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A MULTIVARIATE STUDY OF THE *SOLIDAGO SEMPERVIRENS* COMPLEX (ASTERACEAE: ASTEREAE: *SOLIDAGO* SUBSECT. *MARITIMAE*)

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ABSTRACT

A multivariate morphometric study of the *Solidago sempervirens* complex of *S.* subsect. *Maritimae* was performed to assess statistical support for recognizing *S. azorica*, *S. maya*, *S. mexicana*, *S. paniculata* and *S. sempervirens* as separate species. Specimens of *S. virgata* of the *S. stricta* complex of subsect. *Maritimae* were also included in some analyses. Nine analyses were run, including all or only some of the species. In several analyses, eastern and western specimens of *S. mexicana* were split into two a priori groups. *Solidago paniculata* and *S. azorica* were determined to be the most distinct species in the complex based on both leaf and floral traits. *Solidago maya* was found to be most similar to eastern specimens of *S. mexicana* and to some specimens of *S. virgata* from the southeastern USA. *Solidago maya* has the lowest leaf density in the complex and has inflorescences that are sometimes not apically secund. All species of the *S. sempervirens* complex occur at 0-40 m elevations in coastal plain moist soils and coastal marshes and dunes with the exception of *S. maya*, native to 460-2200 m elevation in Belize, Guatemala, and Chiapas, Mexico and *S. paniculata* native to central Mexico. *Solidago sempervirens* is adventive further inland in eastern North America at higher elevations along roads that are salted in the winter, and it appears to be introduced in a few locations in Florida, Louisiana, and Mexico. The native ranges of distribution of *S. azorica*, *S. maya*, *S. mexicana, S. paniculata*, and *S. sempervirens* are completely or mostly allopatric. Robust individuals are generally easily identified, but smaller or damaged individuals can be more problematic in placing to species.

*Solidag*o subsect. *Maritimae* (Torr. & Gray) G.L. Nesom includes all the bog and marsh goldenrod species with sheathing proximal basal rosette and lower stem leaves. The *Solidago sempervirens* L. complex includes 1) the seaside goldenrods *S. azorica* Hochstetter ex Seubert, *S. mexicana* L., and *S. sempervirens* L. native to eastern North America and some islands in the North Atlantic and 2) two inland species, *S. maya* Semple and *S. paniculata* DC., native to central and southern Mexico, Belize, and eastern Guatemala. These species all have inflorescences that are usually narrowly to broadly secund conical in shape, although *S. paniculata* sometimes has ascending spreading lower branches making the inflorescence somewhat corymbiform. *Solidago azorica* and *S. mexicana* have often been included as varieties or subspecies within *S. sempervirens* (e.g., Cronquist 1968; Semple & Cook 2006). Semple (2012; 2016 frequently updated) treated all three taxa as separate species. Schaefer (2015) reported that plants of *S. azorica* from the Azores differed in their nuclear ITS and ETS sequences plus a number of microsatellite markers from plants of *S. sempervirens* from North America. He also noted that historical records indicated that *S. azorica* was likely present in the Azores in pre-Columbian times with birds being the likely means of the original dispersal from North America in the past. *Solidago maya* is native to the highlands of Chiapas, Mexico, in eastern Guatemala, and central Belize; this species is described in the sister paper to this publication (Semple 2016).

Specimens of *Solidag*o *mexicana* have been confused with *S. virgata* Michx., which is here treated as a member of the *S. stricta* Ait. (sensu Semple 2013) complex of species including, *S. austrina* Small, *S. chrysopsis* Small, *S. gracillima* Torr. & A. Gray, and *S. pulchra* Small. Application of the name *S. stricta* has varied since it was published in 1789; critical for this publication is the misapplication of the name to plants native to the southeastern USA and Mexico (Fernald 1950; Cronquist 1968, 1980; Bell et al. 1968; Correll & Johnston 1970; Nash 1976; McVaugh 1984; Jones & Coile 1988; Semple & Cook 2006; Semple 2012). Other species in the *S. stricta* complex are not dealt with further in this publication. A manuscript on a multivariate analysis of the *S. stricta* complex is in preparation. A multivariate analysis of the remaining small *S. uliginosa* complex of *S.* subsect. *Maritimae* is also nearing completion; this will deal with whether or not the complex can be usefully split into two or three species based on ploidy differences and geographic range differences.

Within *Solidago mexicana*, the western populations from Louisiana to south Texas are tetraploid (Semple et al. 1993, reported as *S. stricta*; additional unpublished reports), while populations further east and north along the Gulf and Atlantic coasts are all diploid (Beaudry 1963; Semple et al. 1984, 1992, 1993; unpublished counts). Because the literature (e.g. Correll & Johnston 1970) and field experience and herbarium sheet examination by the first author indicated that in coastal Texas it was difficult to separate *S. stricta* (sensu authors not Aiton) from *S. sempervirens* var. *mexicana* (= *S. mexicana*), the possibility that the tetraploids were a separate allopolyploid race derived from hybridization of diploid *S. mexicana* and diploids of *S. virgata* in Louisiana was considered by the first author for a number of years. All chromosome count reports for *S. sempervirens* and *S. azorica* are diploid (Beaudry & Chabot 1959; Beaudry 1963; Kapoor 1970; Kovanda 1972; Morton 1981; Semple et al. 1984; 1992, 1993; additional unpublished counts). Thus, the only known tetraploids in the *S. sempervirens* complex occur in the western part of the range from Louisana to south Texas (no reports are known from Mexico). In contrast, polyploidy occurs in multiple species in the *S. stricta* complex.

A multivariate morphometric analysis of the *Solidago sempervirens* complex has not been previously published. Such a study is presented below in order to statistically access the following questions: (1) how significant are the differences between *S. azorica*, *S. mexicana,* and *S. sempervirens* and which characters best distinguish the taxa; (2) whether *S. mexicana* could be usefully divided into eastern and western taxa; (3) whether or not the plants in the complex from the Mexican,Guatemalan, and Belize highlands (*S. maya*) differ significantly enough from *S. mexicana* and *S. virgata* to warrant being placed in a new species and is that new species more similar to *S. mexicana* (eastern and western populations separately or combined) or *S. virgata*; and (4) how different is *S. paniculata* from other species in the complex?

MATERIALS AND METHODS

In total, 119 specimens selected from much larger numbers of specimen from AZU, BM, F, FSU, GH, J.K.Morton personal herbarium in ROM, LL, MEXU, MO, NCU, NY, TEX, USF, and WAT in MT (Thiers, continuously updated) were scored and included in the analysis. Data on *Solidago azorica* (18 specimens; Fig. 1), *S. maya* (9 specimens; Fig. 2), *S. mexicana* (44 specimens; 28 eastern and 16 western; Fig. 3), *S. paniculata* (9 specimens; Fig. 4), *S. sempervirens* (16 specimens; Fig. 5) of the *S. sempervirens* complex, and *S. virgata* (26 specimens) of the *S. stricta* complex were included. Ranges of species in the *S. sempervirens* complex are shown in Fig. 6 along with the locations of samples included in the multivariate analysis. Nineteen vegetative and 19 floral traits were scored when possible: 1-5 replicates per character depending upon availability of material and whether or not the trait was meristic (Table 1). Mean values were used in the analyses, while raw values were used to generate ranges of variation for each trait.

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 were used to define a priori groups along with geographic location. Basal rosette and lower stem leaf traits were not included in the analyses because these were often not present on specimens. No lower stem and rosette leaves were observed on any collections of *Solidago paniculata*, although petiole base scars indicate that the petioles sheathed the lower stem as in other species in the complex.

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 r > |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 in N-dimensional hyperspace. Classificatory discriminant analysis was run on N-1 traits selected by the STEPDISC analysis. If more than N-1 traits were selected, where N = lowest sample size of the a priori groups; in this study N=9 (*Solidago maya* and *S. paniculata*). A COMPLETE analysis would then be run using only eight traits. Geisser probabilities of assignment to each a priori group were generated a posteriori for each specimen 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 or the specimens. 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.

Nine analyses were performed that are reported here. Many preliminary analyses were run on smaller data bases over multiple years as additional specimens and taxa were added to the matrix. The first analysis included specimens of six species level a priori groups: *S. azorica*, *S. maya*, *S. mexicana* (eastern populations, diploid when known), *S. mexicana* (western populations, tetraploid when known), *S. paniculata*, and *S. sempervirens* (including only plants that had been treated as ssp. or var. *sempervirens*). The second analysis included five species level a priori groups: *S. azorica*, *S. maya*, *S. mexicana* (eastern and western populations), *S. paniculata*, and *S. sempervirens*. The third analysis included four species: *S. azorica*, *S. maya*, *S. mexicana* (all populations), and *S. sempervirens*. The fourth analysis included four species level a priori groups: *S. maya*, *S. mexicana* (diploid eastern populations), *S. mexicana* (tetraploid western populations), and *S. virgata* (including diploid, tetraploid, and hexaploid plants when known). The fifth analysis included three species level a priori groups: *S. maya*, *S. mexicana* (eastern and western populations combined), and *S. virgata*. The sixth analysis included three species level a priori groups: *S. azorica*, *S. mexicana* (eastern and western populations combined), and *S. sempervirens*. The seventh analysis included two species level a priori groups: *S. mexicana* (eastern and western populations combined) and *S. sempervirens*. The eighth analysis included two species level a priori groups: *S. maya* and *S. virgata*. The ninth analysis included two species level a priori groups: *S. maya* and *S. mexicana* (western populations only). The number of specimens in a group varied due to absence of some data.

RESULTS

The Pearson correlation matrix yielded r > |0.7| for most pairs of leaf treats reducing the number to be used to either mid leaf length and upper leaf width or mid leaf width and upper leaf length. Lower leaves were often absent and were not included in the discriminant analyses. Both combinations of mid and upper leaf traits were used in preliminary analyses with the more discriminating results being present below. Overall, leaf blade shape is similar in all species and size differences between lower and upper stem leaves varies among and sometimes within species. Lower stem leaves lacked serrations in all cases and were very rarely present in very low numbers on basal rosette leaves.

Figure 1. Example of *Solidago azorica* used in the multivariate study: *Anon. 1277* AZU.

