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A Biosystematic Study of the Genus *Elymus* (Gramineae: Triticeae) in Iowa

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A study of the Iowa taxa of the genus *Elymus* is presented based upon extensive field and herbarium work. Characters used for analysis include anatomy, chromosome number, and morphology. Numerical analyses, distribution maps, and a key to species are included.
INDEX DESCRIPTORS: *Elymus*, Gramineae, biosystematics, taxonomy, Iowa vascular flora.

Elymus is a member of the tribe Triticeae of the Gramineae. Common names include Wild Rye, Terell Grass, and Lyme Grass. Economic importance of the genus is restricted now to grazing and hay, but some species (*E. mollis* and *E. canadensis*) have been used for food by American Indians (Hitchcock, 1951) and Hackel (1890) indicated that in Iceland, grains of *E. arenarius* were once used for making bread.

Many of the species in this genus are extremely variable, and numerous subspecific taxa have been proposed by authors working with this genus (Fernald, 1950; Pammel, Ball, and Lamson-Scribner, 1903; Hitchcock, 1951). In 1903, Pammel, Ball, and Lamson-Scribner published a taxonomic treatment of the Iowa grasses including eight species and three varieties of *Elymus*. Cratty (1933) listed nine species with two varieties, while Sons (1941) enumerated six species, four varieties, and one form of *Elymus* present in Iowa. Most recently, Pohl (1966a) recognized six species and one form for the state. This study is a detailed analysis using anatomy, cytology, morphology, and numerical analyses to evaluate the taxa present within Iowa.

MATERIALS AND METHODS

Studies of anatomy, morphology and chromosome numbers were conducted on material collected in Iowa. Field collections were made throughout Iowa during July through October of 1977 and 1978. Local population samples were made using the "ignorant man" technique of Ward (1974). The number of individuals sampled from each population ranged from 8 to 30 depending upon population size. The collected plants were pressed and dried using electric heat.

Anatomical studies were made on leaf clearings and cross sections of leaf blades. Clearings were made following the technique of Shobe and Lersten (1967). Cross sections were made with a microtome after treatment with hydrofluoric acid and embedding in paraffin. Sections were dehydrated in an EtOH-xylene series, and stained with Johansen's safranin and chlorazol black E. Fresh material of 5 plants from different populations of each proposed taxon was used whenever possible.

Live specimens from population samples were transplanted from the field to a uniform garden on the Hinz farm (owned by Iowa State University), located just north of Ames, Iowa. The plot was fully exposed and lacked any readily observable environmental gradients. Plants were transported in plastic bags and transplanted as soon after collection as possible. Selected culms were bagged prior to anthesis to prevent cross pollination.

Meiotic material for chromosome studies was obtained from wild plants, from the greenhouse, and the garden plot. Newcomer's (Newcomer, 1953) solution was used to preserve young spikes. Anthers were dissected out, squashed, and stained with propiocarmine (Sharma and Sharma, 1965). Slides were made permanent by a freezing technique (Bowen, 1956). Drawings were made with the aid of a Zeiss drawing apparatus on a Zeiss microscope with a 100X oil immersion objective.

Herbarium specimens of *Elymus* were obtained from the University of Iowa (IA), the University of Northern Iowa (ISTC), and Iowa State University (ISC). Measurements were made upon specimens from the field, population samples, herbarium specimens, and garden material. A dissecting microscope fitted with a micrometer disc graduated to 0.1 mm was used for observation. All measurements were made after application of a wetting solution (Pohl, 1965).

Morphological variation was determined by measurement of 19 variables and determination of 5 ratios for 28 populations and numerous herbarium specimens. The variables are as follows:

1. Culm length
2. Spike length
3. First glume length
4. Second glume length
5. First glume width
6. Second glume width
7. Palea length
8. Lemma length
9. Awn length
10. Bowing of glumes
11. Density of spike
12. Lemma pubescence
13. Glume induration
14. Awn curvature
15. Number of florets per spikelet
16. First leaf length
17. Second leaf length
18. Third leaf length
19. Third leaf width
20. Culm length/spike length
21. Leaf width/leaf length
22. Glume width/glume length
23. Palea length/lemma length
24. Lemma length/awn length

All data were standardized (Sokal, 1961) and cluster anlaysis was used to analyze the data from the populations. The Q-technique of Sneath and Sokal (1973) was used to cluster the individuals by variables. Correlation coefficients were used to measure pairwise similarity. The unweighted pair-group mean (UWPGM) method described by McCammon (1968) was used for ordering the operational taxonomic units (OTUs). The computer program used was written by McCammon and Wenninger (1970).

OBSERVATIONS AND DISCUSSION

Epidermal Anatomy

The leaf epidermes of all specimens examined of Iowa *Elymus* were found to be very similar. Cells observed include short cells, silica cells, prickle hairs, stomatal apparatus, and long cells.

