The *Solidago rigida* complex (Compositae: Astereae): a multivariate morphometric analysis and chromosome numbers

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A multivariate morphometric study of herbarium specimens of *Solidago rigida* confirmed that the species was divisible into three groups: a prairie race, a southeastern United States race, and a midwestern–northeastern United States race. These groups are given subspecific rank as ssp. *humilis*, ssp. *glabrata*, and ssp. *rigida*, respectively, on the basis of morphological differences and their largely allopatric distributions. They are most easily distinguished on the basis of pubescence, phyllary, and disc corolla lobe traits. Twenty-seven new chromosome counts in two of the three subspecies are reported. Subspecies *humilis* is diploid ($2n = 18$); ssp. *rigida* is diploid in Oklahoma and tetraploid ($2n = 36$) over most of its range. Subspecies *glabrata* has been reported previously as diploid (four counts). The following new combinations are made: ***Solidago rigida*** ssp. ***glabrata*** and ***S. rigida*** ssp. ***humilis***.

HEARD, S. B., et SEMPLE, J. C. 1988. The *Solidago rigida* complex (Compositae: Astereae): a multivariate morphometric analysis and chromosome numbers. Can. J. Bot. **66**: 1800–1807.

Une étude morphométrique multivariée de spécimens d'herbiers de *Solidago rigida* a confirmé que l'espèce était divisible en trois groupes : une race ses prairies, une race du sud-ouest des États-Unis et une race du mid-ouest–nord-est des États-Unis. À ces groupes sont attribués des rangs de sous-espèces, telles ssp. *humilis*, ssp. *glabrata* et spp. *rigida*, respectivement sur la base de leurs différences morphologiques et de leurs distributions largement allopatriques. On les distingue très facilement sur la base de pubescence et des traits phyllaires et discoïdes des lobes des corolles. Vingt-sept nouveaux comptes de chromosomes chez deux des trois sous-espèces sont rapportés. La sous-espèce *humilis* est diploïde ($2n = 18$); la ssp. *rigida* est diploïde en Oklahoma et tétraploïde ($2n = 36$) dans la majeure partie de sa distribution. La sous-espèce *glabrata* a été rapportée antérieurement comme diploïde (quatre comptes). Les nouvelles combinaisons suivantes sont faites : ***Solidago rigida*** ssp. ***glabrata*** et ***S. rigida*** spp. ***humilis***.

[Traduit par la revue]

Introduction

Solidago rigida L. (Sp. Pl. 880. 1753) is a member of the *Oligoneuron* group of *Solidago*, which have corymbiform capitulescences and phyllaries with one to several pronounced parallel veins (Brouillet and Semple 1981). The *S. rigida* complex is well defined and easily distinguished from other members of *Oligoneuron* and the genus on macroscopic morphological characters.

The complex has been treated nomenclaturally in a number of ways. A western, prairie race was distinguished from the typical material (from Pennsylvania) and described as var. *humilis* Porter. This variety has also been given specific status as *Oligoneuron canescens* Rydb. and as *S. parvirigida* Beaudry. A supposedly more velvety pubescent form was described as *Oligoneuron bombycinum* Lunell. The chromosome number of members of the race has previously been reported as $2n = 18$, whereas that of the typical variety has been reported as $2n = 36$ (Beaudry and Chabot 1959; Anderson et al. 1974; Semple et al. 1981; Semple et al. 1984).

A distinct race of the southeastern United States was recognized as *S. corymbosum* Ell. non Poir.; the same group was described later as *Aster jacksonii* Ktze. and *S. jacksonii* (Ktze.) Fern. The race also has been given varietal status as *S. rigida* var. *glabrata* Braun. Four populations of this race (three in Tennessee, one in Texas) were reported to have a chromosome number of $2n = 18$ (Beaudry 1963; Semple et al. 1984).

Three other varieties have also been proposed. These designate (*i*) a small-headed *S. rigida* var. *microcephala* DC. and (*ii*) a robust *S. rigida* var. *magna* Clute, both known only from single specimens and (*iii*) a smooth-stemmed *S. rigida* var. *laevicaulis* Shinners, from Texas.

The present study was undertaken to clarify the status of the previously named taxa in the *S. rigida* complex and to determine the geographic distribution of cytotypes. The names used below are those that were adopted at the end of the study.

Materials and methods

Herbarium specimens from ALTA, CAN, DAO, DS, F, GA, GH, LL, MO, MT, NY, PH, SMU, TENN, TEX, TRT, US, and WAT, plus personal collections of J. C. Semple, were examined. On the basis of location data and completeness of the specimens, 103 specimens were selected for inclusion in a detailed analysis of morphological variation. For each specimen, the state of each of the 18 characters listed in Table 1 was determined.

After a preliminary examination of the specimens, characters were chosen on the basis of those used in the literature and the second author's knowledge of morphological variation in the Astereae. Informal observations were made on many plants of ssp. *humilis* and ssp. *rigida* grown under cultivation in the greenhouses and experimental garden of the University of Waterloo; these gave an indication of the effects of environment on variation in gross characters, such as stem height. The amount of pubescence was scored separately for different organs, since not all parts of an individual goldenrod (or other Astereae) have the same amount of pubescence. Because the achene hairs of Astereae are morphologically different from those found on other parts of the plant, the amount of pubescence on the fruit body was scored as a separate trait.

