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VARIABILITY OF BLUEGRASS (*POA*) IN SIBERIA

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ABSTRACT

Siberian bluegrass (*Poa*) includes a number of polymorphic species such as *P. arctica* s.l., *P. nemoralis* s.l., *P. palustris* s.l., *P. pratensis* s.l., *P. sibirica* s.l., and *P. smirnovii* s.l., plus numerous hybrids and purported derivatives (e.g., *P. attenuata* s.l., *P. glauca* s.l., *P. urssulensis* s.l.). In Siberia *Poa* is represented by morphologically isolated species and hybrid-apomictic complexes, including both distinct species and taxonomic groups of obscure rank. Section *Stenopoa* is especially rich in these complexes. Most of the key morphological characters used in the taxonomy of bluegrass vary as much within populations as among populations and thus do not support recognition of some previously described taxa. It is likely that karyological or other genetic data would identify regionally distinct taxa. The area of the greatest intraspecific variation of *Poa* in Siberia is the Altai Mountain region based on analyses of distribution and morphology. Geography must be considered during conservation planning activities to avoid impacting locally adapted and morphologically divergent populations of broadly distributed species.

Key words: morphology, *Poa,* populations, Siberia, variability.

INTRODUCTION

The geographic position and size (about 10 million square kilometers) of Siberia, its geological history, and glaciation have resulted an exceptional variety of landscapes and habitats. The region is primarily mountainous, providing numerous refuges and resulting in the isolation and development of morphologically distinct taxa (Malyshev et al. 2000). Widespread introgressive hybridization and polyploidization of species has also been hypothesized (Tzvelev 1974). As a result, common and widespread species have undergone selective adaptation to localized microclimates, resulting in numerous varieties and morphological forms in Siberia. It is possible that there are karyological differences between morphs as well. Documented chromosome counts for *Poa* L. in Siberia are few (Krogulevich and Rostovtseva 1984), but range from $2n = 14$ to 70.

Systematic investigation of the Siberian flora began about 100 years ago culminating in the *Flora of Siberia* (Krasnoborov 2000), but the botany of this enormously diverse landscape remains incompletely documented. Study continues on the taxonomic composition of biodiversity, not only to differentiate species but also taxa at various intraspecific ranks, including subspecies and varieties. Floras are critical for decision-making associated with conservation, therefore shifting taxonomy is at odds with the practical necessity of creating and improving floras since they demand clarity on the number, circumscription, and distribution of species. Siberia is home to 43 species and 61 subspecies of *Poa* distributed in 2 subgenera (*Arctopoa* (Griseb.) Probatova and *Poa*) and 13 sections (Olonova 1999*a,* 2001*b*). Sections *Abbreviatae* Nannf. ex Tzvelev, *Alpinae* (Hegetschw. ex Nyman) Soreng, *Arctopoa* (Griseb.) Probatov, *Bulbosae* Roshev., *Coenopoa* Hyl., *Homalopoa* Dumort, *Nivicolae* (Roshev.) Probatova, *Ochlopoa* (Ascherson et Graebner) Jirásek, and *Oreinos* (Ascherson et Graebner) Jirásek are each represented by one or two species that are readily distinguishable. Taxonomic difficulties exist within sects. *Macropoa* F. Herm. ex Tzvelev, *Malacanthae* (Roshev.) Olonova, *Poa,* and *Stenopoa* Dumort, which represent approximately 75% of Siberian *Poa* species. Bluegrass species are dominant in many plant communities, however, the frequency of hybridization and apomixis make it one of the most difficult genera to characterize systematically. Estimating the biodiversity within species is likely to be equally difficult.

The research presented here assesses the morphological variability of the complex sections of *Poa* in Siberia. The goals of this research include: (1) review the basic morphological characters used in the taxonomy of the most difficult sections; (2) assess the variability of these characters within and among populations; (3) define the areas with the greatest variety of morphological variability.

MATERIALS AND METHODS

The data presented here are based on materials collected by the author since 1972. Plants were collected from the plains of western Siberia, Altai, Baikal, Dauria, Kolyma, Kuznetsk Alatau, and Sayan as well as the European section of the former Soviet Union and Russian Far East (Fig. 1). Specimens from the following herbaria were also studied: KW, LE, MHA, MW, NS, NSK, PE, SSBG, TK, and VLAD (abbreviations follow Index Herbariorum: Holmgren et al. 1990), and those from the vast collections of the Laboratory of Far North Vegetation Research (Institute of Botany, Russian Academy of Sciences). In particular, research on the variability of populations in *Poa arctica* R. Br. was based exclusively on materials from these institutions. Additional specimens were loaned from LD, O, UPS, and US. Taxonomic study follows classical morpho- and phenogeographical methods as described in Yablokov (1976, 1986). Character variability (Table 1) within and among populations used standard statistical methods including principle com-

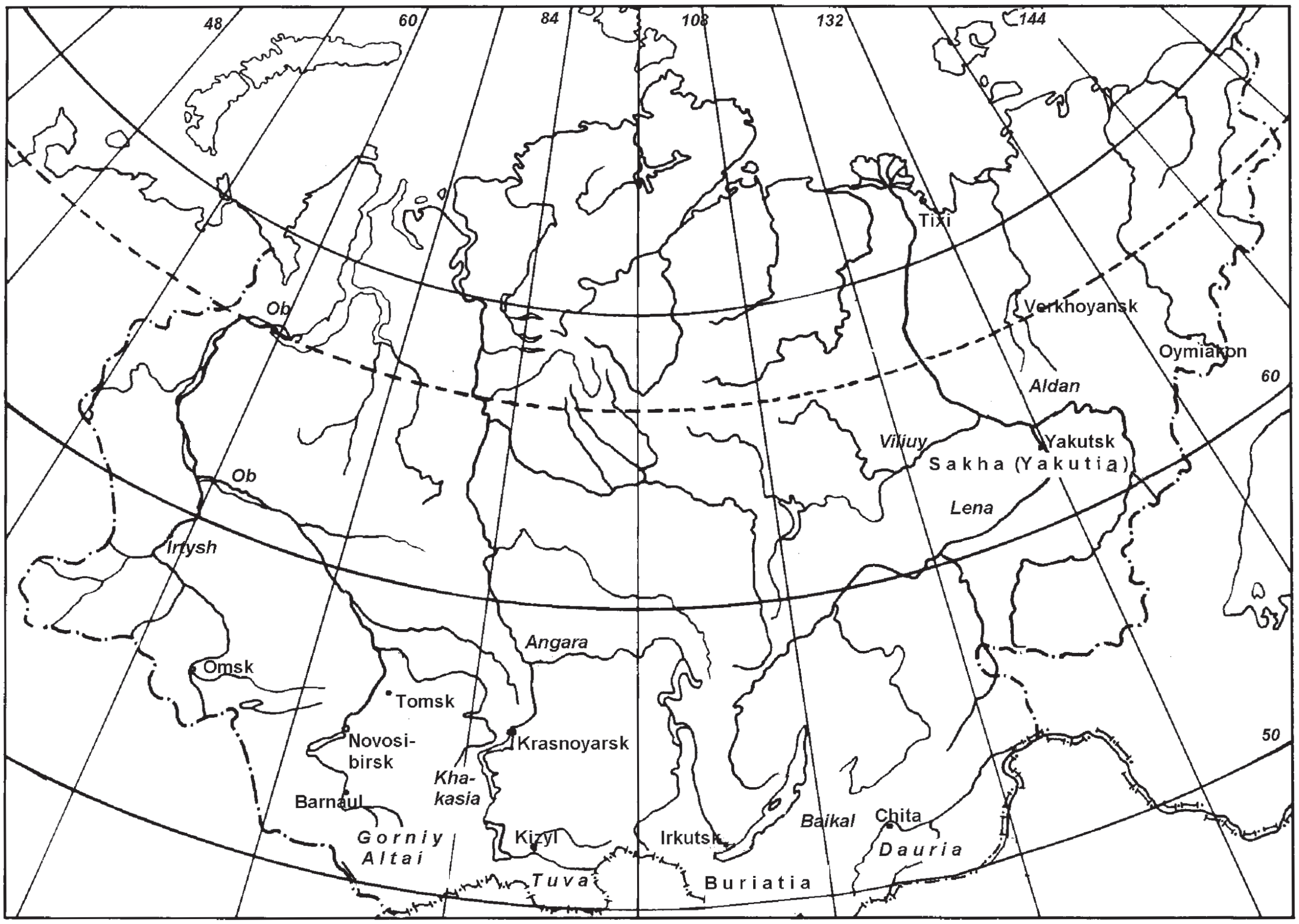

Fig. 1.—Map of Siberia.

Table 1. List of characters used in Siberian bluegrass analysis.

1. Height of plant
2. Distance from base to uppermost node
3. Distance from uppermost node to panicle
4. Length of the second (from the top) internode
5. Length of the flag leaf sheath
6. Length of the flag leaf blade
7. Width of the flag leaf blade
8. Length of the flag leaf ligule
9. Length of panicle
10. Width of panicle
11. No. of branches at 1st panicle nodes
12. Length of the longest panicle branch
13. No. of spikelets per longest panicle branch
14. No. of florets per spikelet
15. Length of spikelets
16. Length of 1st glumes
17. Width of 1st glumes
18. Length of 2nd glumes
19. Width of 2nd glumes
20. Length of lemmas
21. Width of lemmas
22. Rachilla pubescence
23. Lemma callus pubescence
24. Pubescence between veins of lemmas

ponents analysis (PCA) (Zaitsev 1990) and discriminant function analyses (Leonov 1990; Soshnikova et al. 1999).