The short cells often found singly or in pairs were over and between veins. Metcalfe (1960) indicated that they may be found in short rows, but none in that arrangement were observed. Short cells were found more commonly on the abaxial leaf surface. Silica bodies within the silica cells were either rectangular with slightly rounded ends, or oval-circular to crescent-shaped in outline. Metcalfe (1960) reported tall, narrow silica bodies in some species of *Elymus*, but none were observed in this study. Long trichomes were often observed over the veins, and shorter stouter trichomes in the intercostal zones.

Stomata were found only in the intercostal areas. They occur on both surfaces, but are more abundant adaxially. Stomata were consis-

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tantly observed on the edges of furrows arranged in ordered rows 2-4 cells from veins between the adaxial ribs. Metcalfe (1960) observed this to be common in grass leaf blades that tend to become inrolled in dry conditions.

Long cells are generally of two types. In the central intercostal areas, and generally toward the center of the leaf, the long cells were smooth-walled. Toward the margins of the leaves and closer to the ribs ripple-walled cells occur.

Exceptions to the above generalities occur. Plants identified as *E. diversiglumis* had the lowest percentage of ripple-wall cells, with the majority of long cells smooth-walled and tending to be somewhat shorter than those in the other taxa. In *E. canadensis* there were many more short cells than in other taxa examined. Perhaps as a result of this, a greater diversity of silica body shapes was found, including rectangular, oval, circular, and crescent-shaped cells. Often the silica cells were observed to fit into the adjacent cork cell of the short cell pair. The trichomes of taxa identified as *E. villosus* were extremely long and abundant, their structure being the same as trichomes of other species. Taxa identified as *E. wiegandii* lacked trichomes.

Cytology

The basic chromosome number for the genus *Elymus* is $x = 7$ (Brown, 1948; Darlington and Wylie, 1955). The majority of the species and all Iowa species are tetraploids ($2n = 28$). All Iowa *Elymus* examined had $n = 14$, determined from microsporocytes. Chromosome numbers were determined from the following:

Specimen	*Proposed taxon*
Gabel 1323	*E. canadensis*
Gabel 1373	*E. riparius*
Gabel 1372	*E. villosus*
Gabel 1369	*E. virginicus*
Pohl 13312	*E. wiegandii*
Gabel 1355	*E. canadensis*
Gabel 1356	*E. virginicus*
Gabel 1349	*E. villosus*
Gabel 1393	*E. canadensis*
Gabel 1368	*E. riparius*
Gabel 1390	*E. villosus*
Gabel 1387	*E. canadensis*
Gabel 1383	*E. villosus*
Gabel 1993	*E. wiegandii*

Breeding System

Much time and effort has been invested in the study of the breeding systems of the economically important Triticeae. Among the groups studied is the *Elymus-Agropyron-Sitanion* complex. Several authors (Stebbins and Singh, 1950; Dewy, 1966) have suggested that members of this group are more closely related than current taxonomic treatments indicate. Stebbins and Walters (1949) and Stebbins (1956) have even suggested that the tribe Triticeae be regarded as a single genus. Gould (1947) submerged *Agropyron, Sitanion,* and *Hystrix* in *Elymus,* but later (1975) separated *Agropyron* from *Elymus.* Many of the species within the genus *Elymus* hybridize freely and natural or artificial hybrids between many of the species have been reported.

The taxa of *Elymus* studied seem to be capable of self-fertilization as well as outcrossing. Church (1954) reported only 10-20% reduction in seed set due to bagging. Sanders and Hamrick (1980) estimated outcrossing rates at 0-32% in *E. canadensis* using eletrophoresis. Bagging studies conducted at the garden site indicated that although the species of *Elymus* studied are self-compatible (0-32% seed set) there is a higher percentage of seed set without the restriction of the bags (25-90%) (see Table 1). Outcrossing thus appears to be of more significance in the plants studied than has previously been reported.

Numerical Analyses

Operational taxonomic units (OTUs) were grouped based upon the observed variables (listed in Materials and Methods). A comparison of that grouping with traditionally recognized taxa, as well as an evaluation of specific relationships, was made possible by the use of a dendrograph. For convenience, labels based upon traditional taxonomic works (Hitchcock, 1951; Pohl, 1966a; Church, 1967) were assigned to individual plants. The first digit of the label corresponded to the following groups:

1 - *E. canadensis*
2 - *E. virginicus*
3 - *E. villosus*
4 - *E. riparius*
5 - *E. wiegandii*
6 - *E. diversiglumis*

Labeling had no effect upon the clustering process.

A dendrograph was constructed using individuals of 28 population samples (Gabel, 1979). The dendrograph indicated that individuals of any population generally clustered with other individuals of that population. The three most common taxa (1-3) were easily identifiable. Due to a scarcity of populations and a small number of individuals no population samples of material fitting traditional descriptions of taxa 4-6 were available.