Figure 2. Example of *Solidago maya* used in the multivariate study: *Breedlove 27763* F.

Figure 3. Example of *Solidago mexicana* used in the multivariate study: *Kunzer 1207* USF.

Figure 4. Example of *Solidago paniculata* used in the multivariate study: *MacDaniels 611* F.

Figure 5. Example of *Solidago sempervirens* used in the multivariate study: *Semple & Keir 4814* WAT ex JCSemple.

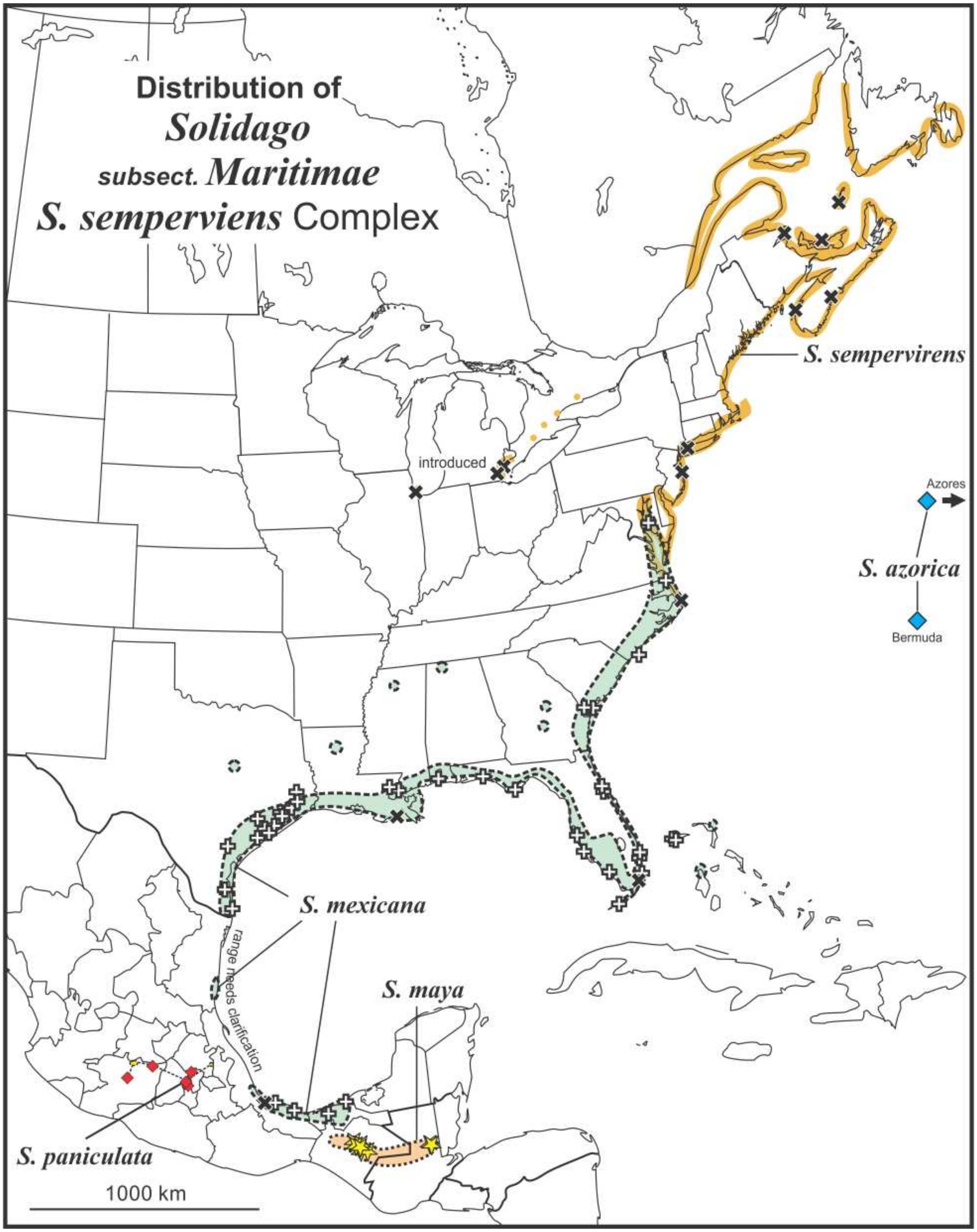

Figure 6. Distribution of the ranges and locations of multivariate samples of the species of the *Solidago sempervirens* complex (*Solidago* subsect. *Maritimae*): *S. azorica*, blue diamonds; *S. maya*, yellow stars; *S. mexicana*, white +s; *S. paniculata*, red diamonds; *S. sempervirens* s.s., black ×s. Symbols indicate a priori group assignments; in a few cases final identification to species of some specimens in the area of range sympatry of *S. sempervirens* and *S. mexicana* in North Carolina to Maryland was difficult.

Table 1. Traits scored for the multivariate analyses of specimens of *Solidago azorica*, *S. maya*, *S. mexicana*, *S. paniculata*, *S. sempervirens*, and *S. virgata*.

Abbreviation	**Description of trait scored**
STEMHT	Stem height measured from the stem base to tip(cm)
UPSTMNOD25	Number of nodes in distal 25% of the stem below the inflorescence
UPSTMNOD 20	Number of nodes in distal 20% of the stem below the inflorescence
BLFLN	Basal rosette leaf length measured from the leaf base to tip (mm)
BLFWD	Basal rosette leaf width measured at the widest point (mm)
BLFWTOE	Basal rosette leaf measured from the widest point to the end (mm)
BLFSER	Basal rosette leaf dentation - number of serrations along (one side)
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 margin - number of serrations (one side)
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 margin - number of serrations (one side)
ULFLN	Upper leaf length measured form the leaf base to tip(mm)
ULFWD	Upper leaf width measured at the widest point (mm)
ULFWTOE	Upper leaf measured from the widest point to the end (mm)
ULFSER	Upper leaf margin - number of serrations (one side)
CAPL	Length of inflorescence (cm)
CAPW	Width of inflorescence (cm)
CAPBRLN	Length of longest lower inflorescence branches (cm)
INVOLHT	Involucre height (mm)
OPHYLN	Outer phyllary length (mm)
OPHYLW	Outer phyllary width (mm)
IPHYLN	Inner phyllary length (mm)
IPHYLW	Inner phyllary width (mm)
RAYNUM	Number of ray florets per head
RSTRAPLN	Ray strap length top of the corolla tube to the tip of the strap (mm)
RSTRAPWD	Ray strap width measured at the widest point (mm)
RACHLN	Ray floret cypsela body length at anthesis (mm)
RPAPLN	Ray floret pappus length at anthesis (mm)
RPUB	Density of hairs on ray floret ovary at anthesis (1-5 scale)
DCORLN	Disc corolla length from the base to tip of the corolla lobes (mm)
DLOBLN	Disc corolla lobe length lobe (mm)
DACHLN	Disc achene length (mm)
DPAPLN	Disc pappus length (mm)
DPUB	Density of hairs on disc floret ovary at anthesis (1-5 scale)

Six species groups analysis

In the STEPWISE discriminant analysis of six species level a priori groups *Solidago azorica*, *S. maya*, *S. mexicana* eastern (mostly or entirely diploids), *S. mexicana* western (mostly or entirely tetraploids), *S. paniculata*, and *S. sempervirens*, the following five traits were selected in a STEPWISE analysis and are listed in order of decreasing F-to-remove values: mid leaf width (27.31), number of ray florets (20.00), number of leaf nodes in the distal 25% of the stem below the inflorescence (9.38), involucre height (9.14), and number of disc florets (8.34). Wilks's lambda, Pillai's trace, and Lawley-Hotelling trace tests of the null hypothesis that all groups were the samples of one group had probabilities of p = 0.000 that the null hypothesis was true. The F-matrix for the discriminant analysis is presented in Table 2. F-values based on Mahalanobis distances between group centroids indicated the largest separations were between *Solidago azorica* and western *S. mexicana* (28.828), *S. azorica* and *S. paniculata* (25.972), *S. paniculata* and *S. sempervirens* (21.985), and *S. paniculata* and western *S. mexicana* (21.253), and the least separation was between *S. maya* and eastern *S. mexicana* (1.082).

In the a posteriori Classificatory Discriminant Analysis of the six species level a priori groups, a posteriori assignments of specimens ranged from 39-94% to their own group. The Classification matrix and Jackknife classification matrix are presented in Table 3. Results are presented in decreasing order of percent correct placement. Seventeen of 18 specimens of *S. azorica* (94%) were assigned a posteriori to the *S. azorica* group; 11 with 93-100% probabilities, 3 with 81-84% probability, 1 from Bermuda with 63% probability (29% to eastern *S. mexicana* and 7% to *S. maya*), and 1 specimens from Bermuda with53% probability (36% to eastern *S. mexicana* and 9% to *S. maya*). One cultivated specimen from N. Bimini, Bahamas (*R. & E. Howard 10104*, NY) included in the *S. azorica* a priori group was placed a posteriori into the eastern *S. mexicana* group with 42% probability (40% to *S. maya*, 17% to *S. azorica*).

Table 2. Between groups F-matrix for the six a priori group analysis (df = 5 80).

