Phytologia (October 1997) 83(4):312-330.

ELYMUS WAWAWAIENSIS: A SPECIES HITHERTO CONFUSED WITH *PSEUDOROEGNERIA SPICATA* (TRITICEAE, POACEAE)

Jack R. Carlson[1] & Mary E. Barkworth[2]

[1]Natural Resources Conservation Service, Fort Collins, Colorado 80526 U.S.A.
[2]Intermountain Herbarium, Department of Biology, Utah State University, Logan, Utah 84322-5305 U.S.A.

ABSTRACT

Elymus wawawaiensis, *spec. nov.*, is native to the valleys of the Snake River and its tributaries in Washington and northern Idaho. It resembles, and was originally confused with, *Pseudoroegneria spicata*, but differs morphologically in having narrower, acuminate to aciculate glumes, a more imbricate spike, and glabrate basal leaf sheaths. It differs cytologically in being an allotetraploid that combines the **St** and **H** genomes, like other North American species of *Elymus*, rather than an **St** diploid or autotetraploid, as are all species of *Pseudoroegneria*. *Elymus wawawaiensis* is considered a useful species for range improvement. A cultivar of the species, 'Secar', has been distributed by the U.S.D.A. under the name Snake River Wheatgrass.

KEY WORDS: *Elymus, Pseudoroegneria*, wheatgrass, Triticeae, Poaceae, plant geography

INTRODUCTION

Pseudoroegneria spicata (Pursh) A. Löve [= *Agropyron spicatum* (Pursh) Scribner & J.G. Sm.] is a common grassland species in western North America. It grows in a wide range of communities, ranging from those of arid habitats where it occurs with *Poa secunda* J. Presl and *Artemisia tridentata* Nutt., to those of more mesic habitats dominated by *Pinus ponderosa* Lawson & C. Lawson or *Pseudotsuga menziesii* (Mirbel) Franco. Several years ago, Dewey (1982) noted that there appeared to be more than one biological element in *Pseudoroegneria spicata*. He commented in particular on a tetraploid accession from southeastern Washington (PI 285272) that differed in its general aspect and heat tolerance from most accessions of *Pseudoroegneria spicata* and formed sterile hybrids when crossed with typical accessions.

More extensive investigation (Carlson 1986), involving several populations of typical *Pseudoroegneria spicata* and additional populations resembling the distinctive accession revealed that the atypical populations are allotetraploids that combine the St genome of *Pseudoroegneria* with the H genome of wild barley (genome designations according to Wang *et al.* 1996). In this they resemble most native North American species of *Elymus* (Dewey 1984), but differ from typical plants of *P. spicata* (and other species of *Pseudoroegneria*), all of which are diploids or autotetraploids. There are no known species of *Elymus* that resemble the distinctive populations. These observations indicate that the distinctive populations should be treated as a new taxon. The purpose of this paper is to substantiate this assertion, characterize the new taxon, and provide it with an appropriate name. In anticipation of the conclusion, we refer to the new taxon as *Elymus wawawaiensis*. For lack of a valid scientific name, those working with it have, until now, referred to it as Snake River Wheatgrass (*e.g.*, Jones *et al.* 1991).

MATERIALS AND METHODS

The materials examined included plants from native populations of *Pseudoroegneria spicata*, *Elymus wawawaiensis*, and *E. lanceolatus* (Scribner & J.G Sm.) Gould, plants grown in uniform gardens from seed accessions obtained during the field studies or through the U.S.D.A., and herbarium specimens at OSC, US, UTC, and WS (herbarium codes from Holmgren *et al.* 1990). Plants of *P. spicata* may have lemmas with strongly divergent awns or lemmas that are essentially unawned. The two variants sometimes occur together, but uniform populations of one or other variant are common. The native populations used in this study consisted of uniformly awned or unawned plants. The seed accessions were also obtained from uniform populations. The emphasis in the morphological studies was on the comparison with *P. spicata* primarily because of the similarity between *P. spicata* and *E. wawawaiensis*, but also because of the Soil Conservation Service's [now the Natural Resources Conservation Service] interest in evaluating the biological diversity within *P. spicata*. We know of no species of *Elymus*, as we interpret that genus, that resembles *E. wawawaiensis*. *Elymus lanceolatus* was included because it grows in the vicinity and can form fertile hybrids with *E. wawawaiensis* although no naturally occurring hybrids were found.

Morphological Studies.--Plants from accessions of *Pseudoroegneria spicata*, *Elymus wawawaiensis*, and *E. lanceolatus* were grown at each of four sites: Evans Farm, Logan, Utah; Utah State University Deer Pen plots, Logan, Utah; Oregon State University Branch Experiment Station, Moro, Oregon; and Oregon State University greenhouse, Corvallis, Oregon. Each accession consisted either of seed from an undetermined number of wild plants growing at a single locality or of seed belonging to a recognized cultivar. The accessions included 37 of *Pseudoroegneria spicata*, 10 of *Elymus wawawaiensis*, 4 of *E. lanceolatus*, and 1 of an artificial cross between *P. spicata* and *E. lanceolatus*. The accessions of *E. lanceolatus* included two awned accessions, i.e., *E. lanceolatus* subsp. *albicans* (Scribner & J.G. Sm.) Barkworth & D.R. Dewey, one of *E. lanceolatus* 'Sodar', and one of the breeding population that eventually gave rise to *E. lanceolatus* 'Schwendimar'.

Table 1. Morphological characteristics of diploid and tetraploid *Pseudoroegneria spicata*, *Elymus wawawaiensis*, and *E. lanceolatus*. Spikelet characters were measured on the spikelet at the third node. Data shown for continuous characters are range, mean and, in parentheses, standard deviation. The units used for length measurements are shown in the table. Vestiture was scored as none (0), sparse (1), moderate (2), dense (3); glume surface was scored as smooth (0), scabrous (1), very scabrous (2). Scores are presented parenthetically, preceded by the number of OTUs with that score. Asterisked characters were used in at least some of the discriminant analyses.

