Status and Use of Important Native Grasses Adapted to Sagebrush Communities

Thomas A. Jones
Steven R. Larson

Abstract—Due to the emphasis on restoration, native cool-season grass species are increasing in importance in the commercial seed trade in the Western U.S. Cultivated seed production of these native grasses has often been hampered by seed dormancy, seed shattering, and pernicious awns that are advantageous outside of cultivation. Relatively low seed yields and poor seedling establishment have also restricted their cultivation. Most are members of the Triticeae tribe. Bunchgrasses include Snake River wheatgrass (*Elymus wawawaiensis*), bluebunch wheatgrass (*Pseudoroegneria spicata*), basin wildrye (*Leymus cinereus*), and squirreltail (*E. elymoide*s and *E. multisetus*). Rhizomatous grasses include western wheatgrass (*Pascopyrum smithii*), thickspike wheatgrass, and streambank wheatgrass (both *E. lanceolatus*), and beardless wildrye (*L. triticoides*). Important non-Triticeae native bunchgrasses include native bluegrasses (*Poa* spp.) and Indian ricegrass (*Achnatherum hymenoides*). These grasses may be either self-pollinated, cross-pollinated, or apomictic. These mating systems are reflected in the patterns of genetic variation characteristic of these species. At the USDA Agricultural Research Service (ARS) Forage and Range Research Laboratory at Utah State University, our goals are to understand distribution-wide patterns of genetic variation and to develop native cool-season grasses that are adapted to rangeland environments, are reflective of natural patterns of genetic variation, and are amenable to commercial seed production. To best accomplish these goals, we are attempting to develop a better understanding of the correlation between *genetic variation* and *ecological adaptation* at a variety of levels ranging from the whole plant to the DNA molecule. Besides ourselves, plant materials of these species have been released by USDA Natural Resources Conservation Service (NRCS) Plant Materials Centers (Bridger, MT; Aberdeen, ID; Pullman, WA; Lockeford, CA; Los Lunas, NM), Forest Service Shrub Sciences Laboratory (FS SSL) (Provo, UT), and Upper Colorado Environmental Plant Center (UCEPC) (Meeker, CO).

Thomas A. Jones and Steven R. Larson are Research Geneticists at the USDA-Agricultural Research Service Forage and Range Research Laboratory, Logan, UT 84322-6300 U.S.A., FAX: (435) 797-3075, e-mail: tomjones@cc.usu.edu, stlarson@cc.usu.edu

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Squirreltail (*Elymus elymoides* [Raf.] Swezey and *E. multisetus* [J.G. Smith] M.E. Jones)

Squirreltail is a short-lived perennial grass that is a prominent understory species in the sagebrush steppe community (Jones 1998). Squirreltail is a complex of five taxa, all of which are found in southwestern Idaho (Wilson 1963). Each taxon can be easily identified by spike morphology using a dichotomous key. *E. elymoides* ssp. *elymoides* is the most common and widespread taxon and is probably most closely related to *E. elymoides* ssp. *californicus*, which is prominent on the eastern slope of the Sierra Nevadas. *E. elymoides* ssp. *brevifolius* is especially common in the central and southern Rockies where plants and seeds are exceptionally large; however, these populations are conspicuously different from *E. elymoides* ssp. *brevifolius* plants originating in the Northwest. *E. elymoides* ssp. *hordeoides* is the most diminutive of the group, and probably the least common overall. *E. multisetus*, commonly called big squirreltail, is often considered a distinct species from the others, a position supported by our molecular data (Larson and others 2003). It is most common in the Northwest.

Squirreltail is a self-pollinated tetraploid ($2n = 28$) that genetically consists of the **St** and **H** genomes, which include 14 chromosomes (7 pairs) each. These two genomes are characteristic of *Elymus* worldwide and are indicative of the evolutionary history of this polyploid genus. The **St** genome originated from the bluebunch wheatgrasses (*Pseudoroegneria* spp.) and the **H** genome from the barleys (*Hordeum* spp.). Most *Elymus* species are predominately self-pollinating, including blue wildrye (*E. glaucus*), slender wheatgrass (*E. trachycaulus*), and Canada wildrye (*E. canadensis*). Prominent cross-pollinated exceptions include thickspike wheatgrass, Snake River wheatgrass, and the introduced species, quackgrass (*E. repens*) (Jensen and Asay 1996; Jensen and others 1990).