Group	*azorica*	*maya*	*mexicana*E	*mexicana*W	*paniculata*
maya	14.463				
***mexicana*E**	18.901	1.082			
***mexicana*W**	28.828	6.454	6.454		
paniculata	25.972	17.406	19.139	21.253	
sempervirens	19.052	15.912	18.252	15.057	21.985

Wilks' lambda = 0.0437 df = 5 5 84
Approx. F = 15.7684 df = 25 298 prob = 0.0000

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

Group	*azorica*	*maya*	*mexicana* E	*mexicana* W	*paniculata*	*sempervirens*	% correct
azorica	17	0	1	0	0	0	94
maya	0	6	3	0	0	0	67
***mexicana* E**	1	8	8	4	0	2	39
***mexicana* W**	0	1	4	10	0	1	63
paniculata	0	0	2	0	7	0	78
sempervirens	1	1	0	1	0	12	80
Totals	19	15	19	15	7	15	68

Jackknifed classification matrix

Group	***azorica***	***maya***	***mexicana* E**	***mexicana* W**	***paniculata***	***sempervirens***	**% correct**
azorica	17	0	1	0	0	0	94
maya	0	6	3	0	0	0	56
***mexicana* E**	1	7	9	4	0	2	35
***mexicana* W**	0	1	4	9	0	2	56
paniculata	0	0	2	0	7	0	78
sempervirens	1	1	0	1	0	12	80
Totals	19	15	19	15	7	15	64

Twelve of 15 specimens of *S. sempervirens* (80%) plus one additional specimen not included in the a priori group were placed a posteriori into the *S. sempervirens* group: 9 specimens were placed a posterior with 91-100% probability; 1 specimen from Louisiana (*Morton & Venn NA6942*, WAT) with 72% probability (19% to western *S. mexicana*, and 7% to eastern *S. mexicana*); 1 specimen from Veracruz, Mexico (*Nee & Taylor*, *29186* F), with 60% probability (28% to *S. azorica*, 10% to eastern *S. mexicana*, and 1% to western *S. mexicana*); and 1 specimen from New Brunswick (*J. & B. Semple*, *1145*3 WAT) with 48% probability (20% to *S. azorica*, 16% to western *S. mexicana*, and 2% to eastern *S. mexicana*). Four specimens of the *S. sempervirens* a priori group were placed a posteriori into other taxa: 1 specimen from Veracruz, Mexico (*Nee & Taylor 29186*, TEX) was placed into *S. azorica* with 98% probability; 1 specimen adventive in southeastern Michigan (*Semple & Suripto 9466*, WAT) was placed a posteriori into *S. maya* with 42% probability (41% to eastern *S. mexicana*, 7% to western *S. mexicana*, and 5% to *S. azorica* and *S. sempervirens*); 1 specimen from Dare Co., North Carolina (*Qualls*, *1252* NCU) was placed a posteriori into eastern *S. mexicana* with 43% probability (28% to *S. maya*, 22% to western *S. mexicana*, and 4% to *S. sempervirens*); and 1 specimen from Dade Co., Florida (*Lakela*, *26882* USF) was placed a posteriori into western *S. mexicana* with 56% probability (30% to eastern *S. mexicana*, 9% to *S. sempervirens*, and 4% to *S. maya*). Seven of the 9 specimens of *S. paniculata* (78%) were assigned a posteriori to the *S. paniculata* group with 91-100% probability. Two specimens were assigned a posteriori into eastern *S. mexicana* with 52% probability (20% to *S. maya*, 16% to western *S. mexicana*, and 8% to *S. paniculata*) and 51% probability (25% to *S. paniculata*, 17% to *S. maya* and 3% to western *S. mexicana*). Six of the 9 specimens of the *S. maya* a priori group (67%) were assigned a posteriori to *the S. maya* group with 42-78% probability (19-40% to eastern *S. mexicana*, and 1-17% to western *S. mexicana*). Two specimens of the *S. maya* a priori group were assigned a posteriori to the eastern *S. mexicana* group with 45% and 52% probabilities (44% and 40% to *S. maya*, respectively). Ten of 16 specimens of the western *S. mexicana* a priori group (63%) were assigned a posteriori to the western *S. mexicana* group: 5 with 97-100%, 1 with 60% (31% to eastern *S. mexicana* and 8% to *S. maya*), and 3 with 44-50% (18-34% to *S. maya* and 12-32% to eastern *S. mexicana*). Six specimens of the western *S. mexicana* group were assigned a posteriori to other groups: 1 to *S. azorica* with 75% probability (24% to western *S. mexicana*); 1 to *S. maya* with 40% probability (34% to western *S. mexicana*, 26% to eastern *S. mexicana*); and 4 to eastern *S. mexicana* with 37-55% probability (2-36% to western *S. mexicana* and 20-45% to *S. maya*). Nine of the 23 specimens of the eastern *S. mexicana* a priori group (39%) were assigned a posteriori to the eastern *S. mexicana* group: 5 with 59-68% probability (31-46% to *S. maya*), 1 with 52% probability (46% to *S. maya*), and 3 with 41-45% probability (1 with 26% to *S. sempervirens*, 19% to western *S. mexicana*, and 13% to *S. maya*; 2 with 31-34% to *S. maya* and 21-23% to western *S. mexicana*).

Two dimensional plots of CAN1 versus CAN 3 and CAN1 versus CAN2 canonical scores for specimens of *Solidago azorica*, *S. maya*, *S. mexicana* eastern and western separately, *S. paniculata*, and *S. sempervirens* are presented in Fig. 7. Eigen values on the first three axes were 2.049, 1.521 and 1.321.

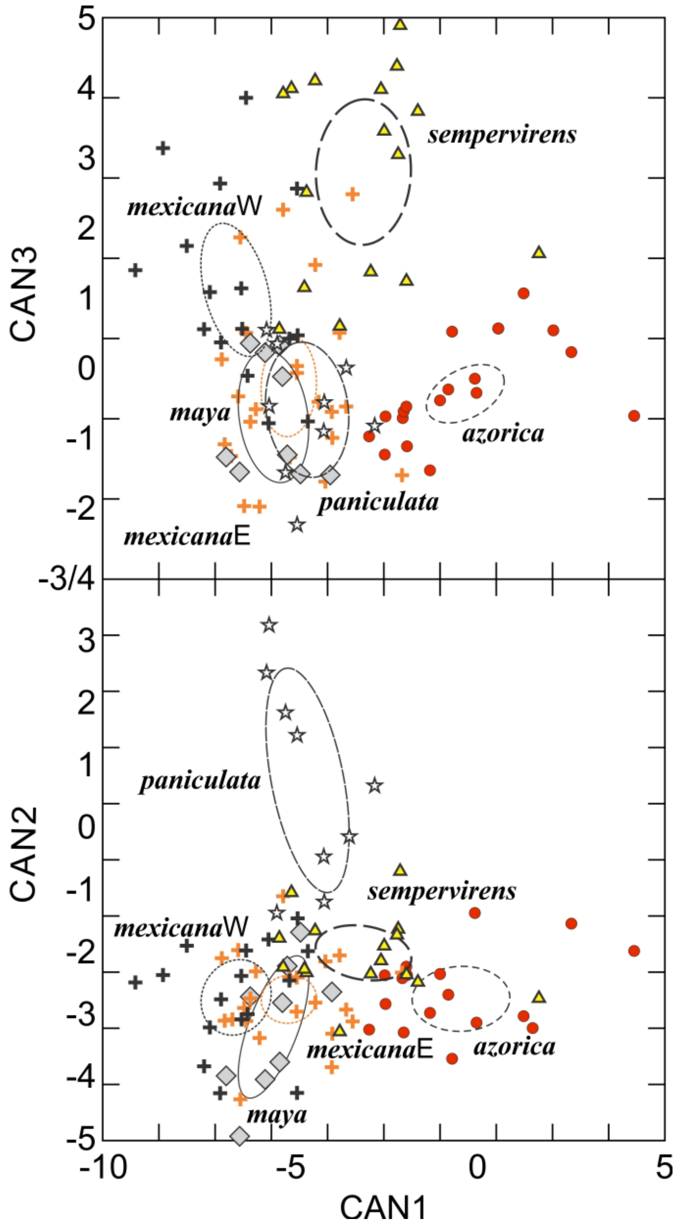

Figure 7. Two dimension plots of CAN1 versus CAN2 and CAN1 versus CAN3 canonical scores for 90 specimens of six a priori groups of the *Solidago sempervirens* complex: *S. azorica* (red dots), *S. maya* (gray diamonds), *S. mexicana* divided into eastern (orange +) and western (black +) groups, *S. paniculata* (white stars), *S. sempervirens* (yellow triangles).

Five species groups analysis

In the STEPWISE discriminant analysis of five species level a priori groups (*Solidago azorica*, *S. maya*, *S. mexicana* eastern and western combined, *S. paniculata*, and *S. sempervirens*), the following six traits selected in a STEPWISE analysis are listed in order of decreasing F-to-remove values: number of ray florets (18.98), involucre height (12.83), mid leaf width (12.61), number of disc florets (9.16), upper leaf length (6.61), and number of nodes in distal 25% of the stem below the inflorescence (4.15). Wilks's lambda, Pillai's trace, and Lawley-Hotelling trace tests of the null hypothesis that all groups were the samples of one group had probabilities of p = 0.000 that the null hypothesis was true. The F-matrix for the discriminant analysis is presented in Table 4. F-values based on Mahalanobis distances of the between group centroids indicated the largest separations were between *Solidago azorica* and *S. paniculata* (22.792), *S. mexicana* and *S. paniculata* (22.733), and *S. azorica* and *S. mexicana* (22.611); the smallest separation was between *S. maya* and *S. mexicana* (1.973).

Table 4. Between groups F-matrix for the five a priori group analysis (df = 6 80).

