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Characterization of diversity among 3 squirreltail taxa

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Abstract

Squirreltail (*Elymus elymoides*, *E. multisetus*) is a complex of 5 taxa whose systematic interrelationships are uncertain. Our objectives were to determine whether the 3 taxa studied here, *Elymus elymoides* ssp. *elymoides*, *E. elymoides* ssp. *brevifolius*, and *E. multisetus*, can be distinguished by several ecological and physiological traits and whether geographical origin is correlated with these traits across accessions within taxa. A multivariate principal component analysis of materials collected in the 10 contiguous western states successfully distinguished taxa, but no pair of the 3 taxa appeared to be more ecologically similar than any other pair. *Elymus elymoides* ssp. *elymoides*, which prevails in the semi-arid cold desert, was shortest and exhibited the lowest total plant dry-matter, earliest phenology, and lowest seed mass. *Elymus elymoides* ssp. *brevifolius*, which prevails in the Rocky Mountains, exhibited slowest emergence, highest specific root length, lowest nitrate reductase activity, and lowest root-to-shoot ratio. *Elymus multisetus*, which is most common in areas with relatively warm springs, exhibited fastest emergence (particularly from deep seeding), greatest root length, and greatest root-to-shoot ratio. *Elymus elymoides* ssp. *brevifolius* accessions clustered into 3 groups: late-maturing high-seed mass accessions originating in Colorado, New Mexico, and Arizona (Group A), early-maturing low-seed mass accessions originating in Colorado and Utah (Group B), and intermediate-maturing low-seed mass accessions originating in the Snake River Plain of southern Idaho (Group C). The ecologically distinct subspecies and groups within ssp. *brevifolius* are indicative of the highly ecotypic nature of the squirreltails, suggesting that restoration practitioners should match site with genetically and ecologically appropriate plant material for these species.

Key Words: *Elymus elymoides*, genetic variation, plant autecology, *Sitanion hystrix*

The squirreltails (*Elymus elymoides* [Raf.] Swezey and *E. multisetus* [J.G. Smith] Burt-Davy) are increasingly important grasses for restoring rangeland communities on disturbed sites in the Intermountain Region of western North America. Systematists generally recognize up to 5 squirreltail taxa (Wilson 1963), which we refer to in this paper as *elymoides*, *brevifolius*, *californicus*, *hordeoides*, and *multisetus*. These taxa have been recognized in

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Resumen

“Squirreltail (*Elymus elymoides*, *E. multisetus*) es un complejo de 5 taxas cuyas interrelaciones sistemáticas son inciertas. Nuestros objetivos fueron determinar si las 3 taxas estudiadas aquí *Elymus elymoides* ssp. *elymoides*, *E. elymoides* ssp. *brevifolius*, y *E. multisetus*, pueden ser distinguidas por varias características ecológicas y fisiológicas y si el origen geográfico esta correlacionado con estas características a través de las accesiones dentro de la taxa. Un análisis multivariado de componentes principales de los materiales colectados en los 10 estados contiguos del oeste distinguió en forma exitosa la taxa, pero ningún par de las tres taxas pareció ser mas ecológicamente similar que cualquier otro par. *Elymus elymoides* ssp. *elymoides*, el cual prevalece en el desierto frío semiárido, fue el más corto y mostró la menor materia seca por planta, la fisiología más temprana y la menor biomasa de semilla. *Elymus elymoides* ssp. *brevifolius*, que prevalece en las Montañas Rocallosas presento la emergencia mas lenta, la mayor longitud específica de raíz, la mas baja actividad de nitrato reductasa y la relación más baja de tallo:raíz. *Elymus multisetus*, que es mas común en áreas con primavera relativamente calientes, mostró la emergencia más rápida (particularmente en siembras profundas), la mayor longitud de raíz y la mayor relación tallo:raíz. Las accesiones de *Elymus elymoides* ssp. *brevifolius* se agruparon en tres grupos: accesiones de madurez tardía-alta biomasa de semilla originarias de Colorado, New Mexico y Arizona (Grupo A), accesiones de madurez temprana -baja biomasa de semilla originarias de Colorado y Utah (Grupo B) y un grupo de accesiones de madurez intermedia-baja biomasa de semilla originarias del Snake River Plain del sudeste de Idaho (Grupo C). Las subespecies y grupos ecológicamente distintos dentro de ssp. *brevifolius* son indicativos de la naturaleza altamente ecotípica de los “Squirreltails, sugiriendo que los que practican la restauración de pastizales deben aparejar el sitio con un el material vegetal genética y ecológicamente apropiado de estas especies.

both *Sitanion* and in *Elymus*, with the latter being the currently preferred classification (Barkworth et al. 1983). However, rank of the taxa varies with taxonomic treatment.

There seems to be little dissension regarding the retention of 2 taxa in *E. elymoides*, namely ssp. *elymoides* and ssp. *californicus*. Wilson (1963) mentioned the marked similarity of their karyotypes. Also, M.E. Barkworth and J.J.N. Campbell (pers. comm. 2000) noted that they appear to hybridize when sympatric.

Taxonomic treatments have varied in their handling of specimens keying to *brevifolius* and *hordeoides* in Wilson's (1963)

treatment. *Brevifolius* was treated as a separate species by Wilson (1963) (*S. longifolium* J.G. Smith), reluctantly treated as a separate species by Holmgren and Holmgren (1977), treated as a subspecies of *E. elymoides* (ssp. *brevifolius*) by M.E. Barkworth and J.J.N. Campbell (2000 pers. comm.), and unrecognized as a separate taxon by Hitchcock (1950) and Arnov (1993). *Hordeoides* has been treated as a separate species by Wilson (1963) (*S. hordeoides* Suksdorf) or as part of a species including *elymoides*, *californicus*, and *brevifolius* by Holmgren and Holmgren (1977) and by M.E. Barkworth and J.J.N. Campbell (pers. comm.).

