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MOLECULAR MARKER ANALYSIS OF *LEYMUS FLAVESCENS* AND CHROMOSOME PAIRING IN *LEYMUS FLAVESCENS* HYBRIDS (POACEAE: TRITICEAE)[1]

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Leymus flavescens (Scribner & Smith) Pilger, yellow wild rye, is a long-lived, strongly rhizomatous, tetraploid (2n=4x=28) perennial grass of the tribe Triticeae distributed throughout central Washington, eastern Oregon, and the Snake River plains of Idaho. Our objectives were (1) to describe chromosome pairing and fertility in F_1 hybrids between *L. flavescens* and North American tetraploids (2n=4x=28) *L. triticoides* and *L. cinereus* and Eurasian tetraploids *L. secalinus*, *L. racemosus*, and *L. alaicus* subsp. *karataviensis* and (2) to utilize genome-specific random amplified polymorphic DNA (RAPD) markers to verify the genomic composition of *L. flavescens*. The hybrids *L. flavescens* × *L. triticoides* (*NsNsXmXm*), *L. flavescens* × *L. secalinus* (*NsNsXmXm*), *L. flavescens* × *L. racemosus* (*NsNsXmXm*), *L. flavescens* × *L. cinereus* (*NsNsXmXm*), and *L. flavescens* × *L. alaicus* subsp. *karataviensis* (*NsNsXmXm*) averaged 13.9, 13.8, 13.6, 13.1, and 11.9 bivalents per cell, respectively. Genome-specific RAPD assay indicates that *L. flavescens* has the *Ns* genome but lacks the *St* genome from the genus *Pseudoroegneria* and the *H* genome from the genus *Hordeum*. On the basis of the bivalent chromosome pairing frequency in the F_1 hybrids of *L. flavescens*, the genomic formula of *L. flavescens* is *NsNsXmXm*. The presence of the *Ns* genome was verified by molecular characterization.

Keywords: Leymus, genome, meiosis, chromosome pairing, interspecific hybrids, taxonomy, systematics.

Introduction

The genus *Leymus* Hochst. is a relatively old genus erected by Hochstetter in 1848 only for *L. arenarius* (L.) Hochst. However, Pilger (1947), Tzvelev (1976), Melderis et al. (1980), Barkworth et al. (1983), and Gleason and Cronquist (1991) recognized the genus. On the basis of the treatments of Tzvelev (1976) and Löve (1984), *Leymus* is subdivided into four sections: (1) sect. Leymus Hochst., which is represented by the North American *L. mollis* (Trin.) Pilger, *L. arenarius* (L.) Hochst., and Eurasian *L. racemosus* (Lam.) Tzvelev (=*Elymus giganteus* Vahl.); (2) sect. Aphanoneuron (Nevski) Tzvelev, which is restricted to Eurasian species typified by *L. angustus* (Trin.) Pilger, *L. secalinus* (Georgi) Tzvelev, and *L. alaicus* (Korsh.) Tzvelev subsp. *karataviensis* (Roshev.) Tzvelev (=*Elymus karatviensis* Roshev.); (3) sect. Anisopyrum (Griseb.) Tzvelev, which is characterized by North American *L. flavescens* (Scribner and Smith) Pilger, *L. ambiguus* (Vasey and Scribner) D. Dewey, *L. salinus* (M. E. Jones) Á. Löve, *L. triticoides* (Buckl.) Pilger, *L. condenstatus* (K. Presl.) Á. Löve, and Eurasian *L. chinensis* (Trin.) Tzvelev, *L. ramosus* (Trin.) Tzvelev, and *L. multicaulis* (Kar. and Kir.) Tzvelev; and (4) sect. Malacurus (Nevski) Tzvelev, which is a monotypic section comprising Eurasian *L. lanatus* (Korsh.) Tzvelev. Sections Aphanoneuron and Malacurus are restricted to Eurasian species. Sections Leymus and Anisopyrum comprise both North American and Eurasian taxa.