Squirreltail germplasms released to date are Sand Hollow (*E. multisetus*; Emmett, ID) (Jones and others 1998), Toe Jam Creek (*E. elymoides ss*p. *californicus*; Tuscarora, NV), Fish Creek (*E. elymoides* ssp. *elymoides*; Carey, ID), and Tusas (*E. elymoides* ssp. *brevifolius*; multiple locations in New Mexico). In addition, several seed growers are producing local proprietary seed sources.

Table 1—Seed production acreages of all classes of certified seed in the United States from 1996 to 2000 for native cool-season grasses commonly seeded on rangelands in the Intermountain Region[a].

Species/Cultivar	1996	1997	1998	1999	2000	Mean
Western wheatgrass	**934**	**959**	**1,626**	**3,029**	**3,371**	**1,984**
Rosana	366	355	992	1,593	1,662	994
Arriba	209	255	286	919	1,055	545
Barton	273	272	272	432	548	359
Rodan	46	37	36	45	66	46
Flintlock	40	40	40	40	40	40
Thickspike wheatgrass	**931**	**1,196**	**1,135**	**2,183**	**3,666**	**1,822**
Critana	459	430	501	1,086	1,840	863
Sodar	345	505	299	596	905	530
Bannock	127	229	312	453	505	325
Schwendimar	0	0	23	48	416	97
Elbee	0	32	0	0	0	6
Native bluegrasses	**469**	**560**	**956**	**1,267**	**1,721**	**995**
Sherman	394	494	836	1,239	1,623	917
Canbar	75	66	120	28	98	77
Snake River wheatgrass/Secar	**313**	**292**	**600**	**949**	**2,054**	**842**
Basin wildrye	**512**	**416**	**572**	**851**	**941**	**658**
Magnar	371	369	445	526	448	432
Trailhead	141	47	127	325	493	227
Bluebunch wheatgrass	**126**	**537**	**603**	**586**	**1,260**	**622**
Goldar	49	422	473	401	965	462
Whitmar	77	115	130	185	295	160
Indian ricegrass	**190**	**126**	**196**	**307**	**944**	**353**
Nezpar	129	107	115	133	499	197
Rimrock	26	3	65	55	251	80
Paloma	35	16	16	119	194	76
Beardless wildrye	**59**	**74**	**93**	**0**	**65**	**58**
Shoshone[b]	59	74	91	0	65	58
Rio	0	0	2	0	0	0
Squirreltail/Sand Hollow	**0**	**0**	**0**	**8**	**8**	**3**
Proprietary (all species)	**30**	**419**	**0**	**289**	**2**	**148**
Total	**3,564**	**4,579**	**5,781**	**9,469**	**14,032**	**7,485**

[a]Figures compiled from AOSCA (1996–2000).
[b]Actually the introduced *Leymus multicaulis*.

Squirreltail exhibits a high degree of racial differentiation, as described for other species by Clausen and others (1947). We evaluated squirreltail accessions (27 in data set 1, 47 in data set 2) for a battery of ecological traits, which could be used to characterize the ecological relationships between and within taxa (Jones and others 2003). For data set 1, 13 traits were measured, including days to seedling emergence, length of the seedling's first leaf, total plant dry matter, root-to-shoot ratio, leaf area, specific leaf area, root length, specific root length, heading date, seed mass, emergence index (from 20 mm), emergence index (from 60 mm), activity of the nitrate reductase enzyme, plant height, and heading date. For data set 2, these same traits were measured except leaf area, specific leaf area, the emergence indices, and nitrate reductase activity. Seed mass was also measured for data set 2.