Some systematists readily recognize *multisetus* as worthy of specific rank (*E. multisetus* [J.G. Smith] Burtt-Davy = *S. jubatum* J.G. Smith) (Hitchcock 1950, Wilson 1963, Barkworth et al. 1983),

while others do so only reluctantly (Holmgren and Holmgren 1977). Wilson (1963) noted that the karyotype of *multisetus* was the most distinctive of the 5 squirreltail taxa. He reported extensive introgressive hybridization between *multisetus* and *elymoides* in southeastern California and southern Nevada, though not in other locales where these 2 taxa are sympatric. Holmgren and Holmgren (1977) suggested that a reasonable approach would be amalgamation of all 5 taxa into a single species.

Wilson (1963) provides a reliable key that easily separates the 5 taxa based on floral appendages. We have used it to identify over 100 accessions in our collection, which includes representatives of all taxa except *hordeoides*. Our objective was to determine how 3 taxa, *multisetus*, *brevifolius*, and *elymoides*, compare for traits

relating to seedling establishment, leaf and root morphology, and phenology because such traits may be correlated with adaptation to particular range sites. We also wished to determine the degree of separation or overlap between the taxa based on these traits and to gather any insights from the relationship between performance and geographical origin of the accessions.

Materials and Methods

Data set 1

Twenty-one of the 27 accessions (Tables 1, 2) in data set 1 originated from USDA-NRCS Plant Materials Centers in Aberdeen, Ida. and Bridger, Mont., or the Upper Colorado Environmental Plant Center in Meeker, Colo.. Two accessions

Table 1. Means for 1 *californicus*, 17 *elymoides*, 5 *brevifolius*, and 4 *multisetus* squirreltail accessions in data set 1 for 8 traits in a 25-day greenhouse trial.

Accession	Collection location	Days to emergence	Leaf length	Total plant dry-matter	Root-to-shoot ratio	Leaf area	Specific leaf area	Root length	Specific root length
			(10 days post-plant)						
		(no.)	(mm)	(mg plant ⁻¹)	(mg mg ⁻¹)	(mm ² plant ⁻¹)	(mm ² mg ⁻¹)	(mm plant ⁻¹)	(mm mg ⁻¹)
<i>californicus</i>									
PI 531604	Toe Jam Creek, Elko Co., Nev.	6.0	73	10.46	0.389	174	31.3	914	324
<i>elymoides</i>									
Acc:1107	sec 32 T22N R22E, Lemhi Co., Ida.	5.4	65	9.56	0.424	148	29.1	916	317
Acc:1108	sec 36 T4N R26E, Butte Co., Ida.	6.3	61	9.57	0.315	168	29.4	698	316
Acc:1109	sec 11 T4N R26E, Butte Co., Ida.	6.0	58	9.26	0.306	182	31.9	652	324
Acc:1110	sec 26 T4N R26E, Butte Co., Ida.	5.8	58	6.98	0.516	110	31.0	687	289
Acc:1111	sec 11 T4N R26E, Butte Co., Ida.	6.2	58	8.38	0.442	158	33.5	853	337
Acc:1112	sec 11 T4N R27E, Butte Co., Ida.	5.1	67	9.79	0.365	175	31.0	838	330
Acc:1113	1737 m, Custer Co., Ida.	5.3	74	8.85	0.423	157	31.3	1057	410
Acc:1114	Morse Creek, Custer Co., Ida.	6.2	54	7.14	0.291	116	27.7	641	410
Acc:1115	Leaton Gulch, Custer Co., Ida.	6.2	62	9.57	0.405	167	32.6	717	270
Acc:1116	Bradbury Flat, Custer Co., Ida.	6.0	64	9.56	0.335	178	33.8	668	275
Acc:1117	Round Valley, Custer Co., Ida.	5.6	62	10.18	0.354	182	32.9	814	322
Acc:1124	Squaw Butte, Harney Co., Ore.	6.1	60	10.27	0.359	150	25.2	960	368
PI 619489	Whitehall, Mont.	5.4	63	8.86	0.427	142	29.0	830	323
PI 619491	Big Piney, Wyo.	5.6	60	10.33	0.352	191	32.1	711	273
PI 619555	Warren, Mont.	6.2	57	9.36	0.285	174	31.7	629	298
PI 619561	Big Piney, Wyo.	5.8	60	9.69	0.436	167	32.0	821	306
9019219	btwn Worland & Ten Sleep, Wyo.	5.8	64	10.15	0.325	214	35.2	667	284
mean		5.8 b[#]	62 b	9.26 c	0.374 b	163 b	31.1 a	774 b	321 a
<i>brevifolius</i>									
Acc:1123	btwn Prairie City & Dixie Pass, Ore.	5.7	70	12.44	0.358	197	27.6	1017	343
Acc:1130	Savageton, Wyo.	6.4	71	9.35	0.280	157	28.0	700	376
PI 531605	btwn N. LaVeta Pass & Gardner, Colo.	7.0	56	10.50	0.267	154	23.8	794	368
9040187	Wet Mountains, Custer Co., Colo.	7.4	49	10.75	0.305	158	25.0	836	361
9040189	Buford, Rio Blanco Co., Colo.	6.3	65	12.10	0.333	210	29.7	943	332
mean		6.6 a	62 b	11.03 b	0.309 c	175 b	26.8 b	858 b	356 a
<i>multisetus</i>									
Acc:1132	Paradise Valley, Nev.	4.8	85	16.60	0.483	269	31.2	1434	268
PI 531603	Lake Tahoe, Nev.	4.4	85	18.48	0.483	303	31.0	1980	335
PI 531606	Central Ferry, Wash.	4.8	82	13.89	0.392	245	32.3	1520	393
PI 619466	Redlands, Lassen Co., Cal.	5.5	84	15.45	0.429	262	31.2	1161	278
mean		4.9 c	84 a	16.11 a	0.447 a	270 a	31.4 a	1524 a	319 a

[#]taxa means followed by different letters in the same column are significantly different at P < 0.05.

Table 2. Means for 1 *californicus*, 17 *elymoides*, 5 *brevifolius*, and 4 *multisetus* squirreltail accessions in data set 1 for 5 traits in field and greenhouse trials.

