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GEOGRAPHY AND MORPHOLOGY OF THE *BROMUS CARINATUS* (POACEAE: BROMEAE) COMPLEX

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ABSTRACT

The *Bromus carinatus* complex comprises several cleistogamous taxa that have been recognized at a variety of taxonomic levels. Our study focused on three taxa: *B. carinatus s.s.*, *B. marginatus*, and *B. polyanthus*, that have received varied taxonomic treatment. We mapped the collection sites of 673 specimens belonging to these taxa to determine whether their geographic distribution would support their recognition as species. We examined the characters customarily used to distinguish among the three entities: longevity, blade width, awn length, sheath vestiture, and lemma vestiture. The geographic data do not support the value of blade width as a taxonomic character but provide some support for use of awn length and the two vestiture characters. Of the three taxa, *B. polyanthus*, characterized as having glabrous sheaths and lemmas and, usually, short awns, was the most geographically distinct taxon. *Bromus carinatus sensu stricto* and *B. marginatus* showed some separation, the former being primarily a coastal taxon and the latter primarily an inland taxon. Based on our observations and published molecular data, we propose that *B. carinatus* and *B. marginatus* be treated as *B. carinatus* var. *carinatus* and **B. carinatus** var. **marginatus** (Nees *ex* Steud.) Barkworth & Anderton, *comb. nov.* respectively, and that *B. polyanthus* be treated as a species.

Key Words: *Bromus*, geography, distribution, morphology, taxonomy, nomenclature, *Poaceae*.

Bromus L. includes approximately 150 species, distributed among 6 sections (Clayton and Renvoize 1986) that are sometimes recognized as genera (e.g., Tsvelev 1976). Section *Ceratochloa* (P. Beauv.) Griseb. is native to the western hemisphere. Its members differ from those of other sections in having strongly keeled lemmas and 3–5-veined lower glumes.

The number of species recognized in sect. *Ceratochloa* varies considerably (Table 1). Hitchcock (1935) recognized five species in his treatment of grasses for the contiguous United States: *B. catharticus* Vahl, *B. sitchensis* Trin., *B. aleutensis* Trin. *ex* Griseb., *B. breviaristatus* Buckley, and *B. carinatus* (Hook. & Arn.). He acknowledged, however, the existence of many forms (using the word in its general, not nomenclatural, sense) of *B. carinatus* that ". . . are connected by numerous intergrades [and] can be distinguished only arbitrarily" (p. 38). He listed *B. marginatus* Nees *ex* Steud., *B. maritimus* (Piper) Hitchc., and *B. polyanthus* Scribn. *ex* Shear as names that applied to such forms.

Some subsequent taxonomists have recognized more species than Hitchcock (e.g., Kearney and Peebles 1942; Chase (*in* Hitchcock 1951); Davis 1952; Harrington 1954; Munz and Keck 1959); others have recognized fewer (e.g., Hitchcock 1969; Scoggan 1978; Wilkens and Painter 1993). There have been similar disagreements concerning the treatment of Mexican and Central and South American members of sect. *Ceratochloa* (e.g., Soderstrom and Beaman 1968; Planchuelo and Peterson 2000; Massa et al. 2004).

Those adopting a broad interpretation of *B. carinatus* have generally cited papers by Stebbins and Tobgy (1944) and Harlan (1945) in support of their treatment. Stebbins and Tobgy (1944) suggested that *B. carinatus* is probably an intersectional polyploid, combining three sets of chromosomes from sect. *Ceratochloa* and one from sect. *Bromopsis* Dumort. [=sect. *Pnigma* Dumort]. They also suggested that the low elevation, coastal members of the complex (*B. carinatus s.s.*, *B. sitchensis* Trin., and *B. aleutensis* Trin. *ex* Griseb.) might involve a different *Pnigma* parent from the inland species (*B. marginatus*, *B. polyanthus*, and *B. breviaristatus* Buckley), pointing out that diploid members of

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TABLE 1. COMPARISON OF THE TREATMENT OF *BROMUS* SECT. *CERATOCHLOA* IN DIFFERENT WORKS. Cells with the same shading density were recognized as a single species. Y—name used at species level. Unshaded empty cells: taxon not mentioned, usually because it is absent from the region treated, occasionally because only limited synonymy was provided. Sources: ASH 1—Hitchcock (1935); ASH 2—Hitchcock (1951); CLH—C.L. Hitchcock (1969); HDH—Harrington (1954); HJS—Scoggan (1978); K&P—Kearney and Peebles (1942); LP—Pavlick (1995); M&K—Munz and Keck (1959); RJD—Davis (1952); W&P—Wilken and Painter (1993); W&W—Weber and Wittmann (1992). [1] *Bromus luzonensis* used to be called *B. subvelutinus* Shear; *B. luzonensis* is the earlier name (Veldkamp 1990). [2] *Bromus willdenowii* used to be called, incorrectly, *B. unioloides* Kunth.

	ASH1	K&P	ASH2	RJD	HDH	M&K	CLH	HJS	W&W	W&P	LP
	1935	1942	1951	1952	1954	1959	1969	1978	1992	1993	1995
	48	AZ NM	48	ID	CO	CA	Pac. NW	Can.	CO	CA	FNA
B. carinatus	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y
B. marginatus		Y	Y	Y	Y	Y					Y
B. polyanthus		Y	Y	Y	Y	Y					Y
B. arizonicus			Y			Y				Y	Y
B. maritimus			Y			Y					Y
B. breviaristatus	Y		Y	Y		Y					
B. luzonensis[1]											Y
B. catharticus	Y	Y	Y		Y	Y		Y		Y	Y
B. haenkeanus						Y					
B. willdenowii[2]									Y		
B. sitchensis	Y		Y				Y	Y		Y	Y
B. aleutensis	Y		Y								Y
B. stamineus						Y				Y	Y

sect. *Pnigma* (e.g., *B. grandis* [Shear] Hitchc., *B. orcuttianus* Vasey, and *B. vulgaris* [Hook.] Shear) have narrow lemmas and long awns and are primarily coastal, whereas the diploid species with broad lemmas and short awns (e.g., *B. anomalus* Rupr. *ex* E. Fourn., *B. ciliatus* L., *B. frondosus* [Shear] Wooten & Standley, *B. kalmii* A.Gray, and *B. suksdorfii* Vasey) are inland or high elevation species.

Dremann (Email to Barkworth; November, 2004) stated that, in the San Francisco Bay region, there were at least five morphologically distinct ecotypes based on his common garden studies: dwarf, small-seeded individuals from windswept coastal populations; matlike sand dune populations; dwarf, hairy, fast-maturing serpentine populations; tall populations from high rainfall areas; and dwarf, hairy, large-seeded populations growing in full sun within areas of low rainfall. He added that there were gradations between these extremes with the region.