RESULTS AND DISCUSSION

Section Macropoa

Poa sibirica Roshev. is the sole representative of sect. *Macropoa* in Siberia. The species grows in both woodlands (mainly montane) and in the alpine mountain belt. Field observation has shown that *P. sibirica* can cross with *P. pratensis* L., forming hybrid swarms. The species is polymorphic (Olonova 2000*b*) and some authors recognize a second species, *P. insignis* Litv. *Poa insignis* differs from *P. sibirica* by having a scabrous (versus smooth) rachilla, scabrous (versus smooth) panicle branches, and a pubescent (versus glabrous) ligule. Additionally, Tzvelev (1976) recognizes *P. sibirica* subsp. *uralensis* Tzvelev, which differs from the typical subspecies by having a thicker stem (2–4 mm versus 1–2 mm), wider leaf blade (2–8 mm versus 1.5–4 mm), and larger spikelets (6–6.5 mm versus 3.5–4.5 mm).

Discriminant analysis of 21 morphological characters (Olonova 2000*a*) revealed significant isolation of alpine and woodland individuals and a strong correlation between predicted ecological groups and morphological characters. For the alpine and woodland group, 84.0 and 93.1% of samples, respectively, were unambiguously assigned. Nonetheless, the limits of almost all of the characters included in the analysis were overlapping, and only four attributes (listed below) had statistically significant distinctions, two of which reflect reproductive biology and are more genetic than ecological.

Basic measured characters of *P. sibirica* s.l. in Siberia vary within the following limits: (1) ligule length from 0.5 to 3.4–4 mm; (2) width of the flag leaf blade from 1.7 to 6 mm; (3) length of spikelets from 3.9 to 6.6 mm; and (4) basal stem thickness from 1 to 4 mm. Approximately the same ranges in variation were observed in Altai, Krasnoyarsk, and Transbaikalia districts.

The majority of alpine individuals had panicle branches that were smooth or almost smooth, while below the timberline, panicle branches were mainly scabrous and frequently rather densely so. In Transbaikalia, the samples with smooth panicle branches occurred quite often in the lower elevations of the mountains as well.

Ligules are pubescent throughout *Poa,* including in *P. sibirica* s.l. The density and length of the hairs fall into three groups: (1) pubescence is sparse and hairs are very short with the length barely exceeding the width, (2) pubescence dense, hairs no more than 0.06 mm in length, (3) hair at regular intervals, length up to 0.25 mm (upper leaves) or even longer on basal leaves. Representatives of Group 1 are widely distributed in all parts of Siberia, from the Altai Mountains to the Amur River. Group 2 is more narrowly distributed than the first and is virtually absent to the east of the Krasnoyarsk region (Yenisei, Siberia). Samples of Group 3 are found mainly in the Altai and adjacent regions. About 20 locations are known (Polozhij and Olonova 1983), primarily near the timberline.

Correlations of the ligule hair length with panicle branch scabrosity or with spikelet length were not observed ($r < 0.3$). The statistical correlations between ligule length, leaf blade width, and spikelet length were also studied ($N = 93$). Results showed a strong correlation between ligule length and leaf blade width ($r = 0.56$) which, however, are known to represent the same structure, and a weak correlation between leaf blade width and spikelet length, as well as between ligule length and spikelet length ($r = 0.19$ and $r = 0.22$, respectively). Analysis revealed neither the presence of diagnostic combinations of character states, nor geographic dependence for any character state except ligule pubescence. Research of morphological variability of *P. sibirica* s.l. in Siberia has revealed the high degree of polymorphism of this species. However, statistical studies of variability of morphological characters used in taxonomy for this group provided insufficient grounds for recognition of new species, nor the maintenance of the already described *P. insignis,* or *P. sibirica* subsp. *uralensis.*

Section Malacanthae

Section *Malacanthae* is represented by five species in Siberia. While there is agreement about three of these species, there is debate on the size and limits of *P. arctica* and especially *P. smirnovii* Roshev. The pubescence of the lemma between veins in *P. arctica* and *P. smirnovii* can vary from densely pubescent to the near absence of pubescence but there are additional variable characters for these two species.

Scandinavian *P. arctica* was investigated by Nannfeldt (1940) who defined six subspecies based on life history and vegetative features. Hultén (1942, 1960) recognized additional subspecies while researching North American materials. Tzvelev (1964) noted the high polymorphism of *P. arctica* in the Arctic areas of the former USSR, but was unable to assign available material of this species to the subspecies described by other botanists. The primary characters most often used in the taxonomy of this group are: plant height, spikelet length, and lemma pubescence. Rachilla pubescence, panicle density, and plant color are less often taken into consideration.

Preliminary research in *P. arctica* confirmed the marked polymorphism of this species in Siberia (Olonova 2000*a*). The characters listed above vary greatly and appear randomly distributed in specimens from this region. Long-stemmed (about 45 cm) samples of *P. arctica* with large spikelets (about 6 mm) occur at the southeast limit of its distribution, are in close contact with *P. smirnovii,* an alpine species that differs by short stems (10–30 cm) and long (up to 7 mm) spikelets. Some tall forms of *P. arctica* resemble *P. sublanata* Reverd., another species that is widely distributed in the Arctic region of Siberia. Character variability of *P. arctica* in Russia was investigated using five populations: (1) Left Sidya-Myutya River on the Tazovskiy Peninsula; (2) herbaceous tundra on the lower reaches of the Salem-Lekambtambda River of Mammoth peninsula, near Cape Honorosale; (3) Cape Trehbugornyj on the Gulf of Ob; (4) middle reaches of the Matyuy-Yaha River on the Yamal Peninsula; and (5) sandy banks of Tit-Ary Island on the lower reaches of the Lena River in the Sakha (Yakutia) Republic.

Siberian samples revealed high variability for plant height, with intra-population variability sometimes exceeding the inter-population variability (Population 1). In populations where average height of samples regularly exceeded the average for this species (Population 2) lower intra-population variability can occur. Spikelet length was also quite variable. For example, in Population 3, it varied continuously from 3 to 6.6 mm, and in Population 4, from 4.9 to 6 mm, while the average was 5.6 mm. This size exceeded the average for this species by almost 22% and corresponds more closely to the southern Siberian alpine species, *P. smirnovii* s.l. Populations of *P. arctica* with completely glabrous lemmas between veins (Population 5) were rarely found in Siberia. The characters of rachilla surface, panicle density, and plant color were also found in random combinations, showing neither geographical nor ecological trends. Based on these data, none of the characters studied can be used as the basis for splitting *P. arctica* into additional species or subspecific taxa. This species is represented by many morphologically different local populations in Siberia and may include a number of different karyological races.

Poa polozhiae Revyakina (1996) was segregated from *P. smirnovii* based on the lack of hair between veins on the lemma; however, detailed research of this character variation in populations of *P. smirnovii* has revealed a high variability of lemma pubescence (Olonova 2000*a*). Most specimens examined (Fig. 2) had dense pubescence between the veins, but a number of glabrous specimens were also examined throughout the range in Siberia, thus this character alone cannot be used to segregate *P. polozhiae* from *P. smirnovii.*

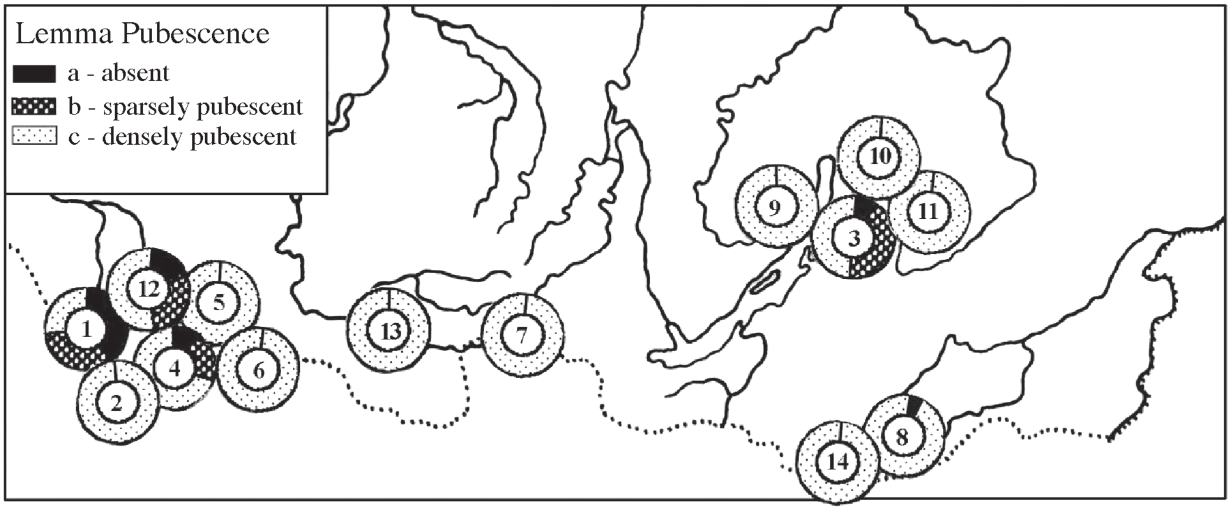

Fig. 2.—Frequencies of pubescence between veins on the lemma surface for *Poa smirnovii* s.l. morphs in Siberia.