Accession	Heading date (days after 30/4/95)	Seed mass (mg seed ⁻¹)	Emergence index		Nitrate
			(20 mm)	(60 mm)	reductase activity (per mg protein)
<i>californicus</i>					
PI 531604	29	4.14	6.36	3.64	7.66
<i>elymoides</i>					
Acc:1107	15	3.27	6.71	3.01	7.83
Acc:1108	27	2.67	6.54	2.01	7.34
Acc:1109	15	2.71	6.62	3.03	7.01
Acc:1110	31	2.95	6.51	2.34	5.38
Acc:1111	19	3.02	6.31	2.80	7.17
Acc:1112	24	2.47	6.74	2.90	6.52
Acc:1113	31	2.94	7.21	3.38	6.03
Acc:1114	17	3.07	6.36	3.50	7.50
Acc:1115	33	3.43	6.67	4.36	8.48
Acc:1116	33	3.49	6.83	4.40	9.46
Acc:1117	36	3.33	7.43	4.80	9.13
Acc:1124	36	3.44	6.64	2.93	6.68
PI 619489	31	3.26	5.71	1.14	7.34
PI 619491	29	3.48	6.44	3.40	8.48
PI 619555	33	3.00	6.60	2.82	7.83
PI 619561	27	2.86	6.56	3.41	8.64
9019219	29	4.07	6.18	4.32	8.64
mean	27 b[#]	3.14 b	6.59 a	3.21 ab	7.62 a
<i>brevifolius</i>					
Acc:1123	47	3.94	5.67	3.73	3.91
Acc:1130	29	3.98	5.92	3.94	6.85
PI 531605	46	6.83	5.05	3.40	4.57
9040187	59	6.32	5.62	3.43	5.54
9040189	45	5.51	5.46	2.94	5.87
mean	45 a	5.32 a	5.54 b	3.49 b	5.35 b
<i>multisetus</i>					
Acc:1132	42	5.29	6.58	4.03	9.62
PI 531603	50	6.33	6.10	4.24	8.64
PI 531606	47	4.89	7.30	4.25	8.15
PI 619466	33	4.69	7.25	3.63	8.15
mean	43 a	5.30 a	6.81 a	4.04 a	8.64 a

[#]taxa means followed by different letters in the same column are significantly different at P < 0.05.

were obtained from USDA-ARS, i.e., W6 22031 (David C. Ganskopp, Burns, Ore.) and W6 20963 (James A. Young, Reno, Nev.). The 4 remaining accessions (PI 531603 through PI 532606), obtained from the National Plant Germplasm System, were originally from the collection of the late D.R. Dewey of our laboratory. We determined the taxon of each accession using the dichotomous key provided by Wilson (1963) that distinguishes the taxa based on number and bifurcation of awns. Seed samples of these accessions are deposited in the National Plant Germplasm System at the USDA-ARS Western Regional Plant Introduction Station in Pullman, Wash. (<http://www.ars.grin.gov/npgs>).

Data were collected from evaluations in the field and 4 greenhouse trials. The field evaluation was established on 2–3 Sept. 1993 at Greenville Farm, North Logan, Ut. (41°45'59" N, 111°48'34" W) on a Millville silt loam (coarse-silty, carbonatic, mesic Typic Rendolls; 2–4% slope).

Accessions were established as field transplants on 0.5-m centers in a 7 x 7 plant block. Each block was filled with 49 plants unless fewer were available. Because the blocks were not replicated, data collected from this trial were only for 2 traits of high heritability, which were heading date (the number of days after 30 Apr. 1995 that the majority of the plants in a plot had at least 1 spike emerge from the boot) and seed mass (mg seed⁻¹ averaged across 1994 and 1995 harvests). Seed harvested from these blocks was used to conduct a seedling growth trial in the greenhouse, 2 depth-of-seeding trials, and a nitrate reductase activity assay in the greenhouse. Because outcrossing in squirreltail is negligible (Jensen et al. 1990), seed harvested from such a block may be presumed to be genetically representative of the original collection.

The seedling growth trial was planted in a greenhouse maintained at 20 ± 5°C on 8 Jan. 1996 in a soil consisting of 3 parts

Kidman fine sandy loam (coarse-loamy, mixed, mesic Calcic Haploxerolls): 1 part peat moss. Five seeds of an accession were planted 5 mm deep in 65 X 255-mm cone-containers. Accessions were assigned to 10 replications in a randomized complete block design. The third seedling to emerge was retained, days-to-emergence was recorded, and the other seedlings were removed. Water was supplied daily with a 32% Rorison nutrient solution (Arredondo et al. 1998). Length of the first leaf was measured on day 10. Plants were harvested on day 25 and divided into shoots and roots. Leaf area was determined with a leaf-area meter (LI-3000, LI-COR, Lincoln, Neb.). Roots were recovered by gentle washing with a slow-moving stream of water. Root length was measured on fresh tissue with 'Branching' software (version 1.52β) (Berntson 1992). Shoots and roots were then oven-dried at 70°C for 48 hours before weighing. Specific leaf area was calculated as leaf area/shoot mass, and specific root length was calculated as root length/root mass.

To measure seedling emergence, 2 greenhouse trials were conducted at 20 ± 5°C at depths of 20 mm and 60 mm. Both trials were planted in above-ground beds filled with the greenhouse soil described above. This was underlain by a gravel layer for drainage. The beds were 1.067-m wide and furrows were 50.8-mm apart. Fifty seeds of an accession were planted per half-length of each furrow. Another randomized accession was planted in the opposite half. Accessions were planted in a randomized complete block design with 6 replications. The 20-mm trial was planted on 9 to 10 Dec. 1996 and seedling emergence was tallied daily. Emergence index was calculated as $\sum[(g_n - g_{(n-1)})/n]$, where $(g_n - g_{(n-1)})$ is the number of seedlings germinating since the previous day and n is the number of days since the germination trial began (Maguire 1962). Therefore, large numbers indicate fast emergence and small numbers indicate slow emergence, the opposite direction of the days-to-emergence variable in the above-mentioned seedling growth trial. The 60-mm trial was planted on 4 Feb. 1997 and conducted similarly.