This study arose from problems encountered in editing Pavlick's (1995) revision of *Bromus* in North America north of Mexico, which he had also submitted as his treatment of *Bromus* for the *Flora of North America* (FNA) series. Unfortunately, Pavlick's health problems precluded his participation in the editing process. One major editorial problem for the FNA series was the need for more precise and better documented distribution data, the other was for increased parallelism in the descriptions.

Pavlick included "shaded area" maps in his revision, but the FNA grass volumes use maps generated from a database system that requires county level data for sites in the contiguous United States and locality data for sites in Canada, Alaska, and Greenland. For species whose taxo-

TABLE 2. CHARACTERISTICS USED TO DISTINGUISH AMONG *BROMUS CARINATUS S.S.*, *B. MARGINATUS*, AND *B. POLYANTHUS*. Those used by Pavlick (1995) are **boldfaced**. Sources: CLH—C.L. Hitchcock (1969); H&H—Holmgren and Holmgren (1977); HDH—Harrington (1954); K&P—Kearney and Peebles (1942); M&K—Munz and Keck (1959); RJD—Davis (1952); W&P—Wilken and Painter (1993).

<table>
<tr><th></th><th>Bromus carinatus</th><th>Bromus marginatus</th><th>Bromus polyanthus</th></tr>
<tr><td rowspan="2">Longevity</td><td>Annual or biennial
(RJD,HDH,M&K)</td><td>Perennial (M&K)
Mostly perennial (HDH)</td><td>Perennial
(RJD,HDH,M&K)</td></tr>
<tr><td colspan="3">Perennial, often flowering first season (CLH, W&P, H&H)</td></tr>
<tr><td rowspan="2">Sheath vestiture</td><td>Pilose to mostly glabrous, throat always with hairs
Pilose to nearly glabrous (HDH)
Smooth or scabrous to sparsely pilose (M&K)</td><td>Pilose to glabrous, throat always with hairs
Pubescent (K&P)
Pilose (M&K)</td><td>Mostly glabrous, sometimes hairy
Glabrous (K&P,M&K)
Usually glabrous (HDH)</td></tr>
<tr><td colspan="3">Usually pilose, sometimes glabrous (CLH, H&H)
Glabrous to soft-hairy (W&P)</td></tr>
<tr><td rowspan="2">Blade width (mm)</td><td>3–6
3–10 (M&K)</td><td>6–12
4–12 (HDH)
4–8(12) (M&K)</td><td>No information
5–15 (M&K)</td></tr>
<tr><td colspan="3">(2)3–12(15) (CLH)
(2)3.5–9(12) (H&H)
3–15(W&P)</td></tr>
<tr><td rowspan="2">Glume vestiture</td><td></td><td>Scabrous or pubescent
Pubescent (HDH)
Scabrous or scabrous-pubescent (M&K)</td><td>Smooth or scabrous
Glabrous or scabrous (HDH)</td></tr>
<tr><td colspan="3">Glabrous to soft-hairy (WP)</td></tr>
<tr><td rowspan="2">Lemma vestiture</td><td>Usually pubescent, sometimes scabrous
Appressed pubescent, rarely glabrous (HDH)</td><td>Pubescent or glabrous
Pubescent (K&P, RJD, HDH)</td><td>Glabrous or scabrous (K&P, RJD)
Pubescent to puberulent (HDH)</td></tr>
<tr><td colspan="3">Glabrous, scabrous, or pubescent (CLH)
Glabrous to scabrous to hirsute (H&H)
Glabrous to densely short-hairy (W&P)</td></tr>
<tr><td rowspan="2">Awn length (mm)</td><td>6–8(15)

7–15
(RJD,M&K,HDH)</td><td>4–7 (M&K)
< 7 (RJD)
4–6 (HDH)</td><td>4–8

4–6
(RJD,HDH,M&K)</td></tr>
<tr><td colspan="3">3–15 (CLH)
(3)4–6(8) (H&H)</td></tr>
</table>

nomic treatment has not changed, data are obtained from many sources (e.g., herbarium databases, floras, checklists, etc.); if taxonomic boundaries have been changed, as was the case for some of Pavlick's taxa, this approach cannot be used.

Pavlick (1995, p. 6) explained that his philosophical approach was ". . . mainly morphological-geographical, modified by available biosystematic evidence . . . . In all cases, the question was asked whether a species concept for a particular taxon would be useful to those that might use this treatment for ecological, resource management or other purposes." He noted that ". . . a number of sometimes neglected taxa are resurrected, and some taxa at infraspecific rank or no rank at all (...) are again treated as species." (*ibid.* p. 7).

Pavlick's treatment of members of the historically challenging *B. carinatus* complex was particularly controversial; some individuals expressed their dismay to Barkworth at his decision to resurrect species that recent works had included in *B. carinatus s.l.*; others praised his insight. In explaining his decision to adopt a narrow interpretation of *B. carinatus*, Pavlick stated that "Despite some intermediate forms, most populations of [sect.] *Ceratochloa* are often easily recognized to species on the basis of their morphology and often occupy different ecological niches and/or geographic zones. There are a number of morphological characters which separate each of the taxa" (*ibid.* p. 95).

His descriptions failed to substantiate the last statement; identification of *B. carinatus*, *B. marginatus*, and *B. polyanthus* was essentially dependent on one or two characters. Moreover, initial examination of specimens suggested that variation in the most frequently used characters was continuous. Consequently, we decided to examine specimens from throughout the range of the three taxa in order to substantiate any decisions we made concerning their treatment in volume 24 of the *Flora of North America* (in prep.). Time constraints precluded extending the study to other taxa in sect. *Ceratochloa.*

In Pavlick's (1995) treatment, the only character distinguishing *B. carinatus* from *B. marginatus* and *B. polyanthus* was longevity (annual or biennial versus perennial) (Table 2). *Bromus carinatus* and *B. marginatus* are described as differing in blade width (3–6 mm versus 6–12 mm); no information on blade width is given for *B. polyanthus*. Other taxonomists have used lemma awn length and lemma and sheath throat pubescence, sometimes in combination with longevity to distinguish among the three taxa (Table 2).

We decided to examine the relationship between the morphological characteristics and geographic distribution of plants belonging to *B. carinatus s.s.*, *B. marginatus*, and *B. polyanthus* more closely, focusing on characters traditionally used for their identification, to determine whether the taxa recognized by Pavlick were morphologically and geographically distinct.

