Semple, J.C., H. Rahman, H., S. Bzovsky, M.K. Sorour, K. Kornobis, R. Lopez Laphitz, and L. Tong. 2015. A multivariate morphometric study of the *Solidago altissima* complex and *S. canadensis* (Asteraceae: Astereae). Phytoneuron 2014-10. 1–31. Published 12 February 2015. ISSN 2153 733X

A MULTIVARIATE MORPHOMETRIC STUDY OF THE *SOLIDAGO ALTISSIMA* COMPLEX AND *S. CANADENSIS* (ASTERACEAE: ASTEREAE)

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ABSTRACT

The *Solidago altissima* complex stretches across much of North America on the prairies and in the eastern deciduous forest. A multivariate morphometric analysis including 28 vegetative and floral traits scored on 162 specimens was performed to assess the classification of the complex in eastern North America proposed by Semple (2014). Discriminant analysis indicated support for recognizing the following taxa: *Solidago altiplanities*, *Solidago altissima* vars. *altissima*, *gilvocanescens*, and *pluricephala*, *S. canadensis* vars. *canadensis* and *hargeri*, and *S. juliae*. A lectotype is designated for *Solidago pruinosa* Greene, which is a synonym of *S. altissima* var. *gilvocanescens*.

The *Solidago altissima* L. complex is part of *Solidago* subsect. *Triplinerviae* (Torr. & A. Gray) G.L. Nesom, which includes 17-18 species (Semple 2014, Astereae Lab web site, continuously updated). *Solidago altissima* (Sp. Pl. 878. 1753) occurs across much of central and eastern North America on the prairies and in disturbed habitats of the eastern deciduous forest (Semple & Cook 2006). Typical *S. altissima* (var./subsp. *altissima*; Fig. 1) occurs from the eastern limits of the Great Plains to the Atlantic coast and has been treated as *S. scabra* Muhl. ex Willd. (Sp. Pl. 3. 2059. 1803) and *S. canadensis* var. *scabra* (Muhl. ex Willd.) Torr. & Gray (Fl. N. Amer. 2: 224. 1842). Use of the latter combination in *S. canadensis* is responsible for much of the ambiguity in the literature about the distribution of *S. canadensis* in Asia, particularly when only the species name is listed. The Great Plains race of the species (Fig. 2) was first described as *S. canadensis* var. *gilvocanescens* Rydb. (Contr. U.S. Nat. Herb. 3: 162. 1895) and subsequently treated as *S. gilvocanescen*s (Rydb.) Smyth (Trans. Kansas Acad. Sci. 16: 161. 1899), *Doria gilvocanescens* (Rydb.) Lunell (Amer. Midl. Nat. 5: 43. 1917), *S. canadensis* subsp. *gilvocanescens* (Rydb.) Löve & Löve (Taxon 31: 358. 1982), *S. altissima* var. *gilvocanscens* (Rydb.) Semple (Phytologia 58: 430. 1985), and most recently as *S. altissima* subsp. *gilvocanescens* (Rydb.) Semple (Sida 20: 1606. 2003). The name *S. altissima* var. *pluricephala* M.C. Johnston (Southw. Naturalist 14: 372. 1970) was based on specimens collected near Brownsville, Texas, but the name was not widely adopted (Fig. 3). Two species in the complex were described relatively recently: *Solidago altiplanities* Taylor & Taylor (Sida 10: 178. 1983) is a narrow-leaved species native to a limited area on the Texas Panhandle and adjacent Oklahoma (Fig. 4); *Solidago juliae* G.L. Nesom (Phytologia 67: 445. 1989) is a more densely hairy species native to parts of the Edwards Plateau in Texas and scattered locations to the west and southwest in Mexico and in isolated mountains in southeastern Arizona (Fig. 5). *Solidago canadensis* var. *hargeri* Fern. can be difficult to distinguish from members of the *S. altissima* complex but usually has more obviously serrate and sometimes narrower upper stem and lower inflorescence leaves.

Taxonomic treatments of the complex have differed greatly in how many taxa were recognized and at what taxonomic rank. Fernald (1915) described a hairy-stemmed, more southern race of *Solidago canadensis* as *S. canadensis* var. *hargeri* Fern. Fernald (1950) treated *S. altissima* as a separate species but included var. *gilvocanescens* in *S. canadensis*. Cronquist (1968) treated *S. canadensis* and *S. altissima* as separate species but did not divide *S. altissima* into varieties and stated its range to be from Québec to Florida west to North Dakota and Arizona; he treated var. *gilvocanescens* as the separate species using the synonym *Solidago pruinosa* Greene [Pittonia 4: 70. 1899. LECTOTYPE, designated here: **CANADA**. **Saskatchewan**. Moose Jaw, Assiniboia, 13 Aug 1895, *Macoun 10894* (CAN!); *Macoun 10893* (CAN!) was collected at the same locality]. Scoggan (1979) included typical *S. altissima* in *S. canadensis* as var. *scabra* and the prairie race as var. *gilvocanescens*; he also included *S. lepida* var. *salebrosa* (Piper) Semple as a variety of *S. canadensis*. Melville and Morton (1982) presented a multivariate study of the some of the taxa of the complex plus *S. lepida*, focusing primarily on those occurring in Ontario. They found support for recognizing the two varieties of *S. canadensis*, *S. altissima* at specific rank, *S. lepida* and *S. gigantea*. In the Flora of North America treatment, Semple and Cook (2006) followed Melville and Morton on *S. canadensis*. In a multivariate analysis of the *S. canadensis*/*S.lepida* complex, Semple et al. (2013) dealt with the varieties in *S. canadensis* but not those within *S. altissima*. *Solidago altiplanities* and *S. juliae* of subsect. *Triplinerviae* have been included in the informal *Tortifolia* Group (Semple 2014, Astereae Lab web site, continuously updated) and are included in the multivariate analysis presented here. Additional multivariate morphometric studies in preparation by the Astereae Lab will cover taxa not included here or in Semple et al. (2013). Lopez Laphitz (2009) included *S. juliae* and putatively closely related North American relatives *S. tortifolia* Ell. and *S. leavenworthii* Torr. & A. Gray in her multivariate analysis of South American members of subsect. *Triplinerviae*. A manuscript presenting this M.Sc. research is submitted and under review.

The systematics of the *Solidago altissima* complex is made more difficult due to multiple ploidy levels occurring in the races of *S. altissima*. Only diploids ($2n = 18$) are known in *S. canadensis*, *S. juliae*, and *S. altiplanities* (Nesom 1989; Turner & Zhao 1992; Semple & Cook 2006; Semple et al. 2013). However, sample sizes for the latter two species are small. The cytogeographic pattern in *S. altissima* was discussed in Semple et al. (1984) in regards to var. *gilvocanescens* and var. *altissima*, while var. *pluricephala* was not considered as a separate taxon at that time. Based on all published and some unpublished counts, var. *gilvocanescens* includes diploids and tetraploids ($2n = 36$) with a few hexaploids ($2n = 54$) in the southwestern part of the range. The more eastern and northern var. *altissima* and the more southern var. *pluricephala* include a few tetraploids in the southwestern and southern portions of the ranges, respectively, and hexaploids are dominant (or exclusively) over the entire ranges. A manuscript on the cytogeography of *S. altissima* is in preparation and will include a large number of chromosome counts by the late John K. Morton and a summary of all published counts.

The purpose of this study is to compare specimens of *Solidago altissima* with specimens of morphologically similar (stems densely short hairy proximally to distally) and putatively closely related species and with *S. canadensis*, which includes specimens (stems densely short hairy proximally to distally) often confused with *S. altissima* as well as specimens that are less likely to be confused (stems densely short hairy only distally; stems glabrous/glabrate proximally). Within *S. altissima*, specimens of three named races and a putative fourth race are compared. Field observations on *S. altissima* were made over more than 40 years of field work by J.C.S. including detailed observations on inflorescence shape variation in the southeastern USA in 2006. The field data suggested that there is a generally unrecognized southeastern USA race within *S. altissima*. While analyzing specimens of *S. lepida* and *S. canadensis* for Semple et al. (2013), a number of collections from Saskatchewan and Manitoba were encountered that did not appear to fit well into *S.*

lepida, *S. canadensis*, or *S. altissima*, although a number of them were closest in appearance to var. *gilvocanescens*. Seven of these specimens are included in the analyses below.

The *Solidago lepida* complex includes *S. brendiae* Semple, *S. elongata* Nutt., and *S. fallax* (Fern.) Semple with two varieties, var. *fallax* and var. *molina* (Fern.) Semple, and is defined by the usually leafy inflorescence with usually ascending short branches. Lower stems tend to be sparsely hairy to hairless regardless of how hairy is the upper stem. In the *S. altissima* group, the inflorescences have spreading to arching lower branches, regardless of branch length, and have lower stems that are usually densely short hairy, even if the hairs are sometimes lost as lower stems age and increase in diameter. Individuals of *S. canadensis* range from *S. lepida*-like in stem features to *S. altissima*-like in stem features and have spreading, arching, usually long lower branches. Upper stem and inflorescence leaves tend to have few or no serrations in the *S. altissima* complex, while those of the *S. lepida*/*S. canadensis* complex often have large serrations on upper stem leaves but are sometimes toothless. Semple (2014) placed *S. canadensis* in the informal *Canadensae* group and *S. altissima* in the informal *Tortifoliae* group. Anyone who has made multiple collections of *S. canadensis* will understand that identification of some individuals can be difficult due to similarities with *S. altissima* individuals in some cases and to similarities with *S. brendiae* and *S. fallax* in other cases. Thus, *S. canadensis* is included in this analysis as well, as it was previously in Semple et al. 2013. Analyses to date of the entire *Triplinerviae* subsection suffer from needing too many different characters to define 17-18 species level a priori groups, leaving too few traits for inclusion in the analyses. Subdividing the subsection into more manageable species groups is one solution to this problem. Morphology alone may not be sufficient to determine the true limits of these subgroups. The subgroups are logical but not necessarily phylogenetically correct because inflorescence branching characteristics and variation in stem pubescence may not be phylogenetic markers. Molecular data is needed to provide guidance.

MATERIALS AND METHODS

In total, 168 specimens from BOON, BRIT, JKM (John Morton's personal herbarium) in ROM, and WAT (Thiers, continuously updated) were selected for inclusion in the analysis of the *Solidago altissima/S. canadensis* complex from an unpublished matrix of 562 plants covering all taxa in subsect. *Triplinerviae*. For each specimen, 14 vegetative and 16 floral traits were scored: 1-5 replicates per character depending upon availability of material and whether or not the trait was meristic (Table 1). Mean values were used in the analyses, while raw values were used to generate ranges of variation for each trait. Sample sizes varied among taxa based on the size of the range of distribution and availability of specimens: 9 *S. altiplanities*, 88 *S. altissima* (31 *var. altissima*, 29 *var. gilvocanescens*, 28 var. *pluricephala*, 7 putative var. nov.), 53 *S. canadensis* (32 var. *canadensis*, 21 var. *hargeri*), and 11 *S. juliae*.

Traits used to define a priori groups were not included in the analyses to avoid circular logic. Differences in general inflorescence shape and branching characteristics, lower stem pubescence density, and leaf pubescence density were used to define a priori groups along with geographic location. Lower stem leaf traits were not included in the analyses because these were often not present on specimens.

All analyses were performed using SYSTAT v.10 (SPSS 2000). A pair-wise Pearson correlation matrix was created to determine which characters were highly correlated. One trait of each pair that had a $> |0.7|$ correlation value was excluded from the analysis to avoid possible pleiotropic effects of a single gene and to make the tests of null hypotheses more stringent. Stepwise discriminant analysis (STEPDISC) was used to select traits that best separated groups based on the Mahalanobis distances between a priori group centroids. Classificatory discriminant analysis was run on N-1 traits selected by the STEPDISC analysis, if more than N-1 traits were selected, where N =

Table 1. All characters scored on specimens included in the study *S. altissima/S. canadensis* complex; traits scored in replicates of five when material available; 1 value for meristic traits.