Section Poa

Section *Poa* is represented by 11 species in Siberia, all of which are similar to *P. pratensis*. *Poa pratensis* shows marked variation for chromosome number and forms numerous chromosome races and agamous complexes (Anderson 1927; Stebbins 1941; Miroshnichenko and Avrasina 1975). Qualitative characters that are often used successfully in bluegrass classification—rachilla surface, lemma callus, area between veins, and ligule length (this character is frequently considered qualitative)—are not taxonomically useful due to low variability for this section of *Poa.* Attempts to circumscribe species based on characters such as lower leaf sheath surface texture, spikelet length, and the shape of the panicle have proved difficult (Rozhevits 1932; Probatova 1971).

Poa *sect.* Poa *interspecific taxa in Siberia.*—The distribution of different character states throughout the range of *P. pratensis* were quantified using samples from the various territories of European Russia. Characters surveyed include lower leaf sheath surface, lower leaf sheath shape, panicle shape, and spikelet length.

The lower leaf sheath surface of *P. pratensis* and close relatives is completely glabrous and smooth, scabrous or hispid (*P. sergievskajae* Prob. and *P. raduliformis* Prob.), or pilose (*P. pratensis* var. *hirtula* Aschers. et Graebn., a widespread species in both Central Europe and Western Siberia). Herbarium material surveys have shown that all of these character states are sporadic within the area studied, although pilose forms frequently occur in wet habitats such as damp meadows and swamps. The four states of the lower leaf sheath surface are not only found in Siberia, they are also encountered in European Russia and adjacent areas. Sheath pubescence is associated with habitat (wetlands). Although the presence of some clinal variability in this case is undeniable, analysis of leaf surface texture distinguished Siberian specimens from European specimens (Fig. 3).

Lower leaf sheath shape is also an important taxonomic character for *P. pratensis.* Individuals with flat sheaths were described as *P. pratensis* var. *anceps* Gaud. This variety was found both in Central Europe (Hegi 1906) and in Siberia (Krylov 1928). *Poa sergievskajae* and *P. raduliformis* differ from *P. pratensis* by possessing flat sheaths. Variation for this character revealed neither a geographical nor an ecological trend.

Panicle shape varies considerably for species closely related to *P. pratensis.* Three types of panicle shape are recognized: (1) dense, pyramidal, with branches, directed upwards (45–80°); (2) lax, wide, pyramidal, frequently with drooping branches; and (3) quite dense, elongated, with branches, directed upwards (45–80°). Preliminary research has shown that Type 2 is more characteristic for Eastern Siberia, but seldom found in Western Siberia and European Russia. A distribution map of this character (Fig. 4) confirms the prevalence of samples with a Type 2 panicle in Western Siberia, but character states are not correlated with habitat or geography.

Reproductive attributes, in particular spikelet length, are taxonomically useful because they are less affected by environment than many other characters. Spikelet length is a quantitative character showing continuous variation. However, for the preliminary analysis, it was convenient to score this character as qualitative, arbitrarily divided into four categories: (1) 3–4 mm; (2) 4.1–5 mm; (3) 5.1–6 mm; and (4) greater than 6 mm. The majority of Russian graminologists describe the length of *P. pratensis* spikelets within the limits of 3.5–6 mm (Rozhevits 1934; Reverdatto 1964; Tzvelev 1964; Prokudin 1977). The distribution of spikelet length categories is represented graphically in Fig. 5 based on 50–67 individuals per sample. Category 2 (4.1–5 mm) dominates all geographic regions. In the European samples, it accounts for more than half of all specimens (from 52% in Transkarpatia to 68% in Eastern Siberian forest-steppe areas), and in Siberia between 39% (Leno-Kolyma district) and 64% (Angaro-Sayansky district) of specimens fall in Category 2. Category 4 encompasses individuals having the longest (greater than 6 mm) spikelets. Long (greater than 6 mm) spikelet length was one of the characters distinguishing *Poa urjanchaica* Roshev. and *P. angustiglumis* Roshev. from *P. pratensis.* Both species are restricted to Siberia; however, individuals with spikelets greater than 6 mm can be found in all investigated districts, with the highest concentration of

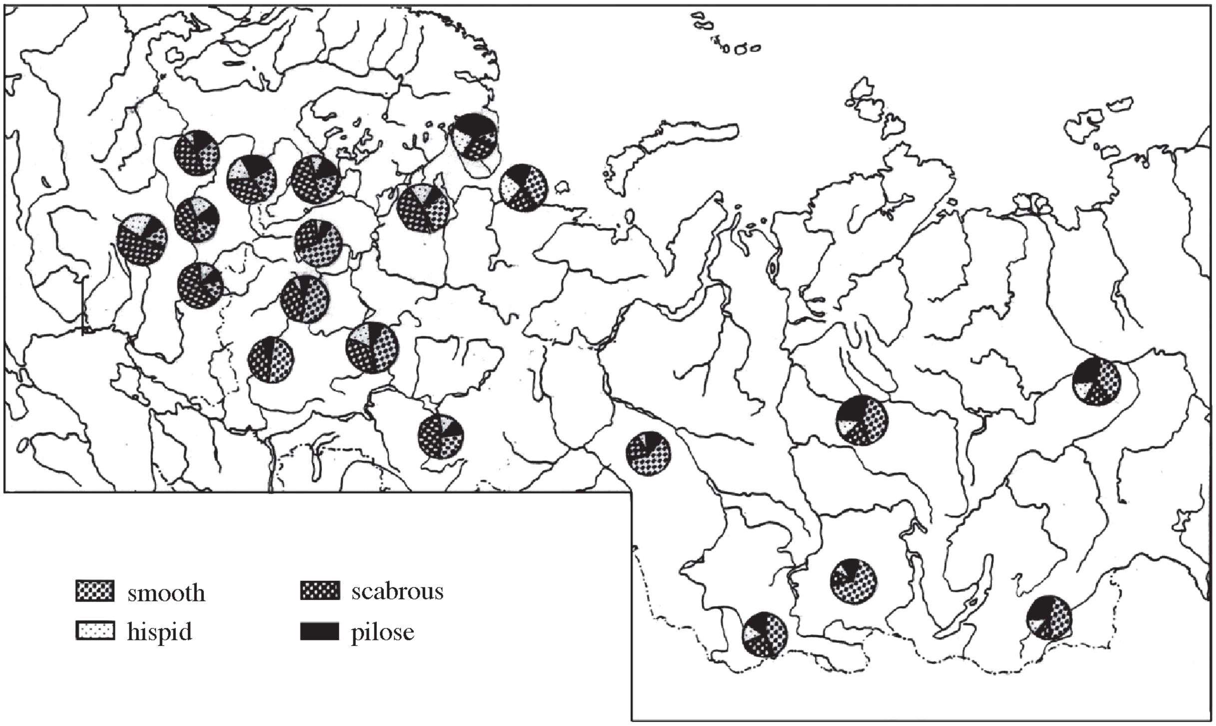

Fig. 3.—Frequencies of lower leaf sheath surface characters for *Poa pratensis* morphs in Siberia and Eastern Europe.

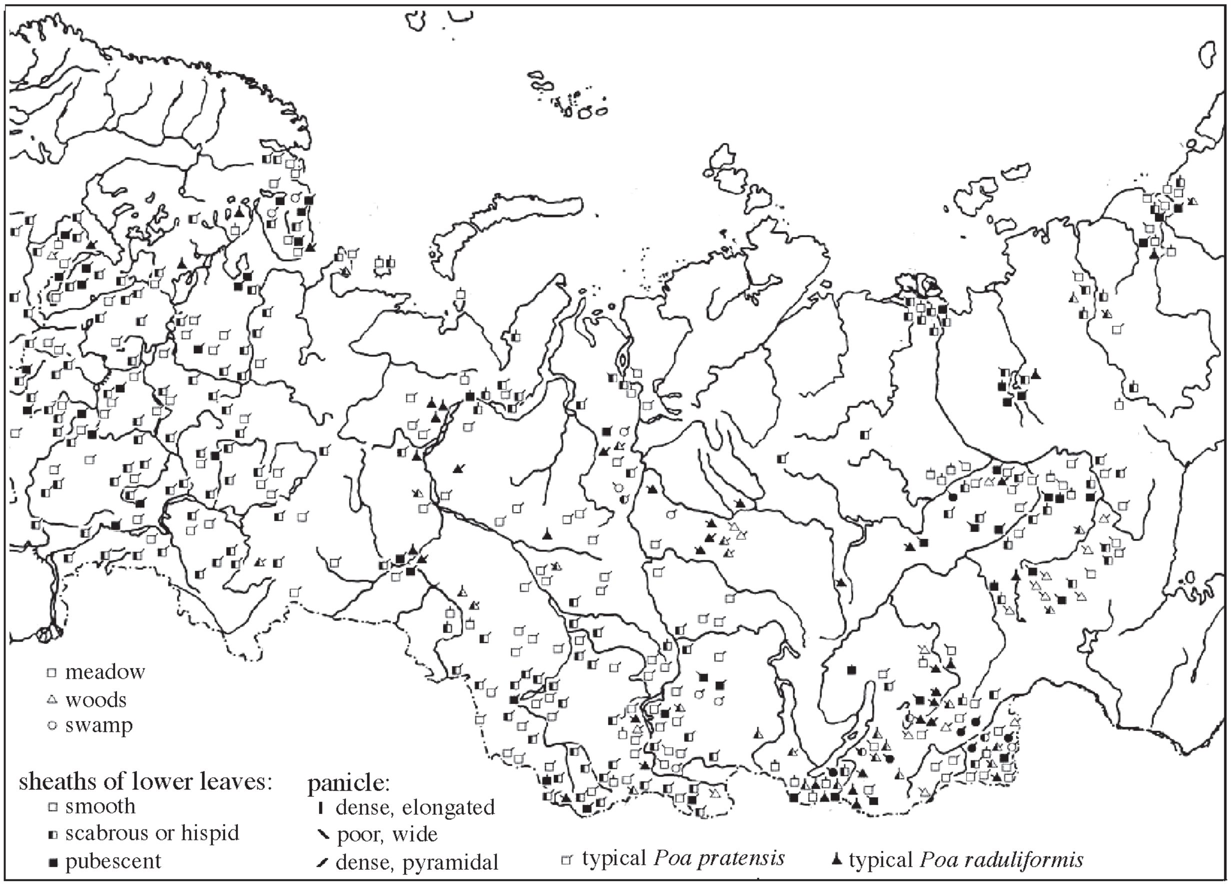

Fig. 4.—Distribution of habitat, sheath, and panicle characteristics for *Poa pratensis* and close relatives in Siberia.