Character	Unawned	Diploid	Tetraploid	Combined	*E. wawa-waiensis*	*E. lanceolatus*
	P. spicata	*P. spicata*	*P. spicata*	*P. spicata*		
Number of OTUs	31	51	19	101	51	10
Culm						
Length (cm)*	27.7-75.6 55.1(12.7)	40.9-80.3 62.9(9.8)	45.7-79.6 62.5(7.3)	27.7-80.3 60.4(10.9)	45-100 70(12)	53.0-95.3 71.7(13.7)
Basal diameter (mm)*	1.0-2.6 1.4(0.4)	1.0-2.2 1.6(0.28)	1.2-2.4 1.6(0.3)	1.0-2.6 1.5(3.3)	1.0-1.9 1.5(0.3)	0.9-1.9 14.8(2.9)
Node (number)*	2-5 3.2(0.7)	2-8 3.4 (1.0)	3-4 3.5 (0.5)	2-8 3.4(0.85)	2-5 3.7(0.7)	3-4 3.5(0.5)
Top internode length (cm)*	20.7-41.6 30.8(5.5)	19.6-48.8 34.4(5.8)	21.3-42.0 34.6(6.0)	19.6-42.0 33.3(5.9)	17.0-47.8 30.4(6.3)	24.7-44.8 34.0(6.7)
Longest leaf						
Sheath length (cm)*	8.8-17.8 12.4(24.0)	8.2-20.3 12.8(2.6)	9.3-18.9 14.1(2.7)	8.2-20.3 12.9(2.6)	7.8-23.9 12.8(3.1)	9.0-16.2 12.0(2.1)
Sheath vestiture	1(2),30(3)	48(0),3(1), 1(3)	19(0)	67(0),3(1), 1(2),31(3)	48(0),3(1)	9(0),1(2)
Ligule length (mm)*	0.1-0.9 3.9(2.4)	0-1.0 0.37(0.23)	0.2-0.7 0.41(0.13)	0.0-1.0 0.4(0.21)	0.1-1.1 0.51 (0.27)	0.2-1.2 0.8(0.3)
Auricle length (mm)*	0.0-0.8 0.25(0.28)	0-1.1 0.24 (0.31)	0.0-0.9 0.3(0.3)	0.0-1.1 0.2(0.3)	0-1.2 0.16(0.25)	0-0.9 0.2(0.06)
Blade length (cm)*	9.1-27.0 18.6(3.9)	12.0-25.3 17.2(3.4)	16.0-27.2 19.9(2.7)	9.1-27.2 18.2(3.4)	8.5-28.2 17.2(4.0)	16.3-25.3 19.0(2.8)
Blade width (mm)*	0.9-6.1 27.6(11.6)	1.8-6.1 3.3(0.8)	2.4-5.1 3.5(0.8)	0.9-6.1 3.2(1.0)	1.7-4.2 2.9(0.5)	2.2-3.6 2.8(0.5)
Ribs in blade (number)*	8-21 12.9(3.3)	9-22 14.8(2.7)	12-21 15.4(2.6)	8-21 14.3(3.0)	9-19 14.1(2)	12-17 14(1.3)
Adaxial vestiture	1(2),30(3)	2(2),49(3)	19(3)	3(2),98(3)	1(0),4(1), 14(2),32(3)	10(3)
Abaxial vestiture	14(0),17(1)	42(0),9(1)	15(0),4(1)	81(0),20(1)	47(0),4(1)	9(0),1(1)
Flag leaf						
Sheath length (cm)*	13.5-26.4 18.3(2.9)	11.8-27.0 18.7(3.4)	13.6-26.2 19.3(3.5)	11.8-27.0 18.7(3.2)	12.1-26.6 19.1(3.8)	16.2-26.7 21.0(3.7)
Blade length (cm)*	1.7-24.7 12.3(4.3)	4.2-20.0 12.3(4.8)	8.3-26.9 15.2(4.7)	1.7-26.9 12.8(4.4)	2.3-17 9.9(1.5)	0.9-8.7 4.8(2.8)
Blade width (mm)*	0.7-5.9 2.3(0.9)	1.4-5.3 3.0(0.8)	2.1-4.7 3.2 (0.7)	0.7-5.3 2.8(0.9)	1.4-4.1 2.1(0.5)	0.9-2.9 1.7(0.6)

Table 1 (continued).

Character	Unawned	Diploid	Tetraploid	Combined	*E. wawa-waiensis*	*E. lanceolatus*
	P. spicata	*P. spicata*	*P. spicata*	*P. spicata*		
Spike and spikelet						
Spike length (cm)*	10.5-20.8 15.4(2.5)	9.4-22.6 15.7(2.9)	11.2-21.7 15.0(2.8)	9.4-22.6 19(2.8)	6.6-17.9 11.2(2.7)	12.4-19.7 15.3(2.6)
Node (number)*	8-18 10.9(2.1)	8-17 11.4(2.2)	9-19 12.6(2.4)	8-19 11.5(2.2)	9-21 12.9(2.5)	12-16 14(1.3)
First spike inter-node length (mm)*	10-39 21.8(6.6)	11-39 22.6(6.8)	11-27 19.5(4.7)	10-39 22(6.4)	6-18 11(3.4)	11-19 15(3)
Third spike inter-node length (mm)*	10-19 14.7(2.6)	9-22 14.9(0.3)	9-16 13.0(2.0)	9-22 14.5(2.8)	5-13 8.3(1.8)	8-12 10(2)
Spikelet length (mm)*	11-24 18.2(2.6)	13-27 19.4(3.1)	15-22 19.25(2.2)	11-24 19(2.8)	9-21 14.5(2.8)	11-18 15(2.2)
Spikelet width (mm)*	1.9-7.0 4.0(1.3)	1.9-7.5 3.8(1.2)	2.2-6.5 4.3(1.4)	1.9-7.5 3.9(1.3)	2.0-8.5 1.4(0.3)	3.0-6.3 4.0(1.2)
Floret number per spikelet*	5-10 7.9(1.3)	5-11 7.6(1.5)	5-8 6.7(0.9)	5-11 7.5(1.4)	3-9 6.6(1.5)	5-9 7(1)
Second rachilla segment (mm)*	1.1-2.4 1.78(0.29)	1.0-2.2 1.6(0.3)	1.5-2.2 1.8(0.3)	1.0-2.4 1.7(0.3)	0.8-2.1 1.4(0.3)	1.2-1.6 1.4(0.13)
First glume length (mm)*	6.8-11.0 8.3(1.1)	5.8-11.2 7.9(1.4)	6.2-10.0 8.1(1.3)	5.8-11.2 8.0(1.3)	3.1-8.3 6.1(1.2)	4.3-8.6 6.6(1.1)
First glume width (mm)*	1.0-1.9 1.5(0.26)	1.0-2.1 1.5(0.3)	1.3-2.2 1.8(2.3)	1.0-2.2 1.5(0.3)	0.5-1.1 0.7(0.1)	0.8-1.3 1.1(0.2)
First glume awn length (mm)*	0.0-0.0	0.0-8.0 0.6(1.4)	0.0-2.0 0.63(0.8)	0.0-8.0 0.4(0.1)	0-6.0 0.5(1.1)	0-1 0.4(0.05)
First glume veins (number)*	2-7 4.4(1.0)	3-6 4.3(0.7)	4-7 4.9(0.81)	2-7 4.4(0.8)	2-4 2.9(0.5)	3-5 3.3(0.7)
First glume adaxial vestiture	3(0),14(1), 14(2)	15(0),23 (1),13(2)	7(0),9(1), 3(2)	25(0),46 (1),30(2)	6(0),28(1), 17(2)	4(1),3(2), 3(3)
First glume abaxial surface	5(0),23(1), 3(2)	5(0),36(1), 10(2)	18(1),1(2)	10(0),77 (1),14(2)	1(0),27(1), 23(2)	3(0),6(1,), 1(2)
Second glume length (mm)*	8.2-12.8 9.9(1.1)	6.7-13.1 8.9(1.4)	7.8-11.2 9.5(1.1)	6.7-13.1 9.3(1.4)	4.0-9.5 6.9(1.2)	5.2-9.1 7.1(1.0)
Second glume width (mm)*	1.2-2.3 1.7(0.3)	1.2-2.2 1.7(2.4)	1.4-2.2 1.9(0.2)	1.2-2.3 1.7(0.3)	0.6-1.2 0.8(1.1)	1.0-1.7 1.3(0.2)
Second glume awn length (mm)*	0.0-0.0	0.0-5.0 0.6(1.2)	0.0-4.0 0.7(1.1)	0.0-5.0 0.46(1.0)	0.0-4.0 0.5(0.1)	0-1 0.4(0.05)
Second glume veins (number)*	3-8 5.1(1.1)	3-8 5.0(0.9)	5-8 5.8(0.9)	3-8 5.2(1.0)	3-5 3.5(0.6)	3-5 3.7(0.7)
Second glume adaxial vestiture	15(1),16(2)	12(0),23 (1),16(2)	5(0),10(1), 4(2)	17(0),48 (1),36(2)	4(0),24(1), 23(2)	4(1),4(2), 2(3)
Second glume abaxial surface	1(0),27(1), 3(2)	4(0),33(1), 14(2)	15(1),4(2)	5(0),75(1), 21(2)	28(1),23(2)	1(0),6(1), 3(0)
First lemma length (mm)*	8.8-13.3 10.5(1.3)	9.0-13.8 10.5(1.2)	9-13 11.2(1.0)	8.8-13.8 10.6(1.2)	7.2-11.7 9.3(1.1)	6.3-10.9 9.6(1.4)
First lemma width (mm)*	1.8-2.9 2.4(0.29)	1.5-3.0 2.3(3.0)	1.8-3.1 2.6 (0.3)	1.5-3.1 2.4(0.3)	1.4-2.8 2.1(0.2)	1.7-2.6 2.1(0.3)