STMHT	Height of the stem from base to the top of the inflorescence (cm)
LLFN	Lower stem leaf length (mm)
LLFW	Lower stem leaf length (mm)
LLFWTOE	Length of lower stem leaf from widest point to tip (mm)
LLFSERNUM	Number of serrations on one side of a lower stem leaf (side with the most)
MLFLN	Mid stem leaf length (mm)
MLFW	Mid stem leaf width (mm)
MLFWTOE	Length of mid stem leaf from widest point to tip (mm)
MLFSERNUM	Number of serrations on one side of a mid stem leaf (side with the most)
ULFLN	Upper stem leaf length (mm)
ULFW	Upper stem leaf width (mm)
ULFWTOE	Length of upper stem leaf from widest point to tip (mm)
ULFSERNUM	Number of serrations on one side of a upper stem leaf (side with the most)
CAPL	Length of inflorescence from tip to base of lowest branch (cm)
CAPW	Width of pressed and dried inflorescence at widest point (cm
INVOLHT	Height of involucre from base to tip of longest phyllary (mm)
OPHYLL	Length of outer phyllary (mm)
IPHYLL	Length of inner phyllary (mm)
RAYNUM	Number of ray florets
RSTRAPL	Length of the ray strap (lamina; mm)
RSTRAPW	Width of the ray strap (lamina; mm)
RACHBL	Length of the ray floret ovary at anthesis (mm)
RPAPL	Length of the ray floret pappus at anthesis (mm)
DISCNUM	Number of disc florets
DCORL	Length of the disc floret corolla in total (mm)
DLOBL	Length of the disc floret lobes (mm)
DACHBL	Length of the ray floret ovary at anthesis (mm)
DPAPL	Length of the ray floret pappus at anthesis (mm)

lowest sample size of the a priori groups; in this study N = 7 (when "var. nov." was included as an a priori group) and N=9 (when *Solidago altiplanities* was included as an a priori group). Geisser probabilities of assignment to each a priori group were generated for each specimen a posteriori based on the Mahalanobis distances from the specimen location plotted in N-dimensional hyperspace to each a priori group centroid. Linear and Jackknifed analyses were run in each classificatory analysis to test the strength of group separation in terms of the numbers of discriminating traits. Results are presented in the form of (1) F-value matrices based on Mahalanobis distances between group centroids and (2) tables summarizing the results of the two methods of doing the classificatory discriminant analyses. Conclusions were reached based on the percents of correct placements of specimens and the probabilities of the placements being correct and visual re-examination of each specimen via high resolution digital images. Lastly, a canonical analysis was performed as a dimension reduction technique to allow visualization of results in 1 to 3 dimensions with the number of dimensions being N-1, where in this case N equals the number of a priori groups in an analysis. While canonical analysis allows for a visual presentation of results, the plots are based on fewer axes

than are used in the statistical analyses and thus do not fully show the multi-dimensional nature of the separation of a priori groups.

Assignment to a priori groups was based on the following traits. All specimens of *Solidago altissima* have upper most stem leaves that were usually not obviously serrate and had abaxial main veins that were moderately to densely pubescent and whitish; var. *altissima* has inflorescence arrays that were less than 1.25 times as long as wide and often wider than long, upper stem leaves were entire or had only a few very small serrations; var. *gilvocanescens* has inflorescence arrays like var. *altissima*, usually has grayer looking leaves than the other varieties and upper stem leaves that were sometimes serrate; and var. *pluricephala* usually has inflorescence arrays that are 1.5 or more times as long as wide and are restricted to the southeastern USA from North Carolina to Arkansas and southward to central Florida and south Texas. All specimens of *S. canadensis* have obviously serrate upper stem and inflorescence leaves that have darker green adaxial surfaces and the abaxial veins are sparsely pubescence and green; var. *canadensis* has lower to mid stems that are glabrous proximally to sparsely pubescent distally, while var. *hargeri* has stems hairy to the base. All specimens of *S. juliae* have grayish stems and leaves due to the high density of short white hairs, elongated inflorescence arrays, linear lanceolate upper stem leaves with fine serrations, and were restricted to southwestern Texas and further west. *Solidago altiplanities* is similar in inflorescence traits and leaf shape to *S. juliae* but has more greenish leaves due to lower hair densities and sometimes obscurely trinervate upper stem leaves. Inflorescence traits and leaf serration traits were not used in the discriminant analyses.

Five separate discriminant analyses were performed and are reported here. The first was performed on four species-level a priori groups and included 161 specimens assigned to one of the a priori groups: 9 specimens of *Solidago altiplanities*, 88 specimens of *S. altissima*, 53 specimens of *S. canadensis*, and 11 specimens of *S. juliae*. A second analysis was performed on 6 variety/species-level a priori groups of 161 specimens: 9 specimens of *S. altiplanites*, 31 specimens of *S. altissima* var. *altissima*, 29 specimens of S. *altissima* var. *gilvocanescens*, 28 specimens of *S. altissima* var. *pluricephala*, 32 specimens of *S. canadensis* var. *canadensis*, and 21 specimens of *S. canadensis* var. *hargeri*. A third analysis was performed on four putative variety-level a priori groups of just 88 specimens of *S. altissima*: 31 specimens of var. *altissima*, 29 specimens of var. *gilvocanescens*, 28 specimens of var. *pluricephala*, and 7 specimens of putative "var. nov." A fourth analysis was performed on 3 putative variety-level a priori groups of 81 specimens of *S. altissima* plus 7 specimens assigned a posteriori to the 3 a priori groups: 31 specimens of var. *altissima*, 29 specimens of var. *gilvocanescens*, 28 specimens of var. *pluricephala*, and 7 unassigned specimens of the northern putative "var. nov." A fifth analysis was performed on specimens of *S. altissima* var. *gilvocanescens*, *S. canadensis* var. *canadensis*, and *S. canadensis* var. *hargeri* in order to determine which traits best separate these three races and to what degree.

RESULTS

The means of means for all traits included in the analyses for all taxa are listed in Table 2 (below Literature Cited).

Four species level analysis

Data on all specimens were used to generate a Pearson Correlation Matrix. The following pairs of traits had correlations greater than |0.7|: CAPL–CAPW, INVOLHT–RPAPL, INVOLHT–DCORL, RSTRAPL–RPAPL, RSTRAPL–DCORL, and RPAPL–DCORL. RPAPL and DCORL were excluded in the discriminant analyses. MLFSERNUM and UPLFSERNUM were excluded from the analyses because they were used in defining a priori groups. CAPL and CAPW were also excluded as these were used to partially define a priori groups. Stepwise discriminant analysis selected the following eight traits as useful in separating the four a priori groups in the analysis in

order of decreasing F-to-remove values (in parentheses): INVOLHT (59.31), DLOBL (47.84), DISCNUM (34.14), ULFW (29.87), ULFLN (16.70), RAYNUM (11.26), RACHBL (6.09), and MLFW (5.99). 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 3. F-values indicate the largest separation was between *Solidago canadensis* and *S. juliae* and second largest between *S. altissima* and *S. juliae*. The smallest separation was between *S. altissima* and *S. canadensis*.

Table. 3. Between Group F-matrix for the four species-level taxa analysis in the *S. altissima* complex.

	altiplanities	***altissima***	***canadensis***	***juliae***
altiplanities	0.000			
altissima	29.169	0.000		
canadensis	38.601	24.425	0.000	
juliae	63.511	112.419	128.119	0.000

Wilks' lambda = 0.0116 df = 11, 3, 157; approx. F= 46.3832, df = 33, 433; prob = 0.0000

In the Classificatory Discriminant Analysis, correct assignments of specimens for taxa ranged from 87% to 100%. The Classification matrix and Jackknife classification matrix are presented in Table 4. Results for individual a priori taxa are presented in decreasing order of percent correct placement. (1) All 11 specimens (100%) assigned a priori to *Solidago juliae* were placed a posteriori in *S. juliae* with all 11 placed with 100% probability. (2) All 9 specimens (100%) assigned a priori to *S. altiplanities* were placed a posteriori into *S. altiplanities* with 8 placed with 100% probability and 1 with 87% probability. (3) 80 of the 88 specimens (91%) assigned a priori to *S. altissima* were placed a posteriori into *S. altissima*, 64 with 95-100% probability, 3 specimens with 90-94% probability, 3 with 70-89% probability, and 3 with 52-58% proability. Of the 8 specimens not placed in *S. altissima*, 7 were placed in *S. canadensis* with 55-95% probabilities, and 1 was placed in *S. altiplanities* with 85% probability. (4) 46 of the 63 specimens (87%) assigned a priori to *S.*

Table 4. Results of the Classificatory Discriminant Analysis of the four species-level groups of the *S. altissima/S. canadensis* complex.

Classification matrix (a priori groups in left column, a posteriori assignments in rows)

	altiplanities	***altissima***	***canadensis***	***juliae***	**% correct**
altiplanities	9	0	0	0	100
altissima	1	80	7	0	91
canadensis	0	7	46	0	87
juliae	0	0	0	11	100
Totals	10	87	53	11	91

Jackknifed classification matrix

	altiplanities	***altissima***	***canadensis***	***juliae***	**% correct**
altiplanities	8	1	0	0	89
altissima	1	78	9	0	89
canadensis	0	8	45	0	85
juliae	0	0	0	11	100
Total	9	87	54	11	88

canadensis were placed a posteriori in *S. canadensis*; 39 specimens with 95-100% probability, 4 specimens with 90-94% probability, and 3 specimens with 52-86% probabilities. All 7 specimens not placed in *S. canadensis* were placed in *S. altissima* with 54-100%.

In the Jackknifed Classificatory Discriminant Analysis, correct assignments did not change or changed little from the linear Classificatory Discriminant Analysis. The largest decrease was for *Solidago altiplanities*, dropping from 100% to 89% correct placement a posteriori, but this was due to only 1 specimen being assigned differently.

Seven specimens not assigned to an a priori group were assign a posteriori to *Solidago* altissima with 97-100% probability. These were the putative "var. nov." specimens of *S. altissima*.

The results of the canonical analysis are shown in Figure 7. Eigenvalues for first three canonical axes were 9.789, 2.600, and 1.214. *Solidago juliae* and *S. altiplanities* are separated from *S. altissima* and *S. canadensis* on the first two axes, while *S. altissima* and *S. canadensis* tend to be separated on the third axis.

Table. 5. Between Group F-matrix for the six variety/species-level taxa analysis in the *S. altissima/ S.canadensis* complex.

	altiplanities	**var. *altissima***	**var. *canadensis***	**var. *gilvocanescens***	**var. *hargeri***	**var. *pluricephala***
altiplanities	0.000					
var. *altissima*	48.265	0.000				
var. *canadensis*	59.744	34.963	0.000			
var. *gilvocanescens*	40.785	9.557	18.863	0.000		
var. *hargeri*	58.631	18.596	12.653	10.281	0.000	
var. *pluricephala*	41.039	3.005	42.942	9.610	20.826	0.000

Wilks' lambda = 0.0485, df = 6 5 144; approx. F = 21.0315 df = 30 558; prob = 0.0000

Six variety/species level taxa analysis

Data on the 150 specimens of *Solidago altiplanities*, *S. altissima* (3 varieties) and *S. canadensis* (2 varieties) were used to generate a pair-wise Pearson Correlation Matrix. The following pairs of traits had correlations greater than |0.7|: CAPL–CAPW, INVOLHT-RPAPL, INVOLHT-DCORL, RSTRAPL-RPAPL, RSTRAPL-DCORL, RPAPL–DCORL, and RPAPL–DPAPL. RPAPL, DCORL and DPAPL were excluded in the discriminant analyses. MLFLN, MLFW, ULFLN, ULFW, INVOLHT, RAYNUM, RSTRAPL, RSTRAPWD, RACHBL, DISCNUM, DLOBL, and DACHBL were included in the STEPWISE analysis. MLFSERNUM and UPLFSERNUM were excluded from the analyses because they were used in defining a priori groups. CAPL and CAPW were also excluded as these were used to partially define a priori groups. Stepwise discriminant analysis selected the following six traits as useful in separating the a priori groups in the analysis including all taxa in decreasing order of F-to-remove value: INVOLHT (50.25), DISCNUM (19.48), MLFW (12.83), RAYNUM (9.18), RSTRAPWD (8.43), and MLFLN (4.85). 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 indicate the largest separation was between *S. altiplanities*

and the two varieties of *S. canadensis*. The smallest separation was between *S. altissima* var. *altissima* and *S. altissima* var. *pluricephala.*

In the Classificatory Discriminant Analysis, the percents of correct a posteriori assignments of specimens to a priori groups ranged from 55-100% with a mean value of 73% (Table 6). Results for individual a priori taxa are presented in decreasing order of percent correct placement. 1) All nine specimens of *Solidago altiplanities* were assigned a posteriori to *S. altiplanities* with 99-100% probability. 2) 31 of 32 specimens (97%) of *S. canadensis* var. *canadensis* were assigned a posteriori to var. *canadensis*: 15 specimens with 90-100% probability, 9 specimens with 70-89% probability, 5 specimens with 50-69% probability, and 1 with 45% probability. One specimen of var. *canadensis* was assigned a posteriori to var. *altissima* with 43% probability. 3) 24 specimens (83%) of var. *gilvocanescens* were assigned a posteriori to var. *gilvocanescens*: 5 with 80-100% probability, 8 with 60-79% probability, 2 with 50-59% probability, 6 with 40-49% probability, and 2 with 32-33% probability. Five specimens of var. *gilvocanescens* were assigned a posteriori to other taxa: two specimens to var. *canadensis* with 42% and 47% probabilities, two specimens to var. *pluricephala* with 39% and 71% probability, and one to var. *hargeri* with 53% probability. 4) Twelve specimens

Table 6. Results of the Classificatory Discriminant Analysis of the four species-level groups of the *S. altissima* complex.