All numerical analyses were performed on mainframe equipment of the Department of Computing Services, University of Waterloo. The clustering analysis was performed using the UPGMA method in the CLUSTAN package of algorithms (Wishart 1978). Statistical analyses were performed using procedures UNIVARIATE, DISCRIM, STEPDISC, and CANDISC available in SAS (SAS Institute 1985*a*, 1985*b*). Each

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variable was transformed by a $\log_{10}$ (continuous data) or a square-root (discrete data) function in an attempt to satisfy the assumption of normality.

Clustering was performed as one means of determining the number of groups to be adopted in the discriminant analysis. The results were compared with indications in the literature of the appropriate number of *a priori* groups to be adopted in subsequent analyses.

Stepwise discriminant analysis (STEPDISC) was used to select a subset of characters that maximized differences among the *a priori* groups. The same subset also can be used as secondary characters in a key to the taxa of the species complex. The primary characters are those used to determine *a priori* group membership and cannot be included in the various discriminant analyses.

Classificatory discriminant analysis (DISCRIM) was used to classify, *a posteriori*, individuals into groups defined *a priori*. Correct classification rates indicate the strength of group separation.

Canonical discriminant analysis (CANDISC) was utilized as a dimension-reduction technique to facilitate visualization of the results of the multidimensional analyses. This analysis was done because the first, or first few, canonical variables may reveal considerable differences among *a priori* groups, even when none of the quantitative variables do so independently. Tests for equality of group centroids (Wilks' λ, Pillai's trace, Hotelling–Lawley trace, and Roy's greatest root) were performed as part of the canonical analysis.

Results of the analyses were used (*i*) to judge the distinctness of the *a priori* groups, (*ii*) to provide some indication of a suitable formal nomenclatural rank, if any, to give each group, and (*iii*) to create a key for the assignment of more than 1800 additional specimens to the appropriate taxa.

Chromosome number determinations were made by J. C. Semple according to the procedure of Semple and Brouillet (1980; mitotic counts) or Semple et al. (1981; meiotic counts). Vouchers of all collections counted have been deposited in WAT; all permanent slides of squashes remain in the possession of J. C. Semple.

TABLE 1. Characters assessed in the morphometric study

Character		Measurement
1	PUB1	Pubescence of inner series phyllary. Nine classes: 0, glabrous, to 8, densely pubescent
2	PUB2	Pubescence of outer series phyllary. Same scale as character 1
3	ACHPUB	Pubescence of achene. Four classes: 0, glabrous, to 4, densely pubescent
4	LFPUB	Pubescence, hairs/mm², non-nerve tissue on underside of a midstem leaf
5	MSPUB	Pubescence, hairs/mm², midstem
6	MSPUBL	Length (mm) of midstem pubescence
7	INFLWD	Width (cm) of capitulescence at widest point
8	INFLHT	Height (cm) of capitulescence from lowest point
9	LDL	Length (mm) of longest disc corolla lobes
10	LDC	Length (mm) of disc corolla
11	LDP	Length (mm) of disc pappus
12	LACH	Length (mm) of immature achene
13	LRS	Length (mm) of ray strap
14	WRS	Width (mm) of ray strap at widest point
15	RAY	Number of rays per head
16	IFL	Total number of florets per head
17	INV	Height (mm) of involucre to tip of longest phyllary
18	PHIW	Width (mm) of inner series phyllary 0.5 mm below tip

NOTE: Values for characters 4–8 are single values for each plant. Other characters were determined in five replicates and the means used for further calculation.

Results

Multivariate analyses

The UPGMA clustering analysis placed the 103 specimens of the *Solidago rigida* complex into two primary clusters with the largest cluster divided into two subgroups. Recognition of any more than three groups would not, in our judgement, have made useful divisions of the complex. Specimens of these three main clusters were examined and differences in phyllary pubescence features were determined to be the traits with which *a priori* groups could be created for disciminant analyses. Traits useful in subdividing the scored plants into more than three groups were not apparent. Each of the 103 specimens was assigned to one of three *a priori* groups. Plants designated as group 1 generally had entirely glabrous phyllaries (treated below as ssp. *glabrata*); these were the specimens from eastern Texas and the Gulf and Atlantic states to North Carolina, and from Kentucky and Tennessee. Group 2 plants had densely pubescent phyllaries (treated below as ssp. *humilis*); these were the specimens from the Great Plains of Canada and the United States and along the foothills into Colorado and New Mexico. Group 3 plants had pubescent outer phyllaries but glabrous to sparsely pubescent inner phyllaries (treated below as ssp. *rigida*); these specimens came from central and northeastern portion of the range of the complex. Membership in the three groups generated by the cluster analysis groups was not completely identical with membership in the three groups examined in discriminant analysis groups. The two phyllary pubescence traits (PUB1 and PUB2; Table 1) were omitted from subsequent analyses because they were used to define the *a priori* groups.

Discriminant analyses showed that discrimination between the groups was possible without the defining characteristics. Correct classification rates were high: 96% (23/24) for group 1, 100% (38/38) for group 2, and 98% (40/41) for group 3. Geisser assignment probabilities were generally higher than 0.95 for specimens correctly identified. Six characters were determined (on the basis of decreasing contributions to Wilks' λ) to be important in discriminating among the groups; these were LFPUB, ACHPUB, LDL, MSPUBL, MSPUB, and PHYLW (Tables 1 and 2). The means and ranges of the 18 characters assessed for the three groups are listed in Table 2.