Table 1 (continued).

Character	Unawned	Diploid	Tetraploid	Combined	*E. wawa-waiensis*	*E. lanceolatus*
	P. spicata	*P. spicata*	*P. spicata*	*P. spicata*		
First lemma abaxial vestiture	31(0)	49(0),2(1)	15(0),4(1)	95(0),6(1)	49(0),2(1)	3(2),7(3)
First lemma awn length (mm)*	0.0-1.0 0.03(0.18)	0-28.0 13.2(6.1)	0.0-16.0 8.1(4.6)	0.0-28.0 8.2(7.5)	0-19.5 17.4(2.9)	0-7.2 0.9(0.02)
Longest awn, lower spikelet*	0.0-1.0 0.03(0.18)	2.0-26.0 16.1(6.0)	0.0-26.0 12.4(5.8)	0.0-26.0 10.5(8.6)	0.0-25.0 15.6(5.0)	1.0-10.0 1.3(3.2)
Longest awn, upper spikelet*	0.0-9.0 0.3(1.6)	3.0-35.0 18.3(7.4)	0.0-24.0 15.7(6.8)	0.0-35.0 12.3(10.1)	0.0-26.0 18.3(5.0)	0.0-17.0 2.1(5.4)
Lemma awn angle*	0-10 0.3(1.8)	0-90 26.2(19.1)	0-35 12.4(10.2)	0-90 1.6(18.3)	0-80 22.7(15.2)	0-35 3.5(11)
Lemma awn longer than 3 mm[1]	0%	96%	84%	66%	100%	14%*
Palea length (mm)*	7.7-11.2 9.2(8.8)	7.3-11.3 9.3(0.9)	8.4-11.2 9.7(7.2)	7.3-11.3 9.3(8.8)	7.2-10.5 8.7(0.8)	5.1-9.9 8.5(1.5)
Palea width (mm)*	1.2-1.9 1.5(0.22)	0.9-2.1 1.6(0.3)	1.6-2.1 1.9(0.12)	0.9-2.1 1.7(0.3)	1.0-1.8 1.2(0.18)	1.1-1.8 1.3(0.2)
Palea adaxial vestiture	9(0),20(1), 2(2)	27(0),21 (1),3(2)	8(0),10(1), 1(2)	44(0),51 (1),6(2)	10(0),30 (1),11(2)	9(1),5(2)
Palea abaxial vestiture	28(0),3(1)	45(0),6(1)	15(0),4(1)	88(0),13(1)	26(0),17 (1),8(2)	2(0),4(1), 6(2),2(3)

[1]Lemma awns were scored as present if one of the lemmas had an awn more than 3 mm long. *Elymus lanceolatus* included subsp. *albicans*, an awned taxon.

The morphological characteristics of the accessions were examined using complete, mature culms from plants grown at the four sites. The number of samples per accession varied from one to ten, the average being 3.1. Except at Evans Farm, the size of the sample was determined by the number of plants that could be grown at each site. In sampling, a conscious effort was made to sample the full range of variation shown by each accession at a given site.

Forty-six morphological characters (Table 1) were selected for examination on the basis of existing treatments (Hitchcock 1951; Hitchcock 1969; Holmgren & Holmgren 1977) and study of native populations. These characters were examined on 166 culms representing 32 accessions grown from seed and 12 plants from a population about 0.5 mi up Wawawai Canyon from the Snake River (Table 2). Flowering culms were visually selected from the tallest third of the culms produced by the plant. Those selected had about average culm and spike lengths among this third. Cauline leaf measurements were made on the longest leaf below the flag leaf. This was usually the second leaf down, but was sometimes the first or third. The number of spikelets per spike was the mean of three tall culms; the number of florets per spikelet was the mean of three spikelets.

Table 2. Source of plants used for morphological studies of *Elymus* and *Pseudoroegneria*.

Source Location and Accession Number	Taxon	Number of OTUs	Ploidy level	Awn?
Columbia Plateau, Lincoln County, Washington (T40592)	*P. spicata*	5	Diploid	Unawned
Columbia Plateau, Lincoln County, Washington (T40593)	*P. spicata*	4	Diploid	Unawned
Columbia Plateau, Douglas County, Washington (T40590)	*P. spicata*	1	Diploid	Unawned
Along Columbia River, Okanogan County, Washington (D3363)	*P. spicata*	2	Diploid	Unawned
Colorado (7031)	*P. spicata*	2	Diploid	Unawned
Snake River Canyon, Wawawai, Whitman County, Washington (DS 120)	*P. spicata*	9	Diploid	Unawned
Palouse Prairie, Colton, Whitman County, Washington (D3363)	*P. spicata*	4	Diploid	Unawned
Logan, Cache County, Utah (D1252)	*P. spicata*	4	Diploid	Unawned
New Meadows, Adams County, Idaho (D2837)	*P. spicata*	8	Diploid	Awned
Slopes above Snake River, Hellers Bar, Asotin County, Washington (DS 117)	*P. spicata*	5	Diploid	Awned
Decker, Montana (D2838)	*P. spicata*	4	Diploid	Awned
Custer, Idaho (BB1600)	*P. spicata*	4	Diploid	Awned
Strevel, Utah (D2836)	*P. spicata*	2	Diploid	Awned
Rocky slopes above Grande Ronde River, Wallowa County, Oregon	*P. spicata*	15	Diploid	Awned
Open *Pinus ponderosa* forest, Avon, Montana	*P. spicata*	5	Diploid	Awned
Grassy valley (old Lake Missoula Lake bed), Deerlodge, Montana	*P. spicata*	4	Diploid	Awned
Open *Pinus ponderosa* forest, Gold Creek, Montana	*P. spicata*	5	Diploid	Awned
Palouse Prairie, Steptoe Butte, Whitman County, Washington	*P. spicata*	15	Tetraploid	Awned
Pinus ponderosa woodland, Clearwater, Idaho (T7681)	*P. spicata*	4	Tetraploid	Awned

Table 2 (continued).