High nitrate reductase activity may facilitate higher assimilation of soil nitrogen, thereby promoting seedling establishment. For the nitrate reductase assay, the 27 accessions were grown in a 20 ± 5°C greenhouse as seedlings in the same soil as the depth-of-seeding evaluations. Fresh samples of leaf tissue were harvested 2 to

4 hours after sunrise, placed directly into liquid N₂, and stored at -80°C until use. Frozen tissue was powdered in liquid N₂ and extracts were made by grinding in 5 to 10 vol. of 50 mM MOPS buffer (pH 7.5) containing 10 mM MgCl₂, 1 mM EDTA, 0.1% Triton X-100, 2.5 mM DTT, 1 mM PMSF, 10 µM leupeptin, and 10 µM chymostatin. After centrifugation of the extracts at 12,000 g for 4 min, the supernatant was transferred to a fresh tube and used immediately to assay total NADH:nitrate reductase activity according to Redinbaugh et al. (1996). Assays were performed in a 200-µl volume containing 50 mM MOPS, 10 mM K-phosphate buffer (pH 7.5) containing 13 mM KNO₃, 500 µM NADH, and 10 µM FAD. Soluble protein in the extracts was determined using a dye-binding assay (Redinbaugh and Campbell 1985).

Data set 2

For the second data set, data were collected from a field evaluation and a greenhouse seedling growth trial. Forty-seven accessions (Table 3) were established as field transplants on 3–4 Sept. 1996 at Evans Farm, Millville, Ut. (41°41'39"N 111°49'58"W) on a Nibley silty clay loam (fine, mixed mesic Aquic Argiustolls; 0–3% slope). All 47 accessions were collected from their native sites in 1995. The planting design was similar to data set 1. Heading date (the mean number of days after 30 Apr. 1997/1998 that the majority

of the plants in a plot had at least 1 spike emerge from the boot), seed mass (the mean mg seed⁻¹ across 1997/1998), and plant height (mean across 1997/1998) were measured on these plots. Seed harvested from these blocks was used to conduct a seedling growth trial in the greenhouse as for data set 1.

The seedling growth trial was planted in a greenhouse maintained at 20 ± 5°C on 12 Mar. 1999 in the same design and soil as used in data set 1. Water was supplied without nutrient solution. Days-to-emergence of the third seedling was recorded and its leaf length was measured 17 days after planting. The plants were harvested 14 Apr. (replications 1 to 3), 15 Apr. (replications 4 to 8), and 16 Apr. (replications 9 to 10) and divided into shoots and roots. For data set 2, we used a Comair root length scanner (Commonwealth Aircraft Corp. Ltd., Melbourne, Australia) to measure root length of fresh tissue that had been stored in refrigerated vials of water. This greatly expedited the process compared to the technique used for data set 1. After scanning, shoots and roots were oven-dried at 70°C for 48 hours before weighing. Specific root length was calculated as root length/root mass.

Statistical analysis

For each trait, differences between means of any 2 taxa were tested for deviation from zero using a t-test at $\alpha = 0.05$. Values for all accessions were standard-

ized to unit variance for each trait before multivariate analysis. Thirteen and 9 orthogonal principal components, the number of variables in each data set, were generated for data sets 1 and 2, respectively (Morrison 1976). Because a large proportion of the total variance was accounted for by the first 2 principal components for both data sets, only the first 2 were retained. These 2 principal components were each defined by a vector of scalars, each representing a trait. These are termed the principal component loadings for Principal Component 1 and Principal Component 2, respectively. Principal Component 1 loadings are the single set of numbers, 13 in the case of data set 1 and 9 in the case of data set 2, that best circumscribes the data set. Likewise, the Principal Component 2 loadings are the second single set of numbers that best circumscribes the variation remaining after Principal Component 1 variation is removed. We rotated principal component loadings using an orthogonal varimax rotation in PROC FACTOR (SAS Institute, Cary, NC) to maximize the amount of information included in the 2 retained principal components (Kaiser 1958). Principal component scores were calculated for each accession for each of the 2 principal components by multiplying the vector of standardized means by the vector of rotated principal component loadings. Accessions were plotted in 2 dimensions based on Principal Component 1 and Principal Component 2 scores. Because 2 of the 13 traits measured in data set 1 and 3 of the 9 traits measured in data set 2 were taken from unreplicated plots, comparisons were made only between taxa rather than between individual accessions. The individual accessions provided replication for their respective taxa.

Results and Discussion

Data set 1

In the 25-day greenhouse trial, *multisetus* accessions emerged faster, had longer leaves at 10 days, and had greater total plant dry-matter at harvest than the other 2 taxa (Table 1). The faster seedling development of *multisetus* may relate to its prevalence in regions with relatively warm springs like the Columbia and Snake River Plains. *Brevifolius* emerged slowest, which may be because of the cooler springs and late freezes of the Rocky Mountains, a region where this taxon predominates. *Elymoides* had the least total plant dry-matter of the 3 taxa, probably

Table 3. Loadings for the first 2 principal components in data sets 1 (13 traits) and 2 (9 traits).

Trait	Principal component	
	1	2
Data set 1		
Days to emergence	-0.563	-0.635
Leaf length	0.818	0.339
Total plant dry-matter	0.968	0.018
Root-to-shoot ratio	0.437	0.526
Leaf area	0.903	0.227
Specific leaf area	0.055	0.854
Root length	0.924	0.059
Specific root length	-0.040	-0.517
Heading date	0.655	-0.552
Seed mass	0.702	-0.593
Germination index (20 mm)	0.028	0.791
Germination index (60 mm)	0.477	0.163
Nitrate reductase activity	0.222	0.749
Data set 2		
Days to emergence	0.353	-0.882
Leaf length	0.082	0.921
Total plant dry-matter	0.512	0.824
Root-to-shoot ratio	-0.754	0.395
Root length	0.441	0.788
Specific root length	0.302	-0.654
Heading date	0.912	0.008
Plant height	0.905	0.001
Seed mass	0.902	0.291

because it is most common in the semi-arid cold desert, a stressful environment where conservative growth is probably advantageous. Root-to-shoot ratio was least for *brevifolius* and greatest for *elymoides*. Evaporative demand, necessitating a greater root-to-shoot ratio, is typically greater in the semi-arid cold desert, where *elymoides* predominates, than in the Rocky Mountains, where *brevifolius* predominates. *Brevifolius* and *elymoides* were similar for leaf area and root length and lower than *multisetus*, which again may relate to the latter's prevalence in warmer regions. *Brevifolius* had lower specific leaf area, i.e., thicker leaves, than the other 2 taxa, but no differences among taxa were observed for specific root length. Likewise, Arredondo et al. (1998) found that 4 *brevifolius* accessions had lower specific leaf area than the *multisetus*, Sand Hollow. Low specific leaf area is associated with high carbon investment and long leaf life-span (Reich 1997), a characteristic of perennials relative to cheatgrass (Arredondo et al. 1998). We are uncertain as to whether *brevifolius* plants have greater longevity in their environments than do *multisetus* or *elymoides* plants.