In data set 1, *E. multisetus* accessions showed greatest seedling vigor and root development. *E. elymoides* ssp. *elymoides* accessions had lowest seed mass and earliest phenological development. *E. elymoides* ssp. *brevifolius* had thickest leaves and slowest germination. Taken together, the 13 traits clearly demarcated the three groups of accessions. In data set 2, *E. elymoides* ssp. *elymoides*, *E. elymoides* ssp. *brevifolius*, and *E. multisetus* accessions again separated discretely, but *E. elymoides* ssp. *brevifolius* accessions separated into three subgroups. Early (subgroup B) and late-maturing (subgroup A) accessions from the Rocky Mountains separated apart from each other and also apart from intermediate-maturing accessions from southwestern Idaho (subgroup C).

Native Bluegrasses (*Poa secunda* Presl.)

Native bluegrasses also serve as important understory components of the sagebrush steppe vegetation. A large number of scientific names (*P. secunda, P. ampla, P. canbyi, P. gracillima, P. incurva, P. juncifolia, P. nevadensis, P. scabrella,* and *P. curtifolia*) have been given to various of the native bluegrasses, but Kellogg (1985, 1990) combined them all into *P. secunda*, except *P. curtifolia*, an endemic from central Washington. Kellogg argued that, because morphological variation among these entities is continuous,