Group	***azorica***	***maya***	***mexicana***	***paniculata***
maya	12.654			
mexicana	22.611	1.973		
paniculata	22.792	17.857	22.733	
sempervirens	14.991	15.604	20.182	18.149

Wilks' lambda = 0.0502 df = 6 4 85
Approx. F= 15.8369 df = 24 280 prob = 0.0000

In the Classificatory Discriminant Analysis of the five species level a priori groups, percents of correct a posterori assignment to the same a priori group ranged from 100% down to 51%. The Classification matrix and Jackknife classification matrix are presented in Table 5. Results are presented in order of decreasing percents of correct placement. All 9 specimens of *S. maya* (100%) were assigned a posteriori into the *S. maya* group; 2 with 87% and 83% probabilities, 2 with 77% and 72% probabilities, 3 with 60-67% probability, and two with 56% and 52% probabilities; all lower probabilities were to *S. mexicana* (eastern and western combined). Seventeen of the 18 specimens of *S. azorica* (94%) were assigned a posteriori into the *S. azorica* group; 13 with 90-100% % probability, 2 with 83% and 81% probabilities, 1 with 70% probability (20% to *S. mexicana* and 10% to *S. maya*), and 1 with 67% probability (16% to *S. mexicana*, 15% to *S. maya*, and 2% to *S. sempervirens*). One specimen of the *S. azorica* a priori group was assigned a posteriori to the *S. maya* group with 43% probability (31% to *S. azorica* and 25% to *S. mexicana*). Eight of the 7 of the 8 specimens of *S. paniculata* (89%; one specimen was excluded) were assigned a posteriori to the *S. paniculata* group; 6 with 98-100% probability and 1 with 86% probability (6% to *S. sempervirens*, 5% to *S. mexicana*, 2% to *S.* azorica, and 1% to *S. maya*). Thirteen of the 16 specimens of *S. sempervirens* (87%) were assigned a posteriori into the *S. sempervirens* group; 10 with 97-100% probability; 1 with 81% probability (18% to *S. azorica*); 1 with 76% probability (18% to *S. mexicana*, 3% to *S. azorica*, 2% to *S. paniculata*, and 1% to *S. maya*); and 1 with 57% probability (34% to *S. azorica* and 8% to *S. mexicana*). Three specimens of the *S. sempervirens* a priori group were assigned a posteriori to other species: 1 to *S. azorica* with 96% probability, 1 to *S. mexicana* group with 51% probability (23% to *S. sempervirens* and 18% to *S. maya*) and 1 to *S. mexicana* with 41% probability (41% to *S. maya* and 10% to *S. azorica*, and 8% to *S. sempervirens*). Twenty of the 39 specimens of the *S. mexicana* (eastern and western combined; 51%;) a priori group were assigned a posteriori into the *S. mexicana* group; 5 with 94-99% probability, 3 with 81-84% probability, 1 with 71% probability (28% to *S. maya*), with 60-67% probability (most lower probabilities to *S. maya*); and 1 with 48% probability (41% to *S. maya* and 10% to *S. sempervirens*). Nineteen specimens of the *S. mexicana* a priori group were assigned a posteriori to other species: 2 to *S. sempervirens* with 90% and 84% probability (6% and 15% to *S. mexicana*, respectively); 1 to *S. azorica* with 77% probability (15% to *S. mexicana* and 8% to *S. maya*); and 14 to *S. maya* with 51-75% probability (nearly all other probabilities to *S. mexicana*).

Two dimensional plots of CAN1 versus CAN 3 and CAN1 versus CAN2 canonical scores for specimens of *Solidago azorica*, *S. maya*, *S. mexicana* (eastern and western combined), *S. paniculata*, and *S. sempervirens* are presented in Fig. 8. Eigen values on the first three axes were 2.247, 1.719 and 1.064.

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

Group	*azorica*	*maya*	*mexicana*	*paniculata*	*sempervirens*	% correct
azorica	17	1	0	0	0	94
maya	0	9	0	0	0	100
mexicana	1	15	20	0	3	51
paniculata	0	0	1	8	0	89
sempervirens	1	0	1	0	13	87
Totals	19	25	22	8	16	74

Jackknifed classification matrix

Group	*azorica*	*maya*	*mexicana*	*paniculata*	*sempervirens*	% correct
azorica	17	1	0	0	0	94
maya	0	7	2	0	0	78
mexicana	1	16	17	0	5	44
paniculata	0	0	1	8	0	89
sempervirens	1	0	1	0	13	87
Totals	19	24	21	8	18	69

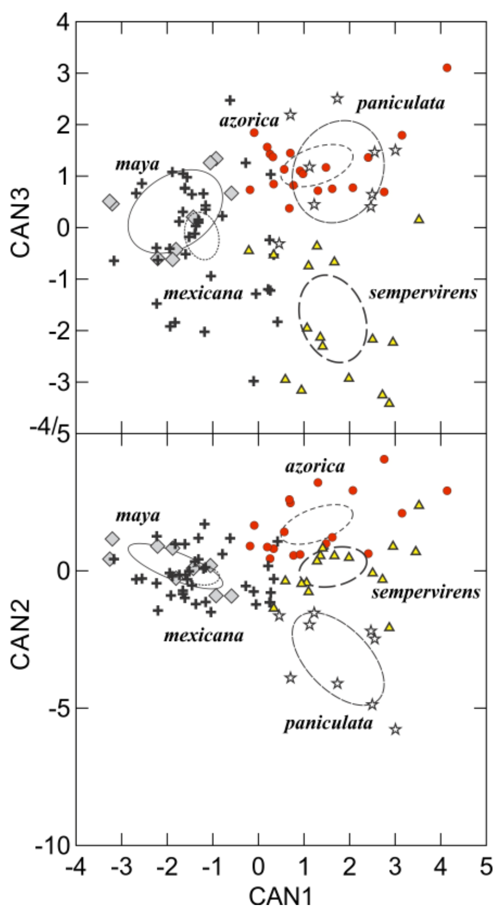

Figure 8. Two dimension plots of CAN1 versus CAN2 and CAN1 versus CAN3 canonical scores for 90 specimens of five a priori groups of the *Solidago sempervirens* complex: *S. azorica* (red dots), *S. maya* (gray diamonds), *S. mexicana* (eastern and western combine, black +), *S. paniculata* (white stars), *S. sempervirens* (yellow triangles).

Four species groups analysis I

In the STEPWISE discriminant analysis of four species level a priori groups (*Solidago azorica*, *S. maya*, *S. mexicana* eastern and western combined, and *S. sempervirens*), the following seven traits were selected in a STEPWISE analysis and are listed in order of decreasing F-to-remove values: involucre height (22.63), mid leaf width (10.99), mid series phyllary length (8.29), upper leaf length (7.13), number of leaf nodes in the distal 25% of the stem below the inflorescence (4.37), mid series phyllary width d (4.35), and ray floret ovary length at anthesis (4.06). Wilks's lambda, Pillai's trace, and Lawley-Hotelling trace tests of the null hypothesis that all groups were the samples of one group had probabilities of p = 0.000 that the null hypothesis was true. The F-matrix for the discriminant analysis is presented in Table 6. F-values based on Mahalanobis distances of the between group centroids indicated the largest separation was between *S. mexicana* and *S. sempervirens* (23.181), and the smallest separation was between *S. maya* and western *S. mexicana* (3.150).

In the Classificatory Discriminant Analysis of the first four species level a priori groups, percents of correct placement a posteriori ranged from 79-100%. The Classification matrix and Jackknife classification matrix are presented in Table 7. All 9 specimens of *S. maya* (100%) were assigned a posteriori to the species; 3 specimens were assigned with 91-96% probability, 2 specimens with 81-84%, 1 specimen with 76% probability, 2 with 67-69%, and 1 specimen with 59% (40% to western *S. mexicana*). All 18 specimens of the *S. azorica* a priori group (100%) were assigned a posteriori into the *S. azorica* group; 11 with 92-100% probability, 3 specimens with 81-85% probability; 2 with 77% probability (14% to *S. mexicana* and 4% to *S. sempervirens*; 15% to *S. maya* and 8% to *S. mexicana*); 1 with 58% probability (29% to *S. maya* and 13% to *S. mexicana*); and 1 with 47% probability 36% to *S. maya* and 17% to *S. mexicana*). Fourteen of the 15 specimens of *S. sempervirens* (93%) were assigned a posteriori into the *S. sempervirens* group; 10 specimens with 90-100% probability; 3 specimens from New Brunswick, Veracruz, and Florida, with 80-85% probability; and 1 specimen from Louisiana, *Morton & Venn NA6942* (WAT), with 52% probability (44% to *S. mexicana* and 3% to *S. azorica*). One specimen of *S. sempervirens* adventive in southeastern Michigan, *Semple & Suripto* 9466 (WAT), was assigned a posteriori to the *S. azorica* group with 40% probability (28% to *S. mexicana*, 18% to *S. sempervirens*, and 18% to *S. maya*). Twenty-eight of the 39 specimens of *S. mexicana* (79%) were assigned a posteriori into the *S. mexicana* group; 7 specimens with 95-100% probability; 7 specimens with 83-88% probability; 11 specimens with 77-79% probability (10 with 21-24% to *S. maya*; 1 with 16 to *S. sempervirens* and 7% to *S. azxorica*); 2 specimens with 61-62% probability (37% to *S. maya*); 3 specimens with 50-56% probability (43-50% to *S.* maya); and 1 specimen with 47% probabilities (44% to *S. maya* and 4% to *S. azorica*). Eight specimens of *S. mexicana* were assigned a posteriori to other species: 7 were assigned to *S. maya* group with 46-84% probability (6 with lower probabilities to *S. mexicana*); and 1 specimen from Texas to *S. sempervirens* with 67% probability (32% to *S. mexicana*).

Two dimensional plots of CAN1 versus CAN 3 and CAN1 versus CAN2 canonical scores for specimens of *Solidago azorica*, *S. maya*, western *S. mexicana*, and *S. sempervirens* are presented in Fig. 9. Eigen values on the first three axes were 2.980, 1.235 and 0.254.

Table 6. Between groups F-matrix for the four a priori group analysis (df = 6 72).

Group	*azorica*	*maya*	*mexicana*
maya	12.407		
mexicana	18.790	3.150	
sempervirens	13.122	17.905	23.181

Wilks' lambda = 0.0887 df = 6 3 77
Approx. F= 15.3562 df = 18 204 prob = 0.0000

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

Group	*azorica*	*maya*	*mexicana*	*sempervirens*	% correct
azorica	18	0	0	0	100
maya	0	9	0	0	100
mexicana	0	7	31	1	79
sempervirens	1	0	0	14	93
Totals	19	16	31	15	89

Jackknifed classification matrix

Group	*azorica*	*maya*	*mexicana*	*sempervirens*	% correct
azorica	16	2	0	0	89
maya	0	9	0	0	100
mexicana	1	9	28	1	72
sempervirens	3	0	1	11	73
Totals	20	20	29	12	79

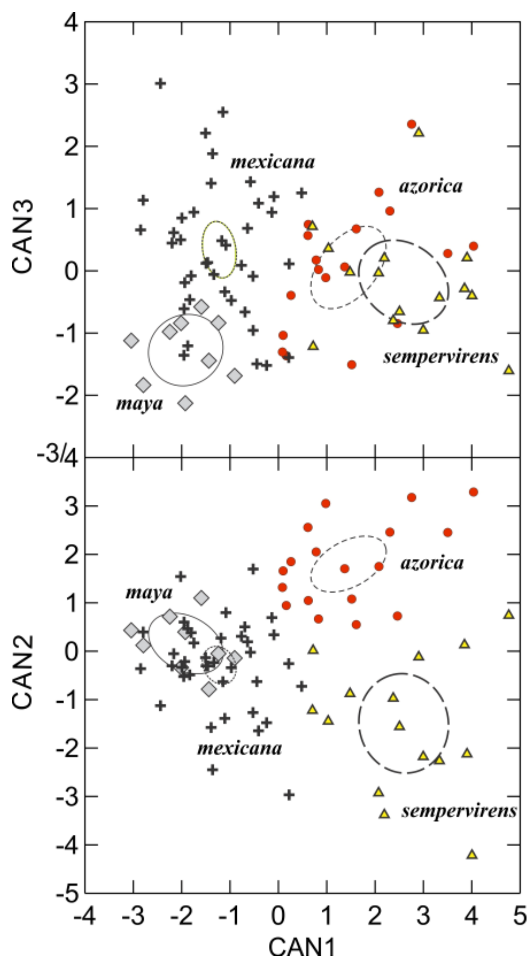

Figure 9. Two dimension plots of CAN1 versus CAN2 and CAN1 versus CAN3 scores for 81 specimens in four a priori groups of the *Solidago sempervirens* complex: *S. azorica* (red dots), *S. maya* (gray diamonds), *S. mexicana* (eastern and western combined, (black +s) groups, *S. sempervirens* (yellow triangles).