Classification matrix (a priori groups in left column, a posteriori assignments in rows)

	altiplanities	**var. *altissima***	**var. *canadensis***	**var. *gilvocanescens***	**var. *hargeri***	**var. *pluricephala***	**% correct**
altiplanities	9	0	0	0	0	0	**100**
var. *altissima*	0	17	0	5	1	8	**55**
var. *canadensis*	0	1	31	0	0	0	**97**
var. *gilvocanescens*	0	0	2	24	1	2	**83**
var. *hargeri*	0	1	3	4	12	1	**57**
var. *pluricephala*	1	10	0	1	0	16	**57**
Totals	10	29	36	34	14	27	**73**

Jackknifed classification matrix

	altiplanities	**var. *altissima***	**var. *canadensis***	**var. *gilvocanescens***	**var. *hargeri***	**var. *pluricephala***	**% correct**
altiplanities	9	0	0	0	0	0	**100**
var. *altissima*	0	15	0	5	1	10	**48**
var. *canadensis*	0	2	30	0	0	0	**94**
var. *gilvocanescens*	0	1	3	21	1	3	**72**
var. *hargeri*	0	1	3	4	12	1	**57**
var. *pluricephala*	1	11	0	1	0	15	**54**
Totals	10	30	54	11	14	29	**68**

(57%) of var. *hargeri* were assigned a posteriori to var. *hargeri*: eight specimens with 80-100% probability, three specimens with 6079% probability; one with 54% probability. Nine specimens of var. *hargeri* with assigned a posteriori to other taxa: four were assigned to var. *gilvocanescens* with 42-69% probability, three to var. *canadensis* with 43-83% probability, one to var. *altissima* with 77% probability, and one to var. *pluricephala* with 39% probability. 5) Sixteen specimens of var. *pluricephala* were assigned a posteriori to var. *pluricephala*: six with 82-91% probability, five with 62-78% probability, four with 52-56% probability, and one with 37% probability. Twelve specimens (57%) of var. *pluricephala* were assigned a posteriori to other taxa: 10 were assigned to var. *altissima* with 43-72% probability, one to *S. altiplanities* with 95% probability, and one to var. *gilvocanescens* with 54% probability.

Two dimensional plots of scores of CAN1 versus CAN 2 and CAN1 versus CAN3 of *S. aliplanities, S. altissima* (three separate varieties) and *S. canadensis* (two varieties) is shown in Fig. 8. Eigenvalues for first three canonical axes were 3.115, 1.905, and 0.397. *Solidago altiplanities* is separated from other taxa on the first and second axes. Symbols for varieties of *S. altissima* are generally more central and those for varieties of *S. canadensis* are placed more to the right in both plots.

Four varietal taxa analysis of *S. altissima*

Data on the 95 specimens of *Solidago altissima* were used to generate a pair-wise Pearson Correlation Matrix. No pairs of traits had correlations greater than |0.7|: CAPL and CAPW were excluded as these were used to partially define a priori groups. Stepwise discriminant analysis selected the following four traits in decreasing order of F-to-remove value as useful in separating the a priori groups in the analysis: DCORL (17.44), MLFW (11.58), RAYNUM (7.11), and MLFLN (3.99). Wilks's lambda, Pillai's trace, and Lawley-Hotelling trace tests of the null hypothesis that all three groups were the samples of one group had probabilities of p = 0.000 that the null hypothesis was true. The F-matrix for the discriminant analysis is presented in Table 7. The largest F-value to separate was between var. *gilvocanescens* and var. *pluricephala*. The smallest F-value to separate was between var. *altissima* and var. *pluricephala*.

Table. 7. Between Group F-matrix for the four variety-level taxa analysis in *S. altissima*.

	altissima	***gilvocanescens***	***pluricephala***	**var. *nov.***
altissima	0.000			
gilvocanescens	8.496	0.000		
pluricephala	5.420	15.226	0.000	
var. *nov.*	9.625	6.421	10.118	0.000

Wilks' lambda = 0.3663 df = 3 3 91; approx. F= 8.9645, df = 12 233; prob = 0.0000

In the Classificatory Discriminant Analysis of the three named varieties and one putative unnamed variety of *S. altissima*, the percents of correct assignments of specimens for *var. altissima*, var. *gilvocanescens*, var. *pluricephala*, and putative "var. nov." were 48%, 59%, 68%, and 57%, respectively. The Classification matrix and Jackknife classification matrix are presented in Table 8. Results for individual a priori taxa are presented in decreasing order of percent correct placement. (1) 19 (68%) of the var. *pluricephala* specimens were assigned a posteriori to var. *pluricephala*; 7 specimens with 82-97% probability, 6 with 67-76% probability, and 4 with 54-65% probability. Nine specimens were assigned to other varieties: 6 to var. *altissima* with 45-74% probability and 3 to var. *gilvocanescens* with 41-47% probability. (2) 17 of the var. *gilvocanescens* specimens were assigned a posteriori to var. *gilvocanescens*; 6 with 81-96% probability, 3 with 70-79% probability, and 4

with 50-63% probability. Twelve specimens of var. *gilvocanescens* were assigned to other varieties: 5 to putative "var. nov." with 38-84% probability, 4 to var. *altissima* with 35-56% probability, and 3 to var. *pluricephala* with 46-56% probability. (3) 4 of the 7 (57%) putative "var. nov." specimens were assigned a posteriori to "var. *nov*." with 80-100% probability. Two were assigned to var. *pluricephala* with 36-37% probability, and 1 to var. *gilvocanescens* with 44% probability. 4) 15 (48%) of the var. *altissima* specimens were assigned a posteriori to var. *altissima*; 2 with 82-90% probability, 5 with 68-72% probability, and 6 with 50-67% probability. Sixteen var. *altissima* specimens were assigned to other varieties: 9 to var. *pluricephala* with 39-79% probability, and 7 to var. *gilvocanescens* with 45-72% probability.

Table 8. Results of the Classificatory Discriminant Analysis of the four variety-level groups in *S. altissima*.

Classification matrix (a priori groups in left column, a posteriori assignments in rows)

	altissima	***gilvocanescens***	***pluricephala***	**var. *nov.***	**% correct**
altissima	15	7	9	0	48
gilvocanescens	4	17	3	5	59
pluricephala	6	3	19	0	68
var. *nov.*	0	1	2	4	57
Totals	25	28	33	9	58

Jackknifed classification matrix

	altissima	***gilvocanescens***	***pluricephala***	**var. *nov.***	**% correct**
altissima	15	7	9	0	48
gilvocanescens	4	17	3	5	59
canadensis	7	3	17	1	61
var. *nov.*	0	1	2	4	57
Total	26	28	31	10	56

probability, three with 70-79% probability, and four with 50-63% probability. Twelve specimens of var. *gilvocanescens* were assigned to other varieties: five to putative "var. nov." with 38-84% probability, four to var. *altissima* with 35-56% probability, and three to var. *pluricephala* with 46-56% probability. 3) Four of the seven (57%) putative "var. nov." specimens were assigned a posteriori to "var. *nov*." with 80-100% probability. Two were assigned to var. *pluricephala* with 36-37% probability, and one to var. *gilvocanescens* with 44% probability. 4) Fifteen (48%) of the var. *altissima* specimens were assigned a posteriori to var. *altissima*; two with 82-90% probability, five with 68-72% probability, and six with 50-67% probability. Sixteen var. *altissima* specimens were assigned to other varieties: nine to var. *pluricephala* with 39-79% probability, and seven to var. *gilvocanescens* with 45-72% probability.

The results of the four variety canonical analysis are shown in Figure 9. Symbols for var. *gilvocanescens* and "var. nov." are distributed to the left on the first axis and var. *altissima* and var. *pluricephala* are central or to the right in the figure. The ellipses for 95% confidence limits are not fully separated. Eigenvalues for the first three canonical axes were 0.785, 0.346, and 0.136.

Three varietal taxa analysis of *S. altissima*

Data on the 88 specimens of *S. altissima* were used to generate a pair-wise Pearson Correlation Matrix. No pairs of traits had correlations greater than |0.7|. CAPL and CAPW were excluded as these were used to define a priori groups. Stepwise discriminant analysis selected the

following six traits in decreasing order of F-to-remove value as useful in separating the a priori groups in the analysis: INVOLHT (31.31), DISCNUM (10.24), DLOBL (7.20), RAYNUM (6.66), RSTRAPL (6.04), and RSTRAPW (5.12). Wilks's lambda, Pillai's trace, and Lawley-Hotelling trace tests of the null hypothesis that all three 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 9. F-values to separate indicate the largest separation was between *var. gilvocanescens* and var. *pluricephala*. The smallest separation was between var. *altissima* var. *pluricephala*.

Table 9. F-matrix for the discriminant analysis of three varietal groups in *S. altissima.*

	altissima	***gilvocanescens***	***pluricephala***
altissima	0.000		
gilvocanescens	13.588	0.000	
pluricephala	3.570	15.036	0.000

Wilks' lambda = 0.2954; df = 7 2 85; Approx. F= 9.4789; df = 14 158; prob = 0.0000

Table 10. Results of the Classificatory Discriminant Analysis of three variety-level groups in *S. altissima.*

Classification matrix (a priori groups in left column, a posteriori assignments in rows)

	altissima	***gilvocanescens***	***pluricephala***	**% correct**
altissima	19	5	7	61
gilvocanescens	0	28	1	97
pluricephala	6	0	22	79
Totals	24	33	30	78

Jackknifed Classification matrix

	altissima	***gilvocanescens***	***pluricephala***	**% correct**
altissima	18	5	8	58
gilvocanescens	1	27	1	93
pluricephala	8	0	20	71
Total	27	32	15	74

In the Classificatory Discriminant Analysis, the percent of correct assignments of specimens for var. *gilvocanescens*, var. *pluricephala*, and var. *altissima* were 97%, 79% and 61%, respectively The Classification matrix and Jackknife classification matrix are presented in Table 10. Results for individual a priori taxa are presented in decreasing order of percent correct placement. (1) Twenty-eight specimens of var. *gilvocanescens* were assigned a posteriori to var. *gilvocanescens*; 15 specimens with 90-100% probability, 5 with 70-89% probability, 8 with 50-69% probability. One specimen was assigned to var. *pluricephala* with 64% probability; this was tetraploid from Montana. (2) Twenty-two specimens of var. *pluricephala* were assigned a posteriori to var. *pluricephala*: 5 specimens with 92-97% probability, 2 with 80-86% probability, 6 with 70-79% probability, 3 with 64-69% probability, and 6 with 50-59% probability. Six specimens were assigned to var. *altissima* with 49-93% probability. These came from North Carolina, Alabama, Louisiana, Florida, and Texas. Two of them were tetraploid and 1 was hexaploid. One of the Texas specimens — *Johnston & Cheatham 12805* (TEX) — was originally identified by M.C. Johnston as var. *pluricephala*; the ploidy level is unknown; the inflorescence array is 13.5 cm tall by 11.5 cm wide and has leaf traits like other specimens of var. *pluricephala*; it was placed a posteriori into var. *altissima* with 57%

probability, into var. *pluricephala* with 34% probability, and into var. *gilvocanescens* with 10% probability. (3) Nineteen specimens of var. *altissima* were assigned a posteriori to var. *altissima*: 3 specimens with 90-94% probability, 6 with 70-86% probability, 5 with 61-66% probability, 4 with 50-58% probability, and 1 with 49% probability. Five specimens were assigned a posteriori to var. *gilvocanescens* with 66-85% probability. Six specimens were assigned to var. *pluricephala* with 51-78% probability.