Source Location and Accession Number	Taxon	Number of OTUs	Ploidy level	Awn?
Riggins, Idaho County, Idaho (D2842)	*E. wawawaiensis*	2	Tetraploid	Awned
Wawawai, Whitman County, Washington (DS 122)	*E. wawawaiensis*	5	Tetraploid	Awned
Penawawa, Whitman County, Washington	*E. wawawaiensis*	10	Tetraploid	Awned
New Meadows, Idaho (D2841)	*E. wawawaiensis*	3	Tetraploid	Awned
Howell Canyon, Whitman County, Washington (D2843)	*E. wawawaiensis*	4	Tetraploid	Awned
Central Ferry, Washington	*E. wawawaiensis*	5	Tetraploid	Awned
Dry coulée, Washtucna, Washington	*E. wawawaiensis*	5	Tetraploid	Awned
Central Ferry, Washington	*E. wawawaiensis*	5	Tetraploid	Awned
Wawawai, Whitman County, Washington [OTUS collected in the field and pressed]	*E. wawawaiensis*	12	Tetraploid	Awned
Artificial hybrid; BB0138	*P. spicata* × *E. lanceolatus*	4		
Canada	*E. lanceolatus* subsp. *albicans*	2	Tetraploid	
Sherman County, Oregon (T21076)	*E. lanceolatus*	3	Tetraploid	
Grand County, Oregon	*E. lanceolatus* cv. Sodar	1	Tetraploid	
Wyoming	*E. lanceolatus* subsp. *griffithsii*	4	Tetraploid	

Discriminant analysis was used to determine which continuous morphological characters would be most valuable in identifying the group to which an OTU belonged. The groups used were a) unawned, diploid *Pseudoroegneria spicata*, b) awned, diploid *P. spicata*, c) tetraploid *P. spicata* (almost all of which were awned), d) *Elymus wawawaiensis*, and e) *E. lanceolatus*. Data from the artificial hybrid were not included (here and elsewhere, "awned" and "unawned" refers to the lemmas, not the glumes). Thirty-seven characters were used in the discriminant analysis (Table 1). The excluded characters were discontinuous with few alternative states.

Table 3. Pooled within-groups correlations between discriminating variables and standardized canonical discriminant functions.

First Function		Second Function		Third Function	
Second glume width	0.669	Lower lemma awn	0.678	Lowest lemma awn	0.385
First glume width	0.571	Upper lemma awn	0.658	Flag blade length	0.285
First glume vein	0.352	Lemma awn angle	0.325	Spike length	-0.227
Second glume vein	0.335	Lowest lemma awn	0.292	Second glume length	0.183
Palea width	0.320	Flag blade width	0.231	Lemma awn angle	-0.160
Second glume length	0.316	Palea width	0.152	Second glume vein	0.159
First internode length	0.302	Cauline blade ribs	0.144	First glume vein	0.149
Spikelet length	0.262	Second glume awn	0.141	Culm diameter	-0.141
First glume length	0.253	Culm diameter	0.140	Spikelet width	0.139
Spike length	0.234	Cauline blade width	0.140	Cauline sheath	0.119

Classification tree analysis was used to explore the ability of the discontinuous and continuous characters for distinguishing between *Elymus wawawaiensis* and the three *Pseudoroegneria spicata* groups. This procedure resembles discriminant analysis in that it works from predefined groups, but it looks for individual characters that will, if used in sequence, most effectively place the objects into the correct group, *i.e.*, it is a divisive method of hierarchical cluster analysis with only one character being used to split an existing cluster. It can be used with both continuous and discontinuous data. *Elymus lanceolatus* was excluded from the analysis because the number of OTUs in the study was too low.

Excel (Microsoft 1997) was used to generate summary statistics for each group, SPSS version 7.5.1 for discriminant analysis (SPSS 1997), S-plus4 for classification tree analysis (MathSoft 1997), and NTSYS-pc (Rohlf 1993) to produce three dimensional projections.

Cytological studies.--Somatic chromosome counts were already available for approximately 110 accessions of *Pseudoroegneria spicata*, *Elymus lanceolatus*, and *E. wawawaiensis*. Counts for an additional 152 populations of these taxa were obtained as part of Carlson's (1986) study. The counts were obtained from root tips that had been pre-treated in ice water for 24 hr, hydrolyzed in 1N HCl at 60°C for 10 min, and stained with Feulgen. For polyploid plants, metaphase 1 of meiosis was also examined using pollen mother cells stained with acetocarmine. In autotetraploid *P. spicata*, quadrivalents predominate (Dewey, oral comm., 1986) consequently the absence of quadrivalents was interpreted as meaning that the plant concerned was an allotetraploid.

Distributional studies.--The morphological characters identified as distinguishing *Elymus wawawaiensis* were used to identify specimens in OSC, US, WS, and UTC. These data, together with the collection data for the seed accessions, were used to determine the geographic and ecological distribution of the species.

RESULTS AND DISCUSSION

Field observations.--Carlson located several cytologically unexamined populations that would have keyed to *Pseudoroegneria spicata* (or *Agropyron spicatum*) in existing floras. These were tentatively identified as being either **StH** allotetraploids or **St** diploids or autotetraploids on the basis of their overall morphology. Subsequent cytological examination demonstrated that the allotetraploids had been correctly identified, but that diploid and autotetraploid populations could not be distinguished from each other.

Morphological studies.--Table 1 summarizes the morphological data obtained. Because the goal of this paper is to establish the need to recognize *Elymus wawawaiensis*, discussion of the data for *Pseudoroegneria spicata* will be presented elsewhere.

The characters that differentiate most clearly between *Pseudoroegneria spicata* and *Elymus wawawaiensis* are glume width and, to a lesser extent, glume venation, rachis internode length, and glume length (Table 1; Figs. 1-3.). The glumes of *E. wawawaiensis* are also somewhat stiffer and more sharply pointed than those of *P. spicata*. Seedlings of the two species can also be distinguished because those of *E. wawawaiensis* have pubescent leaf sheaths that become glabrous as the plant matures, whereas as seedlings of *P. spicata* are glabrous even in seedlings. In this respect, seedlings of *E. wawawaiensis* resemble those of *E. lanceolatus*.

Almost all specimens of *Elymus wawawaiensis* are awned. There were three exceptions among the OTUs, but only one was completely unawned, one of the other two having some shortly (3-6 mm) awned lemmas, and the other having some lemmas with normal (10-18 mm) awns. In the minimally awned plants, the longer awns are on the distal lemmas of a spikelet, as is the case in minimally awned plants of *Pseudoroegneria spicata*. The accessions of *E. wawawaiensis* that produced unawned OTUs came from populations that had populations of both unawned *P. spicata* and unawned *E. lanceolatus* in the vicinity.