A canonical analysis was performed using the same *a priori* groups. Calculation of the Mahalanobis distances between groups and the associated *F*-values showed that each pair of groups was significantly different ($p < 0.0001$). Tests for equality of population centroids showed that the centroids were significantly different ($p < 0.0001$). A plot of the first versus the second canonical variate for each of 103 sample specimens is presented in Fig. 1. There is some overlap in clusters of variate values for specimens of group 3 (ssp. *rigida*) and group 1 (ssp. glabrata), and for group 3 (ssp. *rigida*) and group 2 (ssp. *humilus*), but there is no overlap between group 1 (ssp. *glabrata*) and group 2 (ssp. *humilis*). Symbols for each subspecies group cluster together with no apparently out-of-place symbols, with one exception: one individual of ssp. *glabrata* has a positive CAN2 value, as do most individuals of ssp. *rigida*, while all other CAN2 values for specimens of ssp. *glabrata* were negative.

Chromosome numbers

Previously unreported chromosome counts for the species are listed in Table 3. All individuals of ssp. *humilis* were $2n = 18$. Six individuals of ssp. *rigida* were determined to be $2n = 36$; two individuals of ssp. *rigida* from Oklahoma were $2n = 18$. No new counts for ssp. *glabrata* are reported.

TABLE 2. Summary of statistics for characters used in the numerical study. Values are mean ± SD (range)

Character	Group 1, ssp. *glabrata*	Group 2, ssp. *humilis*	Group 3, ssp. *rigida*
PUBL1	1.1±0.2 (1–1.7)	6.7±0.9 (4.2–8.0)	2.8±1.5 (1–6.5)
PUB2	1.5±1.2 (1.0–5.0)	7.0±0.7 (5.2–8.0)	5.6±1.7 (1.2–7.7)
ACHPUB	0 —	1.2±0.9 (0–2)	0.1±0.5 (0–3)
LFPUB	6.5±7.8 (0–25.8)	36.7±14.1 (18.2–94.9)	22.1±9.0 (7.2–50)
MSPUB	11.4±11.8 (0–42.6)	54.1±22.3 (23.6–130)	36.3±23.1 (10.0–160)
MSPUBI	0.34±0.12 (0.16–0.55)	0.38±0.07 (0.26–0.55)	0.39±0.11 (0.19–0.65)
INFLWD	11.4±4.7 (2.5–23.0)	9.3±3.4 (3.5–18.0)	11.9±5.5 (4.5–27.0)
INFLHT	10.9±4.9 (5.0–24.0)	8.9±5.1 (2.0–24.5)	12.3±8.3 (3.0–34.0)
LDI	1.18±0.12 (1.01–1.47)	1.055±0.12 (0.79–1.33)	1.28±0.14 (1.01–1.60)
LDC	4.9±0.4 (4.3–6.2)	4.7±0.3 (4.0–5.4)	5.1±0.4 (4.3–6.1)
LDP	4.3±0.4 (3.7–5.1)	4.2±0.3 (3.4–5.0)	4.5±0.4 (3.6–5.4)
LACH	1.10±0.21 (0.73–1.58)	1.04±0.16 (0.79–1.52)	1.13±0.20 (0.81–1.68)
LRS	3.9±0.5 (3.2–5.2)	3.4±0.4 (2.8–4.2)	3.8±0.6 (1.4–5.4)
WRS	1.51±0.18 (1.05–1.81)	1.33±0.18 (0.93–1.93)	1.49±0.16 (1.16–1.85)
RAY	9.3±1.6 (6.4–11.8)	10.3±1.6 (7.6–14.2)	9.5±1.4 (6.2–12.8)
IFI	30.4±8.1 (25.0–42.4)	33.8±6.1 (25.0–49.0)	30.3±4.5 (20.4–39.8)
INV	5.7±0.5 (5.1–6.8)	5.5±0.3 (4.6–6.3)	5.8±0.6 (4.6–7.5)
PHLW	1.12±0.11 (0.87–1.31)	0.96±0.14 (0.65–1.25)	1.09±0.15 (0.78–1.4)

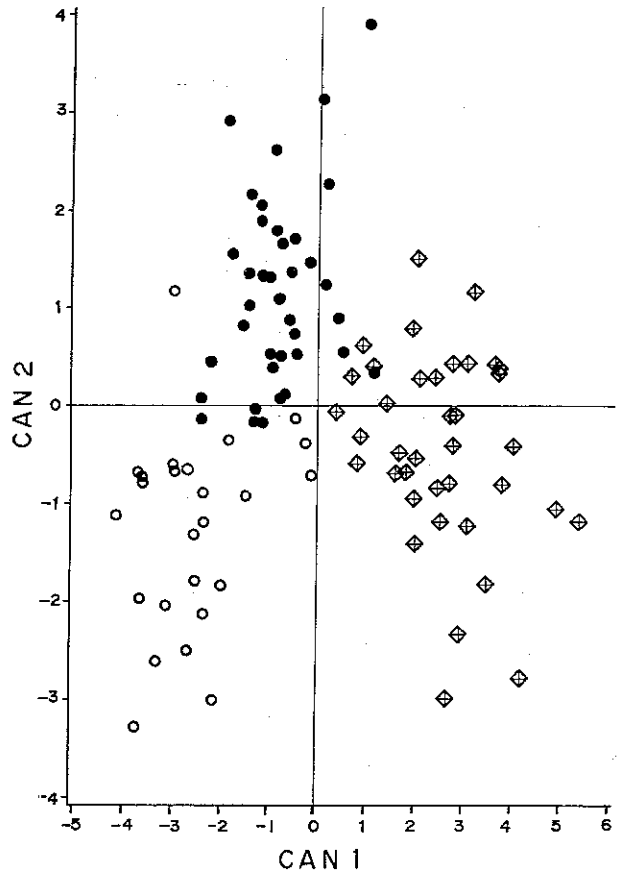


FIG. 1. Plot of first and second canonical (CAN) variates of 103 individuals of *Solidago rigida*. ●, ssp. *rigida*; ⧫, ssp. *humilis*; ssp. ○, ssp. *glabrata*

Discussion

The number of *a priori* groups examined in the discriminant and canonical analyses were considered appropriate for the purposes of the study because, in part, the number of groups recognized traditionally (e.g., Cronquist 1968) in this particular species complex happened to be the same as the number of groups we chose to test statistically after the cluster analysis. More groups could have been tested, but we had no indication from the preliminary analyses that such additional groups could be characterized by a simple set of characters rather than by a computer-generated discriminant function. Discovery of groups that could not be given useful nomenclatural recognition was beyond the scope of the study.