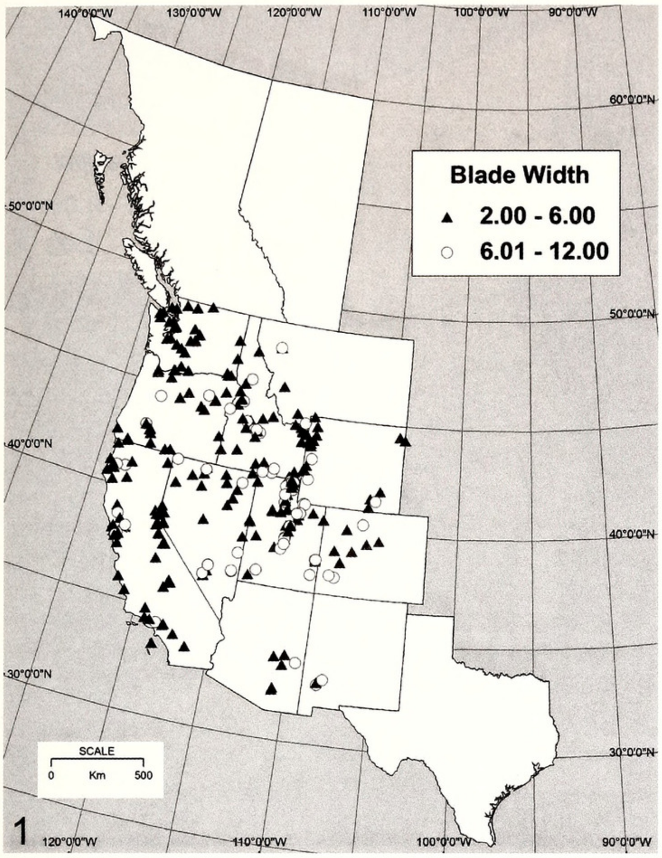
Soreng et al. (2003) recognized two varieties within *B. polyanthus*, var. *paniculatus* Shear and var. *polyanthus*. Pavlick (1995) equivocated with respect to their status, stating that they "are sometimes separated," var. *polyanthus* having erect, contracted panicles, short, erect or ascending branches, and awns 4–6 mm long, and var. *paniculatus* having nodding, open panicles, spreading branches, and awns up to 8 mm long. We measured the lowest panicle branch lengths on a sample of *B. polyanthus* specimens to see whether longer branches were associated with more open panicles and longer awns.

METHODS

We examined 702 herbarium specimens from five herbaria: ARIZ (170 specimens), WTU (88 specimens), NMCR (57 specimens), UTC (269 specimens), and V (118 specimens) (Herbarium codes from Holmgren et al. 1977.) Of the 702 specimens, 29 could not be georeferenced because the label data were inadequate; 30 were not mapped because they were cultivated plants. Because our primary goal was evaluation of Pavlick's treatment, we focused on four of the characters he and earlier taxonomists used for taxonomic delimitation of *Bromus carinatus*, *B. marginatus*, and *B. polyanthus* (Table 2). We were alert to the possibility that there might be other characters that could be used for taxonomic delimitation within the complex, but were unable to identify any.

Longevity was not scored because it is often difficult to determine on herbarium specimens. Blade width was measured on what appeared to be the widest blade of a specimen; it was obtained only for specimens from WTU and UTC for reasons discussed in the following section. Awn lengths were obtained by averaging the length of the longest three awns on a specimen. Sheath throat and lemma pubescence were scored as follows: G for glabrous or scabrous, P– if only a few hairs were visible or if only some sheath throats or lemmas had hairs, P for visible pubescence on most lemmas or sheath throats, and P+ for exceptionally thick pubescence on most lemmas or sheath throats. Panicle branch length was measured on the longest branch at the lowest node on 70 specimens that, according to our criteria, belonged to *B. polyanthus*.

Few specimen labels included georeferencing data. We obtained latitude/longitude data for those lacking them by a variety of methods, depending on the label information. Specimens



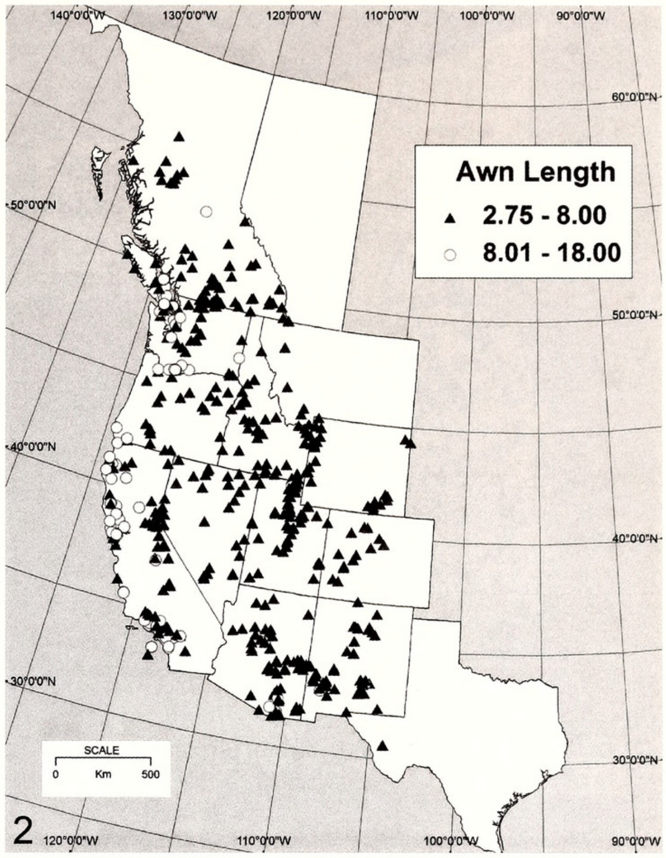


FIG. 1. Distribution of specimens with blade widths narrower or wider than 6 mm. Only the 357 specimens from WTU and UTC were included in this portion of the study.

FIG. 2. Distribution of specimens with awns shorter or longer than 8 mm. Locations of all 673 mapped specimens are shown.

with township, range, and section data were georeferenced using Wefald's (2003) TRS2LL program. For U.S. specimens lacking such data, we used the Geographic Names Information System, refining the estimate where feasible by using maps from TopoZone (Maps a la Carte, 2004). For Canadian specimens, we used Natural Resources Canada's Geographical Names of Canada website. Because we were unable to evaluate the accuracy of specimen label information, our georeference data are only estimates of the original collecting locality, but they are sufficiently accurate to portray the general geographic distribution of the specimens examined; they are not sufficiently accurate to determine ecological characteristics of the collecting site.