In the field trial, *elymoides* headed earlier and produced seed with lower mass than the other taxa (Table 2), suggesting that it is adapted to regions lacking the summer precipitation that is found in the Rocky Mountains, for example. In the greenhouse depth-of-emergence trials, *multisetus* emerged significantly faster than *brevifolius* at both 20 and 60-mm depths. The 25-day greenhouse trial also demonstrated the slow germination rate of *brevifolius*, based on emergence from a shallow 5-mm depth. *Elymoides* emergence was similar to *multisetus* and faster than *brevifolius* at 20 mm, but lagged behind with *brevifolius* at 60 mm. The low seed mass of *elymoides* accessions may have been a disadvantage at the deeper 60-mm planting depth, while the high seed mass of *brevifolius* may have compensated for its inherently slow germinability at this depth. Correlations between seed mass and emergence index were negative ($r = -0.50$; $P < 0.01$) at 20 mm and positive ($r = 0.34$; $P < 0.10$) at 60 mm. Thus, larger-seeded accessions emerged faster at 60 mm, while the reverse was true at 20 mm. Emergence indices at the 2 depths were uncorrelated across accessions ($P > 0.10$).

Nitrate reductase activities were lower for *brevifolius* than the other 2 taxa (Table 2). In agronomic crops, high leaf nitrate reductase activity was correlated with increased plant growth and grain yield,

especially at low (<10 mM) external nitrate concentrations (Johnson et al. 1976, Feil et al. 1993). In addition, barley mutants with low nitrate reductase activity grew slower in the cool early-season and matured later than wild-type plants (Blackwood and Hallam, 1979). Measured nitrate reductase activity is the result of a complex interaction of nitrate, carbohydrate availability, plant development, and light. But plant materials with higher nitrate reductase activity, e.g., *elymoides* and *multisetus*, that can more effectively assimilate and compete for soil nitrogen may grow or become established faster than those with lower nitrate reductase activity, e.g., *brevifolius*. Indeed, the slow emergence of *brevifolius* from a 5-mm planting depth relative to *elymoides* and *multisetus* was noted above. Principal component loadings for days to emergence and nitrate reductase activity were negatively correlated for both principal components 1 and 2, but the relationship was stronger for principal component 2 (Table 3).

Principal Components 1 and 2 explained 38 and 29% of the variation, respectively, among accessions for the 13 traits. Loadings for Principal Component 1 indicate that accessions with higher Principal Component 1 scores had generally more rapid emergence at a 5-mm planting depth, greater day-10 leaf length, and greater total plant dry-matter, root-to-shoot ratio, leaf area, and root length at

harvest in the greenhouse trial; later heading date and greater seed mass in the field; and more rapid emergence from a 60-mm planting depth (Table 3). Principal Component 1 separated *multisetus* (high scores) from *elymoides* (low scores). *Brevifolius* was intermediate between these 2, but closer to *elymoides* (Fig. 1). Loadings for Principal Component 2 indicate that accessions with higher Principal Component 2 scores had generally more rapid emergence at a 5-mm planting depth; greater root-to-shoot ratio, greater specific leaf area (thinner leaves), and lower specific root length (thicker roots) at harvest in the greenhouse trial; earlier heading date and lower seed mass in the field; more rapid emergence from a 20-mm planting depth; and higher nitrate reductase activity. Principal Component 2 separated *elymoides* and *multisetus* (high scores) from *brevifolius* (low scores). Overlap among the 3 taxa was absent in the 2-dimensional scatter plot, but beyond that, accessions did not appear to be organized in any geographical manner.

Values for the lone *californicus* accession, PI 531604, were within the range of *elymoides* accessions for all traits except total plant dry-matter in the greenhouse and seed mass in the field, where PI 531604 had slightly greater values (Tables 1, 2). Accession PI 531604 was clearly more similar to *elymoides* than to *brevifolius* or *multisetus*, supporting a close tax-

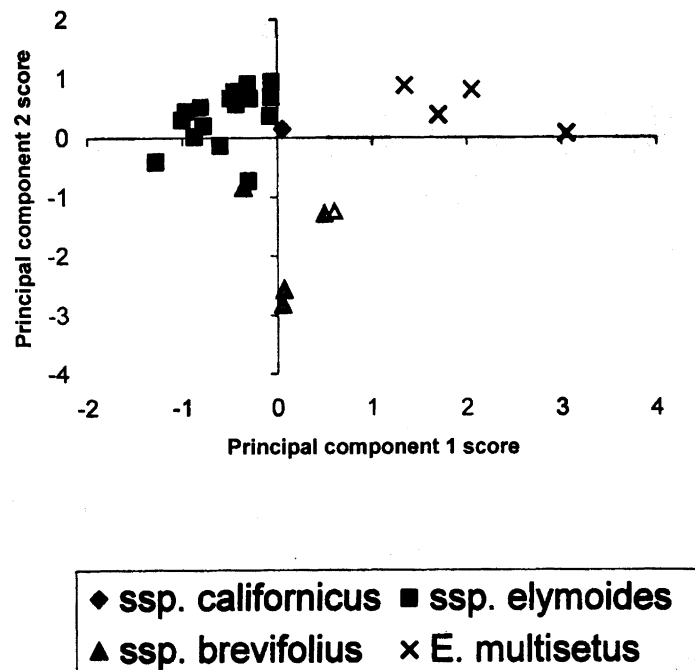


Fig. 1. Plot of the first 2 principal component scores for 27 *Elymus elymoides* and *E. multisetus* squirreltail accessions in data set 1.

Table 4 Means for 10 *elymoides*, 21 *brevifolius*, and 16 *multisetus* squirreltail accessions in data set 2 for 6 traits in a 34-day greenhouse trial.

