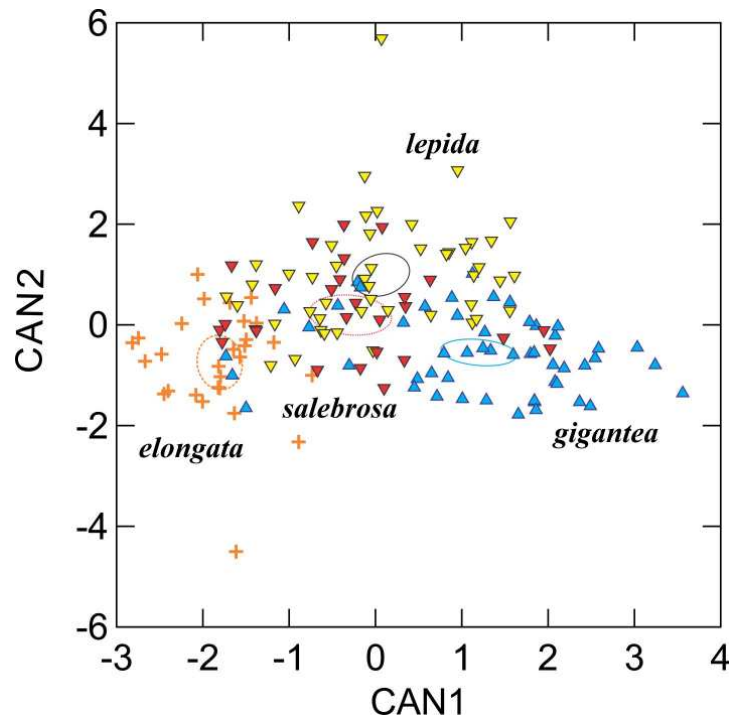


Figure 19. Two dimension plot of CAN1 versus CAN2 scores as in Fig. 17: *Solidago elongata* (orange +s), *S. gigantea* (blue triangles), and *S. lepida* var. *lepida* (yellow inverted triangles) and *S. lepida* var. *salebrosa* (red inverted triangles); 95% confidence ellipses are shown for each taxon.

Twelve specimens of the *S. lepida* a priori group were assigned a posteriori to *S. elongata* with the following probabilities: 91% probability (*Eastham s.n.* UBC from between Kimberley and Fairmont, British Columbia; a small shoot with small heads; var. *salebrosa*), 86% probability (*Semple 11376* WAT from Lake Co., Montana; small shoot, var. *salebrosa*; 2x), 85% probability (*Semple & B. Semple 11367* WAT from Custer Co., Idaho; var. *lepida*; 2x), 83% probability (*Semple 11376 MONTU* from Lake Co. Montana; var. *salebrosa*; 2x), 83% probability (*Semple et al. 11169* WAT from Meilleur River Hotsprings, Nahanni Nat. Park Reserve, Northwest Territories; var. *lepida*; 2x), 77% probability (*Semple & Brouillet 4305* WAT from Nojack, Alberta; var. *lepida*; average height involucre), 76% probability (*Semple 11376* WAT from Lake Co. Montana; var. *salebrosa*; 2x), 75% probability (*Semple & Xiang 10239* WAT from Carbon Co., Montana; var. *salebrosa*; 4x), 69% probability (*Morton & Venn NA14151* TRT from N of Wonowon, British Columbia; var. *lepida* with broadly lanceolate to narrowly ovate leaves; 6x), 68% probability (*Melville BC6* WAT from Surrey, British Columbia; var. *lepida*; 6x), 60% probability (*Eastham s.n.* UBC from Waitabit Creek, British Columbia; a small shoot with small heads; var. *salebrosa*), and 44% probability (*Semple & Brouillet 4376* WAT from Moyie, British Columbia; var. *salebrosa*; 2x).

Frequencies of CAN1 canonical scores for 93 specimens of *Solidago elongata* and *S. lepida* are presented in histograms in Fig. 20. The Eigenvalue on the first axis was 0.976.

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

Group	<i>elongata</i>	<i>lepida</i>	% correct
<i>elongata</i>	24	1	96
<i>lepida</i>	12	56	82
Totals	36	57	86

Jackknifed classification matrix

Group	<i>elongata</i>	<i>lepida</i>	% correct
<i>elongata</i>	24	1	96
<i>lepida</i>	12	56	82
Totals	36	57	86

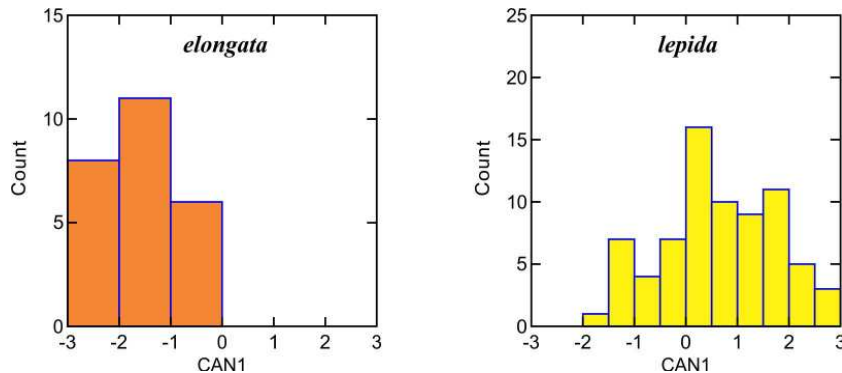


Figure 20. Histograms of the frequencies of CAN1 scores for 93 specimens of *Solidago elongata* and *S. lepida*.

Two species level a priori groups analysis II

The Pearson correlation matrix for data on *Solidago gigantea* and *S. lepida* yielded $r > |0.7|$ for the following three pairs of leaf traits reducing the number to be used: mid stem leaf length and upper stem leaf length, ray floret ovary body length at anthesis and disc floret ovary body length at anthesis, and ray floret pappus length and disc floret pappus length. Mid stem leaf length, disc floret ovary body length at anthesis, and disc floret pappus length were included in the discriminant analysis.

In the STEPWISE discriminant analysis of 116 specimens of *S. gigantea* and *S. lepida*, the following six traits selected in a STEPWISE analysis are listed in order of decreasing F-to-remove values: number of mid stem leaf margin serrations (19.52), ray floret lamina length (9.75), disc floret pappus length at anthesis (6.52), number of ray florets (5.96), involucre height (5.30), and number of upper stem leaf margin serrations (4.18). 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 gigantea* and *S. lepida* had an F-to separate value of 19.2000 (Wilks' lambda = 0.4862 df = 6 1 114; Approx. F = 19.2000 df = 6 109 prob. 0.0000).