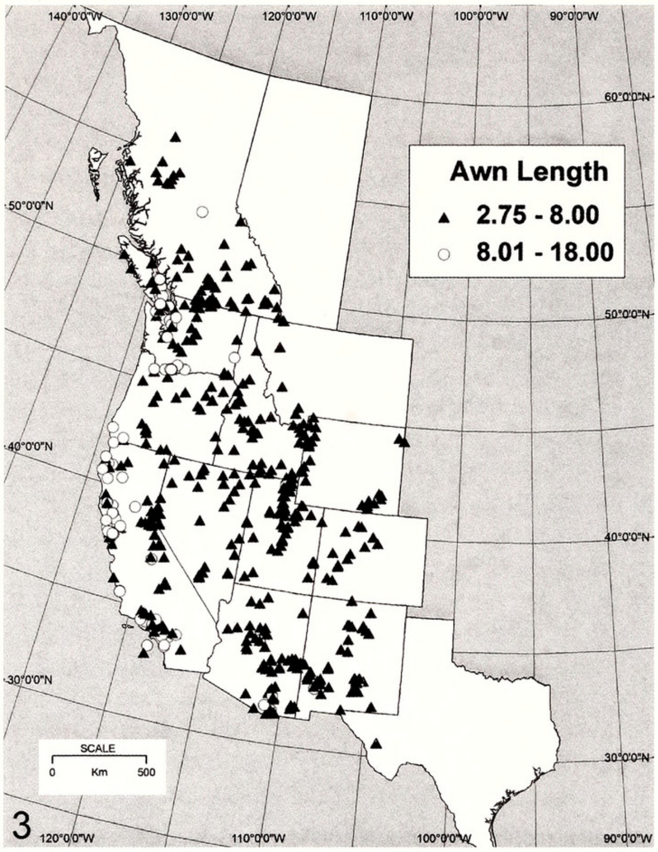
The georeferenced data were combined with the morphological data to relate the morphological variation to geographic distribution. For this analysis, we divided the two continuous characters, awn length and blade width, into two classes each, using breaks indicated by previous treatments (<7 mm and >7 mm, and 3–6 mm and 6–12 mm, respectively). In addition, we used Jenks optimization to calculate the best "natural break" in the data, based on the assumption that two classes were present. Jenks optimization partitions data into classes by minimizing the possible total error (the sum of absolute deviations based on the class median or the sum of squared deviations about the class mean) (Jenks 1967).

Maps were drawn using ArcMap 9.1 (ESRI 1999–2005) and Albers Equal Area Conic projection, datum NAD 83. The layouts were prepared using Creative Suite 2 (Adobe 2005).

RESULTS

The specimens examined came from a wide area (Figs. 1–4; Appendix I). Nevertheless, maps developed from a wider range of sources (Intermountain Herbarium 1999+) demonstrate that Yukon Territory, Alberta, Saskatchewan, Montana, North Dakota, Wyoming, Colorado, South Dakota, Kansas, northern Arizona, northern New Mexico, and Texas are not well represented in this study. The areas represented, however, include those in which the three taxa that were the focus of this study are most controversial (Table 1).

According to Pavlick, *Bromus carinatus s.s.* and *B. marginatus* differ in their blade widths; those of *B. carinatus* being up to 6 mm wide and those of *B. marginatus* being 6+ mm wide. He did not provide information about blade widths in *B. polyanthus.* Mapping of specimens from WTU



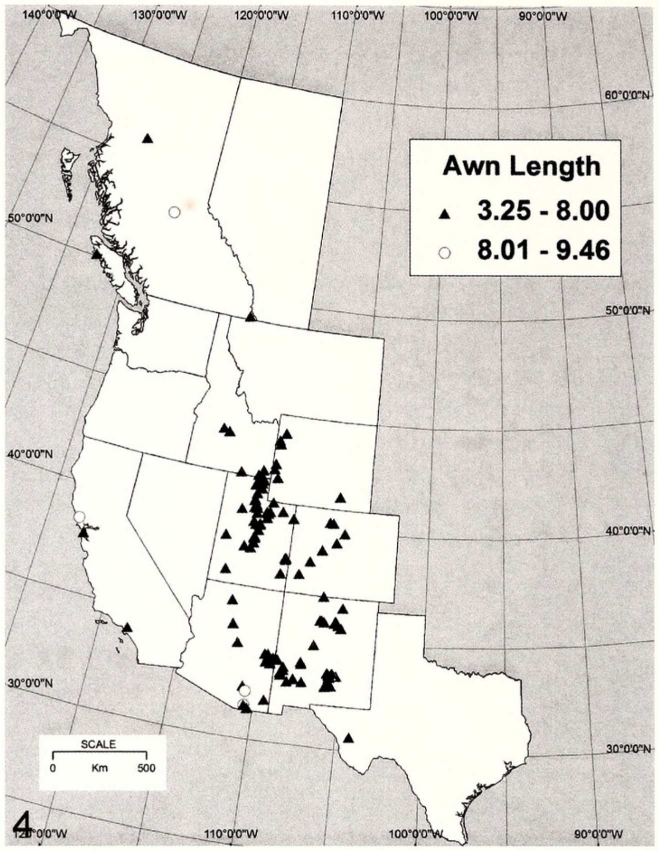


FIG. 3. Distribution of specimens with hairs on their throats and/or lemmas and awns longer or shorter than 8 mm (i.e., *Bromus carinatus* vars. *carinatus* and *marginatus*, respectively).
FIG. 4. Distribution of specimens with glabrous throats and lemmas (i.e., *Bromus polyanthus*) showing origin of specimens with awns shorter and longer than 8 mm.

and UTC revealed no geographic separation of plants with blade widths above and below 6 mm (Fig. 1). Jenk's optimization divided the specimens into two categories at 5 mm. These two categories also were not geographically segregated. We also mapped the specimens with glabrous lemmas and sheaths, (i.e., *B. polyanthus*). These too exhibited no geographic separation between wide- and narrow-leaved specimens (not shown). Thus, we concluded that blade width is not a useful taxonomic character within the taxa under consideration and excluded it from further examination.

Awn length has been used to distinguish *B. carinatus* from both *B. marginatus* and *B. polyanthus* (Table 2). Mapping revealed that almost all specimens with awns 8–18 mm long came from near the coast whereas most specimens with short awns came from inland locations (Fig. 2). Jenks optimization divided the specimens at 7.45 mm; the map using this value as the break point (not shown) was little different from that obtained using 8 mm.

The geographic separation of the short- and long-awned specimens was not absolute. Some short-awned specimens came from near the coast and some long-awned specimens from inland areas in central British Columbia, along the Snake River near the Washington-Idaho border, and southern Arizona and New Mexico. It is, of course, possible that the specimens concerned were collected because they differed from others in the region or that they were collected in unusual habitats within the region. We concluded that the geographic separation, although incomplete, tended to support the taxonomic value of awn length for the portion of the *B. carinatus* complex included in our study.

TABLE 3. NUMBER OF SPECIMENS BY THEIR COMBINATION OF PUBESCENCE CHARACTERISTICS.