Discrimination among the group tested was high even though the traits used to define them (phyllary pubescence traits) were omitted from the analyses. This implies that the groups are real in a phylogenetic sense and are not merely statistical artifacts or arbitrary divisions of a single taxon. Four of the six traits determined to be critical in the stepwise discriminant analysis are pubescence characteristics, but two are not: length of the longest disc corolla lobe (LDI) and inner series phyllary width (*phlw*). Even if the pubescence features are viewed as redundant (ipsative) with the traits defining the *a priori* groups (phyllary pubescence), and we do not view them as such, LDI and PHLW are clearly not. If a phenetic group is also a phylogenetic group, then traits of discriminatory value will be correlated as a consequence of common ancestry, not because they are the result of pleiotrophy.

The geographic ranges of the groups determined from all collections seen in the study (Figs. 2–4) correspond in general to the major floristic provinces of eastern and central North America (Cronquist 1982; Atlantic–Gulf coastal plain, prairie, and Appalachian provinces for ssp. *glabrata*, ssp. *humilis*, and ssp. *rigida*, respectively). The fact that the ranges of the groups match common patterns in plant distributions lends additional support to the validity of the groups defined on morphology because the range limits of a taxon's distribution are the consequence, in part, of a set of inheritable physiological traits.

Specific level status for each group was rejected for two reasons. First, no qualitative diagnostic characteristics were found to distinguish any of the groups from the other two; all differences were quantitative with at least some overlap in ranges of values. Second, *S. rigida* sensu lato forms such a clear natural group within the *oligoneuron* group of *Solidago* that it was thought appropriate to maintain it as a single species. The differences among the groups of the complex are not of the level of differences among species in the genus *Solidago* generally.

The general similarity in morphology of the three subspecies

TABLE 3 Previously unreported chromosome number determinations in *Solidago rigida*

2n	Voucher data (WAI)
	S. rigida L. ssp. *humilis* (Porter) Heard & Semple
9_{II}	U.S.A.: KANSAS: Barton Co.: S of Russell, *7321*; Pawnee Co.: SW of Garfield, *7305*. MONTANA: Musselshell Co.: E of Musselshell, *6988*. NORTH DAKOTA: Golden Valley Co.: I-94 exit to Buffalo Gap, *6977*: Morton Co.: Sweet Briar Lake, *6965*
18	U.S.A.: COLORADO: Boulder Co.: N of Boulder, *S & S 5813*. INDIANA: White Co.: US-241 N of Reynolds, *S & H 8344*. MINNESOTA: Crow Wing Co.: W of Brainerd, *S & H 8793*; Lincoln Co.: S of Lake Benton, *S & Ch 5131*; Stearns Co.: W of Belgrade, *S & Ch 5091*. MONTANA: Wheatland Co.: W of Shawmut, *6998*. NORTH DAKOTA: Stutsman Co.: N of Buchanan, *S & S 6680*. NEBRASKA: Antelope Co.: US-275, E of Co. line, *4501*; Dawson Co.: Overton, *S & S 5840*; Lincoln Co.: North Platte, *S 6528*. SOUTH DAKOTA: Codington Co.: S of Watertown, *S & Ch 5123*; Fall River Co.: W of Hot Springs, *S 6631*; Marshall Co.: E of Britton, *S & Ch 5116*; Potter Co.: US-83 N of Co. line, *S & S 6656*; Stanley Co.: Hayes, *S & S 6653*. WYOMING: Laramie Co.: S of Meridian, *S & S 6614*
	Solidago rigida ssp. *rigida*
18	U.S.A.: OKLAHOMA: Garvin Co.: E of Hennepin on OK-7, *S & H 8250*; Stephens Co.: E of Oklahoma Hills on OK-7, *S & H 8245*
18_{II}	U.S.A.: ILLINOIS: Cook Co.: Northbrook, *6928*. MINNESOTA: Douglas Co.: Garfield, *6949*
36	U.S.A.: KANSAS: Aitchison Co.: S of Aitchison, *S & Ch 5242*; Miami Co.: N of Beagle, *S & Ch 5257*. MINNESOTA. Jackson Co.: Jackson, *S & Ch 5150*. MISSOURI: Camden Co.: E of Preston, *S & Ch 5287*

NOTE: Collections listed by number only are by J. C. Semple and L. Brouillet. *Ch.* J. Chmielewski; *H*, S. Heard; S, J. Semple; *S & S* J. and B. Semple

is reflected in the key below. Several characters had to be utilized to produce a useful key because some overlap occurred in the ranges of all characters measured. Characters not included in the multivariate study were also found useful in the preparation of the key; e.g., capitulescence form.