In the Classificatory Discriminant Analysis of the two species level a priori groups, percents of correct a posteriori assignment to the same a priori group were 87% for *S. lepida* and 81% for *S. gigantea*. The Classification matrix and Jackknife classification matrix are presented in Table 8. Fifty-nine of the 68 specimens of *S. lepida* plus 5 additional specimens included a posteriori were assigned a posteriori to *S. lepida*: 35 specimens with 90-100% probability, 6 specimens with 81-89% probability, 84 specimen with 70-78% probability, 5 specimens with 60-68% probability, and 2 specimens with 53% probability (*Morton & Venn NA14185* TRT from Maidstone, Saskatchewan; var. *lepida* with glands on upper leaves, bracts and phyllaries) and 51% probability (*Semple & Brouillet 4381* WAT from Boundary Co., Idaho; var. *salebrosa*; lanceolate leaves with large serrations; 2x). Nine specimens of the *S. lepida* a priori group were assigned to *S. gigantea*: with 86% probability (*Semple & Brouillet 4416* WAT from Missoula Co., Montana; var. *salebrosa* with lanceolate leaves with big serrations and small involucre), 84% probability (*Semple & B. Semple 5817* WAT from Boulder Co., Colorado; var. *lepida* with broadly lanceolate leaves and small club-shaped inflorescence with glands; 6x), 69% probability (*Semple & Brouillet 7203* WAT; Teton Co., Wyoming; var. *salebrosa*; 6x), 69% probability (*Semple & Heard 8130* WAT; Lincoln Co., New Mexico; var. *lepida* with ascending lower branches in inflorescence; 6x), 60% probability (*Semple & Brouillet 7066* WAT from Valley Co., Idaho; var. *lepida* with ascending branches in small glandular inflorescence; 6x), 60% probability (*Semple & Xiang 10329* WAT from Belt Mts., Broadwater Co., Montana; var. *lepida* with long ascending lower branches in leafy inflorescence; 6x), 57% probability (*Semple & Brouillet 7064* WAT from Boise Co., Idaho; var. *salebrosa* with sparsely pubescent mid and upper stem and glands in inflorescence; 6x), 52% probability (*Morton & Venn NA15876* TRT cult. transplant from Coconino Co., Arizona; var. *salebrosa*; very robust lower and mid stem leaves; 6x), and 52% probability (*Semple & Xiang 10243* WAT from Gallatin Co., Montana; var. *lepida* with large leaves in glandular inflorescence with ascending branches; 6x). Thirty-nine of the 48 specimens of *S. gigantea* were assigned a posteriori to the *S. gigantea* group: 24 specimens with 90-100% probability, 6 specimens with 83-88% probability, 4 specimen with 70-78% probability, 4 specimens with 63-69% probability, and 2 specimens with 54% probability (*Semple & Brouillet 6948* WAT from Douglas Co., Minnesota; glabrous upper stem, narrow upper stem lanceolate leaves with many large serrations and a damaged inflorescence with spreading arching branches; 6x) and 51% probability (*Cheek 1988* NH from KwalZulu-Natal, South Africa; this is a rather typical looks *S. gigantea* upper shoot). Nine specimens of the *S. gigantea* a priori group with yellow rays were assigned a posteriori to *S. lepida*: with 95% probability (*Morton & Venn NA14213* TRT from Roblin, Manitoba; treated as *S. gigantea* but subsequently annotated as *S. lepida* aff. var. *lepida*; ascending

diverging lower inflorescence branches, glandular; 6x), 95% probability (*Morton NA18706* TRT from Crawford Co., Ohio; narrow lanceolate leaves with few small margin serrations, not glandular; 4x), 86% probability (*Semple 11523* WAT from York Co., New Brunswick; very sparsely glandular in narrow inflorescence), 78% probability (*Semple & Brouillet 7292* WAT from Bent Co., Colorado; leaves are lanceolate to narrowly lanceolate; 6x), 60% probability (*Cheek 1987* NH from KwaZulu-Natal South Africa; typical looking *S. gigantea*, not glandular), 59% probability (*Melville 984* WAT from Thunder Bay Dist., Ontario; leafy inflorescence with ascending-diverging branches; 4x), 58% probability (*Semple & B. Semple 11489* WAT from Cape Jourimain, New Brunswick; small leafy inflorescence with short diverging lower branches; 2x), 55% probability (*Melville 1666* WAT from Moosonee, Cochran Dist., Ontario; open inflorescence with ascending lower branches; 4x), and 51% probability (*Semple & B. Semple 6718* WAT from Ingolf, Kenora Dist., Ontario; leaves are lanceolate; 6x).

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

Group	<i>gigantea</i>	<i>lepida</i>	% correct
<i>gigantea</i>	39	9	81
<i>lepida</i>	9	59	87
Totals	48	68	84

Jackknifed classification matrix

Group	<i>gigantea</i>	<i>lepida</i>	% correct
<i>gigantea</i>	39	9	81
<i>lepida</i>	11	57	84
Totals	50	66	83

Frequencies of CAN1 canonical scores for 116 specimens of *S. gigantea* and *S. lepida* are presented in histograms in Fig. 21. The Eigenvalue on the first axis was 1.057.

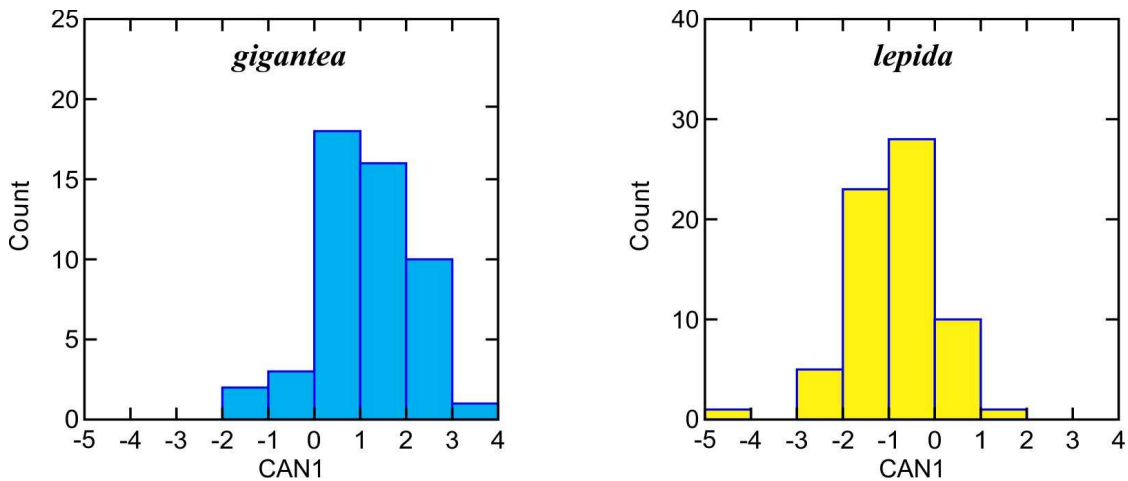


Figure 21. Histograms of the frequencies of CAN1 scores for 116 specimens of *Solidago gigantea* and *S. lepida*.