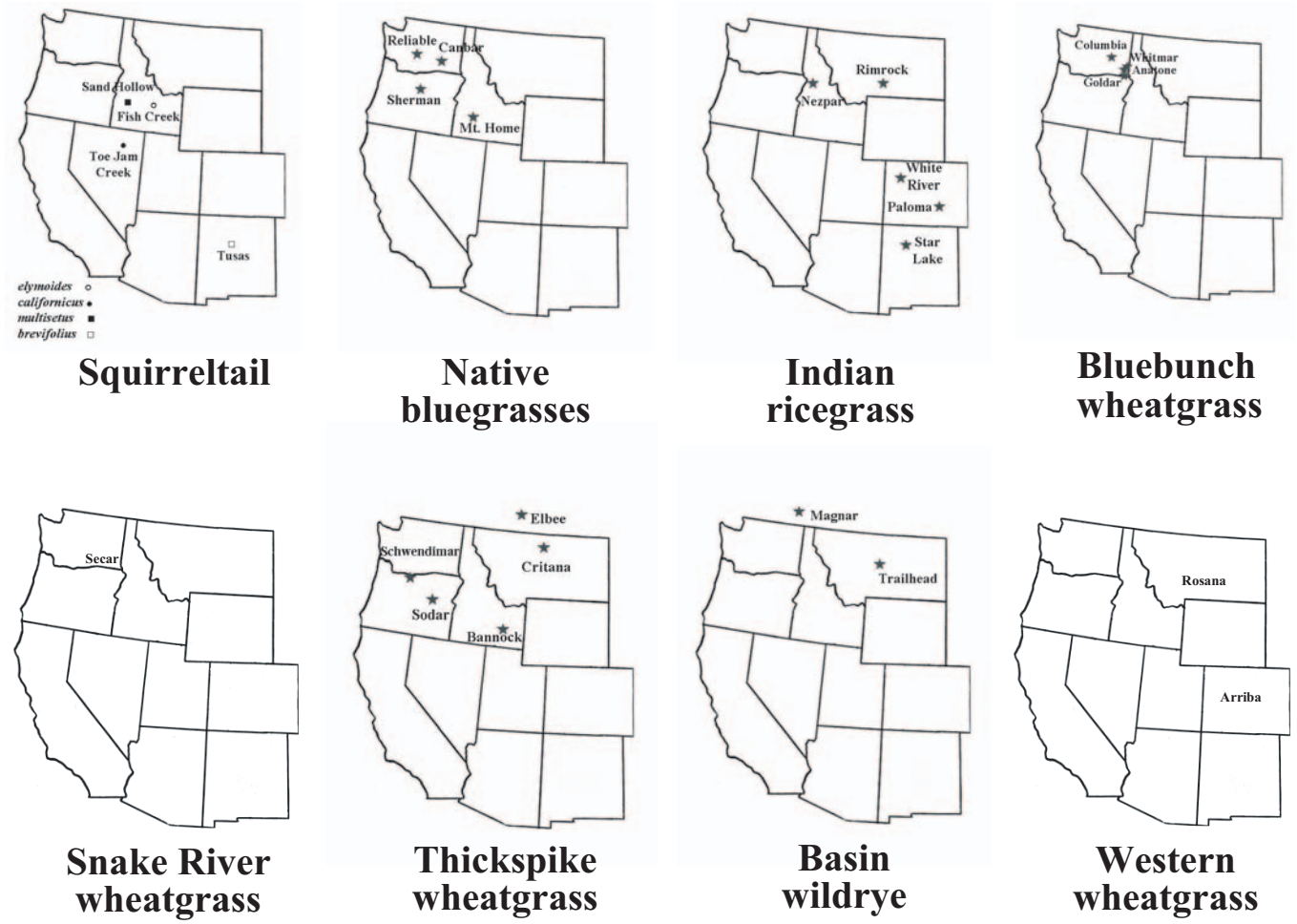

Figure 1—Points of origin of plant materials of squirreltail, native bluegrasses, Indian ricegrass, bluebunch wheatgrass, Snake River wheatgrass, thickspike wheatgrass, basin wildrye, and western wheatgrass.

any attempt to subdivide this group would be arbitrary. Nevertheless, she tolerated the retention of common names within the group.

Releases are 'Canbar' (WA), commonly known as "canby bluegrass," 'Sherman' (OR), commonly known as "big bluegrass" because of its larger stature and longer leaves, and Reliable germplasm (Yakima, WA), commonly known as "Sandberg bluegrass" (fig. 1). Certified seed production acreage of Sherman has greatly increased in recent years, while acreage of Canbar remains low (table 1). Sandberg bluegrass, a diminutive plant, mimics the phenology of cheatgrass. It flowers at least as early as cheatgrass and senesces upon seed ripening in late spring or early summer.

Taxonomic confusion in *Poa* is enhanced by facultative apomixis, an asexual form of reproduction by seed that may preempt sexual reproduction (Kellogg 1987). This means that new genetic variation generated by sexuality can be replicated in large quantities at or close to 84 chromosomes, making them dodecaploids (12*x*), but big bluegrass plants usually have about 63 chromosomes (9*x*) (Hartung 1946). Obviously, this odd number is something that could only be fixed asexually. The frequency with which apomixis occurs probably varies with genotype, but few data have been collected to determine the mean and range among genotypes. Do 63-chromosome plants arise from hybridization of 84-chromosome plants and 42-chromosome (6*x*) plants? Do 63-chromosome plants have a consistently higher level of apomixis than 84-chromosome plants or do they reproduce sexually, spinning off more odd chromosome-numbered plants? We believe a better understanding of these issues would provide a more complete understanding of the taxonomy of the native *Poa* complex.

We used amplified fragment length polymorphism (AFLP) analysis to characterize genetic diversity within Canbar, Sherman, Mountain Home (ID), and Reliable and genetic divergence between them (Larson and others 2001). AFLP methodology involves using sets of DNA primers to copy DNA fragments of different lengths that are then multiplied via the polymerase chain reaction. The resultant array serves as a "fingerprint" of the plant's genotype. Genetic diversities of the wildland collections, Mountain Home and Reliable, are similar to one another, but much greater than Canbar (fig. 2). Sherman shows no genetic diversity whatsoever, which is excellent evidence for apomixis and hints at