The results of the three variety canonical analysis are shown in Figure 10. Symbols for var. *gilvocanescens* are distributed to the left on the first axis and var. *altissima* and var. *pluricephala* are central or to the right in the figure. The ellipses for 95% confidence limits are well separated. Eigenvalues for first two canonical axes were 1.499 and 0.277, respectively.

Var. *gilvocanescens, var. canadensis, var. hargeri* analysis

Data on the 81 specimens of *S. altissima* var. *gilvocanescens*, *S. canadensis* var. *canadensis*, and *S. canadensis* var. *hargeri* were used to generate a pair-wise Pearson Correlation Matrix. The following pairs of traits had correlations greater than |0.7|: INVOLHT-DCORL, INVOLHT-DPAPL, RSTRAPL-DCORL, RPAPL-DCORL, RPAPL-DPAPL, and DCORL-DPAPL. DCORL and DPAPL were not included in the discriminant analyses. MLFSERNUM and ULFSERNUM were not included because these were used in part to define a priori groups. Stepwise discriminant analysis selected the following six traits in decreasing order of F-to-remove value as useful in separating the a priori groups in the analysis: ULFW (23.33), RPAPL (13.82), MLFLN (10.20), OPHYLL (6.53), INVOLHT (6.16), and ULFLN (5.58). Wilks's lambda, Pillai's trace, and Lawley-Hotelling trace tests of the null hypothesis that all three 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 11. The largest F-value to separate was between var. *gilvocanescens* and var. *canadensis*. The smallest F-value to separate was between var. *canadensis* and var. *hargeri* with the F-value to separate between var. *gilvocanescens* and var. *hargeri* on slightly larger.

Table 11. F-matrix for the discriminant analysis of three varietal groups groups *S. altissima* var. *gilvocanescens, S. canadensis* var. *canadensis* and *S. canadensis* var. *hargeri*.

	gilvocanescens	***canadensis***	***hargeri***
gilvocanescens	0.000		
canadensis	26.264	0.000	
hargeri	14.754	11.164	0.000

Wilks' lambda = 0.1791; df = 6 2 78; Approx. F= 16.5822; df = 12 146; prob = 0.0000

In the Classificatory Discriminant Analysis, the percent of correct assignments of specimens for var. *gilvocanescens*, var. *canadensis*, and var. *hargeri* were 89%, 91%, and 81%, respectively. The Classification matrix and Jackknife classification matrix are presented in Table 12. Results for individual a priori taxa are presented in decreasing order of percent correct placement. (1) 29 specimens of var. *canadensis* were assigned a posteriori to var. *canadensis*: 17 specimens with 90-100% probability, 5 with 80-89% probability, 3 with 61-99%, 3 with 53-59% probability, and 1 with 44% probability. Three specimens were assigned a posteriori to var. *hargeri* with 65-78% probability. (2) 25 specimens of var. *gilvocanescens* were assigned a posteriori to var. *gilvocanescens*: 19 specimens with 90-100% probability, 4 with 70-89% probability, 1 with 54% probability. Three specimens were assigned a posteriori to other varieties. One tetraploid specimen from Minnesota was assigned to var. *altissima* with 75% probability. Two specimens were assigned a posteriori to var. *hargeri*; a diploid from Wisconsin had 52% probability of being var. *hargeri* and

42% probability of being var. *gilvocanescens*; a hexaploid from southeastern Colorado had 68% probability of being var. *hargeri*. (3) 17 specimens of var. *hargeri* were assigned a posteriori to var. *hargeri*: 9 specimens with 90-100% probability, 6 with 70-89% probability, and 2 with 64-66% probability. Three specimens were assigned to var. *canadensis* with 71%, 78%, and 86% probabilities, respectively. One specimen was assigned to var *gilvocanescens* with 69% probability; this was a diploid from Ohio with broader lanceolate leaves that were green rather than gray-green.

Table 12. Results of the Classificatory Discriminant Analysis of three variety-level groups *S. altissima* var. *gilvocanescens, S. canadensis* var. *canadensis* and *S. canadensis* var. *hargeri*.

Classification matrix (a priori groups in left column, a posteriori assignments in rows)

	gilvocanescens	***canadensis***	***hargeri***	**% correct**
gilvocanescens	25	1	2	**89**
canadensis	0	29	3	**91**
hargeri	1	3	17	**81**
Totals	26	33	22	**88**

Jackknifed Classification matrix

	gilvocanescens	***canadensis***	***hargeri***	**% correct**
gilvocanescens	25	1	2	**89**
canadensis	1	26	5	**81**
hargeri	1	3	17	**81**
Total	27	30	24	**84**

The results of the three variety canonical analysis are shown in Figure 11. Symbols for var. *gilvocanescens* are distributed to the left and center on the first axis and var. *canadensis* and var. *hargeri* are to the right and to the right and center-right, respectively, in the figure. On the second axis, symbols for var. *canadensis* are generally on the lower half of the graph, while those of var. *hargeri* are generally more on the upper half of the diagram with some overlap in distributions. The ellipses for 95% confidence limits are well separated. Eigenvalues for first two canonical axes were 2.174 and 0.759, respectively.

A plot of the discriminating traits ULFW versus INVOLHT for the three varieties is presented in Fig. 12. The 4 specimens of var. *canadensis* with the larger involucres are from Ontario and New Brunswick. The 3 specimens of var. *hargeri* with larger involucres are from Kentucky (85% probability of being var. *hargeri*), Wisconsin (64% probability of being var. *hargeri*) and Switzerland. The 3 specimens of var. *gilvocanescens* with smaller involucres are from Illinois (52% probability of being var. *gilvocanescens* and 20% of being var. *hargeri*) and Iowa (52% and 70% probability of being var. *gilvocanescens* and 19% and 29% of being var. *hargeri*, respectively); 2 were diploid and 1 is of unknown ploidy level.

DISCUSSION

Based on the results of all the analyses, the following taxa should be recognized: *Solidago altiplanities, S. altissima* var. *altissima, S. altissima* var. *gilvocanescens, S. altissima* var. *pluricephala, S. canadensis* var. *canadensis, S. canadensis* var. *hargeri,* and *S. juliae*. Support was not found for recognizing a new variety in *S. altissima* occurring in Canada along the northern margins of distribution of the species in the prairie / boreal forest ecotone. Additional field and herbarium work might alter this conclusion.

Four species level analysis

Based on the percents of correct assignments and the frequencies of high probabilities of those assignments, *Solidago altiplanities, S. altissima, S. canadensis,* and *S. juliae* are well supported as taxa. The largest F-to separate values in the Results occur in this analysis indicating the greatest amount of separation between species pairs *S. canadensis/S. juliae, S. altissima/S. juliae*, and *S. altiplanities/S. juliae* in the plots of multiple characters in N-dimension hyperspace on which the statistics are determined. In the classificatory discriminant analysis 0-11% decreases occurred in correct a posteriori classification values between the linear and jackknifed analyses. The 11% decrease involves just one specimen of *S. altiplanities*. This is not surprising because visually *S. juliae* is the most distinct species included in the analysis. Surprisingly, it is the most recent of the species to be described (Nesom 1989). Inclusion of *S. juliae* into *S. altissima* or *S. canadensis*, as had been done in floras prior to 1989, expands the ranges of some character traits in either of the latter to species to the point where recognizing the less distinct *S. altiplanities* would have been less defensible. Recognition of the two narrower leaved species *S. juliae* and *S. altiplanities* reduced the size of the problem in dealing with *S. altissima* and assigning specimens to species in the subsect. *Triplinerviae*. Additional analyses discussed below indicate that the real problem in the *S. altissima* complex is not with the relatively narrowly distributed *S. juliae* and *S. altiplanities* but instead with *S. altissima* and its infraspecific races and *S. canadensis* and its infraspecific races.

Six variety/species level taxa analysis

In the analyses involving more than one species and multiple varieties, the nomenclaturally established varieties within a species tended to be less differentiated from each other than from the other species. The largest F-to separate values are between *Solidago altiplanities* and all five varieties included in the analysis. The lowest F-to separate values were between the varieties of *S. altissima.* Within *S. canadensis*, recognition of var. *canadensis* and var. *hargeri* was supported, which was the conclusion reached in Semple et al. (2013) using the same *S. canadensis* data, but in comparison with other species than those included here. The percentages of correct a posteriori placements in the classificatory discriminant analysis were lowest for the three varieties of *S. altissima* and *S. canadensis* var. *hargeri*. The distinctness of these four taxa was explored in the two species/three varietal level analyses discussed below.

Three and four varietal taxa analyses of *S. altissima*

Two analyses were performed on just specimens of *Solidago altissima* to assess the significance of differences between the three named races and a fourth putative race within the species. The difference in level of support for four versus three races was considerable. The F-to separate values between var. *gilvocanescens* and var. *pluricephala* were about the same in the two sets of analyses and were the largest, but still low compared to F-to separate values in the four species analysis. The F-to separate value between var. *altissima* and var. *gilvocanescens* increased when the putative fourth variety was dropped as an a priori group. However, the F-to separate value between var. *altissima* and var. *pluricephala* decreased when the putative fourth variety was dropped as an a priori group, meaning the two varieties were less well supported in the three variety analysis than the four variety analysis in terms of amount of group centroid separation in the N-dimension hyperspace plot of discriminating characters. However, the percentages of correct place increased for all three named varieties when the putative fourth variety was not included as an a priori group; the average value of placement to variety went from 58% to 78%. Inclusion of a putative fourth variety was disruptive. Sample size for this putative variety was small, but the number of characters selected by the stepwise discriminant analysis was lower than the number selected when only three varieties were included as a priori groups. The conclusion that a fourth variety should not be recognized at this time seems obvious based on the data available.

Support for recognizing var. *pluricephala* as a distinctive southeastern USA race of *Solidago altissima* is moderate and much less well supported than treating the western var. *gilvocanescens* as a distinct race from the eastern var. *altissima*. The original trait used to distinguish var. *pluricephala* was an elongated inflorescence array like those found in *S. juliae*, *S. altiplanities*, and *S. leavenworthii*, which was not included in the set of analyses reported here. However, this trait was not consistent and assignment to the a priori groups var. *altissima* and var. *pluricephala* was based primarily on geography with the latter being found on the coastal plain and outer Piedmont in the Carolinas, Georgia, and Alabama. Geography is a somewhat arbitrary trait and this may account for the higher number of "mis-assignments" indicated by the results of the classificatory discriminant analyses. Even a specimen *M.C. Johnston & Cheatham 12805* (TEX) from extreme southern Texas that was identified as var. *pluricephala* by the author of the taxon was placed weakly into var. *altissima*. The specimen vegetatively looks generally more like var. *pluricephala* than var. *altissima*, even if the technical traits are atypical for var. *pluricephala*. This was also true for some of the other var. *pluricephala* specimens assigned a posteriori to var. *altissima*. The fact that 71% of the var. *pluricephala* specimens were assign a posteriori to var. *pluricephala* is noteworthy. It is true that var. *pluricephala* is not always easily distinguished from var. *altissima*, especially in the area where the Coastal Plain flora and the inland-upland-more northern floras come together. It is the first author's opinion that it is useful to recognize var. *pluricephala* and doing so is consist with how other previously ignored species and varieties are now being recognized (Semple, 2014, continuously updated, Classification of Solidago, Astereae Lab web site).