Lemma throat	Glabrous	Sparsely pubescent	Moderately pubescent	Densely pubescent	Total
Glabrous	155	9	26	1	**191**
Sparsely pubescent	18	6	40	2	**66**
Moderately pubescent	43	27	313	6	**389**
Densely pubescent	0	3	16	8	**27**
Total	**216**	**45**	**395**	**17**	**673**

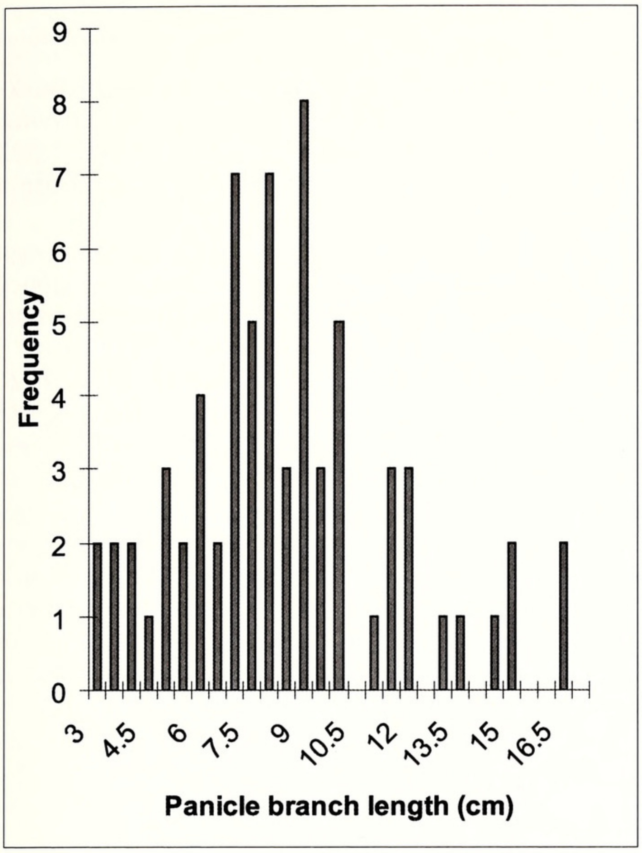


FIG. 5. Histogram of lowest panicle branch lengths in *Bromus polyanthus*.

Vestiture of the sheath and lemma have also been used to distinguish among *B. carinatus*, *B. marginatus*, and *B. polyanthus.* Existing descriptions suggest that there is variation in both characters, but particularly sheath vestiture, within each taxon. We found the association between throat and lemma vestiture was high (Table 3). Of the 673 specimens mapped, almost half (313) had moderately pubescent throats and lemmas; the second largest class of specimens had glabrous lemmas and throats (155). Glabrous lemmas were never found on plants with densely pubescent throats; one specimen with densely pubescent lemmas had glabrous throats. Specimens with hairs on the throats and/or lemmas came from throughout the range of specimens in this study (Fig. 3), whereas those with completely glabrous throats and lemmas, which would correspond to *B. polyanthus*, came primarily from the Rocky Mountains (Fig. 4). Eight of the completely glabrous specimens had awns longer than 8 mm; one was from British Columbia, two from coastal California, three from southern Arizona and two from New Mexico.

Panicle branch lengths for *B. polyanthus* were essentially unimodal (Fig. 5). Some of the specimens with branches longer than 11 cm had open panicles; it was impossible to determine whether the others might have had open panicles if collected slightly later in the season. The correlation between panicle branch length and awn length was 0.44.

DISCUSSION

Our study demonstrates that the taxa Pavlick (1995) identified as *Bromus carinatus*, *B. marginatus*, and *B. polyanthus* have somewhat different geographic distributions, which supports their recognition as distinct taxa at some level. The geographic separation between long-awned and short-awned specimens, as well as that between glabrous and pubescent specimens, supports the use of awn length and pubescence of sheath throats and lemmas as characters delimiting distinct taxa. There were not as many long-awned glabrous specimens (8) as would be expected (26.486) if awn length and pubescence were independent characters (chi-square statistic $= 20.2177$, < 0.0001).

None of the entities circumscribed by the characters examined in this study were completely geographically distinct. Moreover, the morphological separation of specimens based on pubescence of lemmas and sheath throats and average awn length glossed over the fact that several specimens had awns either just under or just over 8.0 mm; variation in pubescence density was also continuous.

The most morphologically distinct group included specimens with completely glabrous sheath throats and lemmas; most also had awns shorter than 8 mm. Specimens with this combination of characteristics came primarily from the Rocky Mountains (Fig. 4). They correspond to *B. polyanthus*.

Massa and Larson's (2005) phylogeographic study of *B. carinatus* confirmed that *B. polyanthus* is more distinct than either *B. carinatus* or *B. marginatus*. Using AFLP, they identified four genetically distinct groups among their samples, all of which they referred to *B. carinatus sensu lato*. Examination of the vouchers deposited at UTC revealed that all three accessions in their group 4 belong to *B. polyanthus*, both morphologically and geographically.

The other specimens in Massa and Larson's (2005) study had awns less than 8 mm long, which placed them within *B. marginatus*. They stated that two of them, CAR03 (PI 202202) and CAR04 (PI 202203), came from seed accessions derived from collections made in Marin County, in coastal California. Of these two, CAR03 was notable for having some awns longer than 8 mm. All the voucher specimens were made from plants grown in a uniform garden near Logan, Utah.

The PI numbers enabled us to obtain additional information for the accessions from the U.S.D.A.'s Germplasm Resource Information Network (U.S.D.A. 2005). Both accessions are derived from seed collections made in 1955. Only PI 232202 was collected in Marin County; PI 232203 is derived from multiple collections made throughout the western U.S. The accessions have been maintained by growing seed up and harvesting seed from the mature plants. Initially, the accessions were grown out in Ames, Iowa; since 1985 they have been grown out in Pullman, Washington. While at Ames and for the first five years at Pullman, seed accessions were grown up without being isolated from other accessions of the same species. It is not known how many times new seed has been collected. This history would have favored a slow shift in gene frequencies to genotypes that are adapted to the climatic conditions at interior locations rather than those of coastal California. Moreover, as Harlan (1945) demonstrated, the taxa are only predominantly cleistogamous; outcrossing may also have occurred between descendants of the original accessions and those of other accessions.

Their history reduces the taxonomic value of the accessions in GRIN. It is possible that the population from which PI 232202 was originally obtained corresponded to *B. carinatus s.s.* There were, however, many wild-collected specimens that, like PI 232202, had some awns more than 8 mm long even though the majority were shorter. Neither the study by Massa and Larson (2005) nor this study eliminated the possibility that the short-awned specimens growing near the coast are environmentally modified representatives of a long-awned taxon. We are also unable to reject Stebbins and Tobgy's (1944) hypothesis that the shorter awned plants have a different parentage from the longer awned plants.

Pavlick (1995) argued that groups should be recognized as species if doing so would "be useful to those that might use this treatment for ecological, resource management or other purposes". We agree that some nomenclatural difference is desirable for taxa that appear to have different ecological characteristics; we do not agree that they need to be recognized as species. Based on the morphological, geographic, and genetic data available, we propose that *B. marginatus* and *B. carinatus* be treated as conspecific taxa and *B. polyanthus* as a distinct species. For consistency with Pavlick's treatment of other species, we are proposing that *B. carinatus sensu stricto* and *B. marginatus* be recognized as varieties. The following key summarizes our findings.