Two varietal level a priori groups analysis of *Solidago lepida*

The Pearson correlation matrix for data on *Solidago lepida* yielded $r > |0.7|$ for the following four pairs of leaf traits reducing the number to be used: mid stem leaf length and upper stem leaf length, mid stem leaf width and upper stem leaf width, ray floret ovary body length at anthesis and disc floret ovary body length at anthesis, and ray floret pappus length and disc floret pappus length. Mid stem leaf length, mid stem leaf width, disc floret ovary body length at anthesis, and disc floret pappus length with included in the discriminant analysis.

In the STEPWISE discriminant analysis of 74 specimens of *Solidago lepida* var. *lepida* and *S. lepida* var. *salebrosa*, the following three traits selected in a STEPWISE analysis are listed in order of decreasing F-to-remove values: upper leaf width (24.85), number of mid stem leaf margin serrations (10.85), and disc floret ovary body length at anthesis (5.95). 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 var. *lepida* and var. *salebrosa* had an F-to separate value of 12.994 (Wilks' lambda = 0.6423 df = 3 1 721; Approx. F= 12.9943 df = 3 70 prob. 0.0000).

In the Classificatory Discriminant Analysis of the two species level a priori groups, percents of correct a posteriori assignment to the same a priori group were 90% for var. *salebrosa* and 73% for var. *lepida*. The Classification matrix and Jackknife classification matrix are presented in Table 9. Twenty-seven of the 30 specimens of var. *salebrosa* were assigned a posteriori to the var. *salebrosa* group: 5 specimens with 90-97% probability, 8 specimens with 80-89% probability, 8 specimens with 72-79% probability, 4 specimens with 61-67% probability, and 2 specimens with 55% probability (*Semple & Brouillet* 7203 WAT; Teton Co., Wyoming; var. *salebrosa*; 6x) and 53% probability (*Semple* 11376 WAT from Lake Co., Montana; small shoot with a narrow elongated inflorescence with ascending short branches longer than the subtending leaves; 2x). Three specimens of the var. *salebrosa* a priori group were assigned a posteriori to var. *lepida*: 1 specimen with 93% probability (*Morton & Venn* NA14195 TRT from Battleford, Saskatchewan; var. *salebrosa* like inflorescence but glandular; 6x), 1 specimen with 90% probability (*Semple & Xiang* 10324 WAT from Edith Lake, Belt Mts., Broadwater Co., Montana; leafy broadly secund conical inflorescence with ascending arching lower branches; 6x; Fig. 11), and 1 specimen with 73% probability (*Morton & Venn* NA15876 TRT wild from Coconino Co., Arizona; var. *salebrosa*, a robust shoot with pubescent mid and upper stem and a narrow secund conical inflorescence; 6x). Thirty-two of the 44 specimens of var. *lepida* were assigned a posteriori to var. *lepida*: 10 specimens with 91-99% probability, 10 specimens with 80-89% probability, 5 specimens with 70-78% probability, 3 specimens with 62-67% probability, and 3 specimens with 56% probability (*Ringius et al.* 940 WAT from Kapiskau R. near James Bay, Kenora Dist., Ontario; upper stem leaves are much reduced in the narrow inflorescence with ascending branches), 56% probability (*Chmielewski et al* CC4714 WAT from N of Good Hope, British Columbia; very leafy inflorescence with ascending lower branches; 4x) and 51% probability (*Oldham* 36842 WAT from Kenogami River junction with Little Drowning River, Thunder Bay Dist., Ontario; open leafy inflorescences with ascending arching lower branches). Twelve specimens of the var. *lepida* a priori group were assigned to var. *salebrosa* with 95% probability (*Chmielewski et al* CC4231 WAT from Fairbanks, Alaska; leafy lower inflorescence, lower branches ascending or diverging; 2x), 83% probability (*Semple & Brouillet* 7066 WAT from Valley Co., Idaho; ascending branches in small glandular inflorescence; 6x), 79% probability (*Semple & Heard* 8130 WAT; Lincoln Co., New Mexico; ascending lower branches in inflorescence; 6x), 73% probability (*Semple et al.* 11167 WAT, Virginia Falls float plane landing dock area, Nahanni Nat. Park. Reserve, Northwest Territories; small plant with small inflorescence with ascending lower branches 2x; Fig 7), 61% probability (*Chmielewski et al* CC4285 WAT from Dalton Hwy at Yukon River, Alaska; small secund conical inflorescence and secund shoot with more club shaped inflorescence with ascending

branches; 2x), 61% probability (*Semple & B. Semple 11367* WAT from Custer Co., Idaho; leafy inflorescence with long ascending lower branches; 2x), 57% probability (*Oldham & Sutherland 25798* WAT from Polar Bear Prov. Park; small conical inflorescence with short spreading branches), 54% probability (*Morton & Venn NA14171* TRT from Elk Is. Nat. Park, Alberta; much reduce stem sparsely villous-strigose mid stem to more densely so distally, leaves just below small conical inflorescence; 6x), 54% probability (*Semple & Brouillet 4305* WAT from W of Nojack, Alberta; broad club shaped inflorescence with ascending to ascending arching branches), 52% probability (*Semple et al. 11167* WAT, Virginia Falls float plane landing dock area, Nahanni Nat. Park. Reserve, Northwest Territories; second shoot on sheet, small plant with small inflorescence with ascending lower branches 2x; Fig 7), 51% probability (55), and 51% probability (*Oldham & Sutherland 24804* WAT from Polar Bear Prov. Park, Ontario; leafy inflorescence with short ascending diverging lower branches).

Table 9. Linear and jackknife classification matrices from the Classificatory Discriminant Analysis of two varietal level a priori groups; a posteriori placements to groups in rows.