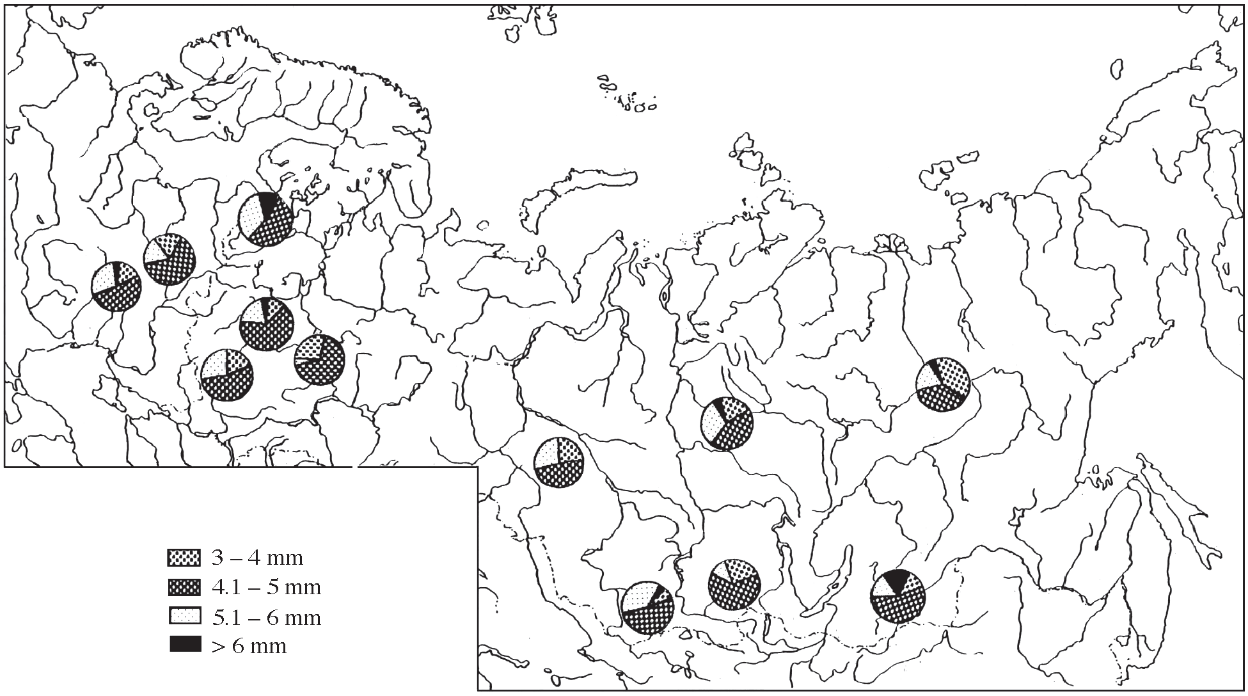

Fig. 5.—Frequencies of spikelet lengths for *Poa pratensis* in Siberia and Eastern Europe.

individuals in Dauria and Leningrad District (16 and 11%, respectively). Comparison of all samples from Siberia and European Russia shows that average spikelet length differs little (4.78 and 4.68 mm, respectively), and distinction by this attribute is not statistically meaningful (Student's *T*).

Thus, the main characters used in the classification of the *P. pratensis* complex show trends (Fig. 3, 5) but did not show any statistically significant geographical, ecological, or morphological correlations (Fig. 4). Therefore, these characters can be used as additional attributes in the taxonomy of sect. *Poa,* not the sole basis for taxonomic change or diagnosis.

Poa pratensis *intraspecific taxa in Siberia.*—The second investigative phase of this research was the study of intraspecific differentiation of Siberian *P. pratensis,* specifically the definition of taxa by discriminant analysis of morphological data. Historically, up to 11 varieties or subspecies were recognized (Reverdatto 1964). Preliminary research of herbarium material has shown that, contrary to European Russia, where *P. pratensis* is found mainly in meadow communities, in Siberia—especially Eastern Siberia—this species is quite common in woodland communities, with the woodland populations somewhat polymorphic.

The woodland populations of *P. pratensis* in Siberia consist of at least two, or even three components: the first and most numerous component—especially in Eastern Siberia—is represented by hybrid populations with morphology intermediate between *P. pratensis* and *P. raduliformis.* The second consists of populations of morphologically pure *P. pratensis* that have become established in woodlands, perhaps as a result of post-glaciation expansion. A third group resulting from hybridization of *P. pratensis* with another (unknown) woodland species, or representing the remnant of an extinct species, now introgressed with *P. pratensis,* may also be present. Discriminant analysis of 20 morphological characters for five woodland populations revealed strong differentiation among them. Discriminant analysis of five meadow populations also showed both heterogeneity and a high degree of differentiation (Fig. 6). Thus, discriminant analysis of morphological variability in *P. pratensis* has shown that *P. pratensis* from Siberia and European Russia differ. The difference is understandable, taking into account the extent and variety of environments in the Siberian territory and also the geological and geographical conditions in which the formation of this group proceeded (Olonova 1999*b*).

Research on the distribution of character states for key morphological characters of *P. pratensis* has shown that diagnostic character states for the taxon may not be typical for specimens from Siberia or other areas of European Russia, but rather occur sporadically in different parts of the distribution range. Clinal variation was observed for some characters, yet none of the studied characters provides a suitable basis for splitting *P. pratensis* s.l. into separate species or subspecific taxonomic entities.

Section Stenopoa

Section *Stenopoa* is represented by 16 species in Siberia. It is considered to be the most taxonomically complex section of *Poa.* The postulated evolution in this section is based on the degree of xeromorphy, and four levels of morphological progression are recognized, expressed in terms of the position of the uppermost node, as well as panicle shape, leaf blade width, and the ratio of the length of the leaf blade to the sheath.

The presumed ancestral condition (Xeromorphy Level I) is characterized by a culm with the upper node more than half way up and typified by species *P. palustris* L. and *P. nemoralis* L. The two species are found in contrasting hab-