The change in rank from variety to subspecies for the three groups is acknowledged to be minor but is made for two major reasons. First, subspecific rank was chosen as the most appropriate treatment for the three groups following the consensus definition presented in Semple (1974): all members of a subspecies share a distinctive morphology and are by and large allopatric from other members of the species. Varieties lack the predominantly allopatric distribution pattern according to the definition in Semple (1974). Intersubspecific and intervarietal hybridization can occur, but less frequently between subspecies than varieties because the former have more limited opportunities to cross-pollinate. With the exception of some overlap in ranges in the midwestern United States, the three groups we recognize on morphology can be separated to a great extent on geographical grounds alone.

Second, the new nomenclature is consistent with that being adopted or proposed by the second author and colleagues for other goldenrods and asters: e.g., *S. nemoralis* Ait. ssp. *nemoralis* and ssp. *decemflora* (DC.) Brammall in Semple (1985), *S. glutinosa* Nutt. ssp. *glutinosa* and ssp. *randii* (Porter) Cronq. (see Ringius and Semple 1987), and *Aster lanceolatus* Willd. ssp. *lanceolatus* and ssp. *hesperius* (A. Gray) Semple and Chmielewski (1987). In each case, only small portions of the total ranges of the subspecies are sympatric.

Individuals with varying degrees of morphological intermediacy between two of the groups were encountered in the appropriate zones of sympatry. However, only some of these are believed to be intersubspecies hybrids. Subspecies *rigida* is known only at the tetraploid level in most of the zone of sympatry with ssp. *humilis*, which is known only at the diploid level throughout its range. Hybrids would be triploid and triploids are very rare in *Solidago* in general (see Semple et al. 1984). Diploids are known in both subspecies in Oklahoma, and it is there that intersubspecific hybrids are expected. Too little is known about cytotypes in ssp. *glabrata* to draw conclusions about the importance of ploidy level. Subspecies *humilis* and ssp. *glabrata* are known to be diploid in eastern Texas.

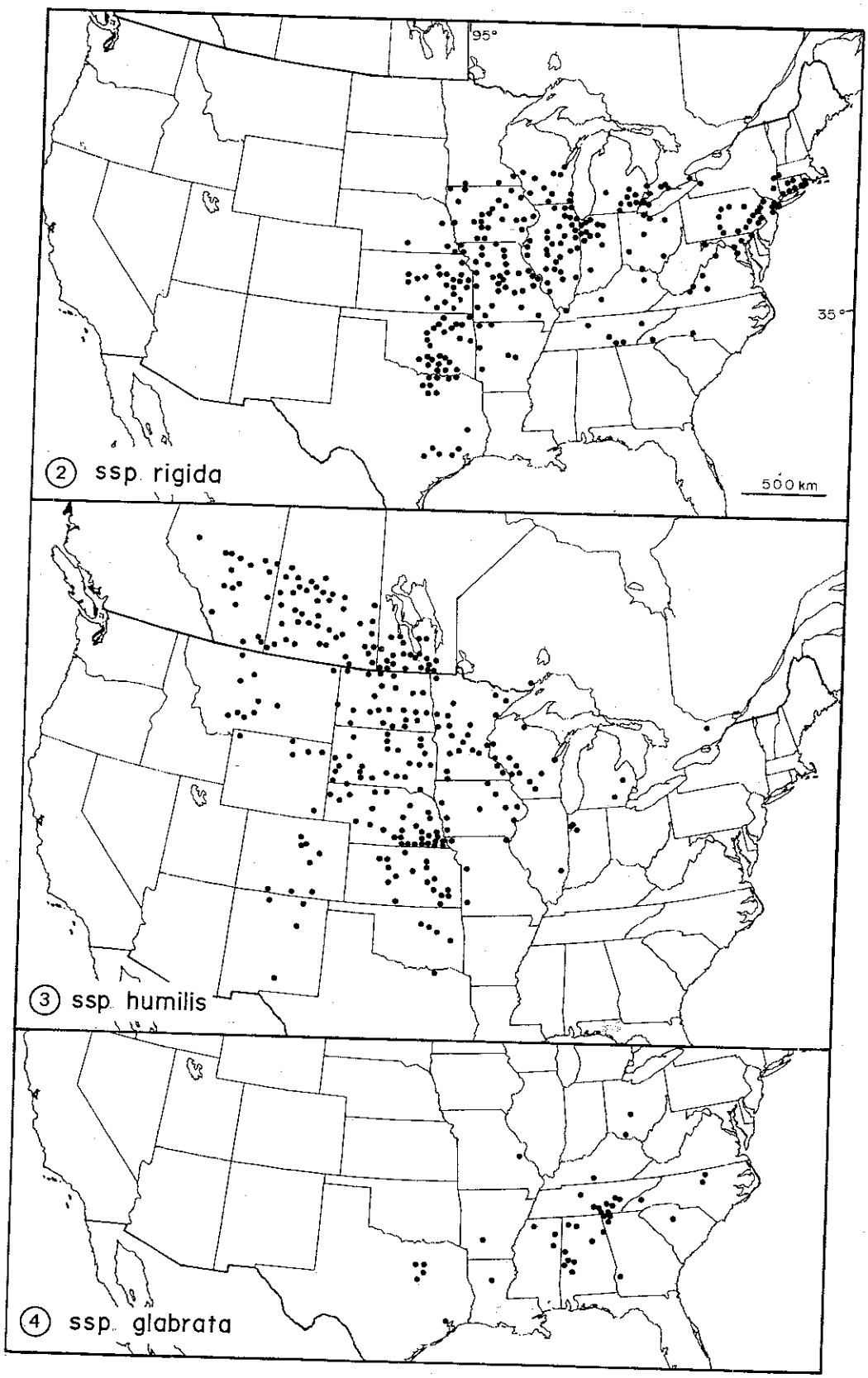
The following hypothesis on the origins of the subspecies is presented as our best estimate of likely past events. The three subspecies are thought to have diverged from a single ancestral taxon in response to different (unknown) conditions that were encountered in the different regions and as the result of stochastic events following isolation during peaks in late Pleistocene glaciation. The most extreme morphological divergence is seen between populations the farthest separated; e.g., individuals of ssp. *humilis* from Alberta and of ssp. *rigida* from Pennsylvania may be distinguished at a glance, whereas the status of plants from Iowa, Kansas, or Oklahoma, where the two ranges meet, can be more difficult to determine.

