The *Leymus* N^s-Genome

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Abstract: N^s-genome specific DNA sequences have been isolated from two *Leymus* species: *L. mollis* and *L. arenarius*. Five out of six clones characterized, i.e. pLmIs1, pLmIs44, pLmIs51, pLmIs53 and pLaIs56, are dispersed retrotransposon-like repeats, and one (pLaIs7) is a chloroplast gene. These sequences are highly specific to *Leymus* and *Psathyrostachys* as they hybridize essentially to these species, while little or no signal can be detected in other *Triticeae* species. Fluorescence *in situ* hybridization (FISH) mapping of these sequences shows that they are dispersed indiscriminately over all chromosomes. Southern hybridization experiments using total genomic DNA as probes confirm that there is nothing else in the *Leymus* genomes but N^s-genomic DNA. Based on these evidences, *Leymus* must be considered autopolyploid having the $(N^s)n$ genome designation or segmental allopolyploid consisting of a variation of the basic N^s-genome. The N^s-genome specific sequences are useful for discriminating N^s-genome in wide hybrids, uncovering phylogenetic relationships among the N^s-species, and solving many discrepancies in the genome-based classification of the *Triticeae*.

Keywords: *Leymus*; N^s-genome; genome-specific DNA sequences; molecular cytogenetics; phylogenetics

Leymus is a genus of about thirty polyploid perennial grass species in the tribe *Triticeae* (Dewey 1984). Most species are rhizomatous. Characteristic features of *Leymus* include stiff leaves, leaf blades strongly ribbed on top but glabrous underneath, awnless glumes and lemmas, 2–7 spikelets, and long anthers (Melderis 1980; Barkworth & Atkins 1984). *Leymus* has its main distribution in the temperate regions of Eurasia and North America. Its natural habitats range from coastal to inland areas, including diverse soil types and climatic conditions. Type species is *Leymus arenarius* (L.) Hochst., or sea lymegrass, which is an octoploid northern European species belonging to large-seed lymegrass group (sect. *Leymus*). Grains harvested from natural stands were used for human consumption, for example in Iceland, until recently. Amphiploids are being developed from crosses between wheat and *Leymus* with the aim of increasing agronomic quality and yield, hopefully making *Triticoleymus* a viable, perennial grain crop for sub-arctic regions (Anamthawat-Jónsson *et al.* 1994, 1997). *Leymus* genepool has also been utilized in wheat breeding as the plants are particularly adapted to nutrient-poor soil and extreme environmental conditions. Wheat containing *Leymus* chromosomes has been developed (Mujeeb-Kazi *et al.* 1983; Qi *et al.* 1997; Ellneskog-Staam & Merker 2001). Some of these wheat breeding lines have shown good quality such as fungal resistance (Merker pers. com.).

Most species of *Leymus* are tetraploid having $2n = 4x = 28$, but a few species have higher chromosome number. *Leymus* was recognized as a genomically distinct genus consisting of two different genomes EN^s (Dewey 1984; Löve 1984), where E(J) is a genome of *Thinopyrum* Löve and N^s is from *Psathyrostachys* Nevski. This genomic constitution is no longer correct as molecular studies have rejected the involvement of the E-genome in *Leymus* (Zhang & Dvorak 1991; Wang & Jensen 1994), leading to a consensus that X^m-genome of unknown origin be used in its place (Wang *et al.* 1994). Several attempts have been made to identify the X^m-genome but no similarity to existing *Triticeae* genomes is discovered. As concluded in the first papers (Zhang & Dvorak 1991; Dvorak & Zhang 1992),

all of the *Leymus* genomes/haplomes probably originated from *Psathyrostachys*, thus making *Leymus* autopolyploid, or segmental allopolyploids having $N^s_1N^s_2$ genomes for a tetraploid species. Nevertheless, some meiotic data do not seem to support autoploidy in *Leymus* (Wang & Jensen 1994; Sun *et al.* 1995). The question is probably whether meiotic pairing can truly reflect homology between genomes, or between homoeologous haplomes. Our studies have indeed shown that complete bivalents in *Triticoleymus* hybrids are not always autosyndetic but can also be intergenomic (Anamthawat-Jónsson & Bödvarsdóttir 1998). Similar observations have been reported by others, e.g. Ellneskog-Staam and Merker (2001). Intergenomic pairing and recombination in interspecific hybrids has become common after the adoption of molecular cytogenetic techniques that allow unequivocal differentiation between parental genomes or species. Such techniques have proven to be powerful and the new results obtained should generally be used to complement or revise the genome classification of the tribe *Triticeae*.

This review is a continuation of the paper presented at the 4th International Triticeae Symposium (Anamthawat-Jónsson 2001), which showed genetic and genomic relationships in the group of large-seed *Leymus* using a variety of molecular techniques. The present paper aims to summarize the process of isolation and characterization of *Leymus* N^s-genome specific DNA sequences (based on Bödvarsdóttir & Anamthawat-Jónsson 2003), to uncover genome composition of the polyploid genus *Leymus*, and to present preliminary results on phylogenetic relationships among species of *Leymus*, *Psathyrostachys* and related genera using these *Leymus* N^s-genome specific sequences.