Whether or not var. *gilvocanscens* should be treated as a separate species because it is more distinct is a reasonable question to ask. The statistics indicate that var. *gilvocanescens* is not as strongly separated from var. *altissima* (and var. *pluricephala*) as are *Solidago altiplanities* and *S. juliae* from *S. altissima*. The size of the F-to separate values, the percentages of correct placements, and the probabililties of those placements are all lower than what the Astereae Lab has found to be usual for species level recognition in asters and goldenrods. Also, var. *gilvocanescens* includes the only diploids known in *S. altissima* and is thus likely the ancestor of both var. *altissima* and var. *pluricephala* which include some tetraploids and mostly hexaploids. Ploidy level alone is not a basis for treating var. *gilvocanescens* as a separate species because it also includes many tetraploids and some hexaploids. Halverson et al. (2008) reported that AFLP marker data suggested that polyploid cytotypes in *S. altissima* likely have multiple origins from different diploid lineages. This means that var. *altissima* and var. *pluricephala* possibly are polyphyletic in the strictest sense. Schlaepfer et al. (2008) concluded that tetraploids in *S. gigantea* were much more likely to have evolved multiple times than from a single event, and they suggested that as many as seven independent origins for tetraploids had occurred in eastern North America. Peirson et al. (2012) reported on the cytogeography of subsect. *Humiles* (Rydb.) Semple (the *S. simplex* complex) and discussed problems with species concepts as applied to the genus. Peirson et al. (2013) concluded the same as Halverson et al. (2008) but regarding the multiple origins for polyploids in subsect. *Humiles* and that "recurrent formation of polyploid lineages is the norm in many plants." Semple and Peirson (2013) treated nearly all of the infraspecific taxa in S. *simplex* listed in Semple and Cook (2006) as separate species. Separate races were not recognized in *S. gigantea*. The races in *S. altissima* appear to be more distinct (more geographically discrete, less intergrading) than those in *S. gigantea*. The patterns of distributions of the different ploidy levels differ in the two species (Semple et al. 1984; Semple & Cook 2006; Peirson et al. 2012). Treating var. *gilvocanescens* as subsp. *gilvocanescens* does not clarify the problem because of differences of opinion on application of the rank subspecies. For consistency, the three races of *S. altissima* have been designated varieties in this paper, without implication that the ranks subspecies and variety are essentially the same or that the former should just be used as a grouping category only.

Var. *canadensis, var. hargeri, var. gilvocanescens* analysis

The results also provide statistical support for the generally held opinion that the *Solidago altissima*/*S. canadensis* identification problem is real. While *S. altissima* and *S. canadensis* should be treated as separate species, the existence of diploids in *S. altissima* var. *gilvocanescens* and only diploids in *S. canadensis* var. *hargeri* increases the difficulty of placing individual specimens into one or the other variety. Smaller headed, proximally hairy-stemmed plants with lower numbers of serrations on upper stem leaves are the main challenge. The plot of upper leaf width versus involucre height in Figure 12 indicates some of the difficulty in separating the three varieties. The var. *canadensis* specimens with larger involucres came from New Brunswick and southeastern Ontario, which are outside the range of var. *gilvocanescens*. The two specimens of var. *hargeri* with larger involucres came from Kentucky and Wisconsin from the portion of the range that overlaps with that of var. *gilvocanescens*; these were placed in var. *hargeri*. The third came from Switzerland in Europe and was placed in var. *canadensis* in this analysis, but it was placed in var. *hargeri* in the analysis in Semple et al. (2013). The three specimens of var. *gilvocanescens* with smaller involucres came from Illinois and Iowa — these were placed in the analysis into var. *gilvocanescens*, and two were known to be diploid. While *S. canadensis* var. *hargeri* generally has greener upper leaves with larger teeth than specimens of *S. altissima* var. *gilvocanescens*, the leaves of both tend to be wider than those of var. *canadensis*. Leaf color can be changed by drying conditions and age, making that trait less reliable. For those who really need an identification that is highly accurate and with high probability of being correct, an alternative method, i.e., molecular, is needed to further explore the relationships of these three varieties and to find more reliable ways of identifying problematic individual specimens. Scoring multiple traits on a specimen and running a discriminant analysis to determine its identification is clearly not a convenient method either.

ACKNOWLEDGEMENTS

This work was supported by a Natural Sciences and Engineering Research Council of Canada (NSERC) Discovery Grants to JCS. NSERC Undergraduate Student Research Awards to HF is acknowledged. Daniel Schlaepfer is thanked for collections of *S. canadensis* from Europe used in this study. Derick Poindexter is thanks for specimens of *S. canadensis* from North Carolina used in this study. Joan Venn is thanked for her help with processing loans in and out of WAT and for assisting the late J.K. Morton in collecting numerous specimens used in this study. The curators of herbaria that loaned specimens are gratefully acknowledged. Jennifer A. Hood, Imram Khamis, Haris Faheemuddin, and Y. Alex Chong are thanked for technical assistance at different stages in the project.

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Table 2. Group means of the means of all taxa of the *S. altissima* complex included in the analyses; mean, standard deviation, minimum and maximum given for each trait.

species	***altiplanites***	***altissima***			***canadensis***		***juliae***
variety		***altissima***	***gilvo-canescens***	***pluri-cephala***	***canaden-sis***	***hargeri***	
STMHT (cm)	**60.5** 16.42 35.5 84.7	**89.9** 25.99 54.5 163.0	**80.1** 25.34 45.8 163.5	**93.0** 24.14 41.0 155.0	**90.6** 29.07 47.5 155.5	**110.5** 45.07 58.0 182.5	**95.2** 38.18 60 180
MLFLN (mm)	**43.4** 6.83 28.3 50.2	**74.1** 14.75 43.6 99.0	**62.6** 12.17 39.8 85.0	**68.8** 14.32 51.5 111.5	**73.7** 15.88 49.6 105.000	**89.6** 25.7 52.0 162.5	**50.2** 11.37 31.8 65.0
MLFW (mm)	**5.1** 1.339 3.7 8.0	**11.0** 2.67 6.8 17.3	**11.2** 2.79 5.6 16.0	**11.4** 1.98 7.8 15.3	**8.4** 2.106 3.4 12.2	**13.3** 3.88 4.25 22.5	**7.2** 2.19 5.1 13.2
MLFSER-NUM	**0.9** 1.25 0.0 3.6	**6.3** 2.64 0.33 11.0	**5.9** 2.63 2.0 14.3	**6.3** 1.54 3.8 10.8	**7.0** 2.28 2.8 11.6	**8.7** 4.146 0.4 16.0	**3.1** 4.49 0.0 13.8
ULFLN (mm)	**29.9** 6.16 23.5 40.0	**45.2** 12.16 26.0 80.0	**41.7** 8.46 25.3 62.7	**45.5** 12.97 26.8 73.5	**47.8** 10.78 27.4 76.25	**49.8** 18.47 14.4 84.5	**46.30** 8.82 30.00 61.25
ULFW (mm)	**3.5** 0.72 2.4 4.3	**7.2** 1.87 4.0 12.3	**8.4** 1.88 5.0 12.0	**8.1** 3.10 5.0 20.3	**5.7** 1.38 3.0 9.0	**7.9** 2.085 3.0 11.8	**14.1** 3.49 10.1 21.8
ULFSER-NUM	**0.04** 0.133 0.0 0.4	**2.7** 1.82 0.0 6.2	**3.8** 2.40 0.0 8.8	**3.8** 1.49 1.0 9.4	**3.4** 2.62 0.0 8.8	**4.2** 3.22 0.0 10.8	**18.0** 7.34 12.2 34.25

Table 2. Continued.

species	***altiplanites***	***altissima***		***canadensis***			***juliae***
variety		***altissima***	***gilvo-canescens***	***pluri-cephala***	***canaden-sis***	***hargeri***	
CAPL (cm)	**14.9** 7.15 8.8 30.0	**18.2** 7.76 7.4 37.0	**17.2** 7.46 5.4 35.7	**19.2** 6.74 7.5 38.0	**12.7** 4.61 4.0 26.0	**19.2** 7.36 8.8 34.5	**21.7** 8.44 11.0 37.0
CAPW cm	**4.7** 4.45 2.2 15.5	**12.6** 5.53 5.0 35.0	**11.8** 5.035 3.8 25.0	**11.1** 4.030 3.5 20.0	**9.2** 3.54 4.0 15.5	**16.0** 7.058 4.0 26.7	**8.3** 1.73 5.5 11.0
INVOLHT (mm)	**4.0** 0.197 3.8 4.4	**3.5** 0.36 2.8 4.4	**2.9** 0.35 2.0 3.5	**3.5** 0.34 2.9 4.4	**2.1** 0.38 1.3 3.2	**2.4** 0.54 1.7 4.2	**3.4** 0.25 2.9 3.7
OPHYLL (mm)	**1.7** 0.94 1.1 4.1	**1.2** 0.16 0.89 1.5	**1.1** 0.20 0.8 1.8	**1.1** 0.132 0.8 1.4	**1.1** 0.27 0.69 2.09	**1.06** 0.23 0.7 1.8	**1.3** 0.13 1.0 1.5
IPHYLL (mm)	**3.5** 0.298 3.06 3.9	**2.6** 0.69 1.4 4.0	**2.1** 0.405 1.6 2.9	**2.6** 0.64 1.7 3.8	**1.8** 0.4 0.9 2.54	**1.9** 0.34 1.1 2.6	**2.8** 0.22 2.5 3.1
RAYNUM	**7.1** 1.73 5.0 9.4	**9.7** 2.42 3.8 13.8	**8.6** 2.14 3.5 11.8	**7.6** 3.02 2.0 11.8	**9.3** 1.9 6. 13	**8.0** 1.83 5 12	**10.4** 1.77 7.3 13.2
RSTRAPL (mm)	**1.6** 0.44 0.8 2.2	**1.3** 0.19 0.9 1.6	**1.2** 0.2 .30 1.625	**1.4** 0.30 0.97 1.8	**0.87** 0.288 0.32 1.45	**0.9** 0.204 0.56 1.3	**1.3** 0.25 0.9 1.6
RSTRAPW (mm)	**0.5** 0.12 0.3 0.7	**0.27** 0.100 0.14 0.48	**0.31** 0.104 0.15 0.50	**0.29** 0.109 0.10 0.60	**0.19** 0.058 0.10 0.30	**0.25** 0.066 0.14 0.38	**0.3** 0.083 0.2 0.5
RACHBL (mm)	**1.1** 0.37 0.6 1.8	**0.75** 0.172 0.43 1.04	**0.75** 0.210 0.43 1.4	**0.73** 0.166 0.40 1.13	**0.79** 0.31 0.30 1.94	**0.68** 0.277 0.3 1.3	**0.79** 0.193 0.54 1.18

Table 2. Continued.

species	***altiplanites***	***altissima***			***canadensis***		***juliae***
variety		***altissima***	***gilvo-canescens***	***pluri-cephala***	***canaden-sis***	***hargeri***	
RPAPL	**3.3**	**2.8**	**2.4**	**2.9**	**1.6**	**1.62**	**2.2**
(mm)	0.34	0.36	0.37	0.34	0.37	0.33	0.45
	2.8	2.1	1.8	2.1	1.0	0.66	1.0
	3.9	3.4	3.1	3.6	2.3	2.04	2.8
DISCNUM	**9.6**	**4.3**	**4.7**	**4.2**	**4.6**	**3.9**	**5.8**
	2.13	0.87	1.33	1.26	1.2	1.18	1.013
	7.4	2.7	2.03	3.0	2	1.8	3.8
	13.2	5.8	8.3	9.2	7	6.2	7.7
DCORL	**3.7**	**3.7**	**3.1**	**3.9**	**2.3**	**2.5**	**3.2**
(mm)	0.457	0.46	0.40	0.55	0.598	0.35	0.23
	2.67	3.0	2.2	3.1	0.6	1.5	2.8
	4.2	5.1	3.9	4.9	3.3	3.0	3.5
DLOBL	**1.1**	**0.77**	**0.83**	**0.85**	**0.53**	**0.65**	**2.0**
(mm)	0.15	0.157	0.240	0.153	0.189	0.187	0.15
	0.8	0.48	0.54	0.50	0.23	0.42	1.8
	1.3	1.01	1.75	1.04	0.90	1.13	2.3
DACHBL	**0.97**	**0.73**	**0.72**	**0.75**	**0.74**	**0.67**	**1.1**
(mm)	0.278	0.136	0.193	0.157	0.22	0.267	0.27
	0.57	0.52	0.43	0.50	0.33	0.40	0.8
	1.52	1.02	1.34	1.22	1.17	1.48	1.7
DPAPL	**3.4**	**3.0**	**2.6**	**3.3**	**1.8**	**1.79**	**2.3**
(mm)	0.40	0.351	0.397	1.36	0.37	0.404	0.26
	2.8	2.5	1.7	2.3	1.2	0.78	2.2
	3.9	3.8	3.3	10.1	2.4	2.51	3.0