Because differences in ploidy level by and large preclude gene exchange and merging of the subspecies in some of the areas of sympatry, morphological similarity is thought to be the result of either parallel evolution or convergence as the subspecies migrated into their present ranges following deglaciation over the last 20 000 years. In the case of ssp. *rigida* and ssp. *humilis* in Wisconsin, the correct interpretation depends on knowing whether or not the ancestors of ssp. *rigida* were more like extant plants seen in Wisconsin than like some other form of the subspecies not as similar to ssp. *humilis*. The data base available is inadequate to clarify this history.

Taxonomic treatment

Solidago rigida L., Sp. Pl. 880. 1753

Stout, rhizomatous perennials. Stems solitary to several, unbranched below the capitulescence, rigidly erect; 40–130 cm tall, 2.5–6 mm thick at the base; glabrate to densely (100+ hairs/mm² at midstem) hispid with hairs 0.3–0.6 mm long; prominently ribbed, the basal 10 cm, and often more, usually anthocyanotic. Basal leaves large, 8–25 cm long and 3–10 cm broad, elliptic to rhombic, long petiolate and the petioles sheathing, usually persistent to flowering, 2–5 per rosette. Stem leaves greatly reduced upwards, alternate, the uppermost 1–2 cm long and 0.5–1 cm broad; lower leaves petiolate, upper sessile; most often ovate but sometimes narrowly elliptic to rhombic, the margins usually entire but sometimes slightly to markedly serrate especially on the lower leaves; venation reticulodromous; indument varying from glabrate to densely (50+ hairs/mm² on midstem leaves) hispid. Capitulescence compoundly corymbiform, flat topped



FIGS 2–4. Distribution of *Solidago rigida* in Canada and the United States based on all collections seen. Fig. 2. Ssp. *rigida*. Fig. 3. Ssp. *humilis* Fig 4. Ssp. *glabrata*

or rounded, 3–30 cm high from lowest branching point, 4–25 cm wide when pressed flat; heads 15–300. Peduncles less than 1 cm long, very densely hispid. Involucres large for the genus, 4.5–7 mm high to tip of longest phyllary and narrowly campanulate. Phyllaries in about 3 unequal series, the central portion chlorophyllous and the margins yellow, 3–5 prominent nerves; ranging in shape from linear to oblong or slightly spatulate, the inner ones 0.7–1.6 mm wide; surfaces glabrous to densely pubescent but margins always ciliate; midrib swollen, translucent. Rays 6–15, yellow (rarely tinged with red), the straps 1–2 mm wide and 3–6 mm long; discs 14–35, yellow, the corollas 4–6 mm long. Pappus single, the bristles barbellate, 3.5–5.5 mm long. Achenes white at maturity with about 20 brown nerves; bluntly fusiform, 1.2–2.5 mm long, 0.5–1 mm broad, corolla usually deciduous at maturity; surface glabrous or with some short hairs on the upper quarter. Flowering period: August–October over most of the range; July and August on the Canadian prairies. Chromosome number: $x = 9$; $2n = 18, 36$.

The species may be distinguished from others in the *Oligoneuron* group of *Solidago* by its stiff, sessile, ovate or elliptic stem leaves; it may be distinguished from others in the genus (particularly forms of *S. wrightii* A. Gray, with which, in the southwest, it could be confused) by the 3- to 5-nerved phyllaries typical of the section and by the usually well developed basal rosettes of petiolate leaves

Key to infraspecific taxa

1. Outer series phyllaries glabrous, leaves and stems glabrous to somewhat hispid . . . . . ssp. *glabrata*
1. Outer series phyllaries pubescent, leaves and stems hispid to densely so
   2. Inner series phyllaries conspicuously pubescent, often linear; plants usually short (3–7 dm) but may be taller; capitulescence compact, pubescence of leaves and stems fine and very dense (>50 hairs/mm²) . . . . . ssp. *humilis*
   2. Inner series phyllaries glabrate to very sparsely pubescent, oblong and bluntly rounded; plants more robust (6–14 dm) with loose, open capitulescence; pubescence coarsely hispid (<50 hairs/mm²) . . . . . ssp. *rigida*

Solidago rigida L. ssp. *rigida*

TYPE: PENNSYLVANIA (holotype: Linn!)

Solidago grandiflora Raf., in Med. Repos. New York 5: 359. 1808. TYPE: not seen

Solidago rigida L. var. *microcephala* DC., Prod. 5: 337. 1836. TYPE: *In horto Parisino* (holotype: DC!)