Species of the genus *Leymus* are long-lived perennials that are distributed from the coastal regions of the North Sea (*L. arenarius*) across central Asia (*L. angustus*—Altai wild rye) to East Asia (*L. chinensis*), Alaska (*L. mollis*), and western North America (*L. cinereus* Á. Löve—Great Basin wild rye, and *L. triticoides*—beardless wild rye). *Leymus* species are characterized by multiple spikelets per node and are for the most part rhizomatous (except *L. cinereus*), long anthered, and variable in their degree of self-pollination (Jensen et al. 1990). On the basis of variation in repeated nucleotide sequences, Dubcovsky et al. (1997) reported similar banding patterns for South American *Elymus erianthus* Phil., and *Elymus mendocinus* (Parodi) Á. Löve and tetraploid *Leymus* taxa, indicating that the distribution of *Leymus* taxa may extend into South America.

Leymus is a polyploid genus that consists of approximately 30 species worldwide, all of which had previously been treated in the genus *Elymus* L. (Dewey 1984). More than half of the *Leymus* species are allotetraploids (2n=28). The higher polyploid species (2n=42−84) are complex autoallopolyploids. Multivalents are seen at metaphase I in octaploid *L. cinereus* and dodecaploid *L. angustus* (Dewey 1972*a*), but their frequency is much less than expected from true autoalloploids, indicating that gene(s) promoting bivalent pairing appear to be operating (Dewey 1984).

The genomic constitution of the genus *Leymus* has traditionally been based on the *Ns* genome from *Psathyrostachys* Nevski and the *J* genome from *Thinopyrum* Á. Löve (Dewey 1984). However, recent cytogenetic and molecular data (Zhang and Dvorak 1991; Wang and Jensen 1994) demonstrate the absence of the *J* genome from *Thinopyrum* in *Leymus* taxa.

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Table 1

Plant Materials Used in Crosses

Species	2n	Genome	Accession number	Collection origin
Leymus flavescens	28	Unknown	Harris	Idaho, U.S.A.
L. triticoides	28	*NsNsXmXm*	Dewey E-7-6	Oregon, U.S.A.
L. secalinus	28	*NsNsXmXm*	PI210988	Afghanistan
L. racemosus	28	*NsNsXmXm*	Jaaska	USSR
L. cinereus	28	*NsNsXmXm*	J. A. Young	Nevada, U.S.A.
L. alaicus subsp. *karataviensis*	28	*NsNsXmXm*	PI314671	USSR

On the basis of repeated nucleotide sequence identity between species and diagnostic hybrid intensities in Southern blots, Zhang and Dvorak (1991) suggested that *Leymus* polyploids originated from hybridization of two unidentified *Psathyrostachys* species. On the basis of these findings, the genomic formula for tetraploid *Leymus* species would be $Ns_iNs_iNs_jNs_j$, where *i* and *j* represent modified versions of the *Ns* genome within the *Psathyrostachys* genus. On the basis of the low frequency of trivalents (0.15–0.40) in eight triploid hybrids between diploid *Psathyrostachys* and tetraploid *Leymus* species (Dewey 1970*a*, 1972*c*, 1976; Wang and Hsiao 1984), chromosome pairing does not support the segmental autotetraploid nature of *Leymus* tetraploid taxa as proposed by Zhang and Dvorak (1991). On the basis of chromosome pairing data, Wang et al. (1994) proposed that the second genome within tetraploid *Leymus* species be designated *Xm*, thus giving *Leymus* the genomic formula of *NsNsXmXm*, where *Xm* is an unidentified genome. However, the actual genomic makeup of *Leymus* is still very much in question and open for further investigation.

Leymus flavescens, yellow wild rye, is a long-lived, strongly rhizomatous, tetraploid (2n=4x=28) perennial grass of the tribe Triticeae distributed throughout central Washington, eastern Oregon, and the Snake River plains of Idaho, with isolated populations in the black hills of South Dakota (Holmgren and Holmgren 1977). The original description of *L. flavescens*, described as *Elymus flavescens*, was made on the basis of material collected on dry sandy soils near Columbus, Klickitat County, Washington, in 1886 (Holmgren and Holmgren 1977). It was transferred to the genus *Leymus* in 1947 by Pilger (Homlgren and Holmgren 1977).