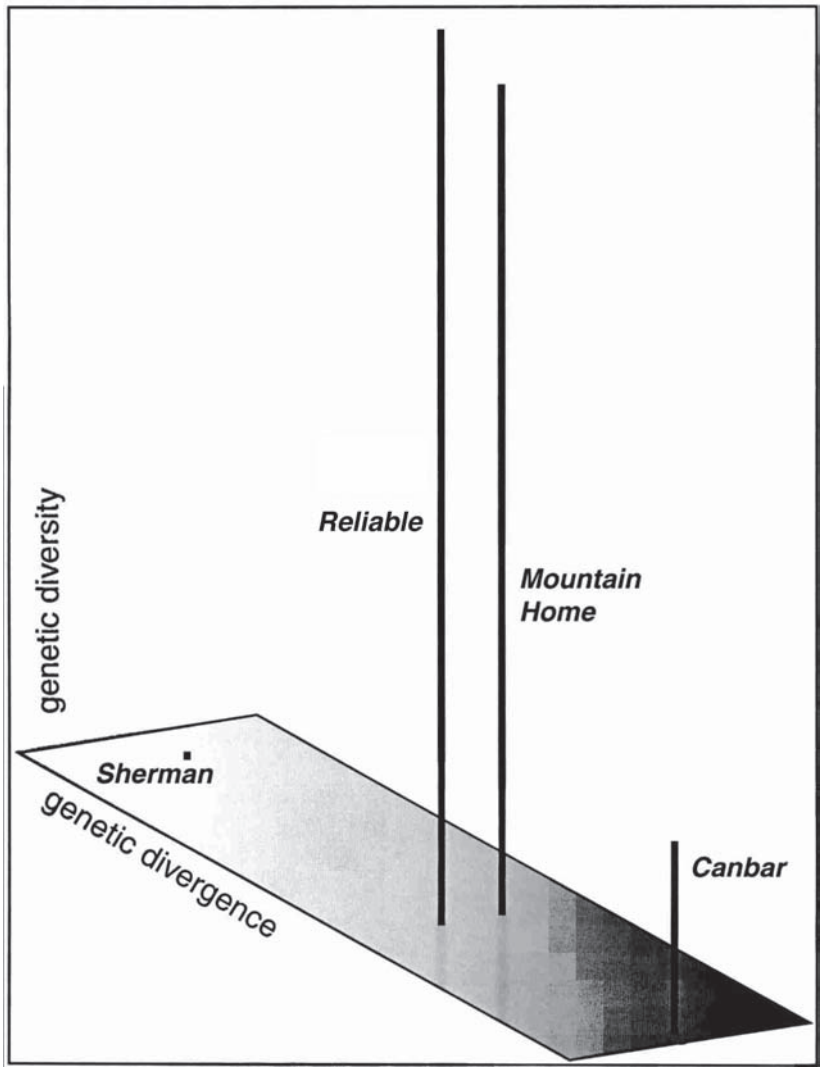

Figure 2—Genetic divergence (plane) and genetic diversity (vertical) of 'Sherman' big bluegrass, 'Canbar' canby bluegrass, and Reliable and Mountain Home Sandberg bluegrass germplasms.

the second question posed in the previous paragraph. Genetic divergence (separation on the plane) between Mountain Home and Reliable is small. These Sandberg bluegrasses are intermediate to Canbar (another 84-chromosome genotype) and Sherman ($2n$ = 63), but more similar to the former.

Indian Ricegrass (*Achnatherum hymenoides* [Roem. & Schult.] Barkworth)

Indian ricegrass is a short-lived perennial bunchgrass that favors light-textured soils, especially fine sandy loams, sandy loams, loamy sands, and sands (Jones 1990). It is found in especially arid environments in the Intermountain Region as well as the Great Plains. Though it is a cool-season C_3 grass, it grows longer into the summer heat than native wheatgrasses and wildryes. This species exhibits great genetic diversity between and within populations. Seed polymorphism is common in Indian ricegrass (Jones and Nielson 1996). Larger seeds typically have greater seed dormancy than the smaller seeds (Young and Evans 1984). These two seed morphs are produced on different plants, which usually differ in other respects as well. Like squirreltail, Indian ricegrass is highly self-pollinating.

Releases are 'Paloma' (Pueblo, CO), 'Nezpar' (White Bird, ID), 'Rimrock' (Billings, MT), and Star Lake (McKinley County, NM), and White River (Rio Blanco County, CO) germplasms (fig. 1). Certified seed production acreage has increased in recent years (table 1).