Analysis of the F_2 generation of a cross between *Elymus wawawaiensis* and unawned plants of *E. lanceolatus* demonstrated that the awn character in these taxa is controlled by a single major gene and that the unawned allele is dominant (T. Jones, in litt., 1998). Such hybrids are easily produced, although few become established under natural conditions. Indeed, the only suggestion that any were present in the populations studied was the presence of unawned specimens in plants raised from

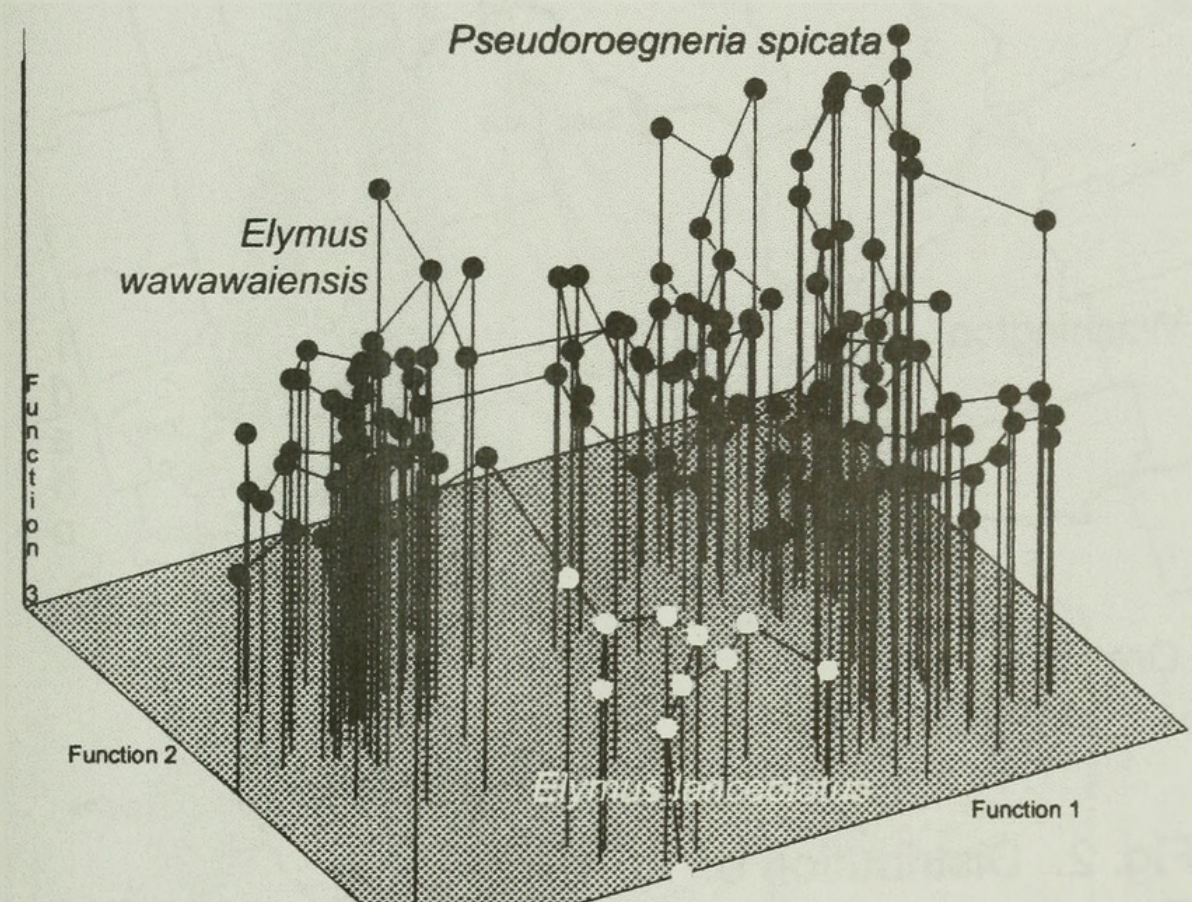

Fig. 1. Position of OTUs on first three discriminant axes

Figure 1. Distribution of *Elymus wawawaiensis*, *E. lanceolatus*, and the three *Pseudoroegneria spicata* groups in the plane defined by the first three discriminant functions. The first function is on the longest axis, the third function on the vertical axis. Light gray - *E. lanceolatus*; dark gray - *E. wawawaiensis*; black - *P. spicata*.

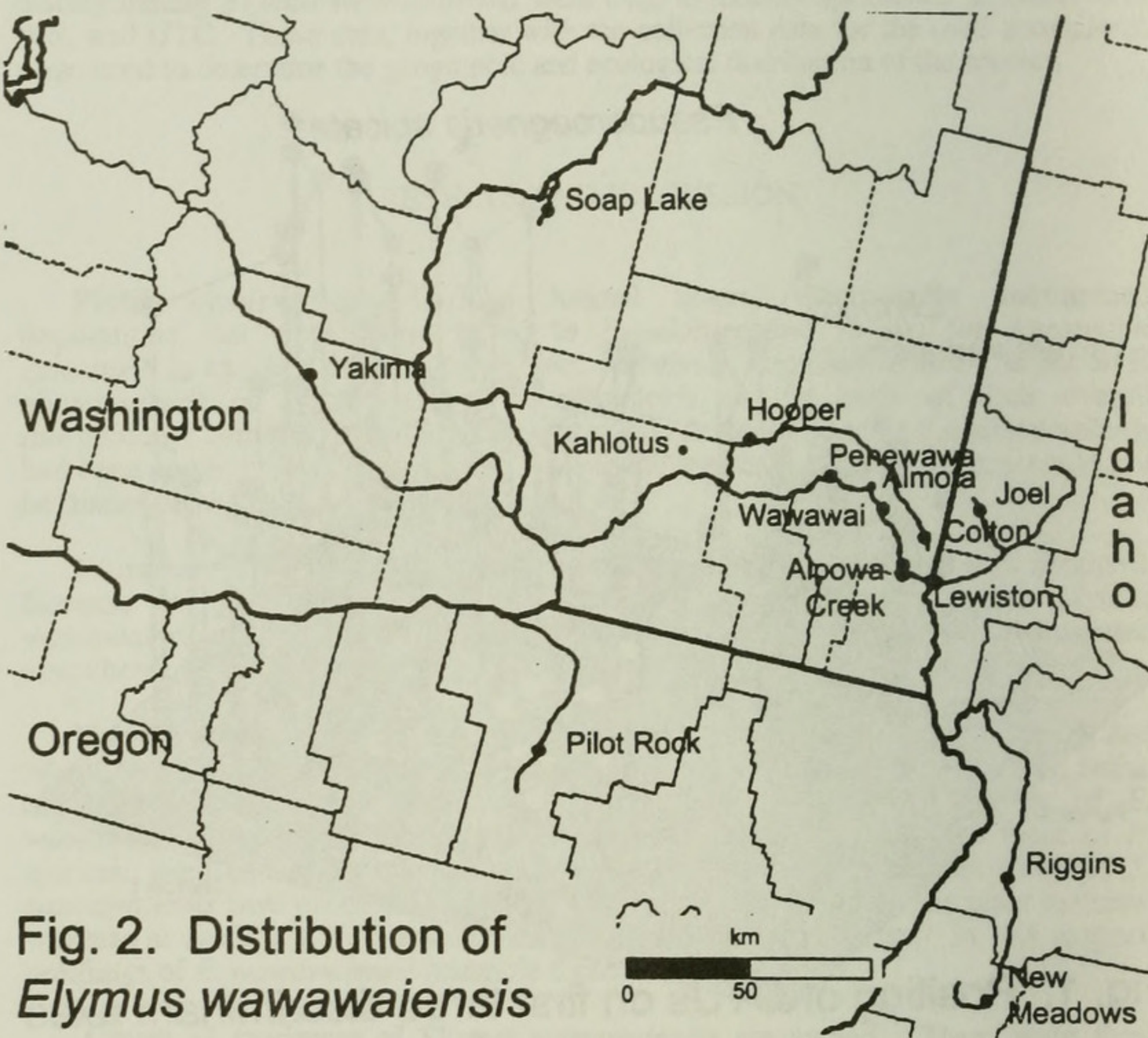

Figure 2. Distribution of *Elymus wawawaiensis*.