Four species groups analysis II

In the STEPWISE discriminant analysis of the second four species level a priori groups (*Solidago maya*, eastern and western *S. mexicana* separately, and *S. virgata*), the following four traits were selected in a STEPWISE analysis as most strongly separating the four groups and are listed in order of decreasing F-to-remove values: upper leaf length (6.93), disc floret pappus length at anthesis (6.82), number of leaf nodes in the distal 25% of the stem below the inflorescence (6.68), and number of disc florets (5,53). 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 8. F-values based on Mahalanobis distances of the between group centroids indicated the largest separation was between eastern *Solidago mexicana* and *S. virgata* (20.055) and the small separation was between *S. maya* and eastern *S. mexicana* (1.067).

In the Classificatory Discriminant Analysis of the second four species level a priori groups, percents of correct assignment a posteriori ranged from 52% to 81%. The Classification matrix and Jackknife classification matrix are presented in Table 9. Twenty-one of 39 specimens of *S. virgata* (81%) were assigned a posteriori to the *S. virgata* group: 9 specimens with 96-99% probability, 7 specimens with 82-88% probability; 2 specimens with 76-79% probability (17% each to *S. maya*); 1 specimen with 59% (20% to *S. maya*, 17% to eastern *S. mexicana*); 1 specimen with 51% (34% to *S. maya*, 8% to western *S. mexicana*); and 1 specimen with 48% (28% to *S. maya*, 15% to eastern *S. mexicana*, and 9% to western *S. mexicana*). Seven of 9 specimens of *S. maya* (78%) were assigned a posteriori to the *S. maya* group; 3 with 51-57% probability (27-42% to eastern *S. mexicana*, 4-27% to western *S. mexicana* and 3-9% to *S. virgata*); 3 with 42-48% probability (10-27% to eastern *S. mexicana*, 10-27% to western *S. mexicana* and 1-21% to *S. virgata*); and 1 with 39% probability (33% to eastern *S. mexicana*, 25% to western *S. mexicana*, and 3% to *S. virgata*). Two specimens of *S. maya* were assigned a posteriori to eastern *S. mexicana*: 1 with 62% (32% to *S. maya*) and 1 with 45% (32% to *S. maya*, and 23% to western *S. mexicana*). Eleven of 17 specimens of western *S. mexicana* (65%) were assigned a posteriori into the western *S. mexicana* group; 1 with 95% probability; 4 with 80-86% probability; 1 with 70%probability; 1 with 60% probabilities; and 3 with 50-57% probability. Six specimens of western *S. mexicana* group were assigned a posteriori to other species: 3 to eastern *S. mexicana* with 57%, 41% and 40% probabilities (38% to western S. mexicana, 25% and 25% to S. maya; respectively); 2 to *S. maya* with 61% and 43% probabilities (21% and 41% to eastern *S. mexicana*; 10% and 12% to western *S. mexicana*; respectively); and 1 to *S. virgata* with 48% probability (26% to western *S. mexicana*; 19% to eastern *S. mexicana*; and 9% to *S. maya*). Fourteen of the 23 specimens of the eastern *S. mexicana* group (52%) were assigned a posteriori into the eastern *S. mexicana* group; 4 with 70-77%% probability, 3 with 63-68%% probability, 1 with 53% probability, 3 with 43-45% probability, and 3 with 30-39% probability. Thirteen specimens were assigned a posteriori to other species: 6 to western *S. mexicana* with 39-77% probability, 6 to *S. maya* with 43-57% probability, and 1 to *S. virgata* with 88% probability.

Two dimensional plots of CAN1 versus CAN 3 and CAN1 versus CAN2 canonical scores for specimens of *Solidago maya*, eastern and western *S. mexicana* separately, and *S. virgata* are presented in Fig. 10. Eigen values on the first three axes were 1.287, 0.341 and 0.047.

Table 8. Between groups F-matrix for the four a priori group analysis (df = 4 72).

Group	***mexicana*E**	***maya***	***mexicana*W**	***virgata***
***mexicana*E**	0.000			
maya	1.067	0.000		
***mexicana*W**	5.443	0.406	0.000	
virgata	20.055	8.467	14.878	0.000

Wilks' lambda = 0.3113 df = 4 3 75; Approx. F= 8.7779 df = 12 190 prob = 0.0000

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

Group	*maya*	*mexicana*E	*mexicana*W	*virgata*	% correct
maya	7	2	0	0	78
***mexicana* E**	2	14	6	1	78
***mexicana* W**	2	3	11	1	65
virgata	4	1	0	21	81
Totals	15	20	17	23	67

Jackknifed classification matrix

Group	*maya*	*mexicana*E	*mexicana* W	*virgata*	% correct
maya	5	3	1	0	56
***mexicana*E**	7	12	7	1	44
***mexicana*W**	3	3	10	1	59
virgata	4	1	0	21	81
Totals	19	19	18	23	61

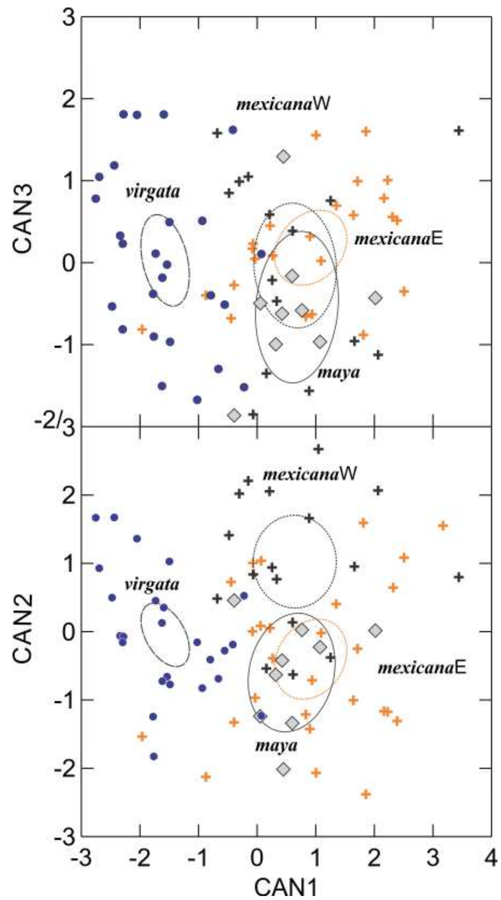

Figure 10. Two dimension plots of CAN1 versus CAN2 and CAN1 versus CAN3 scores for 79 specimens of four priori groups: *Solidago maya* (gray diamonds), *S. mexicana* is divided into eastern (orange +s) and western (black +s) groups, and *S. virgata* (blue dots).

Three species groups analysis I

In the STEPWISE discriminant analysis of the first three species level a priori groups (*Solidago maya*, *S. mexicana* eastern and western populations combined, and *S. virgata*), the following five traits selected in a STEPWISE analysis are listed in order of decreasing F-to-remove values: number of ray florets (9.62), upper leaf width (7.03), disc corolla lobe length (6.69), disc floret pappus length at anthesis (5.22), and number of leaf nodes in the distal 25% of the stem below the inflorescence (4.96). 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 10. F-values based on Mahalanobis distances of the between group centroids indicated the largest separation was between *Solidago mexicana* and *S. virgata* (19.057), and the small separation was between *S. maya* and *S. mexicana* (2.010).

Table 10. Between groups F-matrix for the three a priori group analysis (df = 5 72).

Group	***maya***	***mexicana***
mexicana	2.010	
virgata	7.372	19.057

Wilks' lambda = 0.37418 df = 5 2 76
Approx. F= 9.1428 df = 10 1442 prob = 0.0000

In the Classificatory Discriminant Analysis of the three species level a priori groups, the percents of correct placement a posteriori of specimens to the a priori group ranged from 64-81%. The Classification matrix and Jackknife classification matrix are presented in Table 11. Twenty-one of the 26 specimens of *S. virgata* (81%) were assigned to that species a posteriori: 14 with 90-100% probability; 3 with 80-89% probability; 3 with 70-71% probability; 1 with 58 (25% to *S. maya* and 18% to *S. mexicana*). Five specimens of *S. virgata* were assigned a posteriori to the *S. maya* group with 43-57% probability (with 19-32% probability to *S. mexicana*). Six of the 9 specimens of the S. maya (67%) a priori group were assigned a posteriori to *S. maya*: 1 with 84; 3 with 75-79%; 1 with 59% (39% to *S. mexicana*); and 1 with 42% (35% to *S. virgata* and 23% to *S. mexicana*). Three specimens of the *S. ma*ya a priori group were assigned to S. mexicana with 64%, 62% and 54% probabilities (35%, 36% and 46% to *S. maya*). Twenty-eight of the 44 specimens of the *S. mexicana* a priori group (64%) were assigned a posteriori to the *S. mexicana* group: 3 with 90-94%; 8 with 84-88%; 5 with 72-78%; 3 with 61-65%; and 9 with 45-57%. Sixteen specimens of the *S. mexicana* a priori group with assigned to other species: 4 to S. virgata with 46-76% probability and 12 to *S. maya* with 44-75% probability.