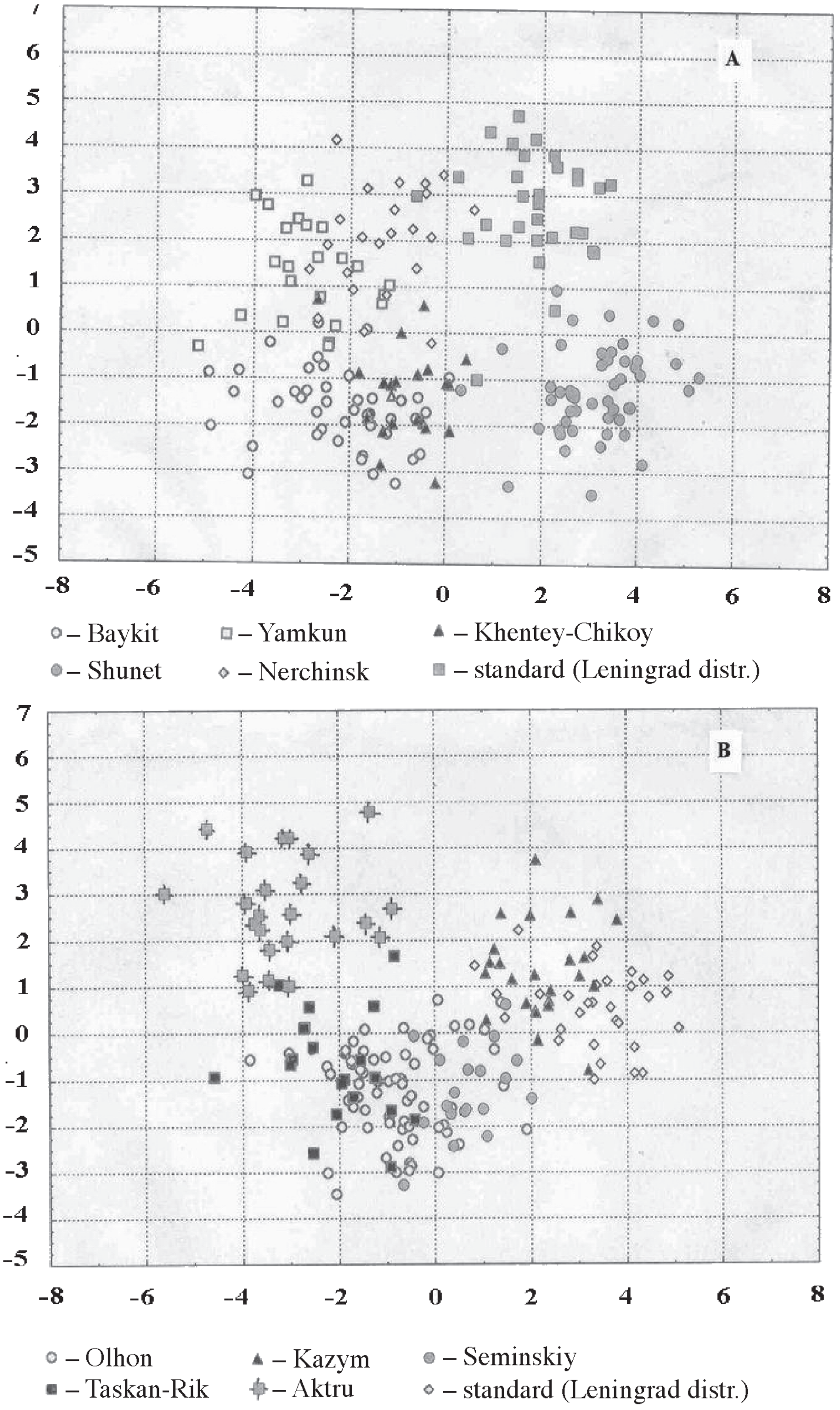

Fig. 6.—Discriminant analysis of 20 morphological characters for 5 populations each from (A) meadow or (B) woodland habitats of *Poa pratensis* (x axis—canonical variable 1; y axis—canonical variable 2). A single population from meadows of Leningrad, European Russia, was included as the standard.

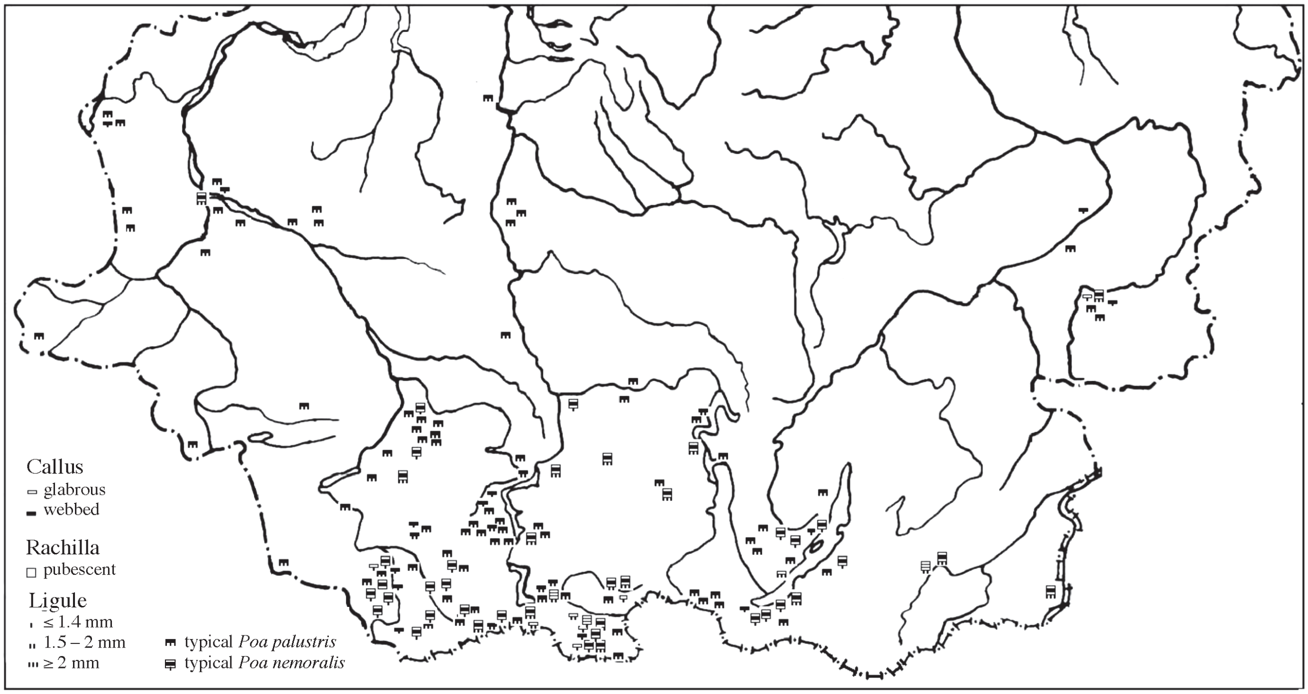

Fig. 7.—Distribution of callus, rachilla, and ligule characteristics for *Poa* sect. *Stenopoa* Xeromorphy Level I species in Siberia.

itats with *P. palustris* a meadow grass and *P. nemoralis* more commonly found in wooded habitats. Tzvelev (1972) hypothesized that these species hybridized during the last glacial period. Among the Siberian members of sect. *Stenopoa,* two lineages are recognized as derived from *P. nemoralis* and *P. palustris.* Although *P. glauca* Vahl s.l. also belongs to sect. *Stenopoa,* it is of hybrid origin and forms an independent and considerably distant branch of evolution. *Poa nemoralis, P. palustris,* and their derivatives differ from one another in two key characters: ligule length and rachilla surface.

Analysis of herbarium material showed that at least half the specimens combine the characters of both lineages, and hybridization is likely to have taken place (Fig. 7). In addition, some specimens have a glabrous lemma callus, unlike either *P. nemoralis* or *P. palustris* which both have a tuft of long hairs on the lemma callus (Olonova 1992). The distribution map of character states and combinations revealed neither geographical trends nor consistent correlation with other factors. The numerous combinations are likely caused by hybridization. The 6- and 8-ploid chromosome numbers, characteristic of xeromorphic species (Probatova 1991), demonstrate the success of this hybridization process. The geographic distribution of the morphological characters supported the hypothesis (Olonova 1992, 1993*b*).

A morphological study of four *P. palustris* × *P. nemoralis* hybrid populations from Tomsk district was carried out to test this hypothesis. Frequencies of the main character states for ligule length, rachilla surface, and lemma callus surface were investigated in the different subpopulations (Fig. 8). Discriminant analyses of 21 quantitative characters confirmed both the heterogeneity of populations and the lack of differentiation among them. Contrary to current opinion, *P. palustris* in Siberia has apparently homogenized with *P. nemoralis* as a result of introgressive hybridization. As a result many populations in Siberia and areas of northeastern Europe combine the characters of both *P. nemoralis* and *P. palustris.* The study of the morphological structure of hybrid populations of *P. nemoralis* and *P. palustris* allows the assumption that in many cases the morphological distinctions between populations are hereditary and confirm the genetic heterogeneity of these populations. This heterogeneity may be retained through apomixis. Siberia possesses not only separate morphologically distinct populations of *P. nemoralis* and *P. palustris,* but also hybrid-apomictic complexes including *P. nemoralis* and *P. palustris* connected with one another by numerous diverse introgressed populations (Olonova 2000*c*). It should be noted that *P. nemoralis* and *P. palustris,* being the ancestral species, have also changed as a result of selection. However, their evolution is assumed to follow the same process as in sect. *Poa.* The two species differ from other species in this section (except *P. glauca*) by forming numerous chromosomal races. This complex is close to the more xeromorphic species of this section.

Poa urssulensis Trin., belonging to Xeromorphy Level II (culm with uppermost node between one half and one third of the way up), is the most complicated taxonomically and might be artificial. It consists of hybrid populations of different parentage, some of which may be drought-adapted hybrids of *P. palustris* and *P. nemoralis,* while others may be hybrids of *P. nemoralis, P. palustris,* and another xeromorphic species such as *P. stepposa* (Kryl.) Roshev. An investigation of populations on the steppe slopes of Salair (Kotorovo, West Siberia) reveals a complex of populations that should be treated as *P. nemoralis, P. palustris* and *P. urssulensis* based on morphological character distributions (Fig. 10). Discriminant analysis of 21 quantitative characters (Fig. 9) confirmed heterogeneity of populations and demonstrated