Little is known about the cytogenetic and genomic relationships between *L. flavescens* and the North American *Leymus* tetraploid species *L. triticoides* and *L. cinereus*. Information is also lacking on genomic relationships between *L. flavescens* and its Eurasian counterparts, *L. secalinus*, *L. racemosus*, and *L. alaicus* subsp. *karataviensis*. *Leymus flavescens* can be distinguished morphologically from its close North American relatives on the basis of its lemmas that are hirsute to densely villous with long yellow-whitish hairs. *Leymus triticoides*, *L. cinereus*, *L. salinus*, *L. simplex*, and *L. ambiguus* are characterized by glabrous to sparsely strigose lemmas (Holmgren and Holmgren 1977). The objectives of this study are to describe chromosome pairing and fertility in F_1 hybrids between *L. flavescens* and North American tetraploids *L. triticoides* and *L. cinereus* and Eurasian tetraploids, *L. secalinus*, *L. racemosus*, and *L. alaicus* subsp. *karataviensis*, and to utilize genome-specific random amplified polymorphic DNA (RAPD) markers to understand better the genomic composition of *L. flavescens*.

Material and Methods

Leymus flavescens (collection A-6484) was collected from sand dunes in the Shelley-Blackfoot region of Idaho by Douglas R. Dewey in the early 1970s. The target and analyzer species used are listed in table 1, including their accession and chromosome numbers, genome designations, and origins. *Leymus cinereus* and *L. triticoides* are North American tetraploids with the *Ns* and *Xm* genomes, the *Ns* genome originating from the genus *Psathyrostachys* and the *Xm* from an unidentified diploid (Dewey 1976; Wang and Jensen 1994). *Leymus racemosus*, *L. secalinus*, and *L. alaicus* subsp. *karataviensis* are

Table 2

Hybrids Synthesized for This Study

Cross (female × male)	Number of unemasculated florets	Number of seeds	Number of hybrids
Leymus flavescens × *L. cinereus*	118	36	35
L. flavescens × *L. triticoides*	110	8	5
L. flavescens × *L. secalinus*	114	5	2
L. flavescens × *L. racemosus*	9[a]	72	2
L. flavescens × *L. alaicus* subsp. *karataviensis*	160	28	16

[a] Number of spikes pollinated instead of number of florets.

Table 3

Chromosome Number and Pairing in F_1 Hybrids of *Leymus flavescens* with *L. triticoides, L. secalinus, L. racemosus, L. cinereus,* and *L. alaicus* subsp. *karataviensis*

Species or F_1 hybrids	2n	Number of plants	Chromosome associations (number/cell)							
			I	II			III	IV	Number of cells	Chiasma/cell
				Ring	Rod	Total				
L. flavescens × *L. cinereus*	28	3								
Configuration mean			1.85	12.0	1.08	13.1	...	...	...	...
Configuration range			0–8	4–14	0–8	10–14	...	...	39	25.08
L. flavescens × *L. triticoides*	28	3								
Configuration mean			0.24	12.6	1.27	13.9	...	...	...	...
Configuration range			0.0–2	11–14	0–3	13–14	...	...	74	26.47
L. flavescens × *L. secalinus*	28	2								
Configuration mean			0.30	13.3	0.48	13.8	...	0.05	...	...
Configuration range			0–2	10–14	0–4	13–14	...	0.0–1	81	27.26
L. flavescens × *L. racemosus*	28	2								
Configuration mean			0.15	11.9	1.70	13.6	0.01	0.17	...	...
Configuration range			0–2	8–14	0–6	13–14	0.0–1	0–2	88	26.11
L. flavescens × *L. alaicus* subsp. *karataviensis*	28	3								
Configuration mean			4.16	10.5	1.39	11.9	...	...	...	...
Configuration range			0–14	6–14	0–4	7–14	...	...	99	22.39

Eurasian tetraploids (Bowden 1957; Petrova 1960; Dewey 1972*c*) suspected of having the *Ns* and *Xm* genomes.

Hybrids produced in this study are listed in table 2. All crosses were made using unemasculated florets of *L. flavescens*. Pollination was achieved by shaking pollen-bearing spikes of the appropriate analyzer parent through an open parchment paper sleeve containing the inflorescence of *L. flavescens*. Seeds from the crosses were germinated on vermiculate and transplanted into plastic tubes (6-cm diameter, 30 cm long) containing 540 cm^3 of steam-sterilized Kidman fine sandy loam soil in the greenhouse. After several months in the greenhouse, the hybrids were transplanted to field plots near Logan, Utah.