1. Lemmas and sheaths completely glabrous, sometimes scabrous. . . . . *B. polyanthus*
1. Lemmas and/or sheaths with some hairs . . . . *B. carinatus*
   2. Most awns 8–17 mm long . . . . *B. carinatus* var. *carinatus*
   2. Most awns 4–7 mm long . . . . *B. carinatus* var. *marginatus*

Bromus carinatus var. **marginatus** (Nees) Barkworth & Anderton, *comb. nov.* Basionym: *Bromus marginatus* Nees *in* Steud., Syn. pl. Glum. 1:322 (1854). Type: Fragment US865445!; Columbia River, Douglas.

Scoggan (1978) attributed this combination to A.S. Hitchcock, but there is no evidence that Hitchcock actually made the combination.

Our data leave the status of the varieties of *B. polyanthus* unclear. Using the criteria that we did for identifying the species, there were a few specimens of *B. polyanthus* that conformed to var. *paniculatus* but they appeared to be extremes of a continuous range of variation. If, however, awn length were given greater weight in identification, Arizonan and New Mexican specimens that we placed in *B. carinatus* var. *carinatus* because they had some hairs on their lemmas or sheaths would be identified as *B. polyanthus* var. *paniculatus.* An additional possibility is that they, together with the long branched specimens we identified as *B. polyanthus*, represent a new, unrecognized taxon.

Clearly, a better understanding of the bases of variability within *B. carinatus* and its relatives is essential to their more satisfactory taxonomic treatment. Developing such an understanding requires an interdisciplinary study involving experimental, cytogenetic, and molecular investigations of wild populations.

Volume 24 of the *Flora of North America* series, which is scheduled for publication in the fall of 2006, will contain keys, descriptions, and illustrations for the three taxa that were the focus of this study as well as the other taxa of *Bromus* that have been found in North America north of Mexico. We hope its publication will stimulate a new round of collaborative, interdisciplinary studies of the genus.

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Appendix I Representative Specimens Examined

Because we did not intend this paper as a revisionary study, we recorded only the data required to relocate an individual specimen among those on loan. Additional specimen information for UTC and WTU specimens is available from the Global Biodiversity Information Facility (2005+). For specimens from NMCR, we include the first collector's initials and collection number because they have no accession number. Canadian specimens do not list county; we show the latitude and longitude of representative specimens. As noted in the text, most such data were obtained retrospectively.

Bromus carinatus var. ***carinatus*** **CANADA. BRITISH COLUMBIA**. V 102110 (48.55N 123.417W), V 113786 (48.833N 123.383W), V 129566 (48.933N 123.45W), V 132360 (49.192N 123.925W), V 132364 (50.9N 119.55W), V132661 (49.183N, 123.933W) V 139379 (48.85N 123.467W), V 151534 (48.417N 123.267W), V

17035 (53N 122.5W), V 177897 (48.658N 123.742W), V 177898 (48.417N 123.667W), V 178359 (49.5N 124.2W), V 178365 (49.5N 124.217W), V 179229 (48.517N 123.417), V 185898 (48.808N 123.63W), V 187492 (48.433N 123.633W), V 20334 (52.85N 132.183W), V 23625 (48.65N 123.4W), V 24304 (50.1N 127.5W), V 453 (48.45N 123.3W), V 467 (54.217N 128.367W), V 469 (48.26N 123.367W), V 66153 (48.5N 123.358), V 66179 (48.27N 123.283W), V 66294 (48.55N 123.458W), V 66352 (48.4N 123.367W), V 66353 (48.625N 123.442W), V 66369 (48.667N 123.400W), V 66386 (48.692N 123.475W), V 66402 (48.683N 123.467W), V 66426 (48.45N 123.467W), V 66555 (48.6N 123.467W), V 75438 (53.05N 119.233W), V 82164 (48.833N 123.517W), V 87217 (48.8N 123.2W), V 8889 (48.55N 123.567W), V 95298 (48.783N 123.15W), V 95586 (49.2N 123.933W), V 96687 (48.43N 123.35W), V 97297 (48.85N 123.283W), V 97389 (48.933N 123.45W), V 98252 (48.483N 123.533W), V 98269 (48.808N 123.908W), V 98535 (48.8N 123.267W). **UNITED STATES. ARIZONA**. Apache. UTC 80085; Cochise ARIZ 255026; Gila ARIZ 329059; Mohave UTC 104006; Pima UTC 238268; Santa Cruz ARIZ 91978; **CALIFORNIA.** Alameda ARIZ 09175; Alpine UTC 195685; Contra Costa UTC 57852; Del Norte WTU 205599; El Dorado ARIZ 30307; Humboldt UTC 99436; Lake UTC 85585; Los Angeles WTU 65528; Madera ARIZ 373904, UTC 116447, WTU 224452; Marin ARIZ 130024, UTC 107945, UTC 107958, UTC 59699, UTC 94689; Mariposa ARIZ 373897; Mendocino ARIZ 373886, ARIZ 373887, ARIZ 373893, ARIZ 373893, ARIZ 373894, ARIZ 373894; Mono UTC 111611; Monterey ARIZ 333966; Napa UTC 230836, UTC 99439; Riverside, ARIZ 317886, ARIZ 317886, UTC 174024, UTC 227709, UTC 236784; San Bernardino ARIZ 258400, ARIZ 373888, ARIZ 373888; San Diego ARIZ 308099, ARIZ 308099, UTC 210342; San Francisco UTC 116608, UTC 126465; San Luis Obispo ARIZ 105998, WTU 121664; San Mateo ARIZ 261182; Santa Barbara UTC 237960; Santa Clara WTU 46684; Shasta WTU 132637; Solano UTC 230923; Sonoma ARIZ 175403, UTC 242988; Trinity WTU 287090; Tulare WTU 192108; Ventura UTC 209582, WTU 116574, WTU 132645; Yolo UTC 147488, UTC 208828; Yuba ARIZ 141375. **NEW MEXICO.** Catron NMCR KA 7578; Eddy NMCR KA 2256; Grant UTC 92709; Lincoln ARIZ 348355; Otero NMCR KA 3100; Sandoval NMCR KA 2547; Sierra ARIZ 126241; Socorro NMCR KA 8433; Torrance NMCR KA 6289; Valencia NMCR KP 391. **OREGON.** Curry WTU 259120; Hood River NMCR JB 6291937; Jackson UTC 243802; Josephine WTU 345697; Lake WTU 25849; Multnomah WTU 238041; Polk ARIZ 258854. **TEXAS.** Jeff Davis ARIZ 373907. **UTAH.** Cache UTC 105779, UTC 93592. **WASHINGTON.** Clallam WTU 313876, WTU 32987; Jefferson WTU 288995; King WTU 54547; Kitsap WTU 288997; Klickitat, UTC 233912, V 44679, WTU 233153, WTU 233970, WTU 233971, WTU 237814, WTU 272747, WTU 272748, WTU 335048, WTU 351971; Pierce WTU 54558; San Juan V 123290; Skagit WTU 233902, WTU 269172; Snohomish ARIZ 373905, ARIZ 373905; Thurston WTU 345274; Whitman WTU 66518.