Taxon/ Accession	Collection location	Elevation (m)	Days to emergence (no.)	Leaf length (17 days post- plant) (mm)	Total plant dry-matter (mg plant ⁻¹)	Root-to- shoot ratio (mg mg ⁻¹)	Root length (mm plant ⁻¹)	Specific root length (mm mg ⁻¹)
<i>elymoides</i>								
T-1173	east of Mountain Home, Ida.	1050	5.7	38	4.09	1.28	640	278
T-1174	west of Mountain Home, Ida.	950	4.4	38	5.18	1.27	860	297
T-1175	Ditto Creek, Elmore Co., Ida.	1000	4.6	42	4.58	1.01	720	313
T-1191	County Rd 10, Moffat Co., Colo.	2150	5.0	41	5.36	1.16	870	302
T-1192	Point of Rocks, Sweetwater Co., Wyo.	2200	4.7	47	5.69	1.39	1090	329
T-1193	Superior, Wyo.	2200	5.9	37	4.04	1.68	730	289
T-1198	btwn Sage Junction & Laketown, Ut.	2200	5.0	42	4.47	1.27	840	336
T-1223	Fish Creek, Carey, Ida.	1450	4.3	49	5.94	1.09	870	281
T-1224	Atomic City, Bingham Co., Ida.	1500	4.5	49	5.26	1.35	770	255
PI 619553	Shoshone, Ida.	1300	4.8	38	5.29	1.20	780	270
mean		1633	4.9 b[#]	42 b	4.99 c	1.27 a	817 c	295 b
<i>brevifolius</i>								
group A								
T-1180	northeast of Wagonmound, N.M.	2000	7.4	30	5.52	0.84	710	282
T-1233	north of Hermosa, Colo.	2000	5.8	44	9.53	0.61	1210	335
T-1238	east of Chimney Rock, Colo.	2050	5.8	44	8.89	0.50	970	327
T-1239	northeast of Pagosa Springs, Colo.	2350	6.4	39	7.33	0.85	1160	345
T-1242	north of Lake City, Colo.	2450	6.4	37	6.16	0.88	1060	367
T-1249	west of Sargents, Colo.	2600	6.8	35	7.68	0.65	1080	356
T-1260	south of Westcliffe, Colo.	2450	6.6	42	6.61	0.76	1060	372
T-1264	north of Colmor, N.M.	1850	7.0	35	5.33	0.74	800	354
T-1265	north of Wagonmound, N.M.	1900	7.1	37	5.56	0.82	980	392
T-1271	southwest of Ocate, N.M.	2300	6.3	45	6.86	0.81	1050	342
T-1272	La Cueva, N.M.	2200	6.4	43	5.46	0.92	850	326
T-1277	Tres Piedras, N.M.	2350	6.6	44	5.70	0.91	1030	380
T-1299	north of Flagstaff, Ariz.	2150	6.2	47	8.44	0.76	1500	411
(mean)		(2204)	(6.5)	(40)	(6.85)	(0.77)	(1035)	(353)
group B								
T-1228	Colton, Ut.	2150	6.5	37	3.70	1.31	910	433
T-1243	north of Powderhorn, Colo.	2750	6.3	39	5.10	1.07	1070	405
T-1308	northwest of Almont, Colo.	2500	5.7	39	4.37	1.07	980	434
(mean)		(2467)	(6.2)	(38)	(4.39)	(1.15)	(987)	(424)
group C								
T-1202	hwy 75 X 20, Blaine Co., Ida.	1350	5.4	42	4.71	1.26	720	274
T-1203	east of Fairfield, Ida.	1500	5.4	52	6.28	0.84	1060	369
T-1204	east of Hill City, Ida.	1550	5.8	43	6.55	1.17	1010	286
T-1205	west of Hill City, Ida.	1600	4.2	44	5.92	1.26	1080	327
T-1206	east of Dixie, Elmore Co., Ida.	1600	5.0	45	5.92	1.18	1080	336
(mean)		(1520)	(5.2)	(45)	(5.88)	(1.14)	(990)	(319)
mean		2100	6.1 a	41 b	6.27 b	0.91 b	1018 b	355 a
<i>multisetus</i>								
PI 619454	A-line canal, Gem Co., Ida.	950	3.9	61	10.49	1.14	1660	297
PI 619456	Cartwright Rd., Ada Co., Ida.	1000	4.1	49	9.00	1.17	1560	321
PI 619457	Little Land & Livestock, Canyon Co., Ida.	800	3.8	64	9.91	1.22	1360	250
PI 619458	northwest of Mayfield, Elmore Co., Ida.	1100	4.0	51	9.92	1.31	1470	262
PI 619459	Boise, Ida.	1000	3.9	55	9.21	1.20	1530	305
PI 619460	Bogus Basin Rd., Ada Co., Ida.	1000	4.3	53	9.05	1.16	1510	311
PI 619461	Barber, Ida.	950	3.9	51	9.24	1.16	1390	280
PI 619462	southeast of Mayfield, Elmore Co., Ida.	1100	3.7	58	8.74	1.39	1360	267
PI 619463	Ditto Creek, Elmore Co., Ida.	1000	3.9	55	9.17	1.34	1490	284
PI 619464	Lower Hatley, Canyon Co., Ida.	800	3.8	56	9.61	0.99	1280	268
PI 619465	Seaman's Gulch Rd., Ada Co., Ida.	1000	4.4	53	9.87	1.23	1510	278
PI 619467	Middle Hatley, Gem Co., Ida.	800	4.3	52	8.25	1.07	1160	272
PI 619564	Ditto Creek, Elmore Co., Ida.	1100	4.9	44	7.38	1.04	1030	273
T-1165	King Hill, Ida.	850	4.3	63	10.87	1.25	1610	267
T-1183	Mountain Home, Ida.	1000	4.2	65	10.26	0.99	1380	270
T-1214	Black's Creek, Ada Co., Ida.	1100	4.2	49	7.99	1.04	1200	294
mean		950	4.1 c	55 a	9.31 a	1.17 a	1406 a	281 b

[#]taxa means followed by different letters in the same column are significantly different at P < 0.05.

onomic relationship between *californicus* and *elymoides*, as favored by Wilson (1963).