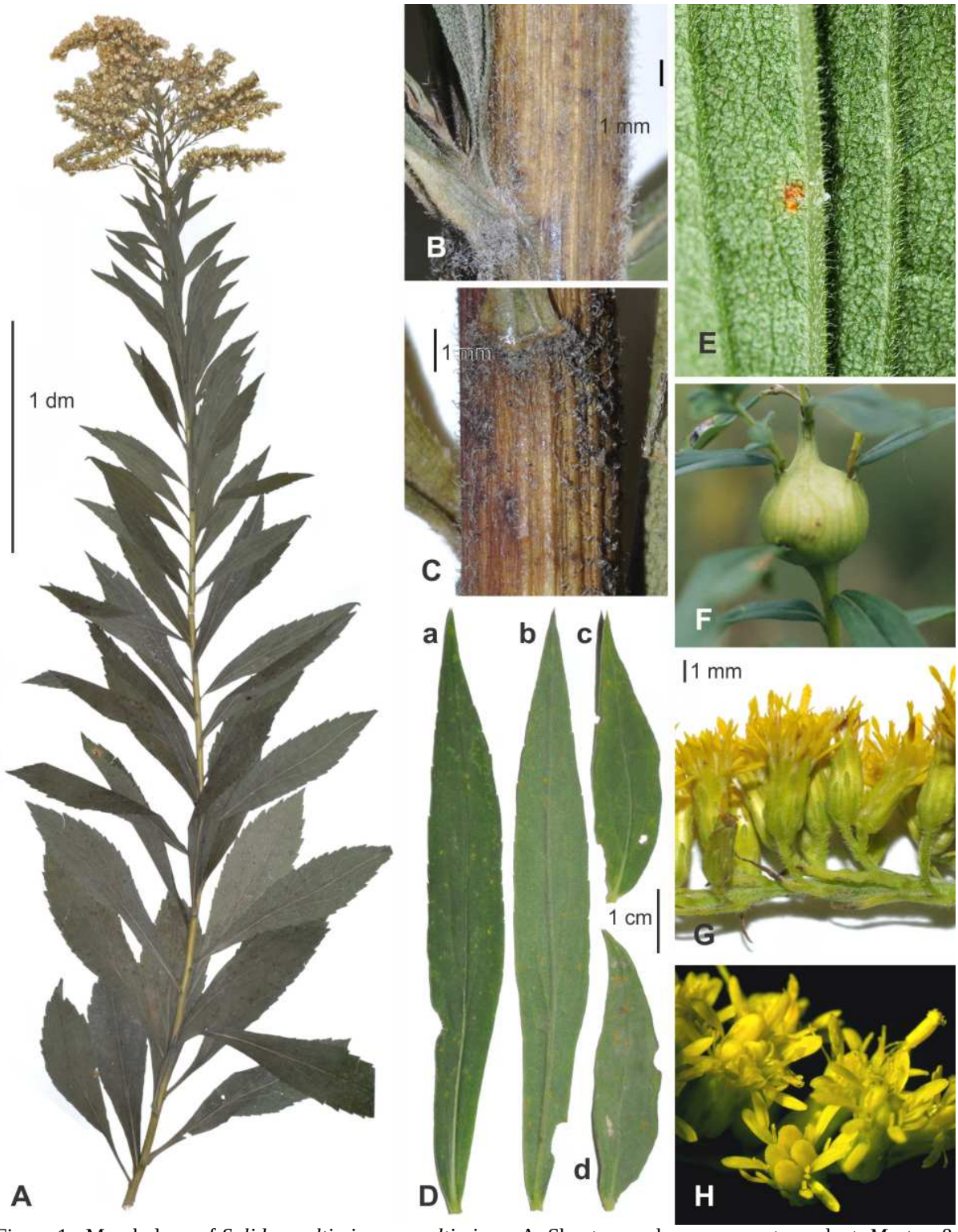

Figure 1. Morphology of *Solidago altissima* var. *altissima.* A. Shoot, greenhouse grown transplant, *Morton & Venn NA176142* (JKM), New Brunswick. B. Upper stem, *Semple & Brammall 2791* (WAT), Ontario. C. Lower mid stem, *Semple 6816* (WAT), New York. D. Mid (a, b) and upper stem leaves (c, d), adaxial surfaces (a, c), abaxial surface (b, d), Ontario. F. Stem ball gall, Ontario. G. Involucres, Ontario. H. Florets, Ontario.

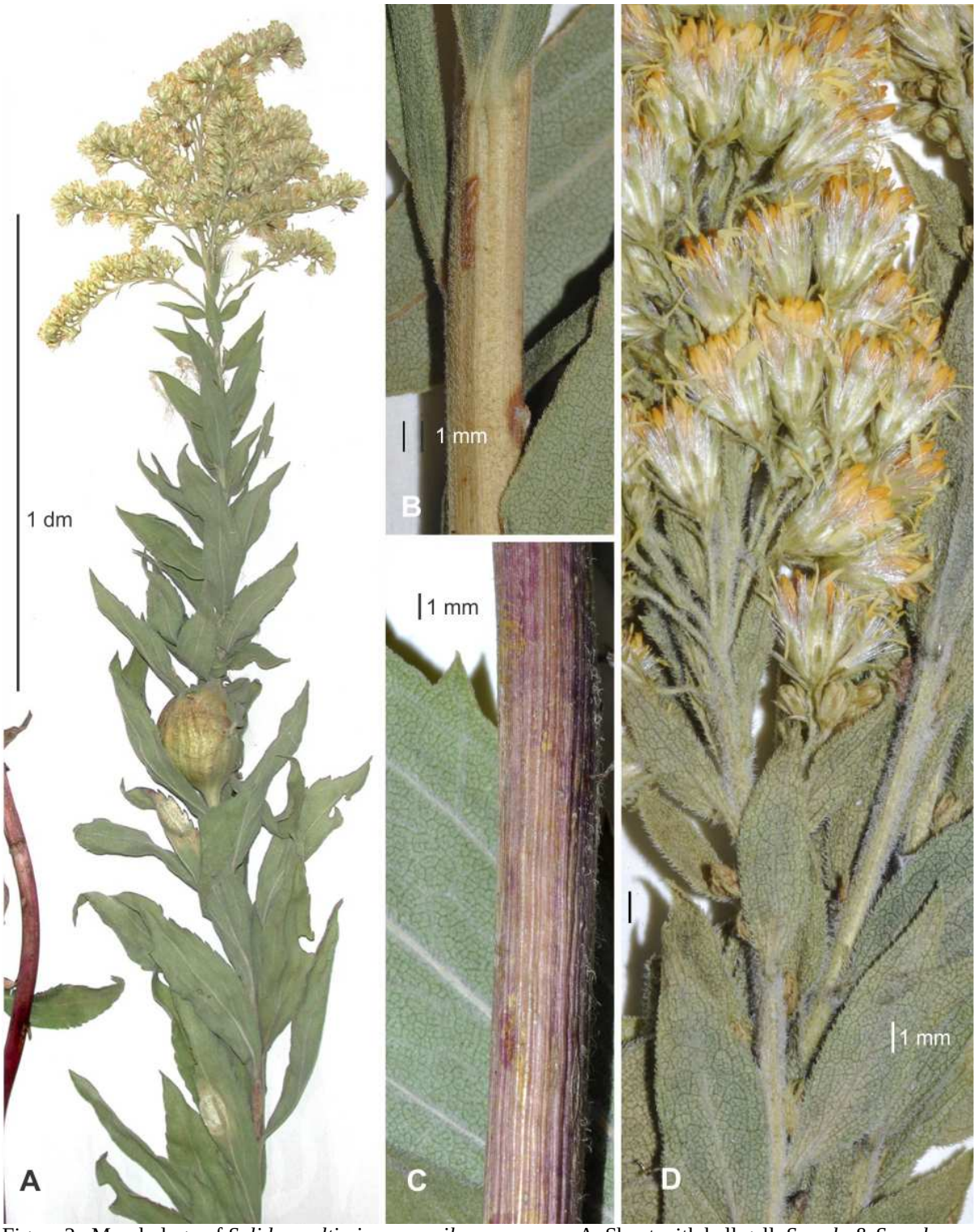

Figure 2. Morphology of *Solidago altissima* var. *gilvocanescens*. A. Shoot with ball gall, *Semple & Semple 6678* (WAT), North Dakota. B. Mid stem, *Semple & Brouillet 6978* (WAT), Montana. C. Lower stem, *Morton & Venn NA15651* (JKM). D. Heads, *Oldham 30688* (WAT).

Figure 3. Morphology of *Solidago altissima* var. *pluricephala*. A. Mid-size shoot, *Semple & Suripto 10076* (WAT). B. Stem, lower, *Morton & Venn NA16471* (JKM). C. Mid stem leaves, Paine Prairie, Florida. D. Inflorescence, Paine Prairie, Florida.

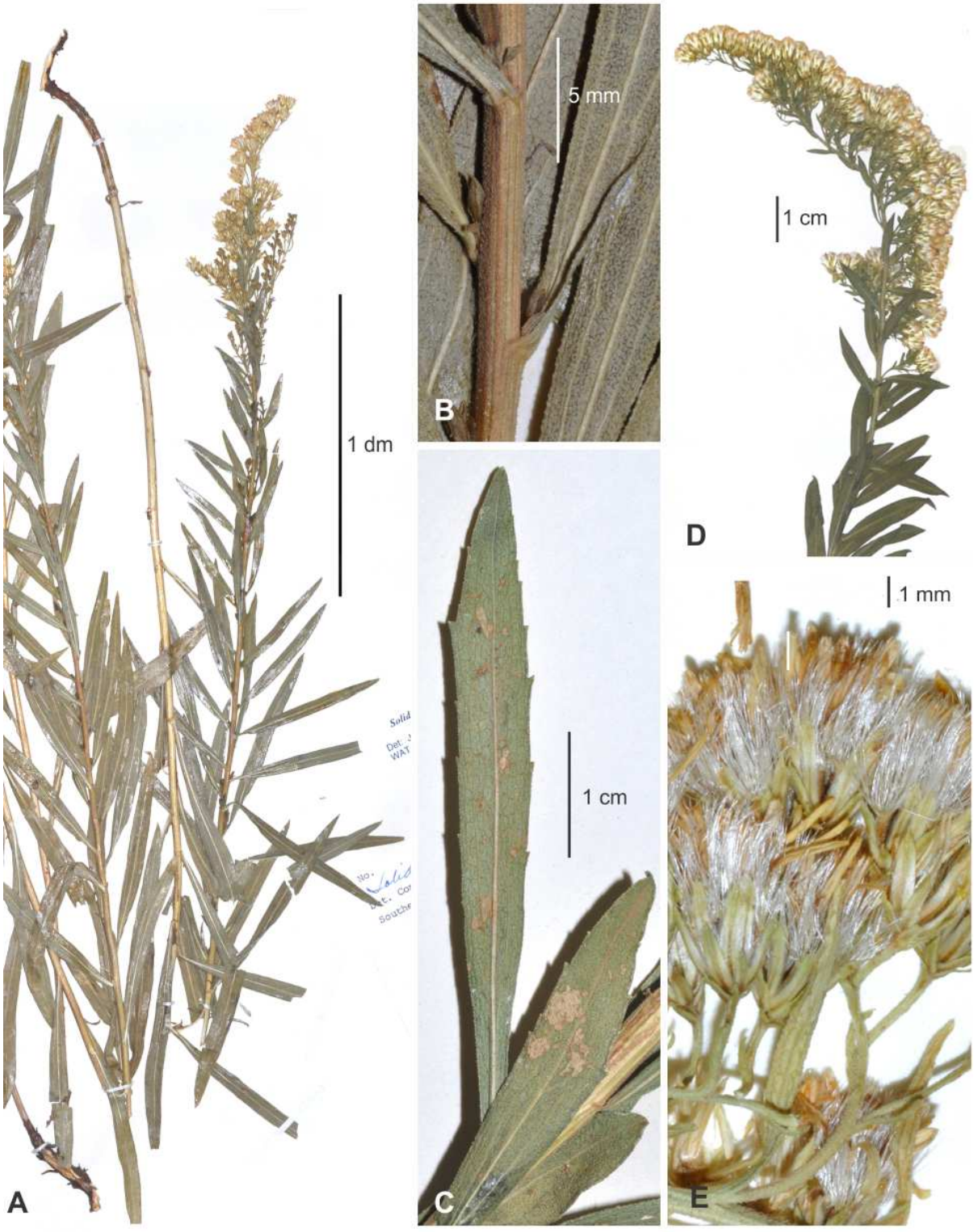

Figure 4. Morphology of *Solidago altiplanities*. A. Shoot, *Pace 150* (BRIT). B. Mid stem, *Correll 13031* (BRIT). C. Lower stem leaves, *Waller 1583* (BRIT). D. Inflorescence, *Correll 38035* (BRIT). E. Heads, *Nesom & O'Kennon LAMR 984* (BRIT).