Population means were then used as OTUs to construct a new dendrograph (Fig. 1). The horizontal axis corresponds to within-cluster similarity, the vertical axis (the arc cosine of correlation coefficients) to between-cluster similarity. Three groups are easily observable. Taxon 1 (extreme left group) corresponds to the traditional *E. canadensis,* the middle group to *E. villosus* (taxon 3) and the extreme right group to *E. virginicus* (taxon 2).

The above population means as well as data from numerous individual herbarium specimens were then used to construct another

Table 1. A comparison of seed set between bagged and unbagged plants.

Collection	Species	Bagged			Unbagged		
		Seed set	Florets	%	Seed set	Florets	%
1333	*E. canadensis*	10	105	9.5	78	97	80.4
1335	*E. virginicus*	0	21	—	50	65	76.9
1339	*E. villosus*	33	117	28.2	47	120	39.2
1347	*E. canadensis*	74	229	32.3	47	71	66.2
1352	*E. canadensis*	0	123	—	83	149	55.7
1353	*E. canadensis*	0	78	—	121	177	68.4
1368	*E. riparius*	0	128	—	79	88	89.8
1377	*E. canadensis*	0	68	—	32	127	25.1
1392	*E. canadensis*	42	199	21.1	64	133	48.1
1525	*E. virginicus*	0	143	—	71	93	76.3

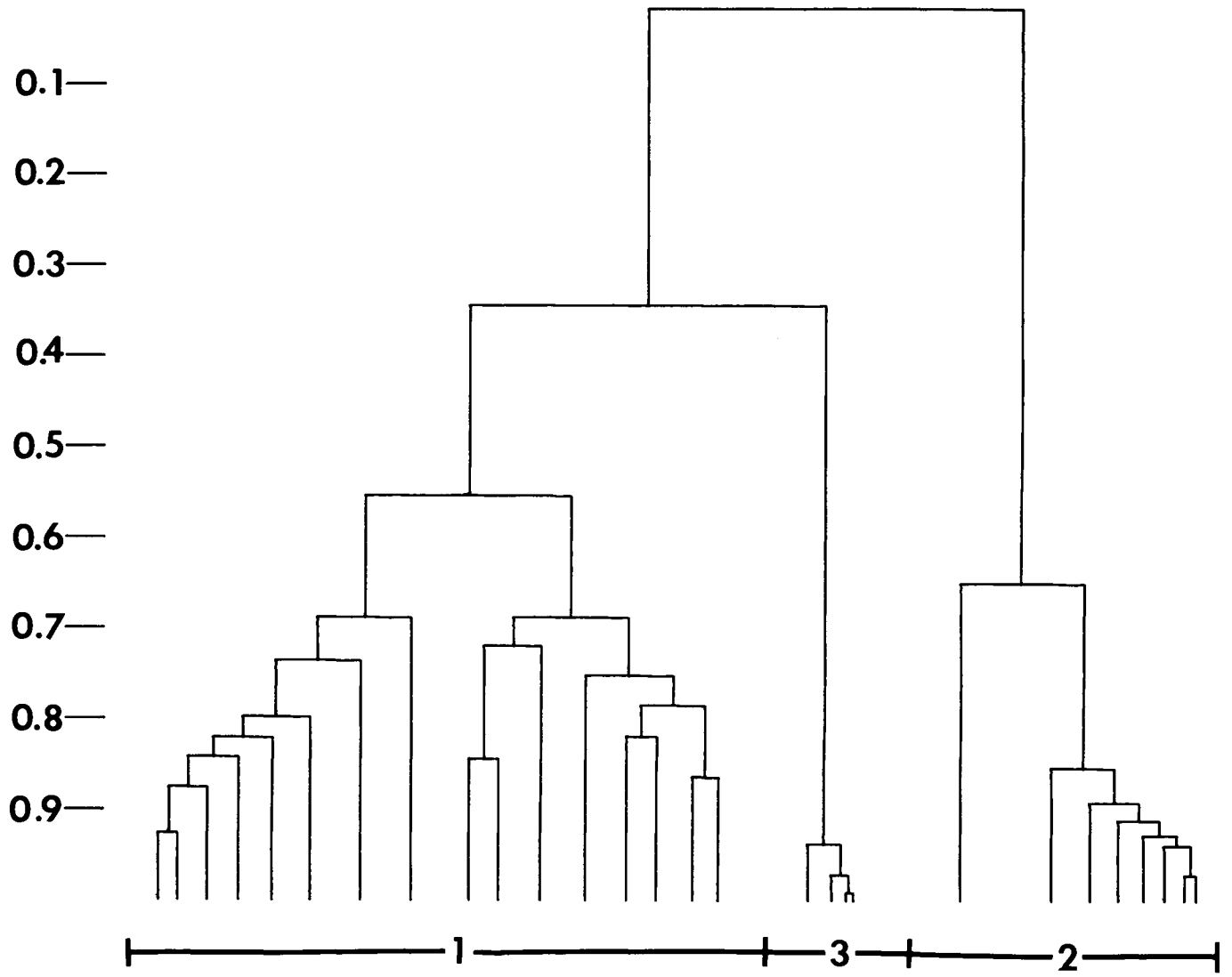

Fig. 1. A dendrograph of population means. Group 1 corresponds to *Elymus canadensis*, group 2 to *E. virginicus* and 3 to *E. villosus*. Axes are explained in the text.