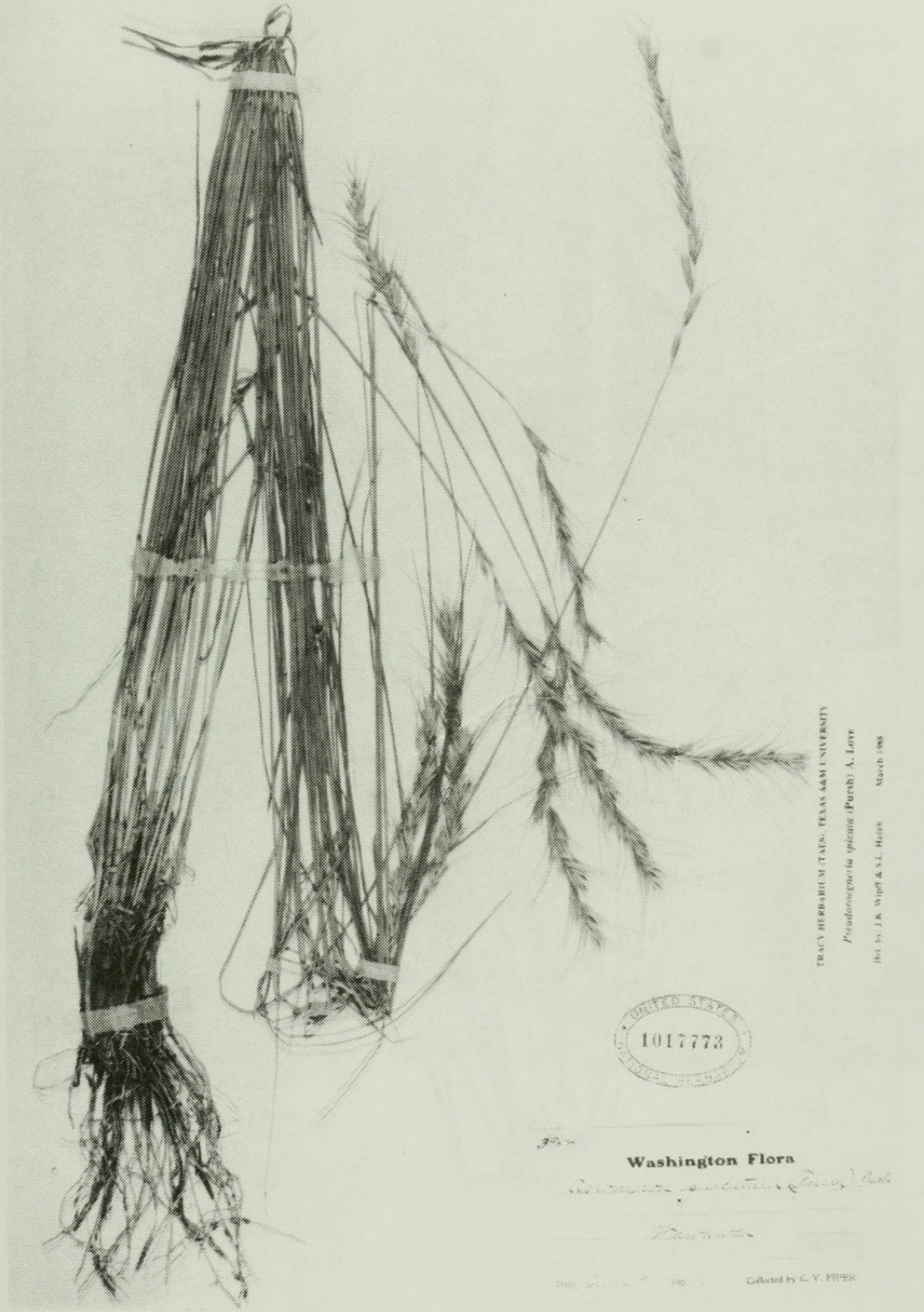

Figure 3. Holotype of *Elymus wawawaiensis*.

Figure 4. Representative of awned *Pseudoroegneria spicata*.