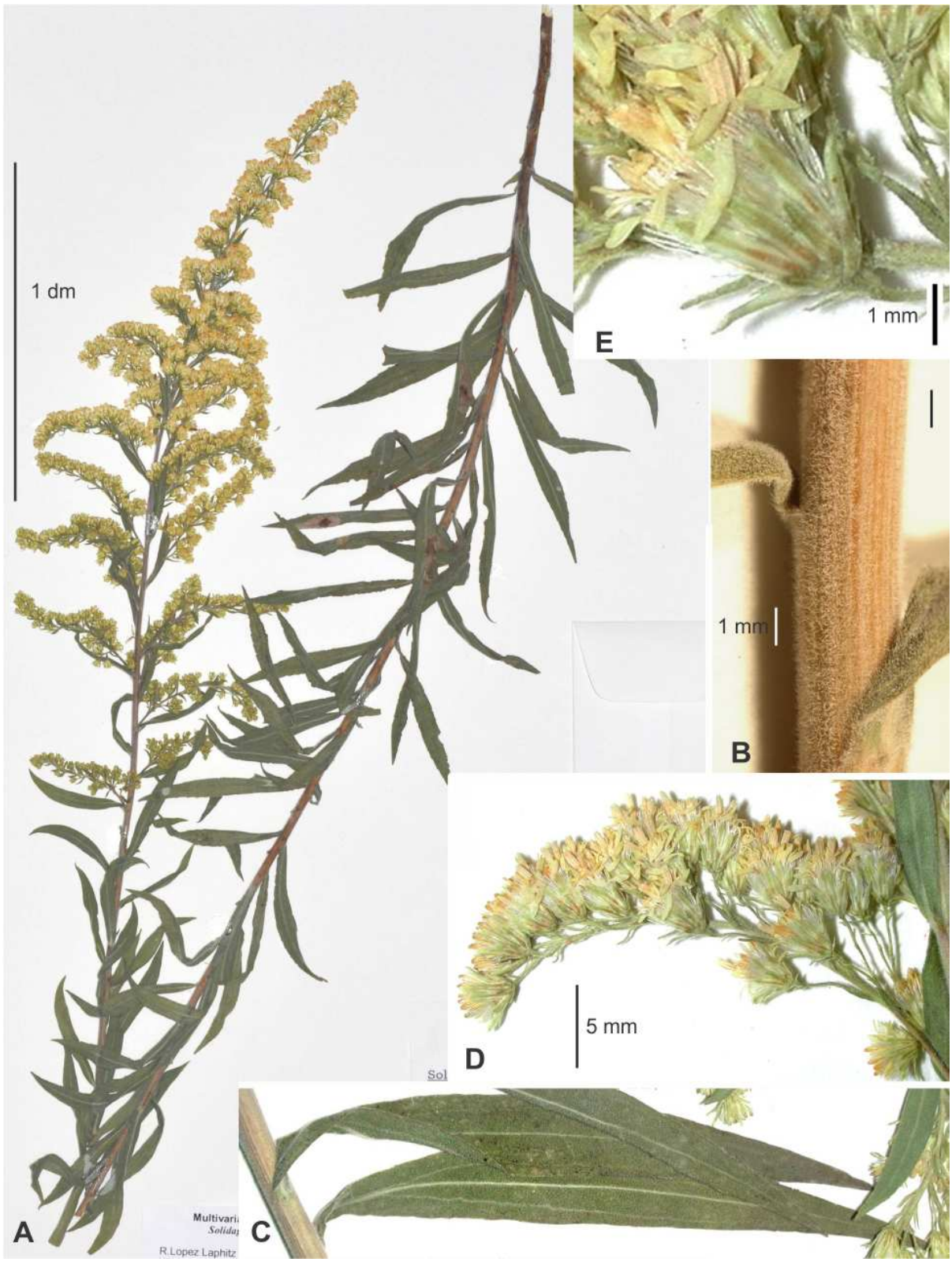

Figure 5. Morphology of *Solidago juliae*. A. Mid-size shoot, *Nesom & Nesom 7211* (WAT). B. Stems. C. Mid stem leaves. D. Inflorescence. E. Heads. Isotype, *Nesom & Nesom 7212* (WAT).

Figure 6. *Solidago altissima* habits and habitats. A. Var. *altissima*, Ontario. B. Var. *gilvocanescens*, sandhills, Nebraska. C. Var. *pluricephala*, prairie, Florida.

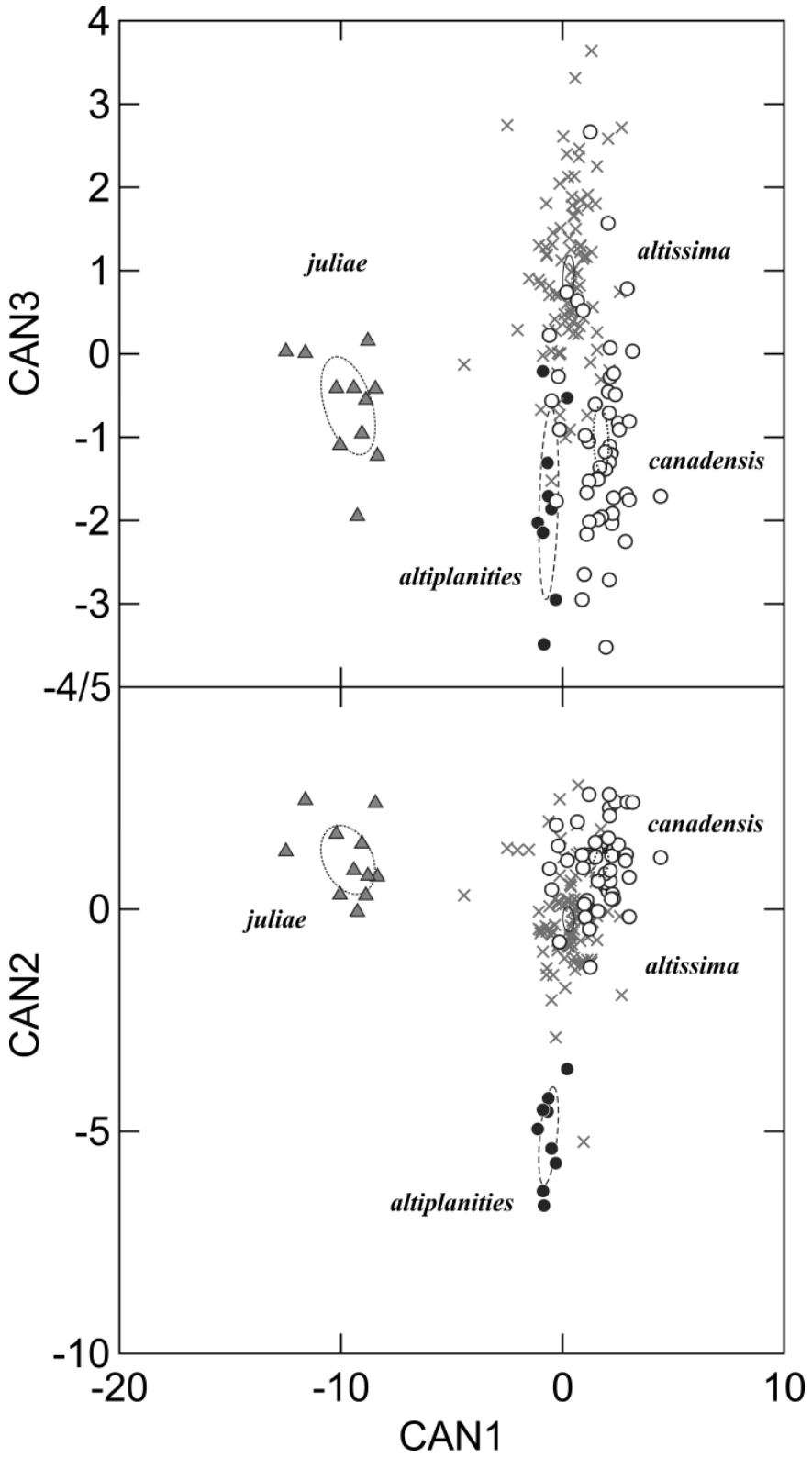

Figure 7. Two dimension plots of CAN1 versus CAN2 and CAN1 versus CAN3 scores generated by the Canonical Analysis of specimens of the *Solidago S. altissima/S. canadensis* complex; solid dots = *S. altiplanities*, gray crosses = *S. altissima*, circles = *S. canadensis*, gray triangles = *S. juliae*; 95% confidence ellipses are shown for each taxon.

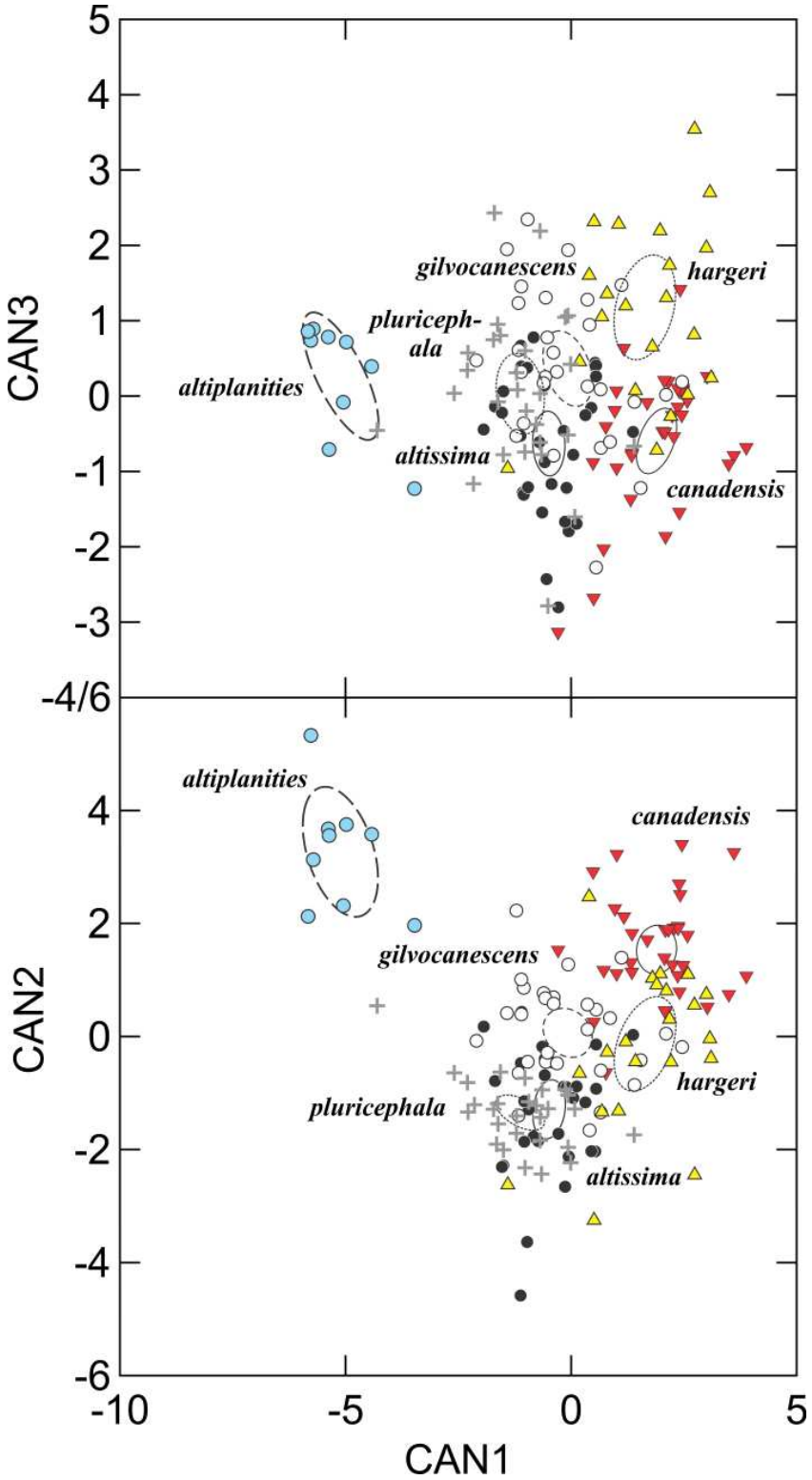

Figure 8. Two dimensional plots of CAN1 versus CAN2 and CAN1 versus CAN3 scores generated by the Canonical Analysis of specimens of the *Solidago altiplanities* and the four varieties of *S. altissima* and *S. canadensis*; blue dots = *S. altiplanities*, black dots = *S. altissima* var. *altissima*, open circles = *S. altissima* var. *gilvocanescens*, gray pluses = *S. altissima* var. *pluricephala*, red triangles = *S. canadensis* var. *canadensis*, yellow triangles = *S.*. *canadensis* var. *hargeri*; 95% confidence ellipses are shown for each taxon.