Group	<i>lepida</i>	<i>salebrosa</i>	% correct
<i>lepida</i>	32	12	73
<i>salebrosa</i>	3	27	90
Totals	35	39	80

Jackknifed classification matrix

Group	<i>lepida</i>	<i>salebrosa</i>	% correct
<i>lepida</i>	31	13	70
<i>salebrosa</i>	4	26	87
Totals	35	39	77

Frequencies of CAN1 canonical scores for 74 specimens of *S. lepida* var. *lepida* and var. *salebrosa* are presented in histograms in Fig. 22. The Eigenvalue on the first axis was 0.557.

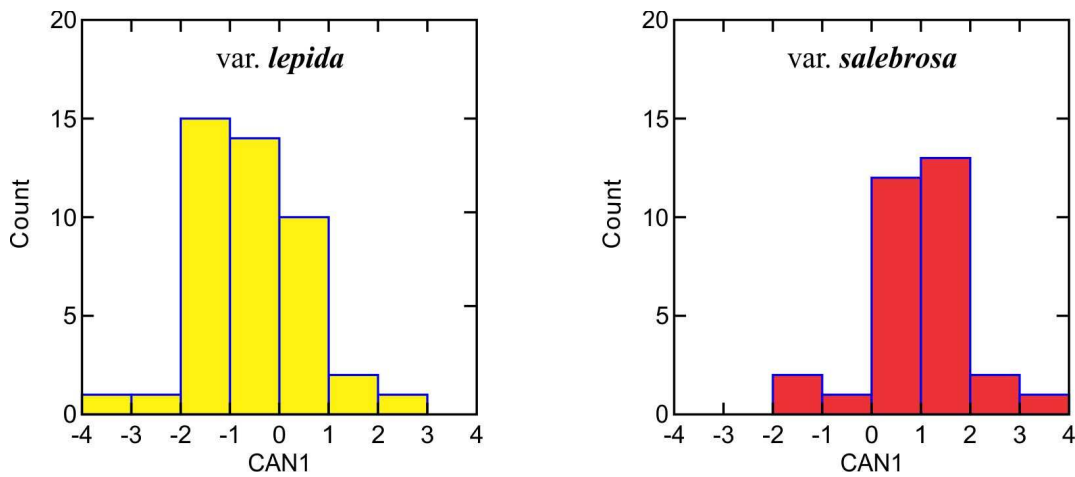


Figure 22. Histograms of the frequencies of CAN1 scores for 93 specimens of *Solidago lepida* var. *lepida* and var. *salebrosa*.

Two varietal level a priori groups analysis of *Solidago gigantea*

In the STEPWISE discriminant analysis of 49 specimens of *Solidago gigantea* var. *gigantea* and *S. gigantea* var. *shinersii*, the following five traits selected in a STEPWISE analysis are listed in order of decreasing F-to-remove values: mid stem leaf width (11.42), upper leaf width (10.07), upper stem leaf length (9.21), outer phyllary length (4.29), and ray floret ovary length at anthesis (4.18). 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 var. *gigantea* and var. *shinersii* had an F-to separate value of 9.437 (Wilks' lambda = 0.4768 df = 5 1 47; Approx. F= 9.4365 df = 5 43 prob. 0.0000).

In the Classificatory Discriminant Analysis of the two varietal level a priori groups, percents of correct a posteriori assignment to the same a priori group were 91% for var. *gigantea* and 87% for var. *shinersii*. The Classification matrix and Jackknife classification matrix are presented in Table 10. Thirty-one of the 34 specimens of var. *gigantea* were assigned a posteriori to var. *gigantea*: 19 specimens with 93-100% probability, 4 specimens with 80-889% probability, 6 specimens with 70-77% probability, 1 specimen with 63% probability, and 4 specimens with 57% probability (*Semple & Keir* 4721 WAT from Cumberland Co., Nova Scotia; 2x), 55% probability (*Morton & Venn* NA 17577 TRT from the Gaspé Peninsula, Québec; 4x), 55% probability (*Morton & Venn* NA 17597 TRT from the Gaspé Peninsula, Québec; 4x) and 53% probability (*Semple & Brouillet* 7373 WAT from Adams Co., Illinois; 4x). Four specimens of the var. *gigantea* a priori group were assigned to var. *shinersii*: 91% probability (*Melville* 1666 TRT, cult. transplant from Moosonee, Ontario; 4x), 84% probability (*Semple & Suropto* 9871 WAT from Kakankee Co., Illinois; 4x), 71% probability (*Morton & Venn* NA 17597 TRT from the Gaspé Peninsula, Québec; 4x), and 57% probability (*Melville* 1685 WAT, from Timiskaming Dist., Ontario; 4x). Thirteen of the 15 specimens of var. *shinersii* were assigned a posteriori to the var. *shinersii* group: 8 specimens with 92-100% probability, 3 specimens with 80-89% probability, 1 specimen with 70% probability, and 1 specimen with 67% probability. Two specimens of the var. *shinersii* a priori group were assigned a posteriori to var. *gigantea*: 1 specimen with 82% probability (*Semple & B. Semple* 6718 WAT from Ingolf, Kenora Dist., Ontario; leaves are lanceolate; 6x) and 1 specimen with 78% probability (*Semple & Brouillet* 7292 WAT from Bent Co., Colorado; leaves are lanceolate to narrowly lanceolate; 6x).

Frequencies of CAN1 canonical scores for 49 specimens of *S. gigantea* var. *gigantea* and var. *shinersii* are presented in histograms in Fig. 23. The Eigenvalue on the first axis was 0.0.791.

Table 10. Linear and jackknife classification matrices from the Classificatory Discriminant Analysis of two varietal level a priori groups; a posteriori placements to groups in rows.