dendrograph (Fig. 2). The herbarium specimens included material from all 6 taxa. A large number of herbarium specimens of taxa 1-3 were used to determine if individuals collected at various times and in various parts of Iowa would be grouped with population means. This would also give an indication of the validity of using herbarium specimens to represent the taxa for which population samples were not available. The closeness of the clustering indicates that individual herbarium specimens give a reasonable representation of "typical" populations represented by the means. As expected, more variation is exhibited by the individuals than the means.

A dendrograph (Fig. 2) also demonstrates the morphological variation of the taxa. At the 0.4 correlation level there are again three major groups present. The group at the left is split into two subgroups at the 0.5 level. The two groups are taxa 3 and 4 (*E. villosus* and *E. riparius* by traditional methods).

The next major group is composed mostly of taxon 2. The extreme left and least correlated of this group is a pair of OTUs labeled taxa 6 and 3. (*E. diversiglumis* and *E. villosus*). Only one specimen of taxon 6 was available for clustering. One specimen does not provide enough information to give confidence in placement.

The major group at the right of the dendrograph is again split into two subgroups at the .45 level. The group at the extreme left is composed of OTUs of taxon 5 (*E. wiegandii*), while the remainder and majority of the major group is taxon 1 (*E. canadensis*).

Four "misplaced" OTUs, identified by traditional means, belong to taxa 1, 3, 4, and 1 respectively, but were placed (using all variables) in taxa 3, 6, 3, and 5 respectively. A reexamination of these "misplaced" individuals indicates that they are probably of hybrid origin, sharing characters of more than one taxon, and do not fit well (have a low correlation) with other individuals in the dendrograph.

The numerical techniques serve to confirm the placement of specimens into taxa by more traditional methods. They also indicated the morphological similarities of *E. villosus* and *E. riparius*, and of *E. wiegandii* and *E. canadensis*. Additionally they gave support to the idea that the most common species of *Elymus* in Iowa are extremely and nearly continuously variable.

Taxonomic Treatment

Elymus L.

Caespitose perennials; inflorescence a terminal balanced spike; spikelets 2 per node (1-6); rachilla twisted at base aligning florets dorsiventrally with rachis; florets 2-6; glumes narrow, dorsally extrorse; lemmas usually awned.

Key to Species

1. Lowest floret and glumes falling from rachis as unit, glumes 1.0 mm or more in width and extremely indurate ..... *E. virginicus*
1. Lowest floret disarticulating from glumes, glumes generally 0.9 mm or less, glumes not indurate 2
   2. Awns straight at maturity (note; immature specimens of all taxa have straight awns) 3
   2. Awns curved at maturity 4
3. Spike and adaxial leaf surface villous, culm 50-80 cm ..... *E. villosus*
3. Spike and leaf scabrous to sparsely pubescent, culm 85-120 cm in length ..... *E. riparius*
   4. Glumes greatly reduced (0.1-1.5 cm long) and/or of distinctly different lengths ..... *E. diversiglumis*
   4. Glumes not reduced (1.2-4.0 cm long) and of approximately same length 5
5. Leaves 9-15 or more per culm, blades broad 1.2-2.0 cm, nerves 60-100 per blade, spike pendant ..... *E. wiegandii*
5. Leaves 3-9 per culm, blade width 1.0 cm or less, nerves 20-40 per blade, spike arching ..... *E. canadensis*

Elymus canadensis L.

E. canadensis L., Species Plantarum 83.1753.
Lectotype: LINN 100.3 (microfiche!)

Plants generally robust, 40-156 cm tall (mean 83.6 cm, s.d. ± 19.7 cm); leaf blades 4-23 mm wide (mean 9.4 mm, s.d. ± 2.3 mm), nearly glabrous to quite pubescent, often scabrous; spikes arching, 7-26 cm long (mean 12.0 cm, s.d. ± 3.9 cm); glumes generally striate, slightly indurate, more or less scabrous, 13-40 mm long (mean 25.8 mm, s.d. ± 4.7 mm), 0.5-1.5 mm wide (mean 0.9 mm, s.d. ± 0.2 mm); lemmas 9.2-15.7 mm long (mean 10.4 mm, s.d. ± 1.4 mm); awns 13.7-49.0 mm long (mean 31.4 mm, s.d. ± 6.6 mm) strongly curved at maturity. Disarticulation above the glumes. Some Iowa specimens have up to five spikelets per node.