Pollen mother cells of the F_1 hybrids were fixed in Carnoy's solution (absolute ethanol : chloroform : glacial acetic acid 6 : 3 : 1 vol/vol) for 24–48 h and then transferred to 70% ethanol and stored in a refrigerator. Pollen mother cells were squashed and stained with 2% acetocarmine solution. Meiotic configurations were tabulated at metaphase I. Seed set was

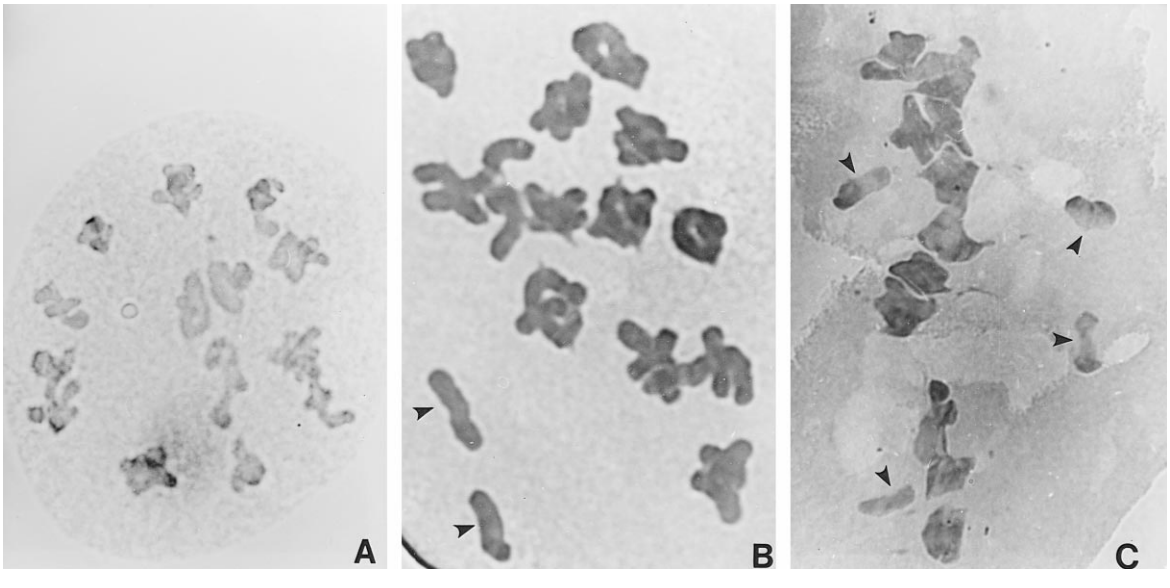

Fig. 1 Chromosome pairing at metaphase I in (*A*) *Leymus flavescens* × *L. racemosus* showing complete bivalent pairing (14 II); (*B*) *L. flavescens* × *L. cinereus* showing 2 I (indicated by arrows) and 13 II; (*C*) *L. flavescens* × *L. alaicus* subsp. *karataviensis* showing 4 I (indicated by arrows) and 12 II.

Table 4

The Presence and Absence of Genome-Specific RAPD Markers in *Leymus flavescens, L. arenarius, Psathyrostachys juncea, Pseudoroegneria spicata,* and *Hordeum bogdanii* Assayed with Primers from Operon Technologies

		Genome-specific RAPD markers				
Template DNA	Ploidy	$OPA20_{400}$	$OPB08_{525}$	$OPN01_{817}$	$OPW05_{338}$	$OPW05_{700}$
L. flavescens	4 ×	−−	+	+	++	−−
L. arenarius	8 ×	−−	+	−−	++	−−
P. juncea	2 ×	−−	−−	−−	++	−−
P. spicata	2 ×	+	++	++	−−	−−
H. bogdanii	2 ×	−−	+	−−	−−	++
None (CK)		−−	−−	−−	−−	−−

Note. ++ indicates an intense band; + indicates a weak band; − indicates the absence of a band.

determined from a minimum of 10 spikes taken from each of the F_1 hybrids.

Genome-specific RAPD markers have been identified for genomes occurring in the tribe Triticeae, thus facilitating the determination of genome compositions in polyploid species (Wei and Wang 1995; Svitashev et al. 1998). *Leymus flavescens* was subjected to RAPD assays along with species with known genomic constitutions following the procedures of Svitashev et al. (1998). Template DNA of *L. flavescens*, *L. arenarius*, *Psathyrostachys juncea* (Fisch.) Nevski, *Pseudoroegneria spicata* (Pursh.) Á. Löve, and *Hordeum bogdanii* Wilenski were amplified with Operon Technologies' primers OPA20, OPB08, OPN01, and OPW05. A negative control, which contained all components of the reaction mixture for RAPD except template DNA, was included for each primer.