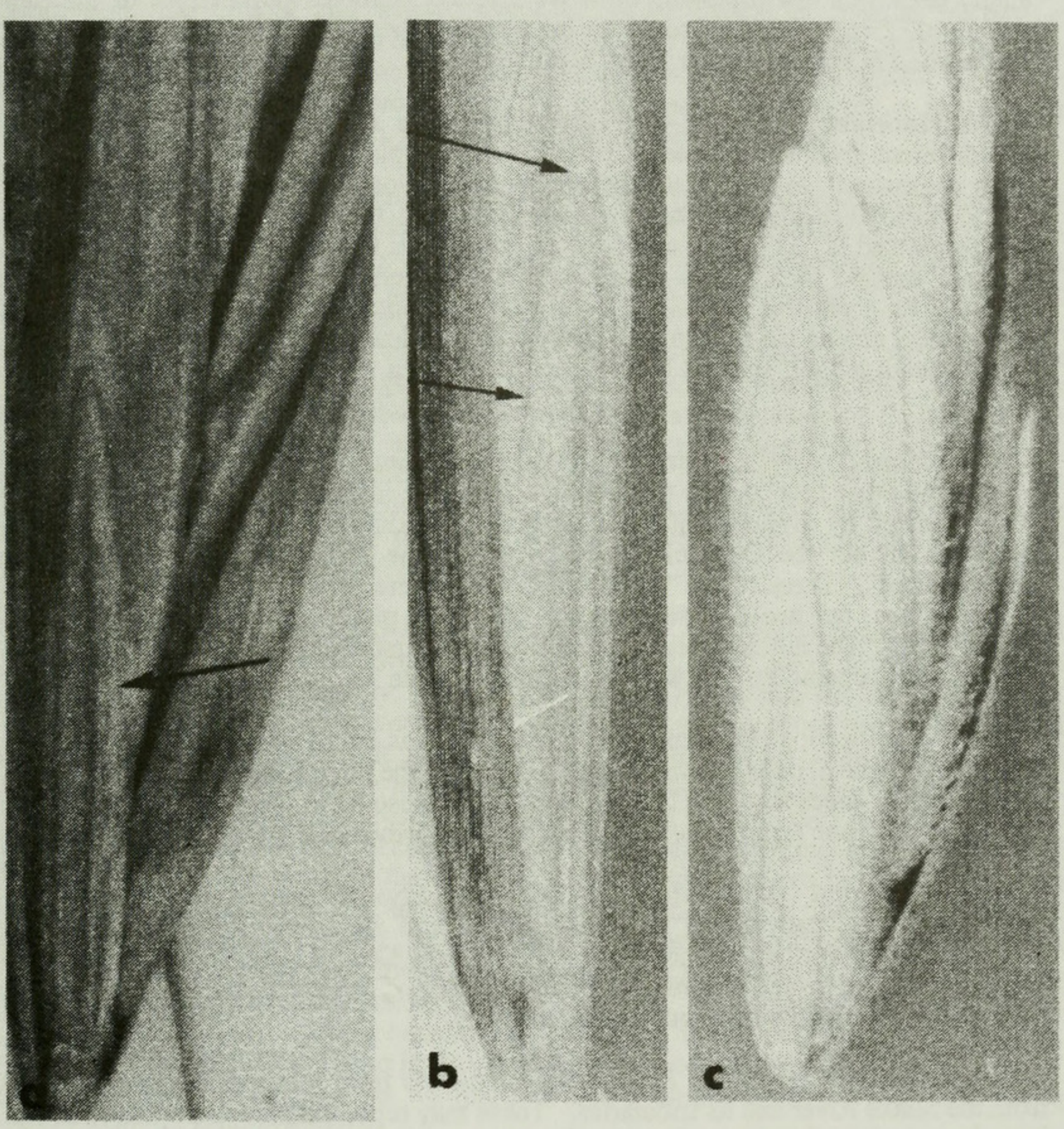

Figure 5. First glume of a) *Elymus wawawaiensis* b) *Pseudoroegneria spicata*, and c) *E. lanceolatus*. Arrows point to the edge of the glume.

seeds obtained in the wild. It is also possible that the unawned *E. wawawaiensis* plants reflect introgression from the unawned *Pseudoroegneria spicata* plants in the vicinity because a few triploid hybrids were found in mixed populations of the two taxa. Further study is needed to determine which of the two scenarios for the origin of the unawned *E. wawawaiensis* plants is correct.

Discriminant analysis.--The *Pseudoroegneria spicata* OTUs were placed in three different groups: unawned diploids, awned diploids, and tetraploids (most of which are awned), to determine whether the morphological characters used could be used to distinguish *Elymus wawawaiensis* even from those plants of *P. spicata* that most resembled it. The addition of the *E. lanceolatus* OTUs brought the number of groups compared to 5. Only six of the 37 characters included in the discriminant analyses had means that showed no significant difference (using P=0.05 as the level of significance) among the five groups. They were flag leaf sheath length, auricle length, cauline sheath length, spikelet length, first glume awn length, and number of cauline nodes.

Discriminant analysis clearly separated the *Elymus wawawaiensis* OTUs from those in the other four groups (Figure 1). When the identification of each OTU was cross-validated by evaluating its identification using discriminant functions based on data from all but the OTU of interest, four of the 152 OTUs were considered "misidentified". Three of the "misidentifications" were between the *Pseudoroegneria spicata* groups, but one *E. wawawaiensis* OTU was placed in the awned diploid *P. spicata* group. The highest correlation between the first discriminant function and the morphological characters was with glume width (Table 3).

With classification tree analysis, the first split was based on second glume width and separated the *Elymus wawawaiensis* OTUs from the three *Pseudoroegneria spicata* groups (the *E. lanceolatus* OTUs were omitted because there were so few of them). There was only one error in the placement of the *E. wawawaiensis* OTUs.

Distributional data.--Most collections of *Elymus wawawaiensis* are from coulées and side canyons of the Snake River and its tributaries in southeastern Washington and northern Idaho (Figure 2). At many sites, *E. wawawaiensis* grows in mosaics with unawned forms of *Pseudoroegneria spicata*. At such sites, *E. wawawaiensis* is easily distinguished by its awns.

There are a few records of *Elymus wawawaiensis* from localities at some distance from the Snake River and its tributaries. These may represent natural populations, but it is also possible that they reflect the distribution of seeds from the population near Wawawai, possibly by Charles V. Piper who founded the herbarium at Washington State Agricultural College (now Washington State University) in 1890, leaving to join the U.S.D.A.

CONCLUSIONS

The atypical populations of *Pseudoroegneria spicata* that Dewey referred to differ from both the diploid and autotetraploid plants of typical *P. spicata* in having narrower, sharper glumes with fewer veins and shorter, more compact spikes, as well as in being allotetraploids. The morphological differences between typical *P. spicata* and the allotetraploid plants are sufficiently great that there is rarely a problem in distinguishing between the two, either in the field or the herbarium.

The values for the distinguishing characters in *Elymus wawawaiensis* are either above or below those of *Pseudoroegneria spicata* and *E. lanceolatus*. This tends to refute the possibility that *E. wawawaiensis* consists of introgressants between the other two taxa. Hybrids may have values that exceed the extremes observed in their parents, but there are no tetraploid populations of *P. spicata* in the vicinity of *E. wawawaiensis*. This does not preclude the possibility that *E. wawawaiensis* originated when an unreduced gamete of diploid *P. spicata* crossed with *E. lanceolatus* but, based on the current distribution of awned and unawned plants of *P. spicata*, one would expect the unawned allele to be present to a significant extent in *E. wawawaiensis* if this were the case. It is, of course, possible that unawned hybrids are rapidly eliminated by selection for the advantages associated with awns. These include greater likelihood that the seeds will be moved to favorable microsites and lodge at the best angle for germination (Peart 1979).

Elymus wawawaiensis and *E. lanceolatus* are not genetically isolated from each other. Hybrids between the two are easy to produce, meiotically regular, and have only slightly depressed fertility. Despite this, the only evidence for the existence of natural hybrids was the discovery of unawned plants among those grown from seed obtained in the wild, a result that could also reflect introgression from unawned populations of *Pseudoroegneria spicata* growing in the vicinity. Although *E. lanceolatus* and *E. wawawaiensis* grow in the same region, they occupy different habitats, *E. wawawaiensis* occupying slopes with high daytime temperatures and shallow, rocky soils whereas the *E. lanceolatus* populations are largely confined to sandy soils, particularly older sand dunes, in the vicinity. The distance between the two kinds of habitat may preclude pollen transfer between natural populations of the two taxa. Alternatively (or additionally), hybrid seed may form but the seedlings be unable to become established under natural conditions. Whatever the reasons, the data suggest that *E. wawawaiensis* constitutes a taxon that is distinct from *E. lanceolatus*, although genomically similar to it. Because the new taxon has a similar origin to other species included in *Elymus*, as we interpret that genus, we include it in that genus rather than in *Pseudoroegneria*.

ELYMUS WAWAWAIENSIS J. Carlson & Barkworth, *spec. nov.* HOLOTYPUS: U.S.A. Washington: Whitman County, Wawawai, June 1902, *C.V. Piper 3954* (US 1017771) (Figure 3). Paratypes: U.S.A., Idaho, Nez Perce County, Lewiston (US 221707); U.S.A., Oregon, Umatilla County, Pilot Rock (US 1017821); U.S.A., Washington, Okanogan County, Okanogan (US 1017759); U.S.A. Washington, Whitman County, Almota (US 23054); U.S.A., Washington, Whitman County, Cow Creek (US 1017790).