Aster rigidus (L.) Ktze., Rev. Gen. 1: 314. 1891

Oligoneuron grandiflorum (Raf.) Small, Fl. S.E. U.S. 1903

Oligoneuron rigidum (L.) Small, Fl. S.E. U.S. 1188, 1339. 1903

Solidago rigida L. var. *magna* Clute, Am. J. Bot. 39: 186. 1933. TYPE: not seen

Subspecies *rigida* is distinguished by a number of characters, all of which overlap to some extent with the other taxa (Fig. 5). Stems robust, 6–13 dm; hispid to densely so (10–70 hairs/mm²), hairs coarse and stiff. Basal leaves very large, up to 25 cm long and 10 cm wide. Leaves hispid on both surfaces, 7–50 hairs/mm². Capitulescence flat topped, usually loose and open; spreading, up to 30 cm high and 25 cm broad when pressed flat. Peduncles densely hispid. Phyllaries of outer series pubescent; those of inner series glabrate to puberulent, oblong to slightly spathulate. Disc corolla lobes deep, 1.1–1.6 mm. Achenes always glabrous. Chromosome number: $2n = 18$ (reported from Oklahoma), $2n = 36$ (most of range).

HABITAT: Glades, savannahs, dry open areas especially on calcareous soils. From Massachusetts in the northeast, south to Tennessee; west to eastern Oklahoma, eastern Kansas, Iowa; southern Minnesota, Wisconsin and Michigan and southwestern Ontario (Fig. 2).

Solidago rigida L. ssp. ***humilis*** (Porter) Heard & Semple, comb. nov.

Solidago rigida L. var. *humilis* Porter, U.S. Dep. Interior Misc. Publ. 4: 63. 1874. SYNTYPES: Wet Mountain Valley, *Brandegee 708*, Aug. 1873, *Porter s.n.*; *Coulter s.n.* Near Denver, *Dr. Smith s.n.* (lectotype: *Brandegee 708*, NY!, designated here; isolectotype: MO!)

Oligoneuron canescens Rydb., Bull. Torrey Bot. Club, 31: 652. 1904. TYPE: WYOMING. Buffalo, 1900, *Tweedy 3117*. (holotype: NY!)

Oligoneuron bombycinum Lunell., Am. Midl. Nat. 39: 183. 1933. TYPE: NORTH DAKOTA, Butte, Benson Co., 9 Sept. 1910, *Lunell* (not seen, not in F)

Solidago canescens (Rydb.) Friesner, Butler Univ. Bot. Stud. 4: 196. 1940

Solidago bombycinum (Lunell) Friesner. Butler Univ. Bot. Stud. 5: 113. 1941

Solidago rigida var. *canescens* (Rydb.) Breitung. Can. Field-Nat. 61: 100. 1947

Solidago parvirigida Beaudry, Can. J. Bot. 37: 224. 1959. TYPE: Based on *Solidago rigida* L. var. *humilis* Porter

Solidago jacksonii (Ktze.) Fern. var. *humilis* (Porter) Beaudry, Can. J. Genet. Cytol. 5: 171. 1963.

Oligoneuron corymbosum (Ell.) Small var. *humilis* (Porter) Beaudry & Kapoor, Can. J. Genet. Cytol. 8: 442. 1966

Subspecies *humilis* is the western, prairie races of the species. It is separated from the typical subspecies on a number of characters (Fig. 5). The differences between this and the typical subspecies are much less near the area of contact of the two. Stems shorter, 4–7(–9) dm, densely hispid (30–70 hairs/mm²) with the hairs less coarse than in ssp. *rigida*. Basal leaves smaller, rarely exceeding 12 cm long and 5 cm broad, and more numerous. Leaves densely hispid (20–60 hairs/mm²) and the hairs less coarse than typical. Capitulescence tightly clumped and usually rounded. Phyllaries of the outer and inner series densely pubescent. Inner phyllaries more nearly linear. Disc corolla lobes shallow, 0.9–1.2(1.3) mm. Achenes pubescent above on about two-thirds of all specimens. Chromosome number: $2n = 18$.

HABITAT: Prairies and open meadows. Edmonton, Alberta, and southeast; prairies of Saskatchewan and Manitoba, scattered south to New Mexico, common in Kansas, Nebraska, and the Dakotas; east through Minnesota and Wisconsin (Fig. 3). One collection from southern Illinois, three from northwestern Indiana, two from Michigan, and one from Renfrew, Ont., are probably introduced. All were collected