A two dimensional plot of CAN1 versus CAN2 canonical scores for specimens of *Solidago maya*, *S. mexicana*, and *S. virgata* are presented in Fig. 11. Eigen values on the first two axes were 1.361 and 0.132.

Table 11. Linear and jackknife classification matrices from the Classificatory Discriminant Analysis of three a priori groups; a posteriori placements to groups in rows.

Group	***maya***	***mexicana***	***virgata***	**% correct**
maya	6	3	0	67
mexicana	12	28	4	64
virgata	5	0	21	81
Totals	23	31	25	70

Jackknifed classification matrix

Group	***maya***	***mexicana***	***virgata***	**% correct**
maya	5	3	1	56
mexicana	14	24	6	55
virgata	5	0	21	81
Totals	24	27	28	63

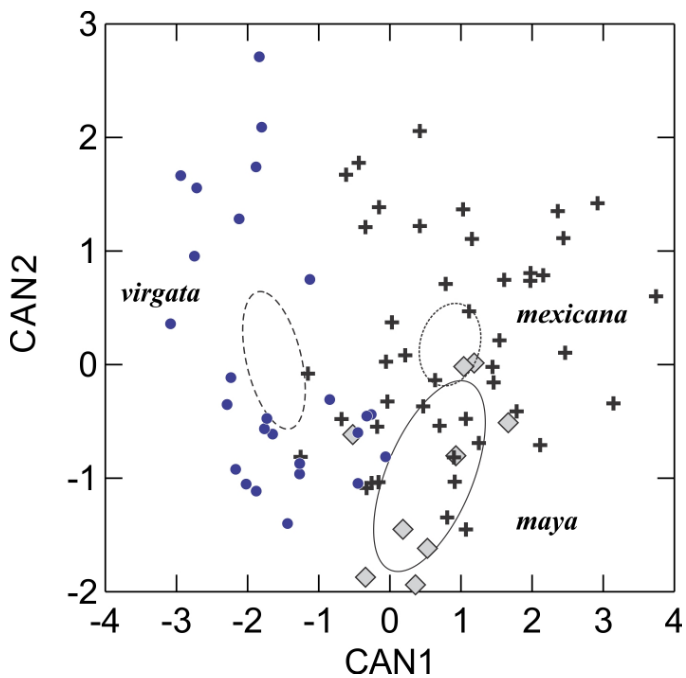

Figure 11. Two dimension plots of CAN1 versus CAN2 and CAN1 versus CAN3 scores for 79 specimens of two priori groups of the *Solidago sempervirens* complex and a third a priori groups of *S. virgata*: S. mexicana includes eastern and western populations.

Three species groups analysis II

In the STEPWISE discriminant analysis of the second three species level a priori groups (*Solidago azorica*, *S. mexicana* eastern and western combined, and *S. sempervirens*), the following seven traits selected in the STEPWISE analysis are listed in order of decreasing F-to-remove values: involucre height (43.85), upper leaf width (23.20), mid leaf length (13.48), mid series phyllary length (9.81), ray floret pappus length at anthesis (5.57), number of leaf nodes in the distal 25% of the stem below the inflorescence (5.33), and mid series phyllary width at widest point (4.48). 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 12. F-values based on Mahalanobis distances of the between group centroids indicated the largest separation was between *Solidago azorica* and *S. mexicana* (24.335), and the smallest separation was between *S. azorica* and *S. sempervirens* (21.948).

In the Classificatory Discriminant Analysis of the three species level a priori groups, the percents of correct placement a posteriori of specimens to the a priori group ranged from 93-100%. The

Classification matrix and Jackknife classification matrix are presented in Table 13. All 18 specimens of *S. azorica* were assigned a posteriori to the *S. azorica* group: 12 specimens were assigned with 98-100% probability; 5 with 91-96% probability; and 1 with 81% probability (16% to *S. sempervirens*). Fifteen of the 16 specimens of *S. sempervirens* (94%) were assigned a posteriori to that species: 11 with 99-100% probability; 1 with 91% probability, 1 with 84% (15% to *S. mexicana*), and 1 with 70% probability (30% to *S. mexicana*). One specimen of *S. sempervirens* was assigned to *S. mexicana* with 77% probability (22% to *S. sempervirens*): the specimen *Semple & Suripto 9466* (WAT) was from an adventive population in southeastern Michigan along Interstate-75. Thirty-nine of the 42 specimens of *S. mexicana* (93%) were assigned a posteriori to the *S. mexicana* group: 36 with 94-100%; 2 with 87-88% probability; and 1 with 70% probability (30 % probability to *S. sempervirens*). Three specimens of *S. mexicana* were assigned a posteriori to *S. sempervirens* with 79%, 64% and 55% probabilities (21%, 36% and 45% to *S. sempervirens*).

A two dimensional plot of CAN1 versus CAN2 canonical scores for specimens of *Solidago azorica*, *S. mexicana* (eastern and western populations combined), and *S. sempervirens* is presented in Fig. 12. Eigen values on the first two axes were 2.559 and 2.252.

Table 12. Between groups F-matrix for the three a priori group analysis (df = 7 67).

Group	*azorica*	*mexicana*
mexicana	24.335	
sempervirens	21.948	22.297

Wilks' lambda = 0.0864 df = 7 2 73; Approx. F= 22.9902 df = 14 134 prob = 0.0000

Table 13. Linear and jackknife classification matrices from the Classificatory Discriminant Analysis of three a priori groups; a posteriori placements to groups in rows.

Group	*azorica*	*mexicana*	*sempervirens*	% correct
azorica	18	0	0	100
mexicana	0	39	3	93
sempervirens	0	1	15	94
Totals	18	40	18	95

Jackknifed classification matrix

Group	*azorica*	*mexicana*	*sempervirens*	% correct
azorica	17	0	1	94
mexicana	0	39	3	93
sempervirens	1	2	13	81
Totals	18	41	17	91

Two species groups analysis I

In the Pearson Correlation matrix of 59 specimens of *Solidago mexicana* and *S. sempervirens*, nearly all leaf traits correlated with some other leaf trait with r >|0.7| resulting in only upper leaf width being included in the analysis. Basal leaves were often absent and were excluded. Not including mid leaf traits allowed one addition specimen of each species to be included in the discriminant analysis.

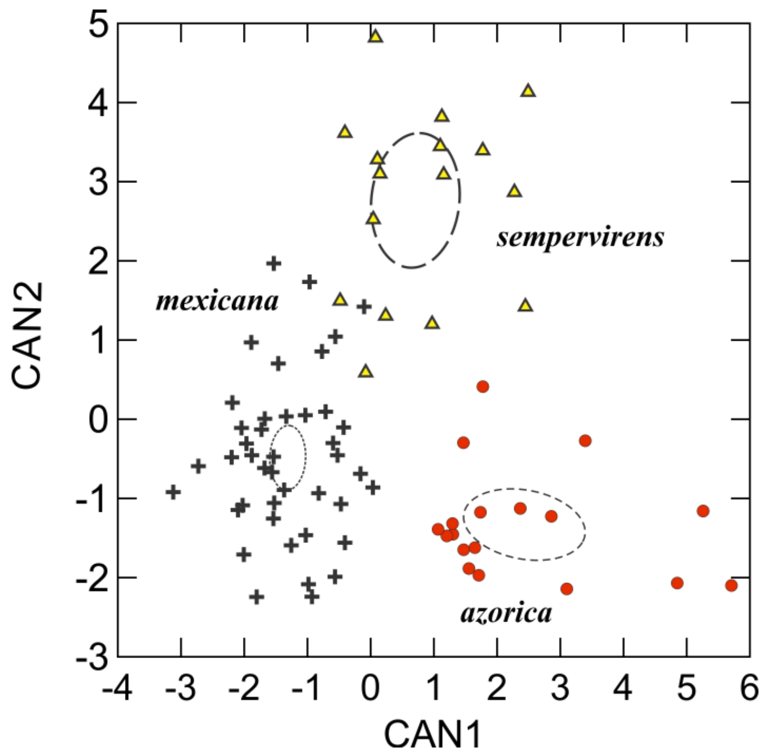

Figure 12. Two dimension plots of CAN1 versus CAN2 for 76 specimens of three a priori groups of the *Solidago sempervirens* complex: *S. azorica* (red dots), *S. mexicana* (eastern and western populations), black +s, *S. sempervirens* (yellow triangles).

In the STEPWISE discriminant analysis of 59 specimens of *Solidago mexicana* and *S. sempervirens*, the following four traits were selected in a STEPWISE analysis and are listed in order of decreasing F-to-remove values: upper leaf width (63.98), involucre height (47.42), mid series phyllary length (14.56), and number of leaf nodes in the distal 25% of the stem below the inflorescence (4.43). 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 14: *S. mexicana* and *S. sempervirens* had an F-to separate value of 34.103.

Table 14. Between groups F-matrix for the three a priori group analysis (df = 4 54).

Group	*mexicana*	*sempervirens*
mexicana	0.0000	
sempervirens	34.104	0.0000

Wilks' lambda = 0.2836 df = 1 57; Approx. F= 34.1030 df = 4 54 prob = 0.0000

In the Classificatory Discriminant Analysis of the two species level a priori groups, the percents of correct placement a posteriori of specimens to the a priori groups were 95% for *Solidago mexicana* and 88% *S. sempervirens*: two specimens of each species was assigned a posteriori to the other a priori group. The Classification matrix and Jackknife classification matrix are presented in Table 15. Forty-one of the

43 specimens of *S. mexicana* (95%) were assigned a posteriori to that species: 39 specimens with 90-100% probability: 1 specimen from Collier Co., Florida, *Semple 5394* (WAT), with 79% probability, and 1 specimen from Volusia Co., Florida, *Ray et al.* 10851 (USF), with 57% probability. Two species of the *S. mexicana* a priori group were assigned a posteriori to *S. sempervirens* with 86% (Veracruz, Mexico. *Vovides AV-569* F; an incomplete specimen not included in other analyses) and with 61% (Texas. *Semple & Suripto 10079* WAT; 2*n*=36). Fourteen of the 16 specimens of *S. sempervirens* (75%) plus one additional specimen not included in the a priori analysis were assigned a posteriori to the *S. sempervirens* group: 13 specimens with 98-100% probability and 1 specimen from Louisiana, *Morton & Venn NA6942* (WAT), with 60% probability. Three specimens of the *S. sempervirens* a priori group were assigned a posteriori to *S. mexicana*: 1 specimen from Michigan, *Semple & Suripto 9466* (WAT), with 98% probability; 1 specimen from Dare Co., North Carolina, *Qualls* 1252 (NCU), with 88% probability; and 1 specimen from Nova Scotia, *Semple & Keir 4814* (WAT; Fig. 5), with 68% probability.