Bromus carinatus **var.** ***marginatus*****. CANADA. BRITISH COLUMBIA.** V 11102B (55.95N 126.617W), V 111787 (49.067N 120.183W), V 11304 (49.85N 123W), V 118639 (51.292N 123.542W), V 122663 (49.583N 126.617W), V 123150 (51.267N 116.6W), V 123175 (51.433N 116.417W), V 127864 (50.317N 122.717W), V 132417 (48.408N 123.625W), V 132723 (50.1N 125.2W), V 13300 (49.667N 117.283W), V 139961 (50.117N 120.45W), V 139968 (50.033N 120.425W), V 141175 (49.133N 114.583W), V 141201 (49.783N 115.867W), V 141845 (49.9N 120.617W), V 142109 (49.825N 119.867W), V 147784 (49.583N 114.85W), V 147785 (50.367N 115.333W), V 147790 (54.117N 127.208W), V 148719 (49.836N 120.607W), V 148747 (49.054N 118.849W), V 158408 (49.067N 121.133W), V 16395 (49.6N 115.883W), V 166870 (50.608N 123.33W), V167607 (49.717N 124.467W), V 168062 (48.533N 123.783W), V 168175 (49.333N 124.7W), V 171056 (49.583N 124.35W), V 175073 (49.7N 115.6W), V 176644 (54.45N 125.3W), V 17711 (54.233N 125.75W), V 17758 (53.8N 126.05W), V 177910 (49.542N 120.9W), V 178365 (49.5N 124.217W), V 179208 (49.717N 117.15W), V 179210 (49.35N 119.9W), V 179211 (49.183N 119.55W), V 179237 (48.817N 123.583W), V 179800 (49.107N 119.675W), V 18083 (49.117N 120.867W), V 18112 (49.117N 120.65W), V 183614 (53.812N 125.925W), V 184038 (53.81N 125.787W), V 185257 (54.033N 125.775W), V 185288 (53.788N 126.833W), V 185433 (49.103N 119.673W), V 186873 (54.692N 126.998W), V 188539 (49.04N 124.338W), V 24476 (50.9N 122.617W), V 29530 (49.5N 117.283W), V 30853 (50.45N 119.2W), V 38852 (49.25N 124.8W), V 45566 (51.85N 120.067W), V 467 (54.217N 129.633W), V 483 (50.167N 120.667W), V 50594 (49.2N 119.833W), V 563 (51.283N 117.583W), V 56595 (51.15N 117.917W), V 66172 (48.45N 123.267W), V 66918 (49.067N 120.7W), V 67268 (49N 120.8W), V 67654 (49.033N 120.933W), V 67661 (49.783N 117.167W), V 68810 (49.267N 120.2W), V 68842 (49.05N 120.967W), V 87217 (48.783N 123.15W), V 88449 (49.133N 119.667W), V 88465 (49.183N 120.083W), V 90176 (49.117N 119.617W), V 90182 (49.117N 119.883W), V 91361 (49.017N 114.104W), V91396 (49.019N 114.106W), V 93615 (49.111N 114.147W), V 93942 (49.032N 114.158W), V 94621 (50.383N 122.35W), V 98620 (48.781N 123.267W), V 66918 (49.117N 120.883W). **UNITED STATES. ARIZONA.** Apache ARIZ 185846; Cochise ARIZ 252313, ARIZ 255027, ARIZ 304977, ARIZ 362097, ARIZ 53657; Coconino ARIZ 109921, ARIZ 109934, ARIZ 160175, ARIZ 196643, UTC 137339; Gila ARIZ 110684, ARIZ 130668, ARIZ 167685, ARIZ 291305, ARIZ 328570, ARIZ 39833, ARIZ 75100, ARIZ 75101, UTC 23485, UTC 23492; Maricopa, ARIZ 109920, ARIZ 37606; Mohave, ARIZ 329394, ARIZ 65255; Pima, ARIZ 133623a, ARIZ 17210, ARIZ 244490, ARIZ 249063; Pinal ARIZ 106150 ARIZ 109914, ARIZ 304300, ARIZ 312982; Yavapai ARIZ 10759, ARIZ 10760, ARIZ 14724, ARIZ 229031, ARIZ 241804, ARIZ 373890, ARIZ 37835, ARIZ 65257, ARIZ 91974. **CALIFORNIA.** Alpine UTC 17509, UTC 17522, UTC 195655, UTC 195680, UTC 195686; Contra Costa NMCR KP CA; El Dorado ARIZ 256250. ARIZ 256250; Humboldt UTC 99433, UTC 99437, WTU 206345, WTU 206981, WTU 219492; Inyo ARIZ 32578, ARIZ 32578 Los Angeles ARIZ 294645, ARIZ 302102, ARIZ 317429, ARIZ 317429, ARIZ 352150, ARIZ 69600; Madera ARIZ 373904; Marin ARIZ 130141, ARIZ 261182, UTC 107959, WTU 51135; Mariposa ARIZ 373897; Mendocino ARIZ 373889, ARIZ 373896, ARIZ 373896; Modoc UTC 101618, UTC 56895; Mono UTC 100739, UTC 103357, WTU 231660, WTU 52787; Monterey ARIZ 373885, UTC 209583; Nevada ARIZ 20728, UTC 107972; Placer UTC 107960, UTC 108713; Plumas ARIZ 112556, ARIZ 112556, UTC 108716; San Bernardino ARIZ 15187, ARIZ 15187, ARIZ 309742, ARIZ 309742, ARIZ 353168; San Diego WTU 57961; Santa Barbara ARIZ 69643; Sierra ARIZ 20728; Trinity UTC 34823; Tulare WTU 179577; WTU 94997; Tuolumne WTU 60470; Ventura ARIZ 69600, ARIZ 69643. **COLORADO.** Gunnison ARIZ 353126, ARIZ 353127; Montrose ARIZ 353128, ARIZ 373908, ARIZ 373908; Routt UTC 245447. **IDAHO.** Adams UTC 108309, UTC 237666; Bear Lake WTU 300978; Blaine UTC 49452; Boise ARIZ 39178, UTC 220838, UTC 71135, UTC 71694; Camas WTU 299870; Cassia ARIZ 202880, UTC 139388, UTC 212111, UTC 234927, UTC 45233; Clark UTC 30055, UTC 46616; Custer UTC 49721; Fremont UTC 163480, UTC 42856, UTC 781; Idaho ARIZ 167569, ARIZ 167569, UTC 108299, UTC 108304, UTC 113111; Lemhi WTU 92426; Oneida UTC 122014; Power V 96380; Shoshone WTU 54560; Twin Falls UTC 150278; Valley UTC 134596, UTC 136838; Washington UTC 134238. **MONTANA.** Granite UTC 212558; Lake UTC 198297, UTC 198299; Madison UTC 72562. **NEVADA.** Carson City ARIZ 20729; Douglas ARIZ 20729, UTC 227143; Elko ARIZ 203021, ARIZ 22296, ARIZ 22296, UTC 108321, UTC 139389, UTC 191913, UTC 29593, WTU 268323; Humboldt ARIZ 203028, ARIZ 20716, ARIZ 20716, UTC 108257, UTC 139600, UTC 142599, WTU 268322; Lander UTC 153102; Lincoln UTC 141291, UTC 149274; Nye UTC 122098, UTC 128132, UTC 128156, UTC 128157, UTC 128158, UTC 128159, UTC 128160, UTC 128187; Washoe ARIZ 20717, ARIZ 373899, UTC 192488; White Pine ARIZ 203029, UTC 135470. **NEW MEXICO.** Bernalillo NMCR KA 7503; Catron NMCR KA 7578; Dona Ana NMCR JS 19; Eddy NMCR KA 2256; Grant NMCR JC 1284, NMCR KA 8380; Lincoln NMCR R 15, NMCR RW 30779; Otero NMCR KA 3100, UTC 151037; Sierra NMCR ER 1203, NMCR ER 636; Torrance NMCR KA 6289; Union NMCR R 15. **OREGON.** Baker UTC 202027, WTU 313742; Douglas UTC 34545, WTU 55398; Grant UTC 231408, WTU 154053, WTU 258386; Hood River WTU 25575; Jefferson WTU 224479; Josephine WTU 298349; Klamath UTC 108719, UTC 72657, WTU 298150, WTU 300994; Lake WTU 282410; Lane ARIZ 373891, ARIZ 373891; Linn UTC 80415; Malheur UTC 154348; Multnomah WTU 238040; Polk ARIZ 258854; Umatilla NMCR JB 28Jun1937; Wallowa WTU 262870; Wheeler WTU 144321. **TEXAS.** Jeff Davis ARIZ 373909; ARIZ 72958. **UTAH.** Cache ARIZ 107237, ARIZ 250271, UTC 217487, UTC 236800, UTC 236820, UTC 236841, UTC 236909, UTC 236979, UTC 237008, UTC 237980, UTC 238116, UTC 238127, UTC 79761; Davis UTC 22350; Garfield UTC 88997; Juab ARIZ 35690; Rich UTC 210376, UTC 237981; Salt Lake UTC 211202; Utah UTC 218590; Washington ARIZ 8803, ARIZ 8804. **WASHINGTON.** Asotin UTC 81926; Chelan V 137652, V 137654, WTU 124466, WTU 215242, WTU 288901, WTU 30296, WTU 322032, WTU 322035; Clallam WTU 21978; Columbia WTU 349068; Ferry UTC 61739; Garfield WTU 341137; Jefferson WTU 38322, WTU 39053; King WTU 23904, WTU 288808; Kittitas WTU 209672, WTU 218776, WTU 322034, WTU 357720; Klickitat WTU 228247, WTU 269216; Lewis WTU 324047; Okanogan V 137653, V 137655, V 137656, WTU 25511, WTU 332998; Pierce WTU 214880, WTU 329976; Skagit WTU 288885; Spokane WTU 14057; Whatcom WTU 25517, WTU 316970, WTU 86726; Whitman UTC 105616; Yakima WTU 31053. **WYOMING.** Albany, ARIZ 373900, ARIZ 45770, ARIZ 69634, UTC 157617, UTC 56755; Big Horn UTC 24473; Carbon ARIZ 125792, ARIZ 45620, UTC 153797; Lincoln UTC 155531, UTC 206601; Park UTC 172297, UTC 210095; Teton ARIZ 373901, UTC 106191, UTC 147161, UTC 185186, UTC 192955, UTC 207599, UTC 231568, UTC 28236.