Results

Cytology and Fertility

***Leymus flavescens* 2n=28 × *Leymus cinereus* 2n=28.** Crossing barriers between these two species appears to be low (table 2). Thirty-five hybrid plants resulted from the pollination by *L. cinereus* of 118 unemasculated florets of *L. flavescens*. The hybrids were moderately rhizomatous with blue-green leaves scattered along the culm and vegetatively and had a closer resemblance to the *L. cinereus* parent. The hybrids were large, robust plants that were much taller than the *L. flavescens* parent but similar in height to *L. cinereus*. The hybrid spikes were upright, had multiple spikelets per node, and exhibited the densely villous yellow-whitish hairs on the lemmas similar to *L. flavescens* but lacking in *L. cinereus*.

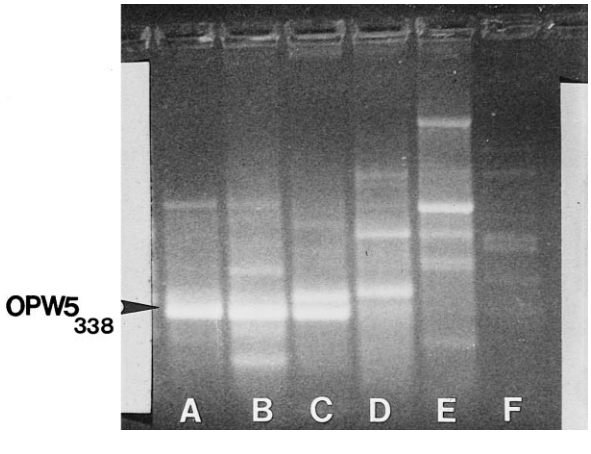

Fig. 2 RAPD profiles of the $OPW5_{338}$ marker, specific to the *Ns* genome, amplified with the template DNA from Triticeae species and hybrids. *A* = *Leymus flavescens*, *B* = *L. arenarius* (*NsNsNsNsXmXmXmXm*), *C* = *Psathyrostachys juncea* (*NsNs*), *D* = *Pseudoroegneria* spicata (*StSt*), *E* = *Hordeum bogdanii* (*HH*), and *F* = check.

Dewey (1970*b*) reported that tetraploid *L. cinereus* consistently formed 14 bivalents at metaphase I (MI) (table 3) and that subsequent meiotic stages were basically stable. Multivalents were not observed or reported for the parent taxa. The hybrids between *L. flavescens* and *L. cinereus* formed 14 bivalents in more than 31% of the MI cells (fig. 1*A*). The most frequently observed association was 2 I and 13 II (fig. 1*B*, table 3), which occurred in 54% of the MI cells. Most of the bivalents were held together by chiasmata in both arms, an indication of close chromosome homologies between *L. flavescens* and *L. cinereus*. Multivalents were not observed (table 3) in the F_1 hybrids between *L. flavescens* and *L. cinereus*. The F_1 hybrids did not set seed under open pollination conditions.

***Leymus flavescens* 2n=28 × *Leymus triticoides* 2n=28.** Hybrid seed resulting from the cross *L. flavescens* × *L. triticoides* was considerably less than that observed in the *L. flavescens* × *L. cinereus* hybrid (table 2). The hybrids were strongly rhizomatous with mostly basal blue-green leaves and culms similar in height to *L. triticoides* (100–120 cm). The hybrid spikes were erect and more slender than those of *L. flavescens*, with the densely villous yellow-whitish hairs on the lemmas similar to *L. flavescens*. The unique morphology and nondehiscent anthers left little doubt as to the validity of the hybrid.

Leymus triticoides is an allotetraploid with two basic genomes, *Ns* and *Xm* (Dewey 1970*b*). Chromosome pairing within *L. triticoides* is predominately 14 ring bivalents with a chiasma occurring on each chromosome arm (Dewey 1970*b*). Chromosome pairing in the *L. flavescens* × *L. triticoides* hybrids was similar to that in the *L. flavescens* × *L. cinereus* hybrids (table 3). Fourteen bivalents (fig. 1*A*), predominantly rings, were observed in 66 of 74 MI cells observed. The remaining eight cells had two univalents and 13 bivalents. Multivalents were not observed in the F_1 hybrid between *L. flavescens* and *L. triticoides*. The above F_1 hybrids did not set seed under open-pollinated conditions.