Bluebunch Wheatgrass (*Pseudoroegneria spicata* [Pursh] A. Löve)

Bluebunch wheatgrass is widespread in the Intermountain Region, foothills, and open slopes of the Rocky Mountains and the northern Great Plains. It is probably most frequent in the region where Washington, Oregon, and Idaho converge. Many populations have been reduced or extirpated because this grass is both palatable and highly susceptible to overgrazing in the spring. Populations may be awned or awnless or are often mixed. Cultivars include the awnless Whitmar (Colton, WA) and the awned Goldar

(Umatilla National Forest, Asotin County, WA) (fig. 1). Certified seed production acreage of Goldar has greatly exceeded Whitmar in recent years. 'Secar' (Lewiston, ID) was released as a bluebunch wheatgrass, but was later discovered to be the newly recognized Snake River wheatgrass (see below). P-7, a multiple-origin polycross of 25 accessions, and Anatone (WA) are recent germplasm releases. Our work at ARS has emphasized selection for grazing tolerance and improved seed production.

Bluebunch wheatgrass may be either diploid ($2n = 14$) or tetraploid ($2n = 28$), with the diploid being far more common. Only the **St** genome is found in bluebunch wheatgrass; it is present in single or double dose depending on ploidy. Tetraploids appear to be most frequent in mesic regions such as southern interior British Columbia and parts of southeastern Washington. Accessions may be mixed for ploidy, but this is not visually obvious because the two ploidys are morphologically indistinguishable. In the past, chromosome number has been measured directly using root-tip cells, but today we typically measure it indirectly using flow cytometry, a much more rapid and convenient technique.

While bluebunch wheatgrass is the only New World species of *Pseudoroegneria*, other taxa are known in the Old World (Jensen and others 1995). These Old World taxa can be morphologically indistinguishable from bluebunch wheatgrass and can be successfully hybridized with it. Both the pollen and the seed of these hybrids are virtually sterile.

AFLP analysis was used to measure genetic diversity and divergence (see Sandberg bluegrass, above) in and among Goldar, Whitmar, and P-7 (Larson and others 2000). As expected, P-7, the multiple-origin polycross, had greater diversity than either Goldar or Whitmar, both of which originated from single sites in southeastern Washington (fig. 3). Divergence was greatest between Goldar and Whitmar, with P-7 being more similar to Goldar than to Whitmar.

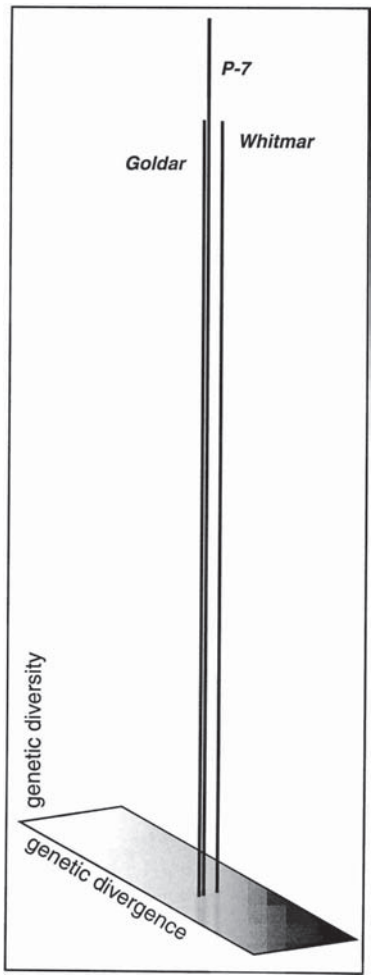

Figure 3—Genetic divergence (plane) and genetic diversity (vertical) of 'Goldar' and 'Whitmar' bluebunch wheatgrass and the P-7 multiple-origin polycross bluebunch wheatgrass germplasm.