Group	<i>gigantea</i>	<i>shinersii</i>	% correct
<i>gigantea</i>	31	3	91
<i>shinersii</i>	2	13	87
Totals	33	16	90

Jackknifed classification matrix

Group	<i>gigantea</i>	<i>shinersii</i>	% correct
<i>gigantea</i>	30	4	88
<i>shinersii</i>	2	13	87
Totals	32	17	88

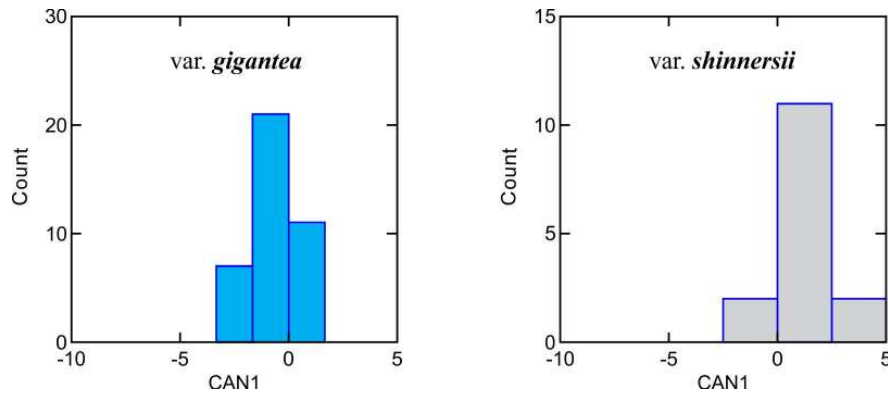


Figure 23. Histograms of the frequencies of CAN1 scores for 93 specimens of *Solidago gigantea* var. *gigantea* and var. *shinersii*.

DISCUSSION

Five species level groups analysis

The results of the five species level analysis support the recognition of *Solidago altissima* (var. *gilvocanescens*), *S. canadensis*, *S. elongata* and *S. gigantea*, although only *S. canadensis* had strong statistical support (89% placement of specimens of the *S. canadensis* a priori group to the group a posteriori). Only 53% of the *S. lepida* a priori group specimens were placed into *S. lepida* a posteriori; 17.6% of the specimens were placed a posteriori into *S. altissima*, 17.6% of the specimens were placed a posteriori into *S. elongata*, 12.2% of the specimens were placed a posteriori into *S. gigantea*, and 0% were placed into *S. canadensis*. However, no individuals of *S. lepida* had lower stem indument densities typical of *S. altissima* var. *gilvocanescens*.

No collections of *Solidago canadensis* from the Pacific Northwest were included in the analysis because none were seen in the 99 specimen UBC loan of “*S. canadensis*” nor in the numerous WAT and J.K. Morton TRT collections examined. A number of collections from British Columbia were included because they superficially looked like *S. canadensis* from eastern North America, but all were placed into western species a posteriori in the analyses. For example, *Eastham s.n.* (UBC) from Waitabit Creek west of Golden, British Columbia, was assigned a priori to *S. lepida* var. *salebrosa* and was placed in *S. lepida* with 50% probability (30% to *S. elongata*; 0% to *S. canadensis*) in the five species analysis, and with 61% probability (39% to *S. elongata*) in the three species analysis. UBC Specimens from British Columbia that had been annotated decades ago as *S. canadensis* were placed into *S. altissima* var. *gilvocanescens* or *S. lepida* var. *salabrosa* in the analyses were originally identified as these two taxa or *S. elongata*, but none as *S. canadensis*. The only UBC collection in the 99 specimens loan that was *S. canadensis* was from New Hampshire. *Solidago canadensis* is native to the northeastern USA and adjacent Canada and is not present in the Pacific Northwest (Semple & Cook 2006; Semple et al. 2013), except as possible garden cultivars.

Solidago altissima var. *gilvocanescens* is either native to a few valleys in southcentral and southeastern British Columbia or has been introduced from the prairies east of the Rocky Mts. and established. These plants can be a bit atypical for var. *gilvocanescens* but have the lower stem hair density of *S. altissima*. Two specimens from the Okanagan Valley in southeastern British Columbia that were assigned a priori to *S. altissima* were assigned a posteriori into *S. altissima* with 77% probability (*McCalla 8345* UBC) and 69% probability (*Gilmore 22* UBC); these both had moderately pubescent stems and leaf veins but otherwise fit well into *S. altissima*. *Canning s.n.* (UBC) from Penticton, British Columbia, was assigned a posteriori to *S. gigantea* with 72% (20% to *S. lepida* and

6% to *S. altissima*) but had the dense stem indument of *S. altissima* and not the glabrous to very sparsely hairy lower stems of *S. gigantea* and *S. lepida*. The plant was short but had robust serrate leaves on the lower and mid stem up to those subtending branches of the inflorescence and were reduced only in the inflorescence. The number of mid stem leaf margin serrations and mid stem leaf width were the second and third most important traits selected for discriminating a priori groups in the five species analysis. These traits were atypical for *Canning s.n.* (UBC) due to the short stature of the plant and few number of stem leaves.

Three species level groups analysis and the two species level groups analyses

The results of the analysis of specimens of *Solidago elongata*, *S. gigantea*, and *S. lepida* strongly support the recognition of *S. elongata* as a separate species, but indicate identification problems are likely with some western specimens of *S. gigantea* in areas where its range approaches or overlaps with *S. lepida*. All 28 specimens of *S. elongata* were placed a posteriori into *S. elongata* in the three species analysis and most were placed with high probability. One specimen, *Wells 699* (UBC) from Tsawwassen, British Columbia, was placed a posteriori into *S. elongata* with 49% probability and slightly less so into *S. lepida*. The lower stem was sparsely canescent and the upper stem densely so; bracts in the inflorescence were obviously glandular. In the *S. elongata/S. lepida* analysis *Wells 699* (UBC) was placed a posteriori into *S. lepida* with 56% probability; all other specimens of *S. elongata* were assigned a posteriori to *S. elongata*. It is therefore possible that *Wells 699* (UBC) was assigned to the wrong species a priori. The presence of very glandular bracts is common in *S. lepida*, while the vegetation of *S. elongata* is glandless or has very few stipitate glands; if glands occur on the upper portions *S. elongata* they are very small and challenging to find. Based on observations from all other species of *Solidago*, a few glands might be encountered even on some individuals of species that usually have none.