Frequencies of CAN1 canonical scores for specimens of *S. mexicana* (eastern and western populations combined) and *S. sempervirens* are presented in histograms in Fig. 13. The eigen value on the first axis was 2.526.

Table 15. Linear and jackknife classification matrices from the Classificatory Discriminant Analysis of three a priori groups; a posteriori placements to groups in rows.

Group	*mexicana*	*sempervirens*	% correct
mexicana	41	2	95
sempervirens	2	14	88
Totals	43	16	93

Jackknifed classification matrix

Group	*mexicana*	*sempervirens*	% correct
mexicana	41	2	95
sempervirens	3	13	81
Totals	44	15	92

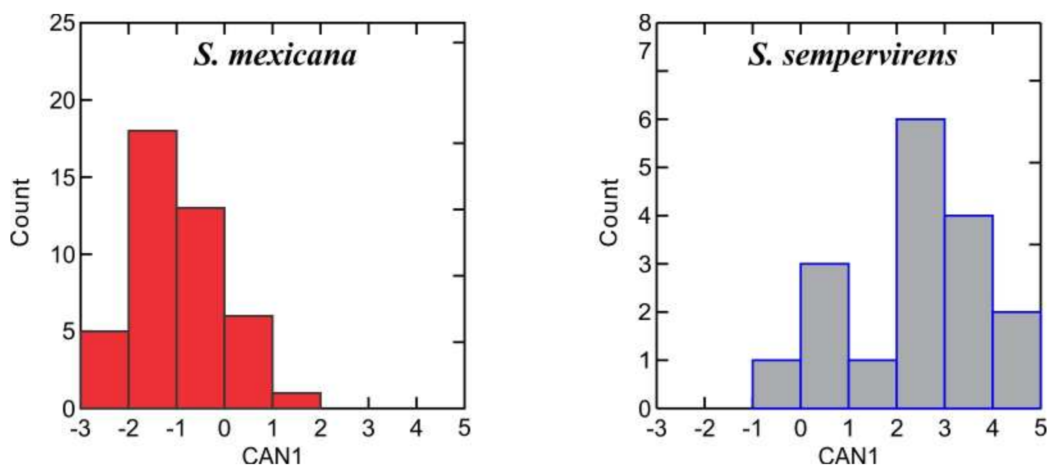

Figure. 13. Histograms of CAN1 canonical scores for 59 specimens of *S. mexicana* (left) and *S. sempervirens* (right).

Two species groups analysis II

In the STEPWISE discriminant analysis of 35 specimens of *Solidago maya* and *S. virgata*, the following two traits were selected in a STEPWISE analysis and are listed in order of decreasing F-to-remove values: mid leaf length (33.00), involucre height (13.79). 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 16: *S. maya* and *S. virgata* had an F-to separate value of 37.540.

In the Classificatory Discriminant Analysis of the two species level a priori groups, the percents of correct placement a posteriori of specimens to the a priori group were 89% for *S. maya* and 96% *S. virgata*: one specimen of each species was assigned a posteriori to the other a priori group. The Classification matrix and Jackknife classification matrix are presented in Table 17. Seven of the nine specimens of *S. maya* (77.8%) were assigned a posteriori to that species with 98-100% probability: 1 specimens was assigned to *S. maya* with 54% probability; and 1 specimen was assigned a posteriori to *S. virgata* with 73% probability. Twenty-three of the 26 specimens of *S. virgata* (75%) were assigned a posteriori to the *S. virgata* group with 97-100% probability: two specimens plus one additional specimen excluded from the STEPWISE analysis were assigned a posteriori to the *S. virgata* group with 91%, 69% and 67% probabilities; and one specimen was assigned a posteriori to *S. maya* with 85% probability.

Frequencies of CAN1 canonical scores for specimens of *Solidago maya* and *S. virgata* are presented in histograms in Fig. 14. The eigen value on the first two axis was 2.346.

Table 16. Between groups F-matrix for the three a priori group analysis (df = 2 32).

Group	*maya*	*virgata*
maya	0.0000	
virgata	37.5398	0.0000

Wilks' lambda = 0.29888 df = 2 1 33; Approx. F= 37.5398 df = 2 32 prob = 0.0000

Table 17. Linear and jackknife classification matrices from the Classificatory Discriminant Analysis of three a priori groups; a posteriori placements to groups in rows.

Group	*maya*	*virgata*	% correct
maya	8	1	78
virgata	1	25	92
Totals	10	26	94

Jackknifed classification matrix

Group	*maya*	*virgata*	% correct
maya	7	2	78
virgata	2	24	96
Totals	9	26	89

Two species groups analysis III

In the STEPWISE discriminant analysis of 25 specimens of *S. maya* and *S. mexicana* (western populations only), the following four traits were used in a STEPWISE analysis are listed in order of decreasing F-to-remove values: length of ray floret ovary at anthesis (14.62), mid leaf length (8.29), number of nodes in distal 25% of the stem below the inflorescence (7.91), and mid series phyllary width

(6.74). 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 = 0.001 that the null hypothesis was true. The F-matrix for the discriminant analysis is presented in Table 16: *S. maya* and western *S. mexicana* had an F-to separate value of 10.767.

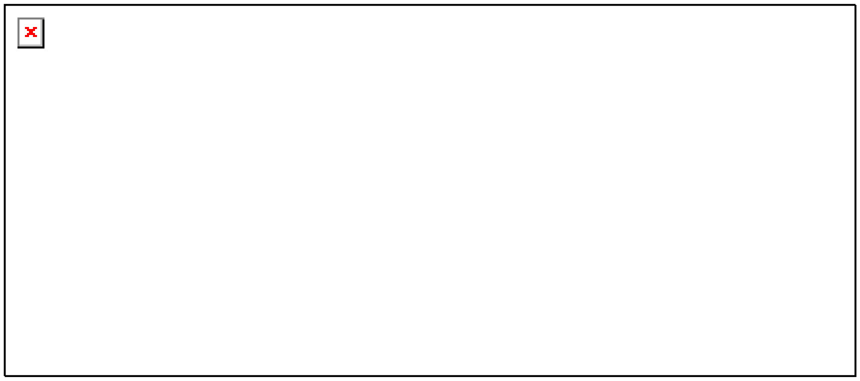

Figure. 14. Histograms of CAN1 canonical scores for 35 specimens of *S. maya* (left) and *S. virgata* (right).

In the Classificatory Discriminant Analysis of the two species level a priori groups, the percents of correct placement a posteriori of specimens to the a priori group were 100% for both *S. maya* and western *S. mexicana*. The Classification matrix and Jackknife classification matrix are presented in Table 17. Six of the nine specimens of *S. maya* (66.7%) were assigned to that species a posteriori with 96-100% probability: 3 specimens were assigned to *S. maya* with 87%, 76% and 70% probabilities. Twelve of the 16 specimens of *S. mexicana* (75%) were assigned a posteriori to the *S. mexicana* group with 93-100% probability: three specimens were assigned a posteriori to the *S. mexicana* group with 65%, 54% and 51% probabilities.

Frequencies of CAN1 canonical scores for specimens of *S. maya* and western *S. mexicana* are presented in histograms in Fig. 15. The eigen value on the first axis was 2.153.

Table 16. Between groups F-matrix for the three a priori group analysis (df = 2 32).

Group	***maya***	***mexicana*W**
maya	0.0000	
***mexicana*W**	10.7666	0.0000

Wilks' lambda = 0.3.1718 df = 4 1 23; Approx. F= 10.7666 df = 4 20 prob = 0.0001

Table 17. Linear and jackknife classification matrices from the Classificatory Discriminant Analysis of three a priori groups; a posteriori placements to groups in rows.

Group	***maya***	***mexicana*W**	**% correct**
maya	9	0	100
***mexicana*W**	0	16	100
Totals	9	16	100

Jackknifed classification matrix

Group	*maya*	*mexicana*W	% correct
maya	8	1	89
***mexicana*W**	4	12	75
Totals	12	13	80

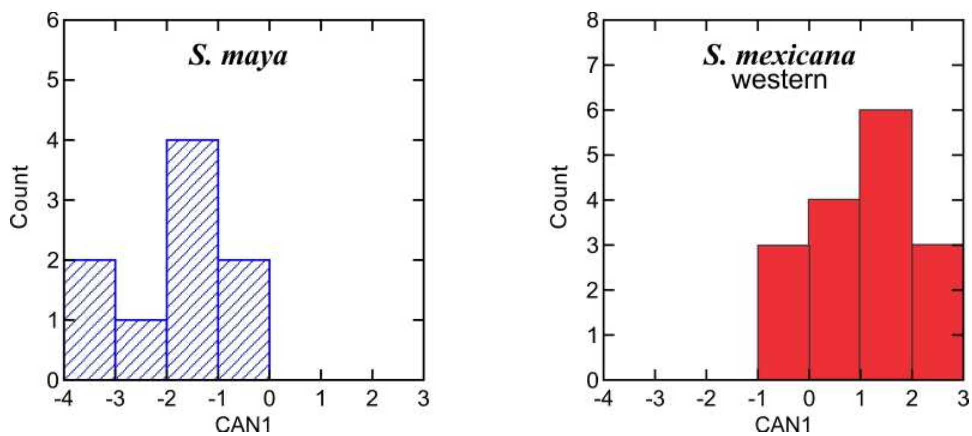

Figure. 15. Histograms of CAN1 canonical scores for 25 specimens of *S. maya* (left) and *S. mexicana* (right; western populations only).