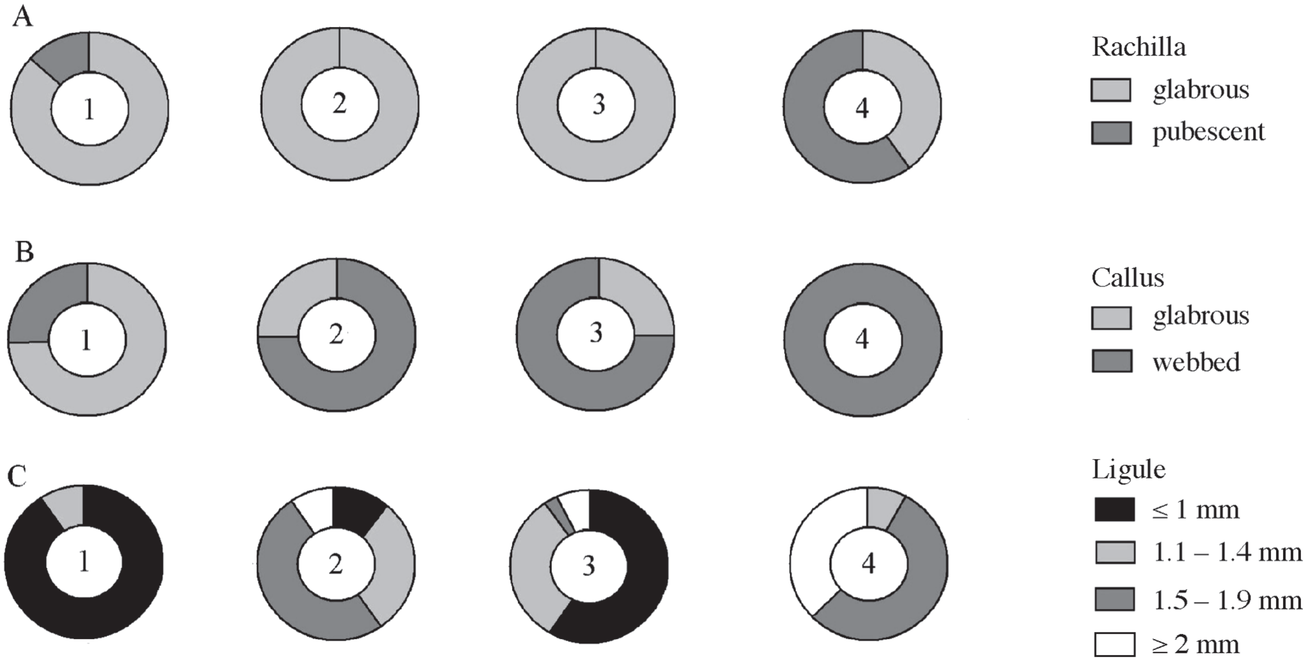

Fig. 8.—Distribution of (A) rachilla surface, (B) lemma callus, and (C) ligule length characteristics for diverse parts of the same hybrid population of *Poa palustris* × *P. nemoralis,* Tomsk district, Western Siberia.

morphological continuity among most of them. The hybrid population seems to be another complex of forms, connected with mesomorphic *P. nemoralis* and *P. palustris,* and xeromorphic *P. stepposa* (Olonova 2001*a*). The same trends can be seen in taxa of Xeromorphy Levels III and IV.

Xeromorphy Level III (culm with uppermost node up to one third of the way up) includes 2 species—*P. stepposa* and *P. skvortzovii* Prob.—xeromorphic derivatives of *P. palustris* and *P. nemoralis,* respectively. The species of this group are closely related both to one another and to species of Levels II and IV. All character state combinations were observed for species at this level too, though this group seems to be the most distinct (Fig. 10).

The species of Xeromorphy Level IV (culm with uppermost node up to one sixth of the way up, usually 1 cm above the base), being the most xeromorphic, are the most difficult to identify because they are the most similar to one another. In Siberia, this group consists of six species, two of them represented by two subspecies. The species forming this group are the most polymorphic and are connected by numerous intermediate populations. Characters such as height of the stem and the characters of the lemma and its callus pubescence (Table 2) are used to distinguish (nominally) the species. Rachilla pubescence and ligule length are characters rarely used in the taxonomy of species at this level. According to Tzvelev (1976) all these species have a glabrous or scabrous—but never pilose—rachilla. In addition to morphological differences, these species occur in different habitats: both subspecies of *P. attenuata* Trin. and *P. rangkulensis* Ovzc. inhabit alpine regions, both subspecies of *P. botryoides* Trin., *P. reverdattoi* Roshev., and *P. argunensis* Roshev. inhabit steppe, and *P. dahurica* Trin. is common to both steppe and alpine habitats. These characters can vary greatly and can be found in almost all parts of the region, though some unusual distributions were identified. Specimens with pubescence between the veins of the lemmas are absent in Buryatia. In western Siberia (Altai) they are found in alpine habitats only, in central Siberia (Khakassia) they are present both in alpine and lower steppes, while in eastern Siberia they are documented only in the lower elevation steppes. Specimens with a glabrous callus prevail in western Siberia.

Species and subspecies for this group are reported to have a unique distribution or at least unique habitats. To test this hypothesis, morphological characters were evaluated using discriminant analyses. In Siberia, xeromorphic species of *Stenopoa* exhibit almost all possible character combinations (Fig. 11). Only one suite of characters is not found in nature: tall plants with lemmas glabrous between the veins, glabrous callus, and a pilose rachilla. The remaining character combinations are found in almost all regions of Siberia, including alpine habitats and steppes. Only one taxon, *P. botryoides* subsp. *orientalis* Olon. from eastern Siberia, has a unique range. Both tall and dwarf plants are found throughout the region. However, in the alpine zone only dwarf plants were found, while at lower elevations both forms existed. It makes doubtful the possibility of discriminating *P. botryoides* from *P. attenuata* or *P. argunensis* from *P. attenuata* subsp. *tshuensis* (Serg.) Olon. on the basis of stem height.

Although such characters as lemma pubescence between the veins, callus and rachilla pubescence, and ligule length appear to vary greatly and unpredictably, the actual variability within and among populations had not been studied. Therefore, 44 populations from Altai, Western Tuva, Yenisei steppes, Southern Buryatia, Baikal, and the Chita and Yakutia districts were investigated, using 25–30 specimens from each population. The study showed that these characters vary within populations (Fig. 12) and cannot be used for the diagnosis of xeromorphic species of sect. *Stenopoa.* The correlation between character states and taxonomic identity has

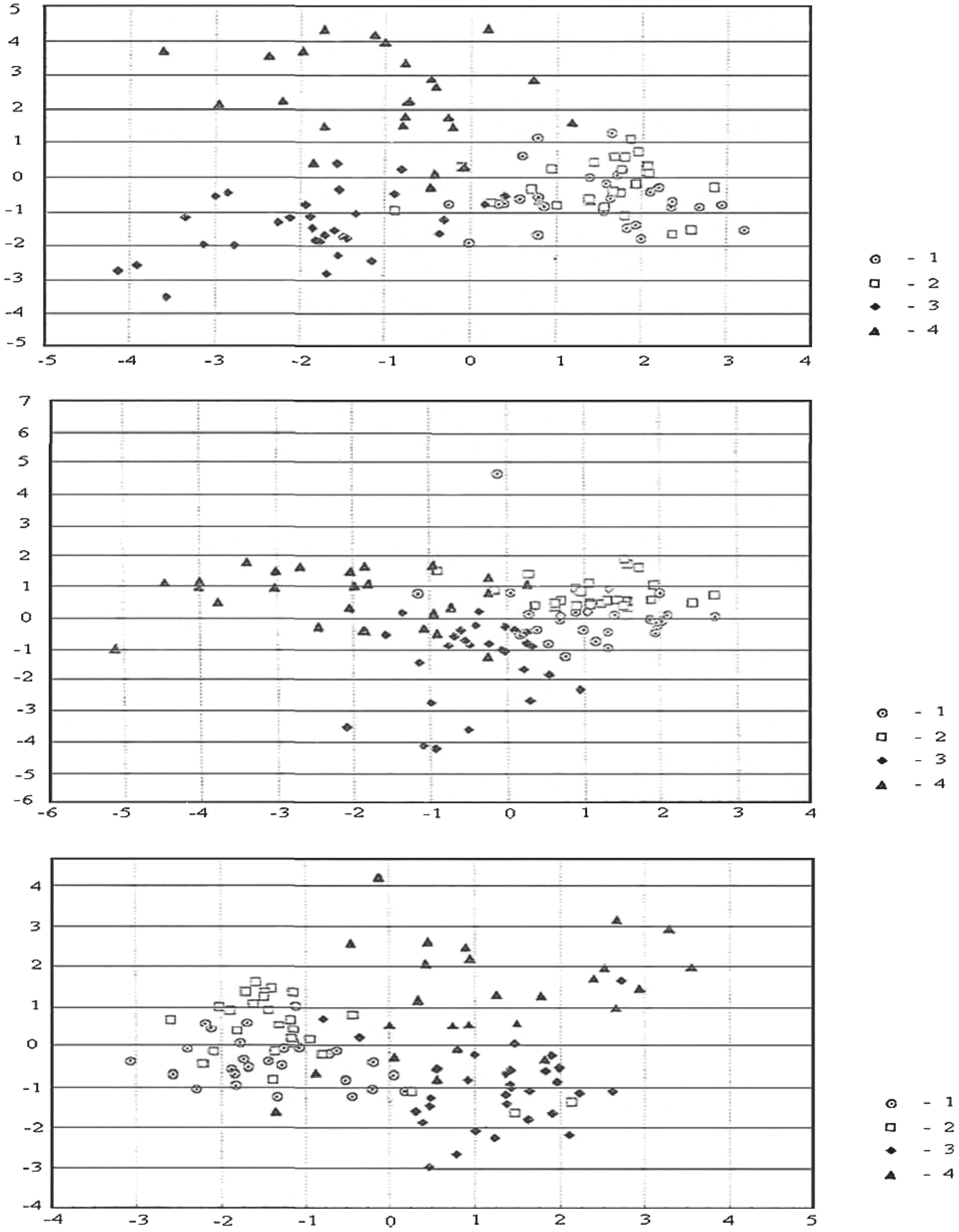

Fig. 9.—Discriminant analysis of 21 morphological characters for a *Poa palustris* × *P. nemoralis* × *P. urssulensis* population from Kotorovo, Western Siberia (x axis—canonical variable 1; y axis—canonical variable 2). (1) Birch wood at the top of the hill; (2) dry grassy slope; (3) fresh grassy slope; (4) wet meadow by the bank of a brook.