Snake River Wheatgrass (*Elymus wawawaiensis* J. Carlson & Barkworth)

Relative to bluebunch wheatgrass, Snake River wheatgrass has a limited distribution within eastern Oregon and Washington and northern and central Idaho. Its frequency has likely been severely reduced because of the high degree of cultivation in that region. Snake River wheatgrass is a bunchgrass with excellent seed production and drought tolerance. It has performed very well in seedings in the Snake River Plain, despite the fact that it is not native to southern Idaho. The most southerly material of which we have knowledge originates from near Cambridge, ID. Snake River wheatgrass is less susceptible to overgrazing than bluebunch wheatgrass (Jones and Nielson 1997). At ARS we are selecting for clipping tolerance to improve its tolerance to grazing.

Until 1985, Snake River wheatgrass was confused with bluebunch wheatgrass (Carlson and Barkworth 1997). In 1980 'Secar' (fig. 1) was released as a bluebunch wheatgrass. Snake River wheatgrass is an **StH** species, thus its hybrids with bluebunch wheatgrass, an **St** species, are cytologically irregular (Carlson 1986). However, hybrids of Snake River wheatgrass with thickspike wheatgrass, another **StH** species, are cytologically regular (Jones and others 1995). It was these observations that initially justified the recognition of Snake River wheatgrass as a separate species apart from bluebunch wheatgrass and its placement in the genus *Elymus* rather than *Pseudoroegneria*. Traditionally, analysis of chromosome pairing in hybrids has been used to determine genomic composition, but we now utilize the FISH (fluorescent in situ hybridization) technique. FISH utilizes DNA-binding dyes that are specific to particular genomes. When used in combination, these dyes generate red or yellow fluorescence, depending on the genome. Intermediate genomes fluoresce orange.

While Snake River and bluebunch wheatgrass share a superficial resemblance, there are many features that distinguish the two from each other (Jones and others 1991). The spike of Snake River wheatgrass is more compact than bluebunch wheatgrass, primarily because the rachis internodes of Snake River wheatgrass are shorter. Snake River wheatgrass is always awned, whereas bluebunch wheatgrass may be awned or awnless. Snake River wheatgrass is always tetraploid ($2n = 28$), while bluebunch wheatgrass is primarily diploid and occasionally tetraploid ($2n = 14, 28$).

Snake River wheatgrass seed is considerably smaller than bluebunch wheatgrass seed. Snake River wheatgrass glumes are more lanceolate in shape than the nontapered bluebunch wheatgrass glumes, but size of the glumes is not diagnostic. Certified seed production acreage of Snake River wheatgrass has greatly increased in recent years and now greatly exceeds that of bluebunch wheatgrass (table 1).

Thickspike Wheatgrass (*Elymus lanceolatus* [Scribn. & J.G. Smith] Gould)

Thickspike wheatgrass is found throughout the Intermountain Region and the northwestern Great Plains, but is most common in Wyoming. Thickspike wheatgrass is a cross-pollinating rhizomatous grass closely related to Snake River wheatgrass. It is generally found on loamy to sandy soils. Like Snake River wheatgrass, thickspike wheatgrass is an **StH** tetraploid ($2n = 28$). Thickspike wheatgrass is much more tolerant of overgrazing than either Snake River wheatgrass or bluebunch wheatgrass. Cultivars appropriate for our region include Bannock (OR, ID, WA), Schwendimar (The Dalles, OR), Elbee (AB, SK), Critana (Havre, MT), and Sodar (Canyon City, OR) (fig. 1). Thickspike wheatgrass rivals western wheatgrass as the most important species for certified seed production acreage (table 1). In recent years Critana has been the leading cultivar, followed by Sodar and Bannock.

Sodar is known in the trade as "streambank wheatgrass," technically a botanical variety of thickspike wheatgrass (Dewey 1969). In Canada, thickspike wheatgrass is known as "northern wheatgrass."