Bromus polyanthus**.** **CANADA. BRITISH COLUMBIA.** V 011102A (55.95N 126.617W), V 141173 (49.133N 114.583W). **UNITED STATES. ARIZONA.** Apache ARIZ 109916, ARIZ 109932, ARIZ 109933, ARIZ 166683, ARIZ 176049, ARIZ 75102; Cochise ARIZ 10393; Coconino ARIZ 113981, ARIZ 113983, ARIZ 113985, ARIZ 257193, UTC 59763; Gila ARIZ 14898, ARIZ 65249; Pima ARIZ 247583, ARIZ 353122; Pinal ARIZ 113986; Santa Cruz ARIZ 223872, ARIZ 255220. **CALIFORNIA.** Los Angeles ARIZ 337375; San Francisco UTC 81091; Sonoma ARIZ 175403. **COLORADO.** Boulder ARIZ 353130; Jackson NMCR JB 23Jun1937; Montrose UTC 184729; Pitkin UTC 163490; Routt UTC 115602, UTC 115621; San Miguel UTC 179420; Summit UTC 163503. **IDAHO.** Blaine UTC 49451, UTC 71399; Cassia UTC 139599; Franklin UTC 213218, UTC 225805; Oneida UTC 782. **NEW MEXICO.** Catron ARIZ 185893, ARIZ 237501; NMCR KA 2333, NMCR KA 2348, NMCR KA 2364; Colfax NMCR JB 1941; Grant ARIZ 353129, NMCR KA 4652, UTC 113375, UTC 124119, UTC 139515; Lincoln ARIZ 109924, ARIZ 109927, ARIZ 109928, ARIZ 173185, ARIZ 173186, NMCR KA 2553, NMCR KA 2557, NMCR KA 2561, NMCR RW 31590, NMCR SA 13; Mora NMCR KA 6935; Otero NMCR KA 5166, NMCR JB 1512, NMCR KA 3098, NMCR KA 8342; Rio Arriba NMCR KA 4991; San Miguel ARIZ 173184, NMCR KA 2454, NMCR RH 76899; Sandoval NMCR JC 264, NMCR KA 2546, NMCR RH 72834; Santa Fe NMCR KA 2454; Sierra UTC 141541; Socorro NMCR KA 8433, NMCR KA 8469; Valencia NMCR KP 24Aug1933. **TEXAS.** Jeff Davis ARIZ 373907. **UTAH** Cache UTC 189028, UTC 20478, UTC 236893, UTC 29726, UTC 30101, UTC 30422, UTC 97270; Davis ARIZ 141064, UTC 23348; Duchesne UTC 146882; Grand UTC 181354, UTC 30102, V 142371; Iron UTC 2751; Salt Lake ARIZ 109929, ARIZ 117069, ARIZ 126498, ARIZ 127529; Sanpete ARIZ 109922, ARIZ 192268, UTC 108056; Sevier UTC 181752; Summit UTC 106940; Tooele UTC 156420; Uintah UTC 146883; Utah ARIZ 35268, ARIZ 35331, UTC 150717, UTC 150718, UTC 150724; Wasatch UTC 239393, UTC 239394. **WYOMING.** Carbon UTC 152076; Lincoln, UTC 154751, UTC 18039, UTC 192732, UTC 20479; Sublette UTC 228446; Teton NMCR GV 1949, UTC 131418, UTC 788.