In the three species analysis, 75% of *Solidago gigantea* specimens were assigned to *S. gigantea*, while 8 were assigned a posteriori to *S. lepida* and 4 to *S. elongata*. The ranges of *S. elongata* and *S. gigantea* are fully allopatric (Figs. 14 and 15) and mid stems of *S. elongata* are usually sparsely to moderately pubescent while those of *S. gigantea* are glabrous. In the two species analysis, 81% of the *S. gigantea* specimens and 87% of the *S. lepida* specimens were placed a posteriori into their respective a priori groups. Very small inflorescences of *S. elongata* (Fig. 2) and *S. gigantea* can be similar (which is true for most species of subsect. *Triplinerviae*), but mid to large ones are very different with those of *S. elongata* being non-secund and club shaped (Fig. 1) while those of *S. gigantea* are secund and conical (Figs. 4-6). Four of the *S. gigantea* specimens assigned to *S. lepida* were tetraploids from the eastern part of the range or invasive in the Old World. Six of the *S. gigantea* specimens assigned a priori to *S. lepida* were hexaploids from the western half of the range (Fig. 15) and only the specimen from Oklahoma was not from a part of the range that is, or potentially is, sympatric with the range of *S. lepida* (Fig. 16). The hexaploid *S. gigantea* specimen from Oklahoma was glandular in the inflorescence. The foothills of the Rocky Mts., the mixed prairie and mountain areas of Montana, along streams and rivers of the eastern Columbia R. drainage system, and the southern edge of the boreal forest-aspen parkland/prairie are the locations where the two species potentially come together and where hybridization between hexaploids is possible. It is not known whether hexaploid *S. gigantea* is natively more glandular in these habitats or whether the presence of such glands on inflorescence parts is evidence of hybridization with *S. lepida*. The Moss revised by Packer (1983) version of the Flora of Alberta did not deal with the problem and separated *S. gigantea* on stems being glabrous below the inflorescence and leaves being glabrous from *S. canadensis* (including *S. altissima* var. *gilvocanescens* as *S. canadensis* var. *gilvocanescens* and *S. lepida* as a synonym of var. *canadensis*) as having more hairy stems and leaves to varying degrees. Gland density was not discussed. The original version of the Flora of Alberta by Moss (1959) did treat *S. lepida* as a distinct species. Presence of stipitate glands in the inflorescence was not discussed.

The late J.K. Morton and the first author had multiple discussions over multiple years about the *Solidago gigantea*/*S. lepida* problem, particularly along the northern edge of the prairie/forest ecotone. Most of the specimens from this area from central Alberta to southern Manitoba of uncertain placement in this study were glandular to some degree and were identified by J.K. Morton as *S. lepida*, while the first author's annotations often were *S. gigantea*. Although Cronquist (1994) may have felt that *S. lepida* belonged in *S. canadensis* as var. *salebrosa*, while *S. gigantea* was a readily recognizable species, the field and lab experiences of J.K. Morton and the first author of this publication disagreed with Cronquist. The real problem is convergence of hexaploid *S. gigantea* and hexaploid *S. lepida*, especially when the leaves of *S. gigantea* are not very broad for the western hexaploid cytotype, var. *shinnersii*. During early analyses of a smaller data set, all the glandular hexaploids from Alberta, Saskatchewan and Manitoba were treated as *S. lepida* and the results yielded much lower percents of correct a posteriori assignments to *S. gigantea* and *S. lepida*. When glands were ignored and only inflorescence branching pattern was emphasized, the a posteriori assignment results improved. Thirteen specimens, 8 of *S. gigantea* and 5 of *S. lepida*, in this study were collected in along a narrow strip from the western edge of Ontario across Manitoba and Saskatchewan to west-central Alberta; all whose chromosome numbers were determined were hexaploid while the ploidy level of the others was not determined. Opinions on the identity of a specimen and the multivariate results differed depending upon the specimen. The hexaploid *Morton & Venn NA14215* (TRT; Fig. 6) a cultivated voucher from a rootstock transplanted from southwestern Manitoba was assigned a posteriori to *S. gigantea* with 97% probability in both the three species and two species analyses involving *S. gigantea* and *S. lepida*; it was identified as *S. gigantea* by both J.K. Morton and by J.C. Semple. The hexaploid *Semple & Brouillet 4287* (WAT) from west of Elk Is. Nat. Park, Alberta was assigned a posteriori to *S. gigantea* in the five species analysis, the three species analysis, and the two species analysis with 80%, 90%, and 69% probabilities, respectively; it has glandular peduncle bracts and phyllaries; it was originally labeled *S. gigantea*, than annotated by J.C. Semple as *S. aff. lepida* in 2005 and then as *S. gigantea* in 2017. The hexaploid *Morton & Venn NA14195* (TRT; Fig. 23) from Battleford, Saskatchewan was identified as *S. lepida* by J.K. Morton and assigned a priori to *S. lepida* because it was obviously glandular in the inflorescence even though it had a relatively open secund conical inflorescence and had been annotated by J.C. Semple in 2017 it as *S. gigantea*. In the three species analysis, *Morton & Venn NA14195* (TRT) was assigned a posteriori to *S. gigantea* with 42% probability (41% to *S. lepida*), but in the two species analysis it was assigned to *S. lepida* with 67% probability. In the five species analysis, *Morton & Venn NA14195* (TRT) was placed a posteriori in *S. lepida* with 66% probability. Is it *S. gigantea* with glands or *S. lepida* var. *salebrosa* (and way east of the range of the variety) or *S. gigantea* × *S. lepida* var. *lepida*? Multivariate morphometric analysis does not provide a clear answer to this question. Which is more informative of identity, the number of mid stem leaf serrations included in the two species analysis or mid stem leaf length, disc corolla length and disc corolla lobe length included in the three species analysis? Both analyses included the number of upper stem leaf serrations, involucre height, number of ray florets, and ray floret lamina length. Using seven traits, *Morton & Venn NA14195* (TRT) was placed a posteriori in *S. gigantea* in the three species analysis, but using six traits it was placed a posteriori in *S. lepida* in the two species analysis. Technical traits requiring dissecting scope examination of parts were critical in both analyses. The final solution may come from DNA sequence analysis of multiple hexaploid plants of both species. *Morton & Venn NA14195* (TRT) will be annotated as *S. gigantea* × *S. lepida* var. *lepida* based on the ambiguous results. Two of the five specimens in the *S. lepida* a priori group from the Alberta to Ontario forest-prairie ecotone were assigned weakly to *S. gigantea* with 68% and 57% probability in the three species analysis but to *S. lepida* in the two species analysis with 53% and 70%, respectively. Based on inflorescence features these are all *S. lepida* var. *lepida*.