Gramina perennia, caespitosa. Culmi 15-130 cm alti. Vaginae foliorum basilium plerumque modice pubescentes juvenes, glabrae maturae, marginibus perspicue ciliatis. Vaginae foliorum caulinorum 6-18 cm longae, glabrae (raro pubescentes sparsim); laminae usque 26 cm longae, 2-5 mm latae, pagina adaxiali plerumque dense pubescenti, solum raro sparsim pubescentes; folia superne perpendicularia in siccitatibus. Spicae 6-20 cm longae, erectae vel erectiusculae, non rumpentes ut maturae; plurima internodia minus quam 1 cm longa. Spiculae solitariae, plus minusve imbricatae, 1-2 cm longae, cum 4-10 flosculis. Glumae 4-10 mm longae, 0.6-1.3 mm latae, lanceolatae ad usque aciculares, cum 1-3 venis; lemmae 7-12 mm longae, rasiles usque ad scabrellas, marginibus sparsim pubescentibus prope basin, aristatae; arista sola 10-25 mm longa, divergentes usque ad squarrosus reflexae ubi maturae; paleae duplicarinatae, sparsim vel modice strigulosae in paginae adaxiali, sparsim strigulosae in pagina abaxiali apicem versus; antherae 3-6 mm longae. $2n$ =28.

Plants perennial, caespitose. Culms 15-130 cm tall. Basal leaf sheaths usually moderately pubescent when young, glabrous when mature, the margins not evidently ciliate. Cauline leaf sheaths 6-18 cm long, glabrous (rarely sparsely pubescent); blades to 26 cm long, 2-5 mm wide, the adaxial surface usually densely pubescent, only rarely sparsely pubescent; flag leaves perpendicular to the stem under drought stress. Spikes 6-20 cm long, erect to somewhat nodding, not disarticulating at maturity; most internodes less than 1 cm long. Spikelets solitary, more or less imbricate, 1-2 cm long, with 4-10 florets. Glumes 4-10 mm long, 0.6-1.3 mm wide, lanceolate to acicular, 1-3 veined; lemmas 7-12 mm long, smooth to slightly scabrous, sparsely pubescent along the margins near the base, awned; awn 10-25 mm long, divergent to squarrose at maturity; paleas 2-keeled, sparsely to moderately strigulose adaxially, sparsely strigulose abaxially towards the tip; anthers 3-6 mm long. $2n$ = 28. Genomes **StH**.

Field and herbarium studies show that *Elymus wawawaiensis* is limited to the coulées and reaches of the lower Snake River drainage, *i.e.*, along the breaks and tributaries of the Salmon, Snake, and Yakima rivers in northern Idaho, northeastern Oregon, and southeastern Washington (Figure 2), habitats initially created during the Spokane and Bonneville floods (Allen *et al.* 1986). The highest concentration of the populations is found along the Snake River between its confluence with the Salmon River and Penewawa, suggesting that the progenitor seedlings became established on the scoured canyon walls in the region and then spread downstream, probably during the Pleistocene. The species will become more widespread through distribution of 'Secar', a cultivar developed by the U.S.D.A. for soil conservation in areas with shallow, rocky soils. The cultivar will probably hybridize with both *E. lanceolatus* and *E. trachycaulus* (Link) Gould if these species are in the vicinity, but whether the hybrids will become established is problematical.

Elymus, even when restricted to alloploids that combine the **St** genome with one or more other genomes, is a morphologically and ecologically diverse genus. North American species combine the **St** genome with the **H** genome from wild barley and range from the strongly caespitose, short-lived, long awned *E. elymoides* (Raf.) Swezey to the rhizomatous, long-lived, unawned *E. lanceolatus*. Given their morphological, ecological, and geographic diversity of **StH** species (they extend from Europe to North and South America), it has always been highly improbable that they had a single tetraploid ancestor in common, but the tools for investigating their ancestry have only recently been developed. Svitashev *et al.* (1996) demonstrated that the **StH** species are polyphyletic, but their sample size was too small to provide reliable information on clades within the species group. *Elymus wawawaiensis* may have originated independently from other North American species of *Elymus*, or it may be derived from another species, possibly through backcrossing with *Pseudoroegneria spicata*. At present there is not enough information available to select between these two scenarios.

ACKNOWLEDGMENTS

We thank the curators of OSC, US, and WS for making their specimens available for this study, and Drs. Kathleen Capels, Jack Maze, and Karen Antell for advice and suggestions that improved our original manuscript, and Dr. Mark Damen for his assistance in writing the Latin description. Carlson's research was supported by the Soil Conservation Service (now the National Resources Conservation Service) and Barkworth's by the Utah Agricultural Experiment Station, Utah State University, Logan, Utah 84322-4810. Approved as journal paper no. 7041 by the Utah Agricultural Experiment Station.

LITERATURE CITED

Allen, J.E., M. Burns, & S.C. Sargent. 1986. *Cataclysms on the Columbia*. Timber Press, Portland, Oregon.

Carlson, J.R. 1986. A study of morphological variation with *Pseudoroegneria spicata* (Pursh) A. Löve (Poaceae: Triticeae). Masters Thesis, Oregon State University, Corvallis, Oregon.

Dewey, D.R. 1982. Genomic and phylogenetic relationships among North American perennial Triticeae. Pp. 51-88 *in* J.R. Estes, R.J. Tyrl, & J.N. Brunken, [Eds.], *Grasses and Grasslands: Systematics and Ecology*. University of Oklahoma Press, Norman, Oklahoma.

Dewey, D.R. 1984. The genomic system of classification as a guide to intergeneric hybridization in the perennial Triticeae. Pp. 209-279 *in* J.P. Gustafson (Ed.), *Gene Manipulation in Plant Improvement*. Plenum Publishing Corporation, New York; New York.

Hitchcock, A.S. 1951. *Manual of Grasses of the United States*. Ed. 2, Rev. A. Chase. U.S.D.A. Misc. Publ. 200, Washington, DC.

Hitchcock. C.L. 1969. Gramineae. Pp. 384-725 *in* C.L. Hitchcock *et al.*, *Vascular Plants of the Pacific Northwest*. University of Washington Press, Seattle, Washington.

Holmgren, A.H. & N.H. Holmgren. 1977. Poaceae. Pp. 175-464 *in* A. Cronquist *et al.*, *Intermountain Flora*, volume 6. New York Botanical Garden, Bronx, New York.

Holmgren, P.K., N.H. Holmgren, & L.C. Barnett. 1990. *Index Herbariorum*. Ed. 8. New York Botanical Garden, Bronx, New York.

Jones, T.A., D.C. Nielson, & J.R. Carlson. 1991. Developing a grazing tolerant native grass for bluebunch wheatgrass sites. Rangelands 13(3):147-150.
MathSoft, Inc. 1997. S-plus4. Seattle, Washington.
Microsoft. 1997. Excel. Redmond, Washington.
Peart, M.H. 1979. Experiments on the biological significance of the morphology of seed-dispersal units in grasses. J. Ecol. 67:843-863.
Rohlf, F.J. 1993. NTSYS-pc: Numerical Taxonomy and Multivariate Analysis System. Exeter Software, Setauket, New York.
SPSS. 1996. SPSS for Windows95/NT, version 7.5.1.
Svitashev, S., B. Salomon, T. Bryngelsson, & R. von Bothmer. 1996. A study of 28 *Elymus* species using repetitive DNA sequences. Genome 39:1093-1101.
Wang, R.R-C., R. von Bothmer, J. Dvorak, G. Fedak, I. Linde-Laursen, & M. Muramatsu. 1996. Genome symbols in the Triticeae (Poaceae). Pp. 29-34 *in* R.R-C. Wang, K.B. Jensen, & C. Jaussi, Eds, Proceedings of the Second International Triticeae Symposium. Forage and Range Research Laboratory, U.S.D.A.-A.R.S., Logan, Utah.