Data set 2

In the greenhouse trial, *multisetus* emerged faster, had longer leaves at 17 days, and had greater total plant dry-matter at harvest than the other 2 taxa (Table 4). *Brevifolius* emerged most slowly from a 5-mm planting depth and *elymoides* had the least total plant dry-matter. Root-to-shoot ratio was least for *brevifolius* and greater for *multisetus* and *elymoides*. Specific root length was greater for *brevifolius* (thin roots), especially group B (see below), than for *multisetus* or *elymoides*. *Multisetus* had the greatest root length with *brevifolius* intermediate and *elymoides* least. In the field trial (Table 5), *elymoides* had the earliest heading date, the lowest seed mass, and the shortest height. *Brevifolius* and *multisetus* did not differ from one another for these traits.

The first 2 principal components explained 41 and 40% of the variation, respectively, among accessions for the 9

traits. Loadings for Principal Component 1 indicate that accessions with high Principal Component 1 scores had generally greater total plant dry-matter, lower root-to-shoot ratio, and greater root length at harvest in the greenhouse trial; and later heading date, greater height, and greater seed mass in the field (Table 3). Principal Component 1 separated *brevifolius* and *multisetus* (high scores) from *elymoides* (low scores) (Fig. 2). Loadings for Principal Component 2 indicate that accessions with higher Principal Component 2 scores had generally more rapid emergence at a 5-mm planting depth; greater leaf length on day 17 and greater total plant dry-matter, greater root length, and lower specific root length (thicker roots) at harvest in the greenhouse trial. Principal Component 2 separated *multisetus* (high scores) from *elymoides* and *brevifolius* (low scores). This separation resulted in plots that oriented the 3 taxa in a similar manner to data set 1 (Fig. 1). Variation among accessions was greater for *brevifolius* than the other 2 taxa; this was reflected mostly by Principal Component 1 scores.

Together, Principal Components 1 and 2 separated *brevifolius* accessions into 3 groups (Fig. 2). "Group A" accessions were late-maturing with high-seed mass and originated from medium to high elevations (1850 to 2600 m) in Colorado, New Mexico, and Arizona. "Group B" accessions were early-maturing (as early as *elymoides*) with low-seed mass and originated from high elevations (2150 to 2750 m) in Colorado and Utah. "Group C" accessions were intermediate-maturing with low-seed mass and originated from low to medium elevations (1350 to 1600 m) in southern Idaho. Amplified fragment length polymorphisms (AFLP), a DNA marker technique, have verified that these 3 groups are genetically distinct (Larson et al. 2003).

In the greenhouse (Table 4), days to emergence were generally lesser for Group C accessions and more similar to *elymoides* than were Group A or B accessions. Total plant dry-matter was generally greatest for Group A accessions, least for Group B accessions, and intermediate for Group C accessions. Root-to-shoot ratio

Table 5. Means for 10 *elymoides*, 21 *brevifolius*, and 16 *multisetus* squirreltail accessions in data set 2 for 6 traits in a 2-year field trial.

Taxon/ Accession	Heading date (days after 4/30)	Plant height (m)	Seed mass (mg seed ⁻¹)	Taxon/ Accession	Heading date (days after 4/30)	Plant height (m)	Seed mass (mg seed ⁻¹)
<i>elymoides</i>				<i>brevifolius</i>			
T-1173	21	0.28	2.21	group A			
T-1174	21	0.32	2.37	T-1180	60	0.66	4.81
T-1175	22	0.31	2.16	T-1233	62	0.64	4.51
T-1191	18	0.28	3.29	T-1238	47	0.75	5.10
T-1192	20	0.27	2.83	T-1239	49	0.75	5.34
T-1193	15	0.38	2.36	T-1242	42	0.77	5.36
T-1198	20	0.48	2.91	T-1249	46	0.68	5.71
T-1223	26	0.42	3.01	T-1260	51	0.53	4.58
T-1224	24	0.42	2.73	T-1264	65	0.71	4.86
PI 619553	23	0.38	3.05	T-1265	60	0.71	5.02
mean	21 b	0.35 b	2.69 b	T-1271	57	0.72	5.23
<i>multisetus</i>				T-1272	57	0.72	5.48
PI 619454	44	0.53	4.88	T-1277	53	0.63	4.51
PI 619456	42	0.58	5.50	T-1299	63	0.66	6.16
PI 619457	42	0.58	4.72	(mean)	(55)	(0.68)	(5.13)
PI 619458	42	0.68	5.83	group B			
PI 619459	41	0.53	5.05	T-1228	23	0.51	3.39
PI 619460	42	0.58	5.01	T-1243	24	0.53	3.77
PI 619461	41	0.64	5.18	T-1245	17	0.58	3.37
PI 619462	45	0.65	5.07	(mean)	(21)	(0.54)	(3.51)
PI 619463	45	0.57	4.72	group C			
PI 619464	44	0.63	4.87	T-1202	34	0.50	3.75
PI 619465	42	0.61	5.14	T-1203	32	0.54	3.74
PI 619467	42	0.56	4.62	T-1204	34	0.58	4.61
PI 619564	42	0.66	4.87	T-1205	38	0.62	3.47
T-1165	33	0.53	4.15	T-1206	38	0.60	3.27
T-1183	41	0.62	5.39	(mean)	(35)	(0.57)	(3.77)
T-1214	41	0.60	5.49	mean	45 a	0.64 a	4.57 a
mean	42 a	0.59 a	5.03 a				

#taxa means followed by different letters in the same column are significantly different at P < 0.05.