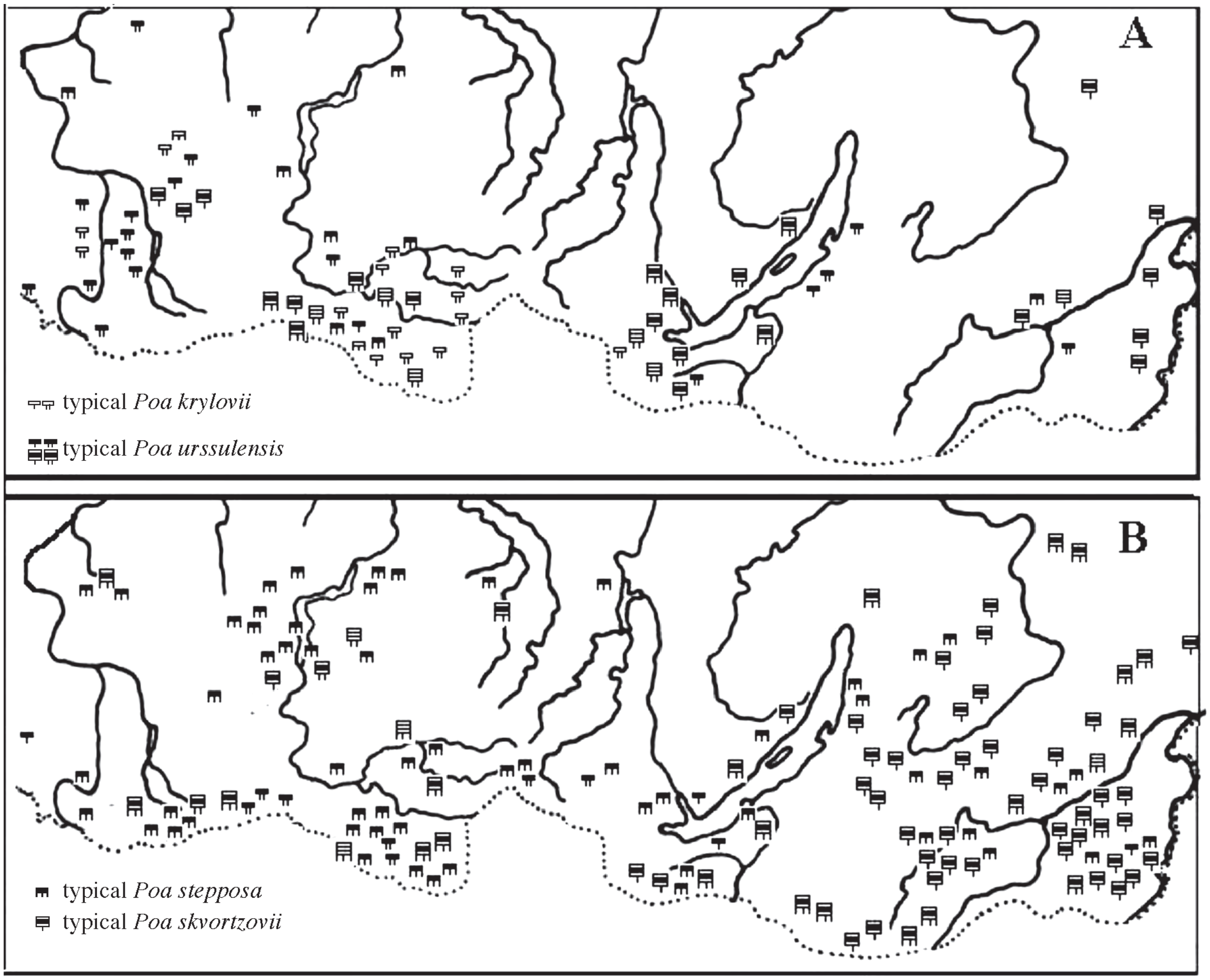

Fig. 10.—Distribution of callus, rachilla, and ligule characteristics for *Poa* sect. *Stenopoa* Xeromorphy Level II and III species in southern Siberia.

likely been lost because of hybridization. All species of sect. *Stenopoa,* mentioned above are closely related to one another, and inside this group it might be possible to designate 3–4 specific complexes.

Poa glauca s.l. is the most complicated taxon in this section and may be the result of hybridization of a xeromorphic species of *Stenopoa* with a species from another section. Analysis of the distribution of the four most important characters (pubescence between lemma veins, presence or absence of a tuft of hairs on the lemma callus, rachilla pubescence, and ligule length) showed that all characters and various combinations of characters were found throughout Siberia (Olonova 1993*a,* 1998, 2001*b*). The characters were correlated neither with ecological nor with geographical conditions in most cases (Fig. 13), but some trends could be noted. In northern Siberia the forms with pubescent lemmas prevail, while the frequency of samples with a pubescent rachilla is greater in Scandinavia. Populations of *P. glauca* show marked variability for these characters too. The study of morphological differentiation in *P. glauca* based on specimens from three geographical races (Scandinavian, northern Siberian and southern Siberian) showed great complexity among races, and divergence between the three races was significant. However, all morphological characters were

Table 2. The main morphological differences between Siberian Xeromorphy Level IV species of *Poa* sect. *Stenopoa.*

	Lemma between veins			
	Glabrous or scabrid		Pilose	
	Height greater than 25 (30) cm	Height less than 25 (30) cm	Height greater than 25 (30) cm	Height less than 25 (30) cm
Lemma callus				
Glabrous	*P. botryoides* subsp. *orientalis*	*P. daurica*	*P. reverdattoi*	—
With tuft of hair	*P. botryoides*	*P. attenuata*	*P. argunensis*	*P. attenuata* subsp. *tshuensis* *P. rangkulensis*

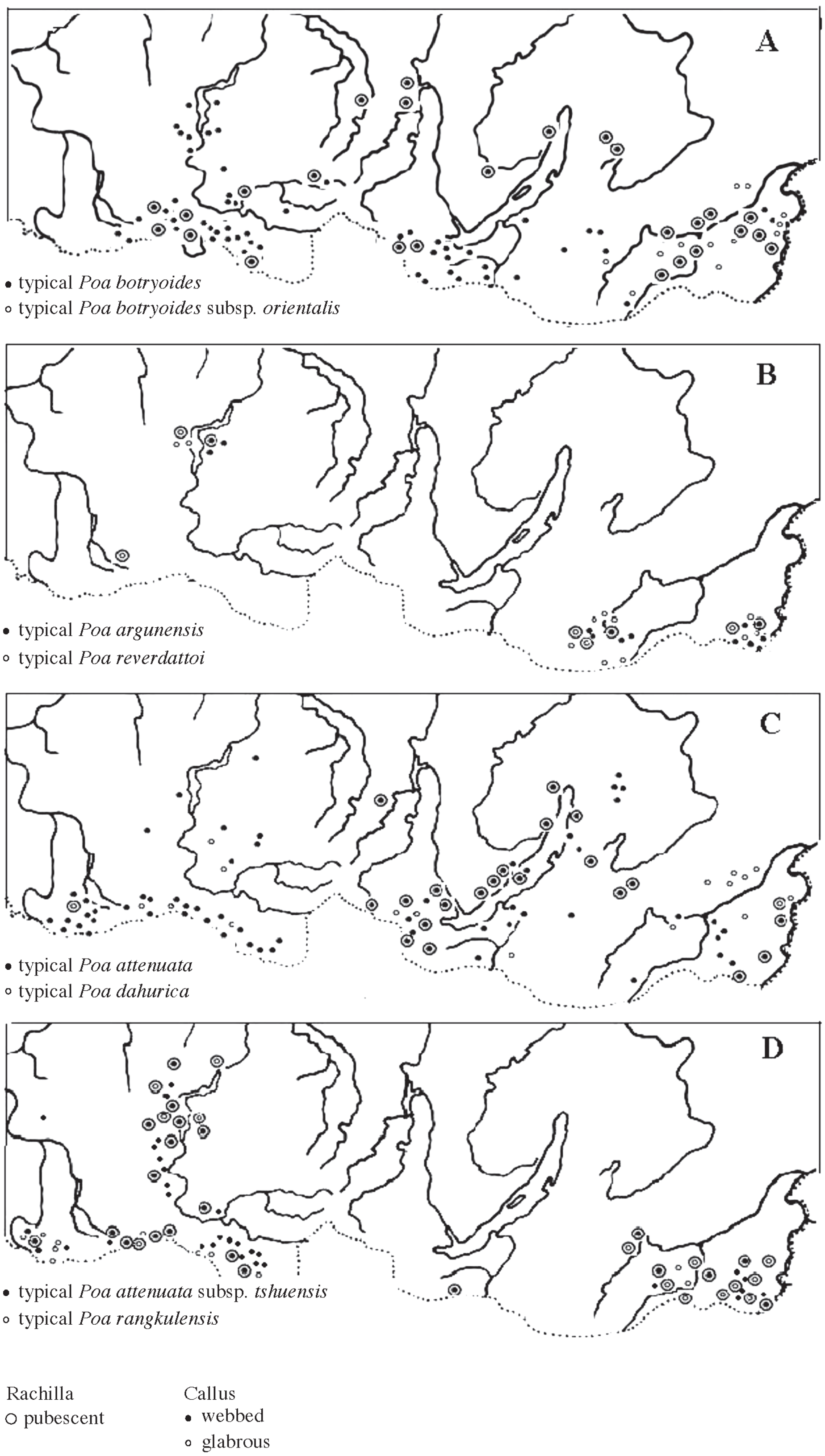

Fig. 11.—Distribution of callus, rachilla, and ligule characteristics for *Poa* sect. *Stenopoa* Xeromorphy Level IV species in southern Siberia.