E. canadensis (Canada wild rye) is common throughout the northern and central United States and southern Alaska and Canada. It is found commonly in road ditches, prairies, and other areas of open ground. In Iowa, *E. canadensis* occurs throughout the state (Fig. 3a).

The awn curvature of mature florets is dependent upon the relative humidity. An increase in humidity causes the awn to straighten, while drying causes curvature. Awns are antrorsely scabrous. This characteristic seems to contribute to the dispersal of mature florets. Immature (straight awned) florets will not be pulled from their position in the spikelet by a foreign object brushing against them. As the floret matures, the awns curl, orienting the points of the prickles in such a manner that a slight abrasion will cause their removal. Mature florets have been observed in clothing and the fur of dogs. Some spikelets observed do not disarticulate in the fall, but remain in position through the winter. Occasionally, I have observed florets sliding with the wind over the crusted snow. Nearly all spikelets examined in the field had disarticulated by mid to late spring. Glumes may fall from the rachis at this time.

E. canadensis has been called the most valuable species in the genus for forage use (Richards and Hawk, 1945). It is said to provide good quality hay if harvested at a young stage.

This vast and variable group of plants has been renamed and subdivided many times since the time of Linnaeus. Part of the confusion was due to Linnaeus himself who described *E. canadensis*

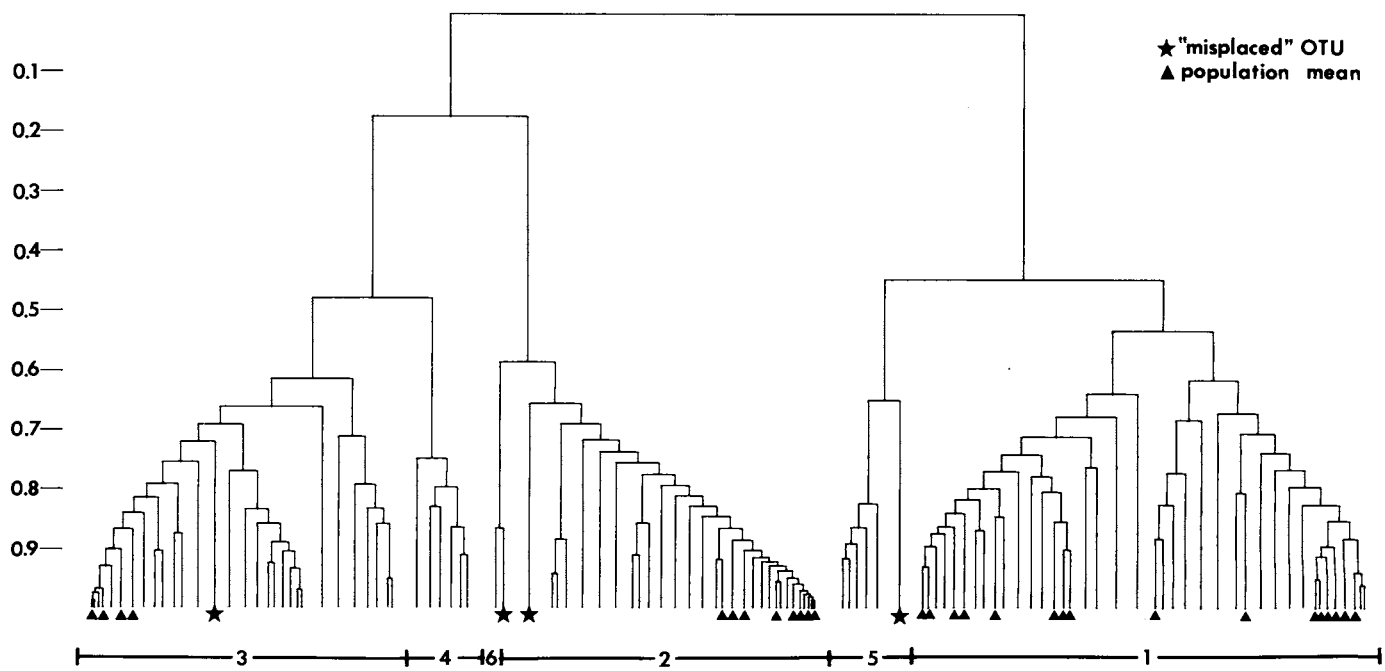

Fig. 2 A dendrograph of population means (from Fig. 1) and data from herbarium specimens. Group 1 corresponds to *Elymus canadensis*, group 2 to *E. virginicus*, group 3 to *E. villosus*, group 4 to *E. riparius*, group 5 to *E. wiegandii*, and group 6 to *E. diversiglumis*. "Misplaced" OTUs are explained in the text.