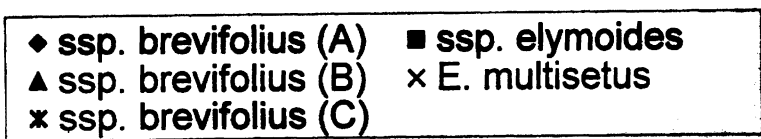
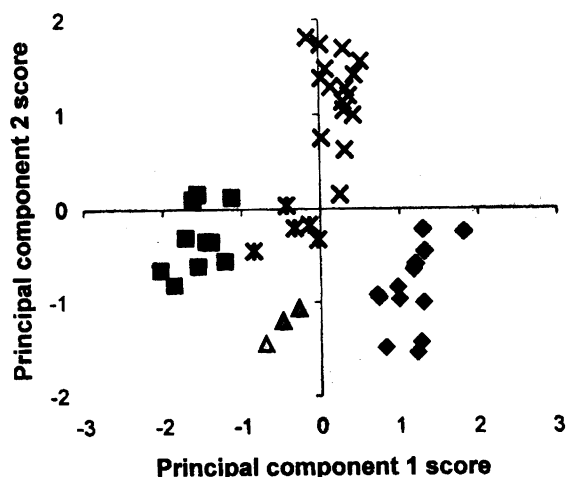


Fig. 2. Plot of the first 2 principal component scores for 47 *Elymus elymoides* and *E. multisetus* squirreltail accessions in data set 2.

was generally lower for Group A accessions than Group B or C accessions, which were more similar to *elymoides* and *multisetus*. Specific root length was generally greater for Group B accessions than Group A or C accessions, which were more similar to *elymoides* and *multisetus*. In the field trial (Table 5), seed mass was generally greater for Group A accessions, which were more similar to *multisetus*, than Group B or C accessions, which were more similar to *elymoides*. Plant height was generally greater for Group A accessions than Group B or C accessions, which were more similar to *multisetus*, which in turn was greater than *elymoides*.

While the geographical range of Group C is clearly separate from Groups A and B, Groups A and B themselves are overlapping and may occur as biotypes at the same site. Accession T-1245, a group B accession originating northwest of Almont, Colo., was collected at the same site as T-1308, which was not included in data set 2, but has been confirmed as a Group A accession based on its AFLP profile (Larson et al. 2003). Likewise, T-1264, a Group A accession originating north of Colmor, N.M., was collected from the same site as T-1309, also not included in data set 2. Based on its early maturity (unpublished data), however, T-1309 is likely a Group B accession.

Relative to Group A, Group B is earlier

in maturity, is shorter, and has greater root-to-shoot ratio, greater specific root length (thinner roots), lower total plant dry-matter, and lower seed mass. We wonder whether some or all of these traits may be associated with adaptation to higher elevations. In fact, T-1243 (Powderhorn, Colorado), a Group B accession, was collected at 2,750 m, the highest elevation of any accession. While our elevation data (Table 4) do not directly support this speculation, we may have missed a trend by failing to collect at higher elevations than we did.

Conclusions

In both data sets, the 3 squirreltail taxa were easily separated by the traits examined. Data set 1 had 13 traits and data set 2 had 9 traits. The 8 traits in common to both data sets were days to emergence from 5 mm; leaf length (at 10 days in data set 1 and 17 days in data set 2), total plant dry-matter, root-to-shoot ratio, root length, and specific root length at harvest; heading date; and seed mass. In addition to the 8 traits in common, data set 1 included leaf area, specific leaf area, days to emergence from 20 mm, days to emergence from 60 mm, and nitrate reductase activity. In addition to the 8 traits in common,

data set 2 included plant height. With 1 exception (root-to-shoot ratio) the 2 data sets ranked the taxa in the same order for all 8 common traits. However, for 3 of these traits (root-to-shoot ratio, root length, and specific root length), significant differences among taxon means were slightly different. For root-to-shoot ratio, data set 1 grouped middle-ranking *elymoides* with lowest-ranking *brevifolius*, while data set 2 grouped highest-ranking *elymoides* with middle-ranking *multisetus*. For root length, data set 1 grouped lowest-ranking *elymoides* with middle-ranking *brevifolius*, while data set 2 grouped lowest-ranking *elymoides* apart from middle-ranking *brevifolius*. For specific root length, data set 1 grouped all 3 taxa together, while data set 2 separated highest-ranking *brevifolius* apart from *elymoides* and *multisetus*.

Of all taxa, *elymoides* was the earliest, shortest, and had the lowest seed mass, seedling dry-matter, and root length. *Brevifolius* had the lowest root-to-shoot ratio, specific leaf area, and nitrate reductase activity, the highest specific root length, and generally the slowest emergence from a normal planting depth. Low specific leaf area is associated with high carbon investment and great leaf life-span (Reich 1997). *Multisetus* had the fastest emergence from a normal planting depth, longest leaf length at 10 days (data set 1) or 17 days (data set 2) post-plant, and greatest seedling dry-matter, leaf area, and root length.

Wilson (1963) stated that *brevifolius* displays the greatest ecological diversity of the 5 squirreltail taxa, being found in desert to montane habitats from 600 to 3000 m elevation and with extreme variation in size. Variation among accessions was similar for the 3 taxa in data set 1, but *brevifolius* had the greatest variation in data set 2, perhaps because these *brevifolius* accessions represented a wider geographical distribution than the other 2 taxa. Nevertheless, we found a greater degree of discontinuity, e.g., Groups A, B, and C, within *brevifolius* than within *multisetus* or *elymoides*. In data set 2, accessions that plotted near the convergence of the 3 taxa were from the environs of southern Idaho, a region with ample representation of all 3 taxa. Overall, Group C accessions were more similar to *elymoides* and *multisetus* than were Group A or B accessions (Fig. 2).

Five *brevifolius* accessions in data set 1 can be reinterpreted based on findings of data set 2 and subsequent AFLP analysis (Larson et al. 2003). Three late-maturing,

high seed-mass accessions, 9040189, 904187, and PI 531605, qualify as Group A, according to AFLP data. While no AFLP data have been collected on the fourth accession, Acc:1123, it appears to be a member of Group C based on its Oregon origin, fast emergence (Table 1) and low seed mass (Table 2). It should be noted, however, that its heading date is similar to the 3 Group A accessions. The fifth accession, Acc:1130 (Savageton, Wyo.), is unique in this study. Based on AFLP results, it belongs to "Group D", accessions of which we have collected on the High Plains from Alberta to Colorado.

Our data support the recognition of *elymoides*, *brevifolius*, and *multisetus* taxa, but they do not provide direction as to whether each merits specific or subspecific rank. From an ecological perspective, these data do not support the suggestion that any one pair of *elymoides*, *multisetus*, and *brevifolius* is more similar than any other pair. Furthermore, these results provide guidance as to which specific commercially available plant materials should be planted in which locations. For example, the 3 distinct groups of *brevifolius* accessions, as well as the different taxa, are ecologically distinct and are likely adapted to regions in which their particular group is found in nature. These results reflect the highly ecotypic nature of the squirreltails.

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