***Leymus flavescens* 2n=28 × *Leymus secalinus* (=*Elymus dasytachys* Trin.) 2n=28.** Only two hybrids resulted from 114 unemasculated florets of *L. flavescens* pollinated with pollen from *L. secalinus*. Both hybrids were strongly rhizomatous spreading to a diameter of more than 2 m within 2 yr. The hybrid spike characteristics were intermediate to both parents. The hybrid lemmas were highly pubescent with subappressed yellow-whitish hairs similar to both parents.

Leymus secalinus has been reported to be a meiotically stable allotetraploid comprised of the *Ns* and *Xm* genomes (Dewey 1970*b*; Wang et al. 1994). This particular hybrid combines the genomes from North American *L. flavescens* and Eurasian *L. secalinus*. Despite the diverse origins of *L. flavescens* and *L. secalinus*, their F_1 hybrids exhibited close bivalent pairing (table 3). Fourteen bivalents (fig. 1*A*), most of them rings, were observed in 65 of 81 MI cells. The next most common configuration was two univalents and 13 bivalents (fig. 1*B*), which occurred in 15% of the MI cells. One to two multivalents, usually quadrivalents, were observed in 5% of the MI cells. The F_1 hybrids did not set seed under open-pollinated conditions.

***Leymus flavescens* 2n=28 × *Leymus racemosus* (=*Elymus giganteus* Vahl) 2n=28.** Of the 72 seeds harvested from the cross *L. flavescens* × *L. racemosus*, only two hybrids resulted, with the remainder resembling *L. flavescens*, indicating that *L. flavescens* has some self-fertility (table 2). The hybrids are large robust plants that bear a closer overall resemblance to the *L. racemosus* parent. Spikes of the hybrid are almost as dense as those of *L. racemosus*, and the hybrids have longer spikelets, more florets per spikelet, and longer glumes than *L. flavescens*. However, the hybrid lemmas exhibit the long yellow-whitish hairs of *L. flavescens*. Their leaves are mostly basal and resemble *L. racemosus*.

The Eurasian tetraploid *L. racemosus* possesses the same two basic genomes as *L. secalinus* (*NsNsXmXm*) and *L. alaicus* subsp. *karataviensis* (*NsNsXmXm*) (Dewey 1972*a*). Dewey (1972*a*) reported nearly complete bivalent formation in *L. racemosus* with a mean of 13.98 and 13.95 bivalents per MI cell, respectively. The hybrids formed 14 bivalents in more than two-thirds of the MI cells (fig. 1*A*). Eighty-seven percent of the bivalents were rings (table 3), an indication of close genome homologies between the genomes of *L. flavescens* and *L. racemosus*. The second most frequent association was two univalents and 13 bivalents, in 6% of the MI cells. One or two quadrivalents were observed in 11% and 3% of the MI cells, respectively. Neither of the F_1 hybrids set any seed under open pollination.

***Leymus flavescens* 2n=28 × *Leymus alaicus* subsp. *karataviensis* (=*Elymus karataviensis* Roshev.) 2n=28.** Sixteen hybrids and 12 selfs were obtained from 160 unemasculated florets of *L. flavescens* exposed to *L. alaicus* subsp. *karataviensis* pollen, supporting the previous conclusion that *L. flavescens* may be partially self-fertile. Although *L. flavescens* × *L. alaicus* subsp. *karataviensis* hybrids are moderately rhizomatous, similar to *L. flavescens*, they are the weakest of all the different hybrids in this study. Overall morphological appearance and spike characteristics were intermediate to both parents. The lemmas of the hybrids, however, expressed the long yellow-whitish hairs similar to *L. flavescens*.