(1753) as having four florets. Examination of the microfiche of type material revealed that it was a young plant having straight awns at the time of its collection. Linnaeus (1759) described another species which was said to be identical to *E. canadensis* with the exception of having six florets per spikelet. Linnaeus named this *E. philadelphicus*. Since that time, numerous synonyms and many subspecific taxa have

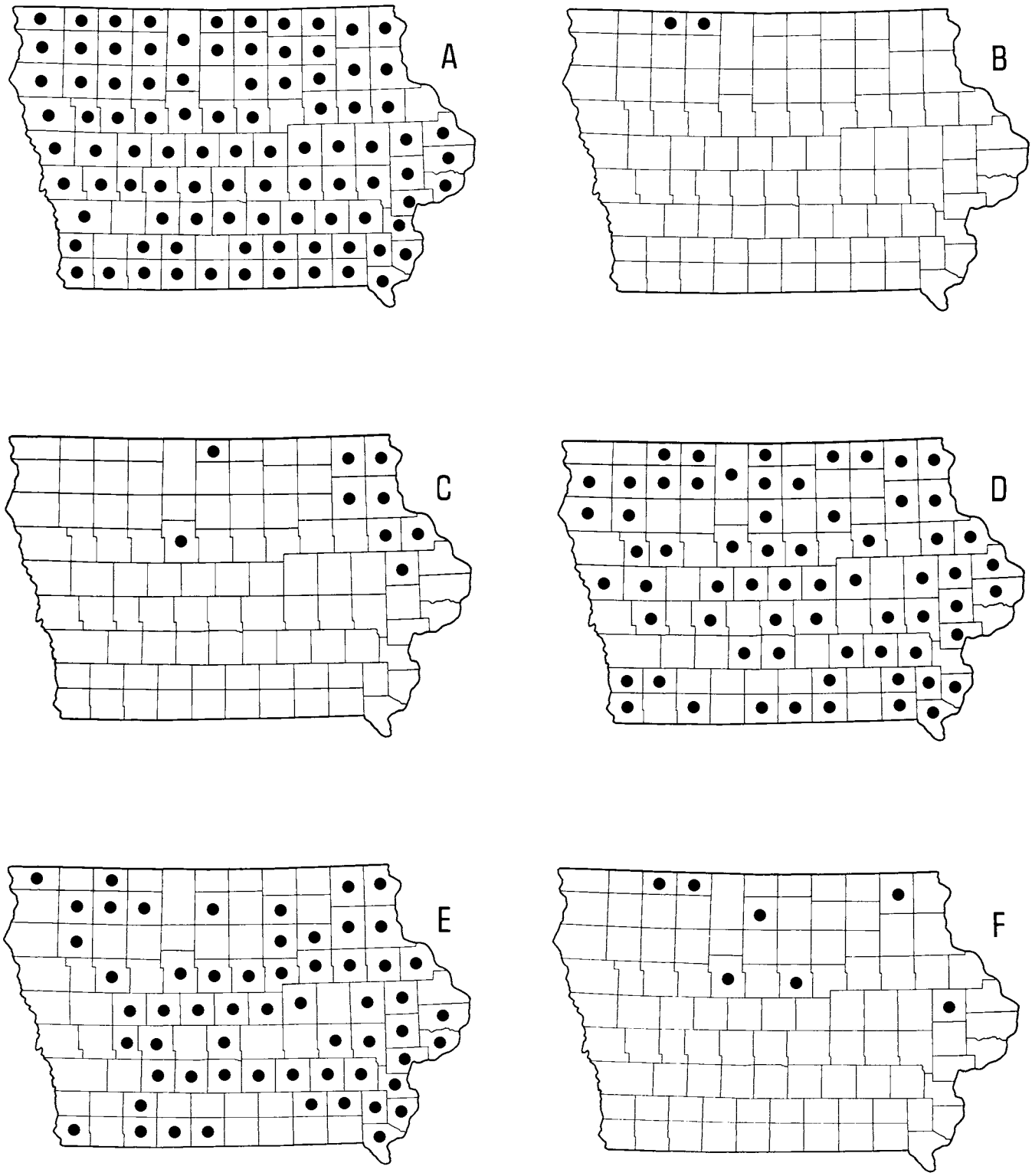

Fig. 3. Iowa distribution of A) *Elymus canadensis*, B) *E. diversiglumis*, C) *E. riparius*, D) *E. villosus*, E) *E. virginicus*, and F) *E. wiegandii*.

been proposed.

I can only conclude that there are many intermediates and intergradations exhibited by individuals of this species. It seems fruitless to attempt to designate subspecific taxa for an almost infinite amount of variation. I recommend that none be designated for *E. canadensis* in Iowa.

Elymus diversiglumis Scribn. and Ball

E. diversiglumis Scribn. and Ball, U.S.D.A. Div. Agrost. Bull. 24:48-49. 1901.

Type: Williams 2653, Bear Lodge Mtns., Wyo. U.S.!