Basin Wildrye (*Leymus cinereus* [Scribn. & Merr.] A. Löve)

Basin wildrye is a large-statured bunchgrass that is prominent in the Intermountain region. It is valued for winter grazing and for the shelter it provides during calving. In the Snake River Plain, basin wildrye is often found in locations with deep soils and high water-holding capacity. Basin wildrye has two chromosome races, tetraploid ($2n = 28$) and octoploid ($2n = 56$), that feature the **Ns** and **Xm** genomes in single or double dose, respectively. The **Ns** genome originated in *Psathyrostachys*, the Russian wildryes, but the origin of the **Xm** genome is uncertain.

The octoploid race, characterized by more robust plants that exhibit a glaucous blue color under drought conditions, is found in central and northeastern Oregon, northern Idaho, eastern Washington, and interior British Columbia. The tetraploid race, with somewhat smaller plants that remain green (rather than turning blue) in response to drought, is found in Central and southeastern Oregon, southern Idaho, Nevada, Utah, Colorado, Wyoming, Montana, Alberta, and Saskatchewan. Magnar is an octoploid cultivar (BC) and Trailhead is a tetraploid cutivar (Roundup, MT) (fig. 1). Magnar is the older cultivar, but its certified seed production acreage has remained stagnant in recent years (table 1). Trailhead's acreage has greatly increased in recent years and it now is equal to Magnar's. ARS is assembling several accessions into a multiple-origin polycross oriented towards northern Nevada, similar to the approach used in the development of P-7 bluebunch wheatgrass.

Beardless Wildrye (*Leymus triticoides* [Buckley] Pilger)

Beardless wildrye is a rhizomatous corollary to the bunchgrass basin wildrye in the genus *Leymus*, much as thickspike wheatgrass is to Snake River wheatgrass in the genus *Elymus*. Beardless wildrye is most common in northern Nevada, eastern Oregon, and northeastern California. It is an important riparian species, but it is also adapted to arid upland sites. Beardless wildrye and basin wildrye often occupy the same site and hybrids are common in such locations. Beardless wildrye has very high levels of seed dormancy, even higher than Indian ricegrass, a feature that is not prominent in basin wildrye. The only cultivar of beardless wildrye is Rio (Stratford, CA), which is propagated commercially by rhizomes because of its poor germination. 'Shoshone' is prominent in the seed trade where it is known as beardless wildrye, but it is now known to be *Leymus multicaulis*, an introduced species. *Leymus triticoides* and *L. multicaulis* are easily distinguished when the two species are grown side-by-side. Shoshone certified seed acreage has not increased in recent years (table 1).

Western Wheatgrass (*Pascopyrum smithii* [Rydb.] A. Löve)

Western wheatgrass is a cross-pollinating rhizomatous grass like thickspike wheatgrass. These two grasses are often confused, but they may be distinguished on the basis of glume shape. The glume of western wheatgrass is asymmetrical, while the thickspike wheatgrass glume is symmetrical. However, determination of ploidy is the most foolproof method to separate these grasses; thickspike wheatgrass is always tetraploid ($2n = 28$) and western wheatgrass is always octoploid ($2n = 56$) (Dewey 1975).

Western wheatgrass is believed to have originated from hybridization of thickspike wheatgrass and beardless wildrye (Dewey 1975). Western wheatgrass combines the **St** and **H** genomes of *Elymus* with the **Ns** and **Xm** genomes of *Leymus*. The frequency and distribution of western wheatgrass exceed either of its parents. Western wheatgrass is rhizomatous because both of its parents are rhizomatous. Western wheatgrass has an intermediate level of seed dormancy because beardless wildrye has high seed dormancy and thickspike wheatgrass does not exhibit seed dormancy. Compared to thickspike wheatgrass, western wheatgrass is more rhizomatous, better adapted to heavier soils, and less adapted to arid conditions.

All cultivars of western wheatgrass originate in the Great Plains. The two most widely used in the Intermountain Region are Rosana (Forsyth, MT) to the north and Arriba (Flagler, CO) to the south (fig. 1). Certified seed production acreage has increased greatly in recent years (table 1). Rosana is the leading cultivar (table 1). Western wheatgrass and thickspike wheatgrass acreages are similar and are greater than those of other species discussed herein.

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