Dewey (1972*c*) reported that of 181 MI cells of *L. alaicus* subsp. *karataviensis*, 180 formed 14 bivalents; the remaining cell had two univalents and 13 bivalents. He also reported that the degree of self-fertility varied in plants of *L. alaicus* subsp. *karataviensis*. Chromosome pairing declined in the *L. flavescens* × *L. alaicus* subsp. *karataviensis* hybrids, which averaged 11.9 bivalents per MI cell compared to other tetraploid hybrids within the study (table 3). The three most frequently observed associations were 4 I and 12 II (fig. 1*C*), 2 I and 13 II (fig. 1*A*), and 6 I and 11 II, which occurred in 29%, 25%, and 24% of the MI cells, respectively. Multivalents were not observed. Complete pairing (14 II) was observed in only 10% of the MI cells. The F_1 hybrids failed to set seed under open-pollinated conditions.

Molecular Characterization of Leymus flavescens *with Five Markers*

The genomic delineation for *L. flavescens* was also supported by results of RAPD assays (table 4). Assays for *St*-genome-specific RAPD markers $OPA20_{400}$, $OPB08_{525}$, and $OPN01_{817}$ indicated the absence of the *St* genome in *L. flavescens* as well as the slight difference between *L. flavescens* and *L. arenarius*, another *NsXm* species. The presence of the *Ns* genome in these *Leymus* species was confirmed by the *Ns*-specific RAPD marker $OPW05_{338}$ (fig. 2). The *H* genome, a common genome in many *Elymus* species, was not present in these *Leymus* species, as indicated by the absence of $OPW05_{700}$. On the basis of genome specific RAPD markers, *L. flavescens* is more closely related to *L. arenarius* (*NsNsNsNsXmXmXmXm*), and *Psathyrostachys juncea* (*Ns*) than *Pseudoroegneria spicata* (*St*) and *Hordeum bogdanii* (*H*).

Discussion

The alloploid genomic structure of tetraploid *Leymus triticoides, L. cinereus, L. secalinus, L. racemosus*, and *L. alacius* subsp. *karataviensis* is firmly established (Dewey 1970*a*, 1970*b*, 1972*a*, 1972*b*, 1972*c*, 1972*d*). Chromosome pairing in the tetraploid hybrids between *L. flavescens* and *L. triticoides* (*NsNsXmXm*), *L. cinereus* (*NsNsXmXm*), *L. secalinus* (*NsNsXmXm*), *L. racemosus* (*NsNsXmXm*), and *L. alacius* subsp. *karataviensis* (*NsNsXmXm*) indicates that the two genomes in *L. flavescens* are *NsNsXmXm*, and the six species have a common ancestry. However, their genomes have since become sufficiently differentiated to ensure their integrity as distinct species, as evidenced by the complete sterility in the F_1 hybrids. Such a strong barrier would inhibit introgression and continued genetic exchange between the species. The most obvious differences in the genomes were between *L. flavescens* and *L. alaicus* subsp. *karataviensis* (table 3). However, the lack of multivalents in the *L. flavescens* × *L. alaicus* subsp. *karataviensis* hybrids resulted in very little restructuring of the original genomes from reciprocal translocations. The higher level of chromosome pairing in the other tetraploid hybrids among *L. flavescens* and *L. triticoides, L. cinereus, L. secalinus*, and *L. racemosus* (table 3) points to somewhat less differentiation between their genomes. The low frequency of multivalents is probably the result of residual homologies between the different genomes rather than possible structural re-

arrangements between the different genomes of the parental taxa. This same relationship was observed in fertile F_1 hybrids between *L. cinereus* and *L. triticoides* (Dewey 1970*b*; K. B. Jensen, unpublished data). On the basis of chromosome pairing in the F_1 hybrids, the genomic formula for *L. flavescens* should be written as *NsNsXmXm*. The presence or absence of diagnostic bands from genome-specific RAPD markers confirms some of the previous conclusions on the basis of chromosome pairing that *L. flavescens* does possess the *Ns* genome.

Despite the diverse geographical origins (table 1) and the different sectional treatments taxonomically (Tzvelev 1976; Löve 1984), *L. flavescens, L. triticoides, L. cinereus, L. secalinus, L. racemosus*, and *L. alaicus* subsp. *karataviensis* are basically the same genomically. There are no apparent chromosomal structural rearrangements between taxonomic sections. On the basis of chromosome pairing and genome relationships, there appears to be very little genomic differentiation between sections *Leymus*, *Aphanoneuron*, and *Anisopyrum* (Löve 1984) within the genus *Leymus*. Section *Malacurus* has not been included in any previous studies.

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