Plants usually erect, with a slender drooping spike. The glumes may vary in length on the same spikelet, or be extremely reduced, especially the sterile glumes. The lemmas are commonly hirsute with divergent awns.

This species is found in clearings, margins of woods, and riverbanks of parts of north central United States and adjacent Canada. It has been collected only twice in Iowa. See Fig. 3b. No measurements will be cited for Iowa specimens of this species for that reason.

E. diversiglumis of Scribner and Ball is not synonymous with *E. interruptus* of Buckley (1862) from Texas (PH!) Some authors (e.g. Hitchcock, 1951) have mistakenly used the name *E. interruptus* when dealing with species from the north central United States. *E. diversiglumis* seems to have a close affinity to *E. canadensis*.

Elymus riparius Wiegand

E. riparius Wiegand, Rhodora 20:84. 1918.

Type: Eames and McDaniels 3567 Ithaca, New york. GH!

Plants rather slender 7-141 cm tall (mean 99.2 cm, s.d. ± 17.9 cm); leaf blades scabrous; spike nodding, 8-19.5 cm long (mean 13.5 cm, s.d. ± 3.5 cm); glumes moderately indurate and terete at the bases, rarely showing striations, 14.4-26.0 mm long (mean 19.5 mm, s.d. ± 3.4 mm) and 0.3-1.0 mm wide (mean 0.6 mm, s.d. ± 0.1 mm; lemmas 7.3-13.2 mm (mean 9.5 mm, s.d. ± 1.5 mm); paleas 5.5-8.6 mm long (mean 7.3 mm, s.d. ± 0.6 mm); spikelets disarticulating above the glumes; awn straight when mature (Fig. 28), 13.1-34.6 mm in length (mean 24.2 mm, s.d. ± 5.2 mm).

E. riparius is common throughout northeastern United States and southeastern Canada, extending west to Minnesota and Nebraska, and south to Arkansas, Tennessee, and North Carolina. In Iowa it occurs chiefly in the northeast and has recently been found in Woodman Hollow (Fig. 3c). The species is commonly found in wooded areas, or the edges of woods.

E. riparius is often confused with *E. canadensis* or *E. villosus*. It can be distinguished from the former by its shorter lemmas and straight awns (at maturity) and lack of striations at the bases of glumes. It is different from the latter in its nearly glabrous leaf blades and sheaths, its slightly longer paleas, and generally taller stature.

Elymus villosus Muhl.

E. villosus Muhl. in Willd., Enum Pl. 1:131. 1809.

Type: Muhlenberg, Pennsylvania. B Willdenow 2297 (microfiche!)

Culms 36.5-103-5 cm tall (mean 67.9 cm, s.d. ± 13.7 cm); sheaths glabrous to pilose; blades pubescent (villous) on upper surface, glabrous to scabrous beneath; spikes 2-21 cm long (mean 6.3 cm, s.d. ± 1.9 cm), arching; glumes striate, somewhat indurate 10.3-32.4 mm long (mean 17.7 mm, s.d. ± 3.5 mm) 0.3-0.7 wide (mean 0.5 mm, s.d. ± 0.1 mm); lemmas hirsute, 5.6-8.8 mm long (mean 6.6 mm, s.d. ± 0.7 mm); paleas 4.8-7.1 mm in length (mean 6.0 mm, s.d. ± 0.5 mm); awns straight at maturity, 8.8-31.0 mm long (mean 19.4, s.d. ± 5.0).

This species is found from Vermont to Wyoming, south to Texas and South Carolina, and rarely in Ontario and Quebec. In Iowa it is found throughout the state, most commonly in and around wooded areas. (Fig. 3d).

E. villosus is perhaps the least variable of the species present in Iowa. It is usually differentiated easily from the other species by the presence of the trichomes covering the adaxial surfaces of the leaves, sheaths, and inflorescence.

There are some plants which do not have trichomes, or have few. Scribner and Ball (1901) noticed this and designated a new species (*E. arkansanus*) which they said "is distinguished by having the empty and flowering glumes minutely scabrous instead of hirsute." Fernald (1933) reduced the species to a form of *E. villosus*.

Counts of the trichomes on one square millimeter of the backs of lemmas (at the widest point) in all specimens believed to be *E. villosus* indicated that the mean number of trichomes was 30.9 (s.d. = 13.3) and the actual number ranged from 0-74 per square millimeter. In population number 1386 (8 individuals), there were individuals that had no trichomes as well as some with up to 26/mm^2. There seems to be little value in designating sub-specific taxa for this species on the basis of a characteristic that varies within one population.

Pammel et al. (1903) delimited a variety from Iowa called *E. striatus* var. *ballii* which seems to have wider glumes than other *E. villosus*. It was suggested by Pohl (1966b) that this is merely an introgressant with *E. virginicus*. I concur with this evaluation.