DISCUSSION

The results of the multivariate analyses support the recognition of *Solidago azorica*, *S. maya*, *S. mexicana*, *S. paniculata*, *S. sempervirens*, and *S. virgata* as separate species. The results do not support dividing *S. mexicana* into a diploid eastern and a tetraploid western species at this time; in each analysis where *S. mexicana* was divided into two groups, the percents of correct placement and the probabilities of those placements were relatively low compared to analyses in which *S. mexicana* specimens were not divided into two groups. *Solidago paniculata* from marshes around Mexico City and further west in Michoacán state was strongly separated from most other species in the *S. sempervirens* complex. A single specimen of *S. paniculata* was weakly assigned to *S. mexicana* (all specimens) in one analysis.

The strong results for treating *Solidago azorica* as a separate species are indicated by the large F-to-separate values between *S. azorica* and other species and the high percents of specimens assigned a posteriori to the *S. azorica group*. Thus, the morphological results are in agreement with Schaefer's (2015) molecular results indicating that *S. azorica* and *S. sempervirens* are sufficiently different to warrant treating them as separate species. Plants of *S. azorica* from Bermuda are more likely to be confused with plants of *S. mexicana* and *S. sempervirens* than those from the Azores based on lower percents of correct placements a posteriori to *S. azorica*. One specimen was not assigned to *S. azorica* in the first two analyses; this was a short garden cultivated collection from the Bahamas that was considered to be a specimen of *S. sempervirens* in early stages of the study and by the collector R.A. Howard. It was assigned a priori to *S. azorica* on the basis of geography and the assumption its source was possibly Bermuda or the Azores. In the third analysis including *S. azorica*, the Howard collection was assigned to *S. azorica* with 81% probability. When *S. azorica* arrived in Bermuda and whether or not is it native or just relatively recently introduced is unknown. Additional molecular work involving *S. azorica* from Bermuda might be informative. Short plants of *S. azorica* and *S. sempervirens* can be difficult to place to species as can specimens of *S. azorica* with narrower upper stem leaves. A very short collection of *S. sempervirens* from the Magdalen Islands, Quebec, located midway between Prince Edward Island and Newfoundland (*Oldham 21146* WAT) was placed into *S. sempervirens* with 100% probability in the first three analyses indicating that short stature is not necessarily a problem with correct identification of the seaside goldenrods.

Numbers of ray and disc florets have been used to separate *Solidago mexicana* and *S. sempervirens* historically (e.g., Cronquist 1980; Weakley 2015) with *S. mexicana* having 7–11 rays and ca. 10–16 disc florets and *S. sempervirens* having 12–17 rays and ca. 17–22 disc florets (Semple and Cook 2006). Fernald (1950) noted the var. *mexicana* had narrower leaves and that the heads were "slightly smaller", but not the numbers of rays and discs in particular. In the analysis of *S. mexicana* (both eastern and western populations combined) and *S. sempervirens*, STEPDISC selected the following as most useful in separating the two species: upper leaf width, involucre height, mid series phyllary length, and number of leaf nodes in the distal 25% of the stem below the inflorescence. The numbers of ray and disc florets were not found to be as useful in separating the two species. Fernald's choice of narrower leaves is thus a better way to separate the two species than on numbers of florets. However, the mean number of rays and discs do follow the pattern indicated by Cronquist (1980), Semple and Cook (2006), and Weakley (2015) but the ranges overlap considerably. A Maryland plant of *S. mexicana* (*Semple & Ringius 7633* WAT) included in the analysis had the narrower and shorter upper stem leaves of *S. mexicana*, but had some of the highest numbers of ray and disc florets for the species (10-11 rays, 13-16 discs). In our sample, the lowest number of rays for a specimen of *S. sempervirens* was 4 and the lowest number of discs was 8, which was well below the means values. Our conclusion is that plants with the highest numbers of rays and discs are *S. sempervirens*, but the overlap in high end for *S. mexicana* and low end for *S. sempervirens* (ca 10-14 rays and 14-17 discs) reduces the traits to secondary characters in distinguishing the two species.

Confusion in separating *Solidago mexicana*, *S. sempervirens*, and *S. virgata* is understandable and complicated by multiple ploidy levels known in *S. mexicana* (2x, 4x) and *S. virgata* (2x, 4x, 6x). However, in those analyses including *S. virgata*, specimens of *S. virgata* were generally more strongly separated from the other species based on F-to-separate matrix values and in having the highest percents of correct placement a posteriori. Western populations of *S. mexicana* were more similar to *S. sempervirens* in some traits (involucre height) than to the eastern populations of *S. mexicana*. This is most likely a consequence of the western being tetraploid plants and the eastern being diploid plants because involucre height is strongly influenced by ploidy level within a species in the genus *Solidago*, e.g., in *Solidago altissima* (Semple et al. 2015). It appears that there are some collections of *S. sempervirens* from areas well into the range of *S. mexicana*; specimens from Louisiana and Mexico really look like *S. sempervirens* overall. These are likely chance adventives introduced by human activity. On the other hand, some of the collections of *S. sempervirens* from introduced populations in the southern Great Lakes region in Michigan and Ontario can have more reduced upper stem leaves than other shoots in the same population. It seems more likely that these are just outlier forms of *S. sempervirens*, then really being long distance disjunct plants of *S. mexicana*. Molecular work might clarify the situation. In some of the analyses, overall typical looking tetraploid specimens of *S. mexicana* were placed in other taxa on technical traits. Only diploid counts are known for *S. sempervirens* and *S. azorica*. It seems unlikely that adventive tetraploid individuals of *S. azorica* or *S. sempervirens* are present along the Gulf coast in Texas. Additional work is needed to determine the origins of the tetraploid populations of *S. mexicana* from Louisana and Texas (are they autopolyploid?) and to determine ploidy levels of *S. mexicana* (and adventive *S. sempervirens*) and *S. maya* from Mexico.

The ecological species concept is particularly useful in dealing with *Solidago* taxa (Peirson et al. 2012). For example, the initial impression of the first author regarding the specimens from Chiapas, Mexico, and Guatemala was that there was no way a species found throughout its entire range from Newfoundland in Canada to along the Gulf coast in Veracruz and Tabasco, Mexico and occurring at 0-30 m elevation could also be growing at 2200 m in Chiapas, Mexico. The strong disjunction in elevation of the habitats suggested that the highland specimens likely belonged in a separate species, which is here and in Semple (2016) treated as the new species *S. maya*. Accumulating data on enough specimens to statistically demonstrate that *S. maya* and *S. mexicana* were distinct and also not just specimens of *S. sempervirens* s.l. or *S. virgata* took a considerable amount of effort over multiple years. During that time early results of multivariate analyses with fewer specimens and including all species of subsect. *Maritimae* indicated that *S. sempervirens* should be divided and *S. mexicana* should be treated as a separate species. Also, as (1) unpublished results became available supporting splitting the *S. stricta* complex into multiple species (e.g. *S. austrina*, *S. gracillima*, *S. stricta* sensu Ait. not sensu others, e.g. Semple & Cook 2006) that occurred in different habitats, and (2) as unpublished and published results from other subsections of *Solidago* also began to indicate the same problem, it became increasingly obvious that there had been too much lumping of distinct species in *Solidago* by Cronquist (e.g. 1980) and those who followed him (e.g., Semple and Cook 2006). Historically, specimens of *S. maya* have been treated as either belonging in *S. sempervirens* in the broad sense or *S. stricta* in the misapplication-of-the-name sense (*S. virgata* would have been the correct name to use) based on herbarium label and annotation label identifications and the floristic literature covering Chiapas, Mexico and Guatemala (e.g., Nash 1976). The results of the multivariate analyses taken together indicate that *S. maya* should be treated as a separate species but that it is more similar to eastern *S. mexicana* and *S. virgata* than to western *S. mexicana*. No chromosome number has been reported for *S. maya*, but based on involucre height it is more likely to be diploid than tetraploid or hexaploid. Some collections of diploid *S. mexicana* from Florida can be difficult to separate from some *S. maya* and *S. virgata* collections; this is true in the field and with herbarium specimens. Specimens of *S. virgata* always have inflorescences that are narrow with short ascending branches and a non-secund apex. When tall stems (1.5 m plus) arch over from the weight of the inflorescence as it develops, then all branches of the inflorescence can be oriented upward in the field making the entire array secund. Most specimens of *S. mexicana* have inflorescences with longer more spreading lower branches and an erect secund conical shape. Sometimes the apex of the inflorescence is only weakly secund on individual shoots. When the bend in the apex of the inflorescence is flattened out by the angle at which the inflorescence is pressed and dried, then misidentification to *S. virgata* is much more likely. Inflorescences of *S. maya* vary from clearly secund conical in shape to non-second and narrowly erect like *S. virgata*. If all of *S. mexicana* along the Gulf coast in Mexico is tetraploid as it is in Texas, then the question arises as to what is the origin of putatively diploid *S. maya* in central Mesoamerica. Changes in the distribution of diploid *S. mexicana* and *S. virgata* due to changes in climate associated with glacial advances and retreats during the past 60,000 years may account for the arrival and subsequent isolation and divergence of members of the *S. sempervirens* complex or the *S. stricta* complex in Mesoamerica into the highlands species *S. maya*. Preference for moist soil habitats continued, as this is critical for all species of *S.* subsect. *Maritimae*. The origins of *S. maya* with morphological affinities to relatives in Florida may be similar to the origins of *Pityopsis graminifolia* (Pursh) Nutt. populations disjunct in Guatemala from the eastern Gulf coast and Florida populations of the species (Semple & Bowers 1985; Semple 2006). If there are diploids in *S. mexicana* in Mexico or *S. maya* is found to be tetraploid, then alternative hypotheses on the origins of *S. maya* may be needed.

In conclusion, the *Solidago sempervirens* complex is best treated as a group of five morphologically similar species occurring in wetter soil habitats. Like members of other species complexes in *Solidago*, some difficulty in identifying some collections to species is to be expected. While the multivariate analyses reported here have led to a much better understanding of the complex, they do not provide a 100% fool proof solution to the challenges of identifying goldenrods in the complex.

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Erratum:

The following reference cited in text was inadvertently omitted from the Literature Cited in the original posting:

Schaefer, H. 2015. On the origin and systematic position of the Azorean goldenrod, *Solidago azorica* (Asteraceae). Phytotaxa 210: 047–059.