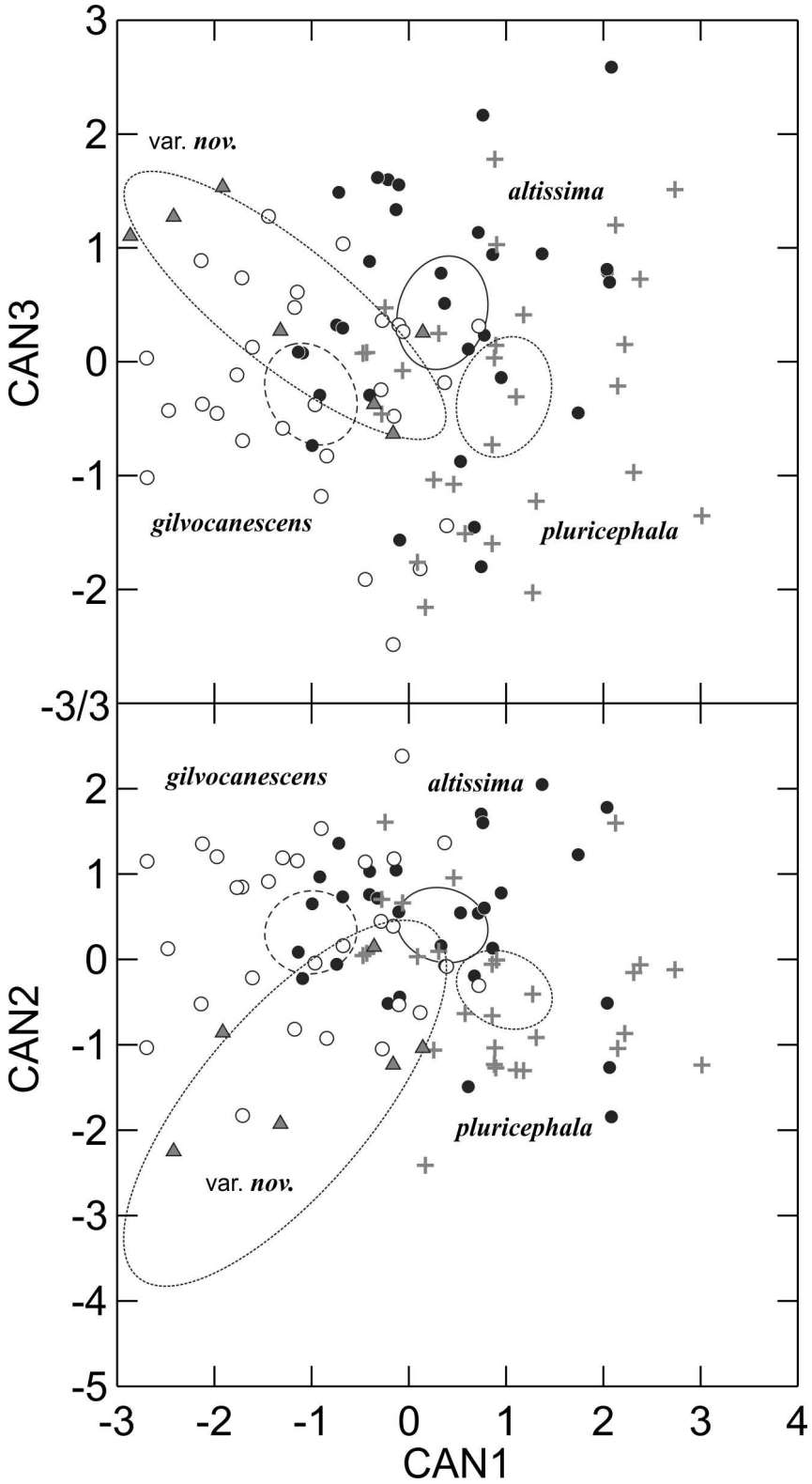

Figure 9. Two dimensional plots of CAN1 versus CAN2 and CAN1 versus CAN3 scores generated by the Canonical Analysis of specimens of four possible varieties of *Solidago altissima*; black dots = var. *altissima*, var. open circles = var. *gilvocanescens*, gray pluses = var. *pluricephala*, gray triangles = var. *nov.*; 95% confidence ellipses are shown for each taxon.

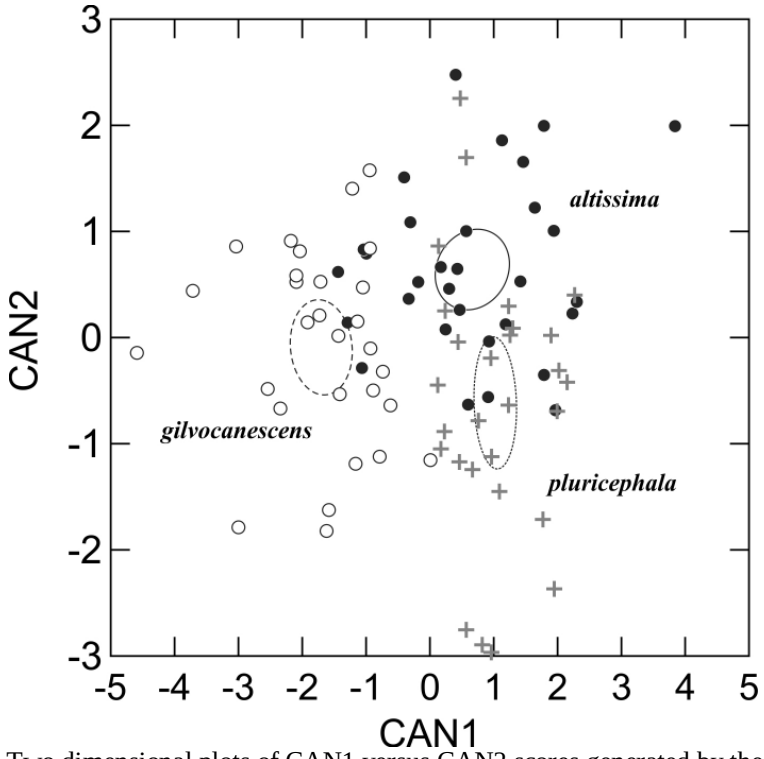

Figure 10. Two dimensional plots of CAN1 versus CAN2 scores generated by the Canonical Analysis of specimens of three varieties of *Solidago altissima*; black dots = var. *altissima*, var. open circles = var. *gilvocanescens*, gray pluses = var. *pluricephala*; 95% confidence ellipses are shown for each taxon.

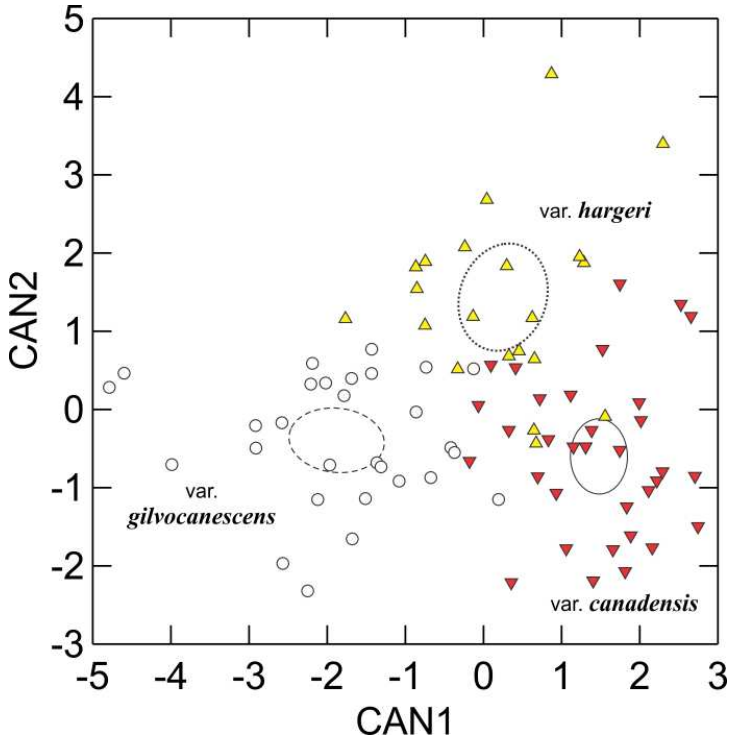

Figure 11. Two dimensional plots of CAN1 versus CAN2 scores generated by the Canonical Analysis of specimens of *Solidago altissima* var. *gilvocanescens*, *S. canadensis* var. *canadensis* and *S. canadensis* var. *hargeri*; open circles = var. *gilvocanescens*, red triangles = var. *canadensis*, yellow triangles = var. *hargeri*; 95% confidence ellipses are shown for each taxon.

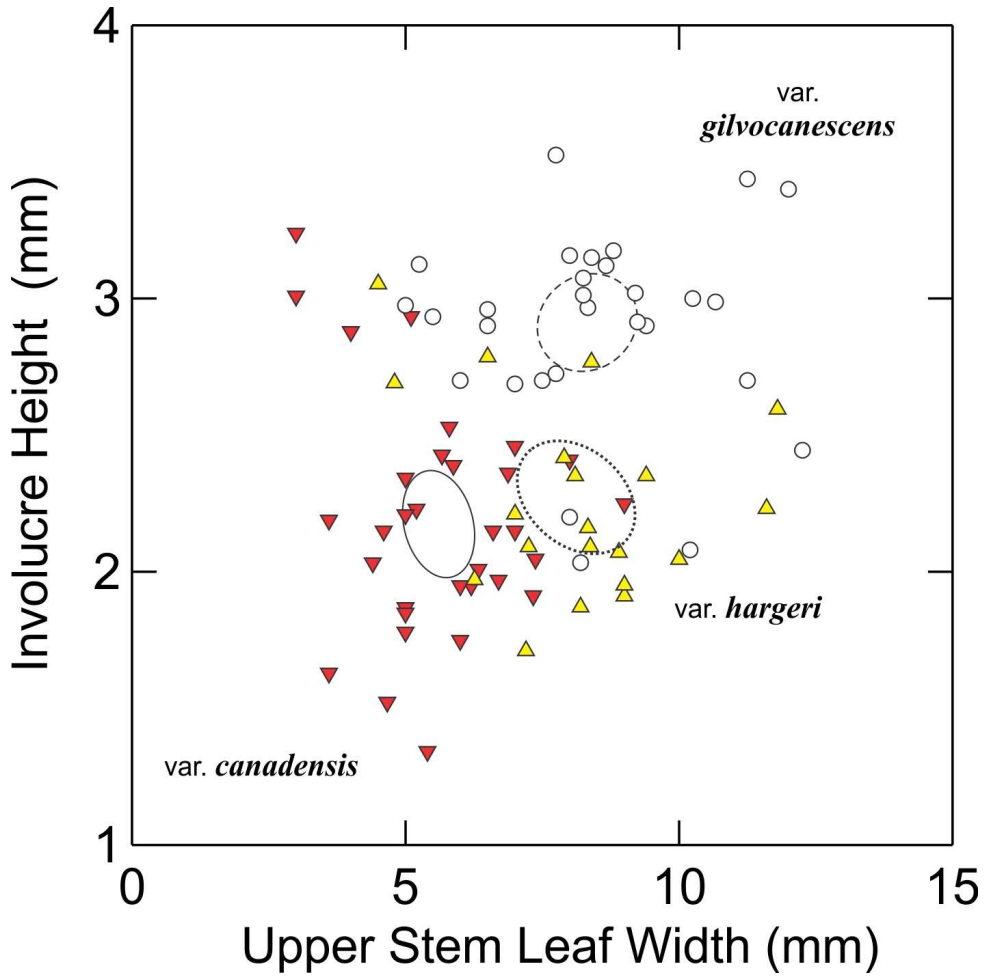

Figure 12. Two dimensional plot of upper leaf width versus involucre height for specimens of of *Solidago altissima* var. *gilvocanescens, S. canadensis* var. *canadensis* and *S. canadensis* var. *hargeri*; open circles = var. *gilvocanescens*, red triangles = var. *canadensis*, yellow triangles = var. *hargeri*; 95% confidence ellipses are shown for each taxon.