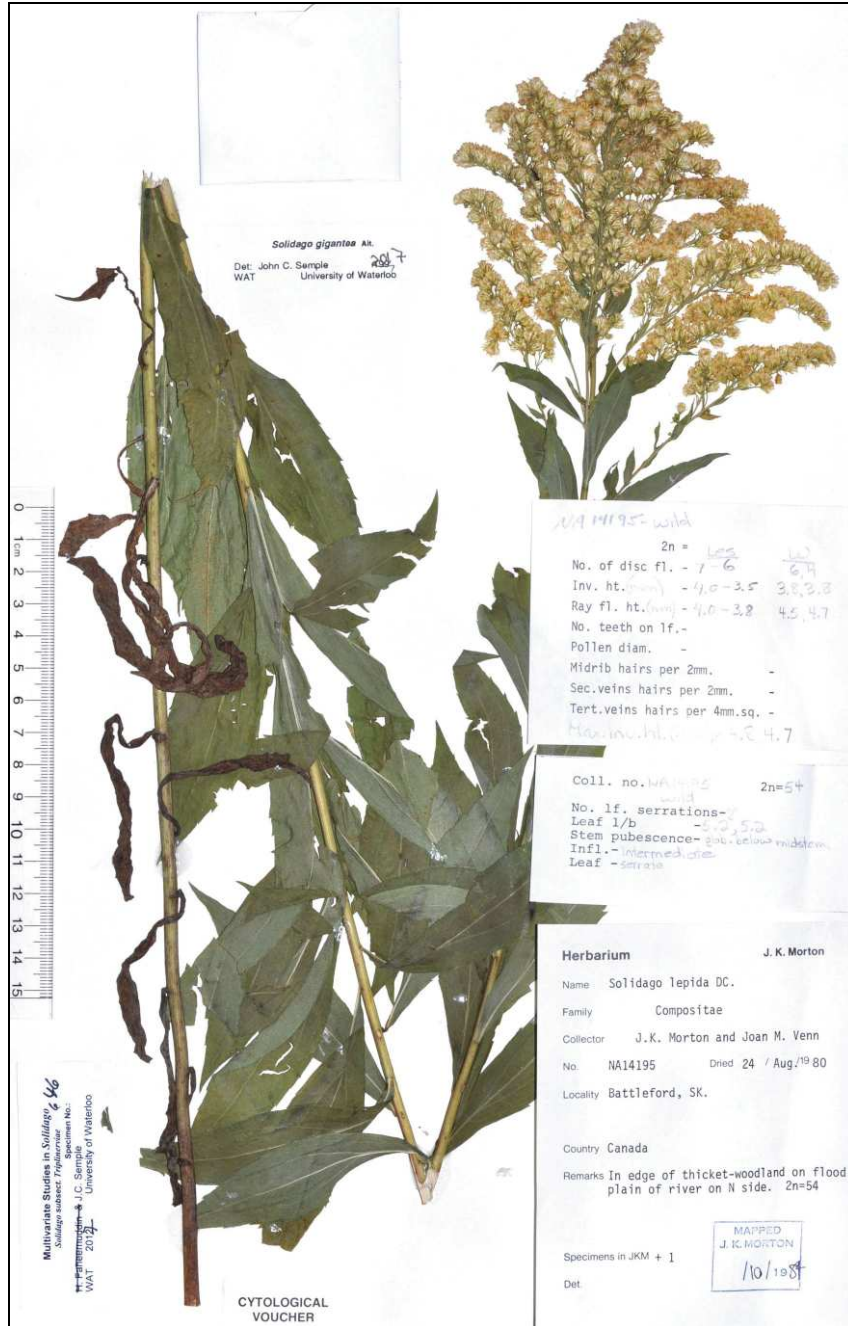


Figure 23. Morton & Venn NA14195 (TRT) from Battleford, Saskatchewan. Is it *S. gigantea* with glands or *S. lepida* or *S. gigantea* × *S. lepida* var. *lepida*?

Included in the analyses were three hexaploid specimens treated a priori as *Solidago gigantea* from Idaho and eastern Washington. These represent a larger group of collections from southeastern British Columbia, eastern Washington and central and Northern Idaho area of very *S. gigantea*-like specimens, some of which are glandular and some of which are not. *Semple & Brouillet* 4387 (WAT) from Whitman Co., Washington (very few glands on bracts and phyllaries), and *Semple & Brouillet* 4403 (WAT) from Idaho Co., Idaho (glands on phyllary apices; Fig. 24), were assigned in the five

species analysis to *S. gigantea* with 97% and 100% probability, respectively; in the three species analysis to *S. gigantea* with 99% and 98% probability, respectively; and in the two species analysis to *S. gigantea* with 98% and 96% probability, respectively. *Semple & Brouillet 4396* (WAT) from E of Lewiston, Idaho (glands on the upper leaves, peduncle bracts and phyllaries), was assigned a posteriori in the five species analysis to *S. lepida* with 74% probability, but to *S. gigantea* in the three species analysis and two species analyses with 98% and 83%, respectively. All three are mapped in the disjunct area of the range in Washington and Idaho on the range map of *S. gigantea* in Fig. 15. Potentially, *S. gigantea* occurs in scattered locations along streams and rivers further north and west in other areas of the Pacific Northwest including British Columbia, but the presence of some glands will make identification to *S. gigantea* rather than *S. lepida* more difficult. The occurrence of hexaploid hybrids between the two species in the Pacific Northwest is also possible, further complicating the identification task. No putative specimens of *S. gigantea* from British Columbia were included in the analyses. However, *F. Lomer 7497* (WAT, UBC) with immature heads from Castlegar, British Columbia, was annotated as *S. gigantea*; the ploidy level was not determined but the heads were small enough to possibly be diploid or tetraploid, which would make the collection introduced; if more mature heads would have been larger than it would likely be hexaploid and native. A collection from Okanagan, British Columbia (*Hill s.n.*, UBC), appears to be *S. gigantea*, but the collection consists of only one large stem leaf and a piece of stem with a small number of flowering heads.



Fig. 24. A shoot of *Solidago gigantea* from near Kooskia, Idaho held by graduate student at the time Luc Brouillet, 4 Sep 1979; the shoot grew along a river bank and was moved for the photograph.

The results of the multivariate analyses indicate that there is a problem with how best to treat the western diploids included in *S. lepida* in this study. Eight of the *Solidago lepida* specimens assigned a posteriori to *S. elongata* in the two species analysis were known diploids or likely diploids from southwestern Northwest Territories, eastern British Columbia, central Idaho, and western

Montana; most of these were small to mid height var. *salebrosa*. In contrast, 11 of the smaller var. *salebrosa* diploids from Alaska, Northwest Territories, Alberta, Idaho, Wyoming, and Colorado were placed a posteriori in *S. lepida* with high probabilities. Because diploids in *S. lepida* are generally less obviously glandular than polyploids, it is more difficult to identify the diploids as *S. lepida*. Many of these collections were originally identified as *S. elongata*, but all of them from were outside the range for the species shown in Fig. 14. When all the diploid *S. lepida* plants were placed into *S. elongata* or into their own a priori group in preliminary multivariate analyses, the results did not support these alternative interpretations as being more likely correct. Thus, all the diploids from the Rocky Mts. were included in *S. lepida* in the analyses presented here.