Elymus virginicus L.

E. virginicus L., Sp. Pl. 84. 1753.

Lectotype: LINN 100.5 (microfiche!)

Culms 36-129 cm long (mean 71.8 cm, s.d. ± 20.5 cm); leaves generally scabrous; spike almost always erect, 2-16 cm long (mean 7.7 cm, s.d. ± 3.0 cm); glumes indurate, 0.7-1.9 mm wide (mean 1.3 mm, s.d. ± 0.3 mm), 8.9-22.4 mm long (mean 16.9 mm, s.d. ± 2.8 mm); lemmas 6.1-10.1 mm long (mean 8.0 mm, s.d. ± 0.8 mm); paleas 6.1-9.4 mm long (mean 7.5 mm, s.d. ± 0.7 mm); awns 1.0-19.7 mm long (mean 11.2 mm, s.d. ± 3.3 mm), remaining straight at maturity. Florets disarticulating from each other, but the lowest remaining attached to the glumes which fall from the rachis.

Elymus virginicus (Virginia wild rye) is found throughout the United States (with the exception of the far Southwest) and southern Canada. It occurs throughout Iowa (Fig. 3e). It is commonly found in open woods, stream banks, and clearings as well as road ditches and prairies.

Variation in this species is great. So-called "typical" specimens are easily distinguished from other species by erect spikes, wide glumes, disarticulation below the glumes, and straight awns. Pohl (1966b) enumerates the following characteristics in which variation has been observed: glume width and induration, pubescence of spikelet and rachis, bowing of glumes, exsertion of spikes, color, length of awns. To these, I would add lengths of culm and spike, and especially the lemma length: awn length ratio.

From the above, one may note that the major diagnostic characteristics of the species are variable. This has caused many misidentifications and has muddled the literature with countless synonyms (Fernald, 1933). In Iowa, the plants are less diverse but nonetheless display great variability. In field or herbarium work a student of the species is likely to encounter many intermediates which do not fit existing keys.

The late disarticulation below the glumes of the spikelets is unique to this *Elymus* species in Iowa. This characteristic has been largely ignored by recent authors (Hitchcock, 1951; Pohl, 1959; Bowden, 1964).

Elymus wiegandii Fernald

Elymus wiegandii Fernald, Rhodora 35:192. 1933.

Type: Fernald 197. St. John River, St. Francis, Maine, GH!

Generally robust, 98-148 cm tall (mean 127 cm, s.d. ± 23.6 cm); leaves 9-15 (−27) per culm, broad 0.8-2.2 cm wide (mean 127 cm, s.d. ± 0.4 cm); nerves 60-100; spikes 11.5-19.5 cm long (mean 15.1

cm, s.d. ± 3.5 cm); glumes 11.9-20.1 mm long (mean 15.2 mm, s.d. ± 3.5 mm), 0.5-0.6 mm wide (mean 0.5 mm, s.d. ± 0.05 mm) showing some induration and striation at base; lemmas 11.2-16.3 mm (mean 13.1 mm, s.d. ± 2.0 mm); paleas 9.6-12.9 mm long (mean 10.9 mm, s.d. ± 1.2 mm); awns curved, 15.5-26.1 mm long (mean 20.7 mm, s.d. ± 4.0 mm). The spikes of live plants exhibit a very distinct droop rather than just a gentle arching. This feature is often lost in processing herbarium specimens.

E. wiegandii is found throughout southeastern Canada to Saskatchewan, and northeastern United States westward to Wyoming (Fig. 3f).

E. wiegandii is often confused with *E. canadensis* where the ranges overlap. The differences are the pendant spike, numerous wide leaves, and striated glume base. *E. wiegandii* is generally found in rich alluvial soils in shaded areas.

Hitchcock (1951) and Bowden (1964) have stated that *E. wiegandii* is merely a variety of *E. canadensis*. The cytological work by Vilkomerson (1950) demonstrating the unique meiotic behavior of *E. wiegandii* and crossing studies by Church (1967) showing a low affinity between *E. canadensis* and *E. wiegandii* have verified the distinctness of the two species. Morphologically, the spikelets are very similar and indicate a close relationship between the species.

Exclusions

Exluded from the genus in this presentation are *Elymus macounii* and *Hystrix patula*. The former is actually *XAgrohordeum macounii* (Vasey) Lepage, shown by Boyle and Holmgren (1955) to be series of hybrids between *Agropyron trachycaulum* (Link) Malte and *Hordeum jubatum* L.

Hystrix patula (L.) Moench has been included in the genus by several authors (Linnaeus, 1753; Bowden, 1964). Church 1954, 1967) has shown it is possible to cross *H. patula* to some species of *Elymus*, but with difficulty. Critical judgment of generic limits cannot be undertaken in work with very limited geographical boundaries. The relationship of these widely distributed genera has been used as is commonly accepted at the present.

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