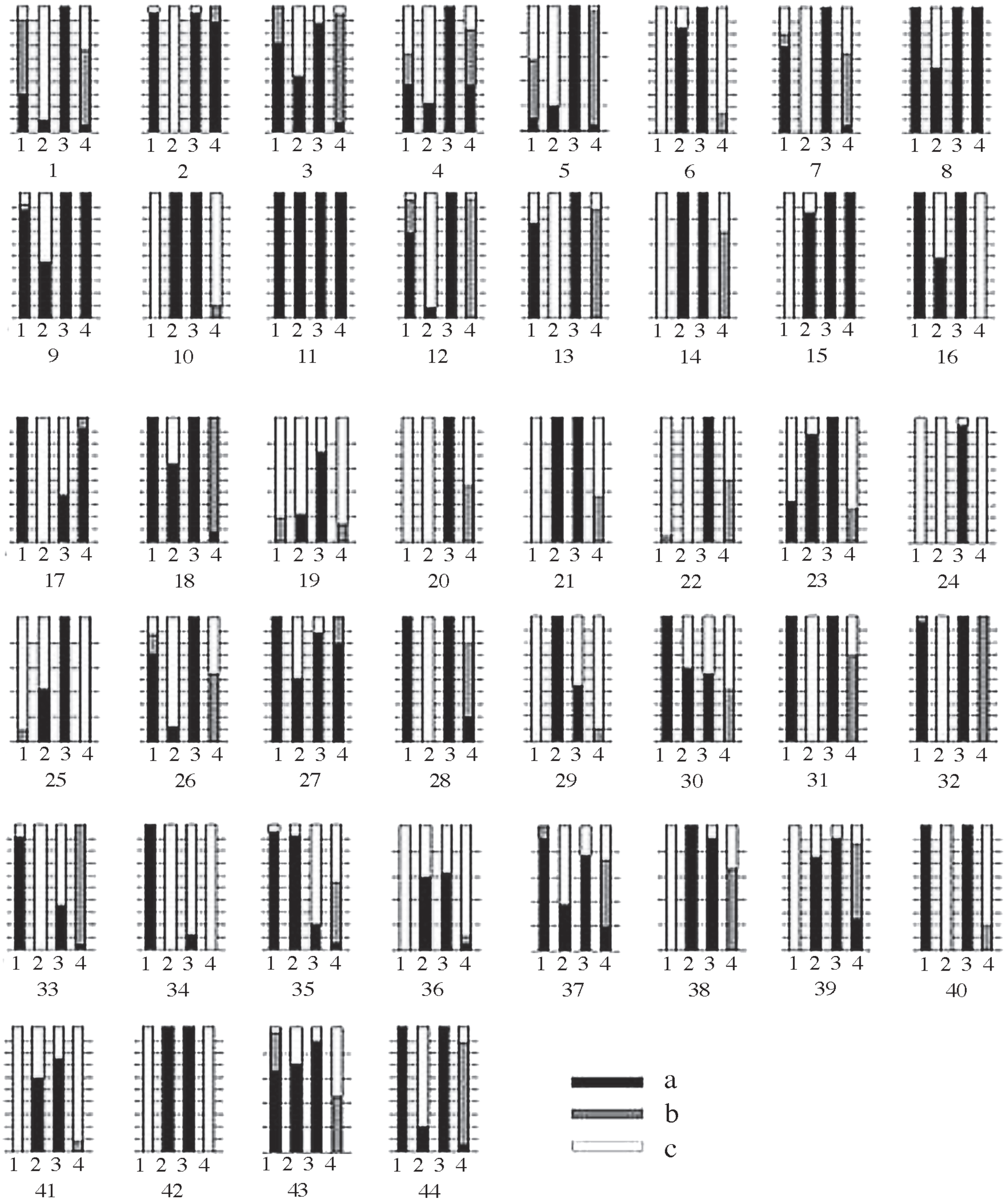

Fig. 12.—Frequencies of lemma, callus, rachilla, and ligule characters for 44 populations of xeromorphic Siberian *Poa* species. (1) Lemma pubescence between veins: (a) densely pubescent, (b) sparsely pubescent, (c) glabrous; (2) callus surface: (a) glabrous, (b) webbed; (3) rachilla pubescence: (a) glabrous, (b) pubescent; (4) ligule length: (a) <1 mm, (b) 1–2 mm, (c) ≥2 mm. Populations 1–12 Altai; 13–18 Western Tuva; 19–27 Yenisei; 28–31 Southern Buryatia; 32–36 Baikal; 37–43 Chita District; 44 Yakutia.

overlapping, arguing against subdivision of *P. glauca* into three species.

In conclusion, the most polymorphic Siberian species of bluegrass are *P. arctica* s.l., *P. smirnovii* s.l., *P. sibirica* s.l., *P. pratensis* s.l., *P. palustris* s.l., *P. nemoralis* s.l., and their numerous hybrids and derivatives *P. urssulensis* s.l., *P. attenuata* s.l., and *P. glauca* s.l. In Siberia, sect. *Stenopoa* is the most variable and represented not so much by separate morphologically isolated species as by hybrid-apomictic complexes, including species and taxonomic groups of obscure rank connected by numerous diverse populations. Many specimens in this section cannot readily be attributed to any species or subspecific taxon. They cannot be described as new species either because of the extraordinary variability of the main taxonomic characters. Most of these characters vary within populations, so they cannot be used for diagnosis of species. Variability of key morphological characters should be taken into account when describing new

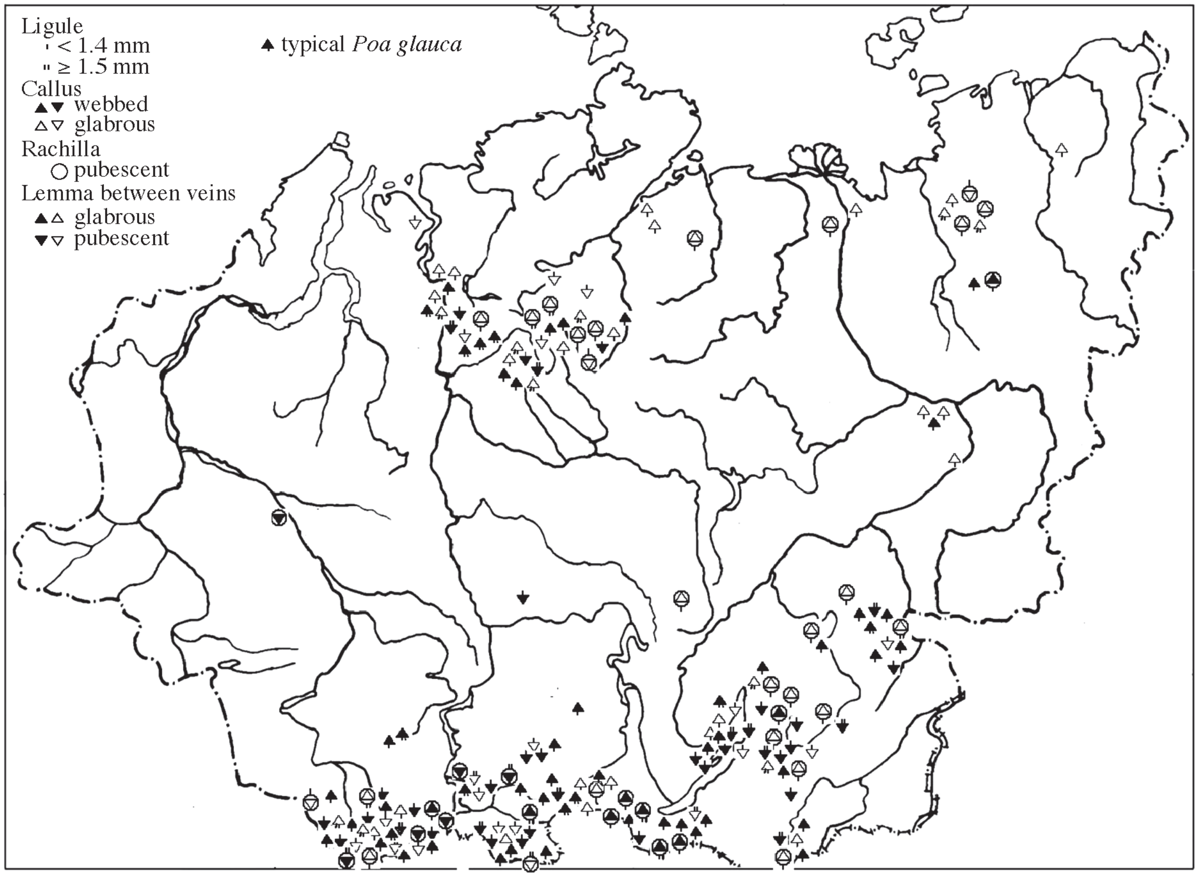

Fig. 13.—Distribution of callus, lemma, ligule, and rachilla characteristics for *Poa glauca* s.l. in Siberia.

species. Descriptions of taxa made on the basis of these characters may not reflect phylogeny, thus additional studies should be conducted to determine the rank and circumscription of these taxa.

The analysis of the distribution of various forms in Siberia has shown that the area with the greatest intraspecific variety of this genus is in the Altai Mountains (Olonova 1992, 1993*b*), a finding supported by the data of L. I. Malyshev and his colleagues regarding richness of species in the regions of Siberia (Malyshev et al. 2000). This information should be taken into account when planning species conservation work.

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