The following is a possible history of the *Solidago lepida* complex. It seems likely that at one point in the early history of *S. lepida* diploids were the only ploidy level in the species and these occurred in the Rocky Mts. from Alaska south to at least New Mexico and possibly south into eastern Mexico (no diploid counts are known for the species from Mexico). Tetraploids and hexaploids evolved from the diploids in the Rocky Mts., potentially multiple times, and these spread eastward all the way to northern Ontario and eastern Québec much more recently. Much earlier expansion(s) of the diploid range across Canada and subsequent isolation in glacial peak times is likely to have resulted in eastern diploids evolving in isolation into *S. brendiae*, *S. canadensis*, and *S. fallax*, although when is unknown. Diploids also expanded early into the Cascade Mts. in the Pacific Northwest, where they diverged and evolved in isolation into *S. elongata* with its distinctive inflorescence and very low numbers of or lack of glands and then spread south to the mountains in California. Some of the diploids of *S. lepida* in the Rocky Mts retained some of the more ancestral features and these are the specimens that were assigned a posteriori to *S. elongata* in the analyses, but are nonetheless individuals of *S. lepida*. When diploid *S. gigantea* diverged and evolved in eastern North America is also unknown. Whether it arrived along a southern route across North America or a more northern route from diploid southwestern ancestors is unknown, but we speculate here that an earlier divergence from diploid *S. lepida* or proto-*S. lepida* via a southern route into the southeastern USA is likely. From there the range expanded in part via the evolution of tetraploids and hexaploids into new habitats and subsequently westward across the Great Plains to the base of the Rocky Mts. from Alberta to New Mexico and further west in Montana into Idaho and Washington along rivers. British Columbia plants may be part of the western Columbia River drainage populations or more recent adventives from the western Canadian prairie populations.

Two variety level groups analysis of *Solidago lepida*

The results of the multivariate analysis of var. *lepida* and var. *salebrosa* provide support for recognizing the two varieties. In the two variety analysis, 90% of the var. *salebrosa* a priori group specimens were assigned a posteriori to var. *salebrosa*. One of the three specimens of var. *salebrosa* assigned a posteriori to var. *lepida* (Semple & Xiang 10325, WAT, a hexaploid from Montana; Fig. 12) clearly has the broad inflorescence with diverging lower branches characteristic of var. *salebrosa*, but was placed a posteriori into var. *lepida* with 90% probability. The mean value for upper stem leaf width was 8.25 mm for var. *salebrosa* and 12.5 mm for var. *lepida*. Thus, narrow upper stem leaves and arching spreading lower and mid inflorescence branches distinguish var. *salebrosa* from var. *lepida* most of the time. Some robust specimens of var. *salebrosa* have larger and broader upper stem leaves but still have the broad second conical inflorescences with broadly spreading branches. In var. *lepida* the inflorescence branches are more often ascending, but in some cases branches are spreading but subtended by large leaves either much exceeding the branch length or nearly so. The ranges of the two varieties overlap throughout much of the western mountains. Further east var. *lepida* appears to be the only variety present, unless one includes some of those problematic *Solidago gigantea*-like plants in *S. lepida*. If so, then the range of var. *salebrosa* extends eastward to Saskatchewan in the forest-prairie ecotone. Our conclusion is that hybridization with *S. gigantea* may be occurring in the

ecotone area, yielding some odd *S. lepida* var. *lepida* plants or F1 hybrids with traits of both *S. gigantea* and *S. lepida*.

Two variety level groups analysis of *Solidago gigantea*

The results of the multivariate analysis of var. *gigantea* and var. *shinnersii* provides some support for recognizing the western hexaploids as the taxonomically distinct race var. *shinnersii*. The widths of mid and upper stem leaves are the most useful traits in separating the two varieties with means of 15.16 mm for mid stem leaves and 10.7 mm for mid and upper stem leaves var. *lepida* and 19.95 mm and 14.89 mm for var. *shinnersii*. All var. *shinnersii* plants with known chromosome number are hexaploid, but not all hexaploids have broad mid and upper stem leaves. This accounts for a posteriori correct assignment to a priori groups of 91% for var. *gigantea* and 87% var. *shinnersii*. Outer phyllary length and ray ovary body length at anthesis were also selected as useful in separating the two varieties and these traits are influenced by ploidy level and both were on average longer in var. *shinnersii* than var. *gigantea*. All three of the Washington and Idaho specimens of *Solidago gigantea* discussed above were placed a posteriori into var. *shinnersii* with 94-98% probability. One of the Alberta *S. gigantea* collections (Turner 3205, WAT) was treated as var. *gigantea* a priori and was placed into that variety a posteriori with 95% probability; the specimen included two smaller shoots with small narrowly lanceolate mid and upper stem leaves; the ploidy level is unknown. The other Alberta *S. gigantea* collection (Semple & Brouillet 4287, WAT) was a more robust hexaploid included in var. *shinnersii* a priori and was placed a posteriori in var. *shinnersii* with 89% probability. It is therefore possible, that growing conditions as indicated by plant height and leaf size may limit full development of the broad var. *shinnersii* form of mid and upper stem leaves. This would not be the case for environmentally stressed eastern plants because they would normally not produce very broad leaves under more favorable growing conditions. Three of the four var. *gigantea* specimens placed a posteriori into var. *shinnersii* were tetraploids from Illinois, northern Ontario near James Bay, and the Gaspé Peninsula, Québec. The fourth specimen was most likely tetraploid and was from Matachewan, Timaskaming Dist., in northern Ontario. Only the Illinois plant had leaves approaching the shape of those of typical var. *shinnersii*.

In conclusion, while there are difficulties in identifying individual specimens to species of subsect. *Triplinerviae* in the northern Cascade Mts., the mid latitude Rocky Mts., and the northern edge of the prairies into the adjacent woodlands across Alberta, Saskatchewan, and Manitoba, the following taxa should be recognized as native: *Solidago altissima* var. *gilvocanescens*, *S. elongata*, *S. gigantea* var. *shinnersii*, *S. lepida* var. *lepida*, and *S. lepida* var. *salebrosa*. *Solidago canadensis* is not native in western North America. The only modifications to the key to the subsection in Flora North America (Semple & Cook 2006) is the addition to *S. gigantea* of var. *shinnersii*, which is hexaploid, sometimes stipitate glandular on inflorescence parts, usually has broadly lanceolate to narrowly ovate midstem leaves, and has involucre at the higher end of the range for the species.

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