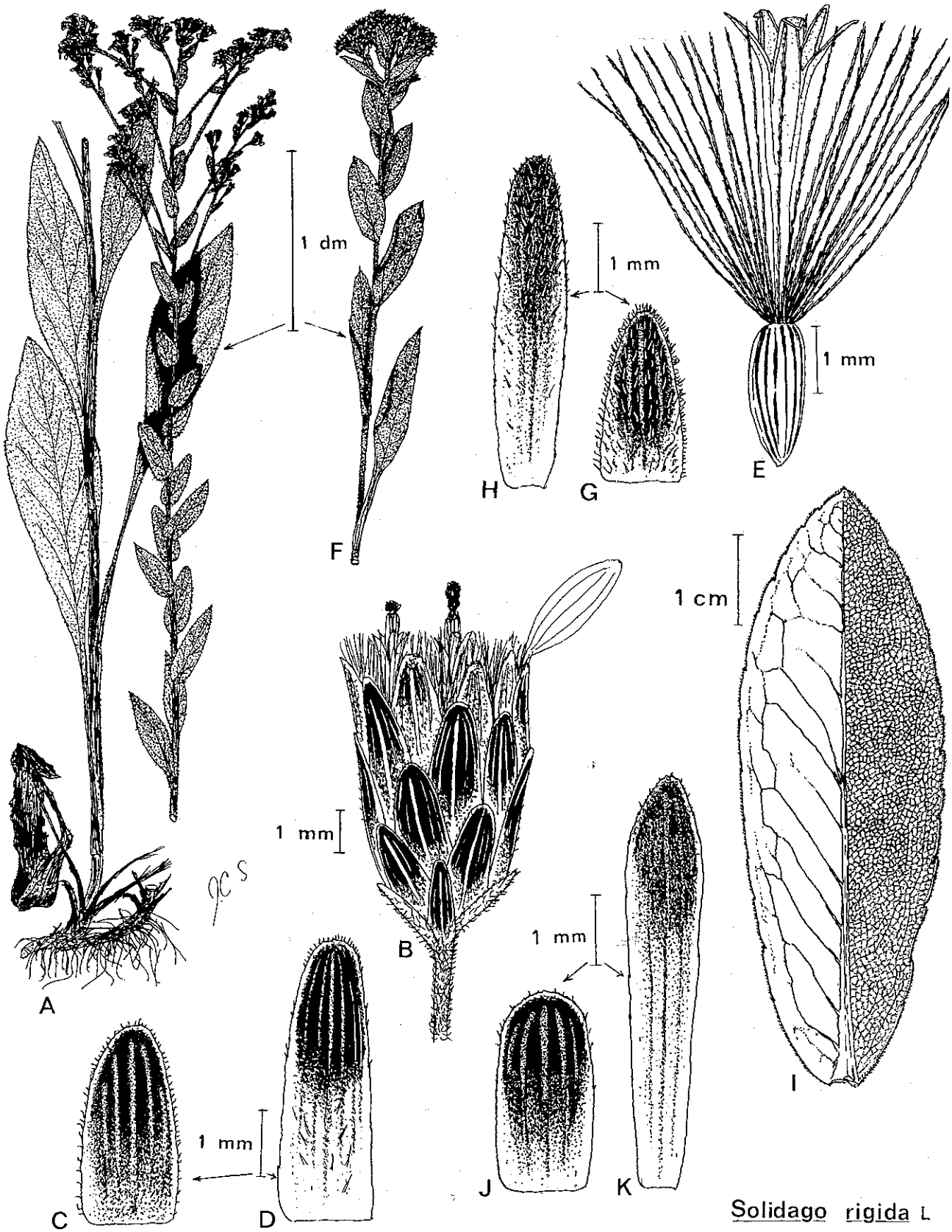


FIG. 5. Morphology of *Solidago rigida*. (A–E) ssp. *rigida* (A) Habit. (B) Head with only some florets drawn. (C and D) Outer and mid series phyllaries, respectively; chlorophyllous zone dark; scale the same in Figs. 5C, 5D, 5G, 5H, 5J, and 5K. (E) Mature disc floret achene with corolla still attached. (F and H) Ssp. *humilis*. (F) Capitulescence and upper stem; scale the same as in Fig. 5A. (G and H) Outer and inner series phyllaries, respectively; chlorophyllous zone dark. (I and K) Ssp. *glabrata* (I) Midstem leaf; upper surface on left, lower surface on right. (J and K) Outer and inner series phyllaries, respectively; chlorophyllous zone dark.

along railroad tracks, which may provide routes for the transport of achenes

Solidago rigida L. ssp. ***glabrata*** (Braun) Heard & Semple, comb. nov.

Solidago rigida L. var. *glabrata* Braun, Rhodora, 44: 3 1942. TYPE: Kentucky. Dry soil with prairie plants, near Cave City, Barren Co., 13 Sept. 1940, *Braun Ky-3629* (holotype: GH!; isotype: E. L. Braun)

Solidago corymbosa Ell., Sketch Bot. S. Carol. and Georgia, 2: 378. 1824. non Poir., Encycl. Suppl. 5: 461. 1817. TYPE: GEORGIA. Louisville, *Mr. Jackson s.n.* (holotype/lectotype: CHARL?, not listed in Weatherby (1942), presumed lost or destroyed)

Leiolego corymbosa (Ell.) Raf., Fl. Tell. 2: 42. 1836.

Aster jacksonii Ktze., Rev. Gen. 1: 314. 1891. TYPE: Based on *Solidago corymbosa* Ell.

Oligoneuron corymbosum (Ell.) Small, Fl. S.E. U.S. 1188, 1339. 1903.

Oligoneuron jacksonii (Ktze.) Small, Fl. S.E. U.S. 1361. 1903.

Oligoneuron jacksonianum (Ktze.) Small, FL. S.E. U.S. 1509. 1903. Orthographic variation of *O. jacksonii*.

Solidago jacksonii (Ktze.) Fern., Rhodora, 38: 229. 1936.

Solidago rigida L. var. *laevicaulis* Shinners, Field & Lab. 9: 35. 1951. TYPE: TEXAS. Dallas Co. 2 mi. N of Cedar Hill, 11 Nov. 1947, *Whitehouse 19269* (holotype: SMU!; isotypes: GA! NY!, SMU!(8), TEX!, US!)

Subspecies *glabrata* differs from the typical subspecies in its reduced pubescence. Phyllaries, of both inner and outer series, are completely glabrous. Peduncles, while still hispid, are only sparsely to moderately so. Leaves and stems vary from completely glabrous (the type specimen is such) to quite hispid (stem 0–25 hairs/mm^2; leaves 0–20 hairs/mm^2). Leaves tend also to be thinner and less stiff, more often rhombic, and may be 5 or more times as long as broad. Otherwise, the subspecies is quite similar to ssp. *rigida*. Chromosome number: $2n = 18$ (three reports from Tennessee and one from Texas; Beaudry 1963; Semple et al. 1984).

HABITAT: Glades, savannahs, dry open areas, especially on calcareous soils. Northeast Texas east to North Carolina; north through Tennessee and Kentucky into Ohio (Fig. 4).

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