N^s-genome specific DNA sequences

N^s-genome specific sequences have been isolated from two *Leymus* species, the North American tetraploid *L. mollis* and the northern European octoploid *L. arenarius* (Table 1). Restriction enzyme digested repetitive DNA fragments specific to *Leymus* were identified and isolated the same way as described in Anamthawat-Jónsson and Heslop-Harrison (1993), with modifications as in Bödvarsdóttir and Anamthawat-Jónsson (2003). The fragments corresponding in size to those identified in Southern genomic blots were excised from agarose gels, purified and cloned in pUC18 according to standard method of molecular cloning. More than 50 cloned fragments were then screened with labeled total genomic *L. mollis* probe by dot-blot hybridization, using dots of genomic *L. mollis* DNA and water (no DNA) as references. Dots that showed strong hybridization signal presumably contained repetitive DNA fragments abundant in the probe species. Six clones were then selected for further

Table 1. Plant species used in this study and their genome designation, chromosome number and origin

Species	2n number	Accession	Origin
Leymus Hochst. (N^s)n			
L. cinereus (Scribner & Merr.) Löve	28	H 10779	Nevada, USA
L. mollis (Trin.) Pilger	28	Múlakot (Iceland)	Alaska
L. racemosus (Lam.) Tzvelev	28	H 5053	Romania
L. arenarius (L.) Hochst.	56	Seltjarnarnes	Iceland
L. karelinii (Turcz.) Tzvelev	56	H 7548	China
L. angustus (Trin.) Pilg.	84	H 7526	China
Psathyrostachys Nevski (N^s)			
P. fragilis (Boiss.) Nevski	14	H 4375	Turkey
P. huashanica Keng	14	H 3087	China
P. lanuginosa (Trin.) Pilger	14	H 8803	China
P. juncea (Fisch.) Nevski	14	DJ 4034	former Soviet Union
Elytrigia repens (L.) Nevski (HXX)	42	Is 9604	Iceland

characterization by Southern blot hybridization and sequencing (Table 2). Five of these clones, i.e. pLmIs1, pLmIs44, pLmIs51, pLmIs53 and pLaIs56, are dispersed retrotransposon-like repeats, whereas one clone (pLaIs7) is a chloroplast gene. Three of the dispersed repeats are specific to *Leymus* and *Psathyrostachys*, particularly pLmIs44, as they hybridize essentially to these species. Little or no signal can be detected in most other *Triticeae* genera.

Genome-specific sequences may differ from their closely related sequences in the nucleotide composition (single or low-copy genes, such as pLaIs7), or they may occur in several genomes but in a much higher copy number (repetitive sequences, e.g. pLmIs44 and other repeats in this study). The proportion of such sequences has been estimated to be between 16% and 45% in the cereal genome, and consists mostly of repeated DNA segments, interspersed with other sequences, along with long tandem arrays of the same repeating units (Anamthawat-Jónsson & Heslop-Harrison 1993). Such genome-specific DNA sequences are therefore most suitable for differentiating genomes (haplomes) in allopolyploids, especially in the tribe *Triticeae* where the majority of species are polyploids. The N^s-genome specific sequences isolated here should be able to verify N^s-genome in wheat × *Leymus* wide hybrids in the same manner as GISH (genomic *in situ* hybridization, Anamthawat-Jónsson *et al.* 1990). Similar genome-specific sequences were used to identify *Hordeum* chromosomes in wide hybrid between barley and rye (Anamthawat-Jónsson & Heslop-Harrison 1993). Many other sequences have been used to differentiate particular genomes/haplomes in allopolyploids, for example the sequence pTa1 hybridizes specifically to D-genome of *Triticum* and *Aegilops* (Bradsley *et al.* 1999), whereas the rye sequence pSc119.2 preferentially hybridizes to the B-genome (Castilho *et al.* 1997). Dispersed retrotransposon-like repeats, like the N^s-genome specific sequences isolated here, are clearly among the most common genome-specific sequences found in plants. This is not surprising as such sequences may undergo rapid change in nucleotide sequence or are amplified in a relatively short time (San Miguel *et al.* 1998; Bennetzen 2002; Zhang & Wessler 2004). In conclusion, the present paper shows that (1) genome-specific sequences are mostly retroelement-like repeats and (2) isolation of such sequences can be simple and requires no prior molecular information about the genome of interest.

Genome designation of *Leymus* should be $(N^s)n$

Mapping of the retroelement-like repeats (Table 2) on chromosomes by fluorescence *in situ* hybridization (FISH) shows that the sequences are dispersed over all chromosomes of *Leymus* and *Psathyrostachys* species investigated (Figure 1). These sequences are often distributed over the whole length of chromosomes except the chromosomal regions where tandem repeats occupy such as centromeres, telomeres and nucleolar organizing regions (NORs). Among these dispersed repeats, the sequence pLmIs44 shows the most spotted

Table 2. N^s-genome specific DNA clones isolated from *Leymus*

Clone (in pUC18)	GenBank accession No.	Cloning site	Insert size (bp)	Hybridisation to *Leymus-Psathyrostachys*	Significant cross hybridisation	Sequence type based on homology searching
pLmIs1	AY188516	*Hin*dIII	1.277	relatively specific	*Elytrigia repens*	*Gypsy*-type LTR retroelement (wheat, barley)
pLmIs44	AF493969	*Hin*dIII	1.164	highly specific (most abundant)	none	*Gypsy*-type LTR retroelement (wheat)
pLmIs51	AY188517	*Hin*dIII	1.514	not specific	to all species examined (smear)	*Gypsy*-type LTR retroelement (wheat)
pLmIs53	AY188518	*Hin*dIII	1.424	relatively specific	*Elytrigia repens*	*Copia*-type LTR retroelement (barley, rice)
pLaIs7	–	*Eco*RI	2.1	highly specific Ns-fragment	exists in all species examined (single band)	Chloroplast sequence (rice, maize)
pLaIs56	AY188519	*Eco*RI	1.514	not specific	to all species examined (bands)	Retroelement-like sequence (*Triticeae*)

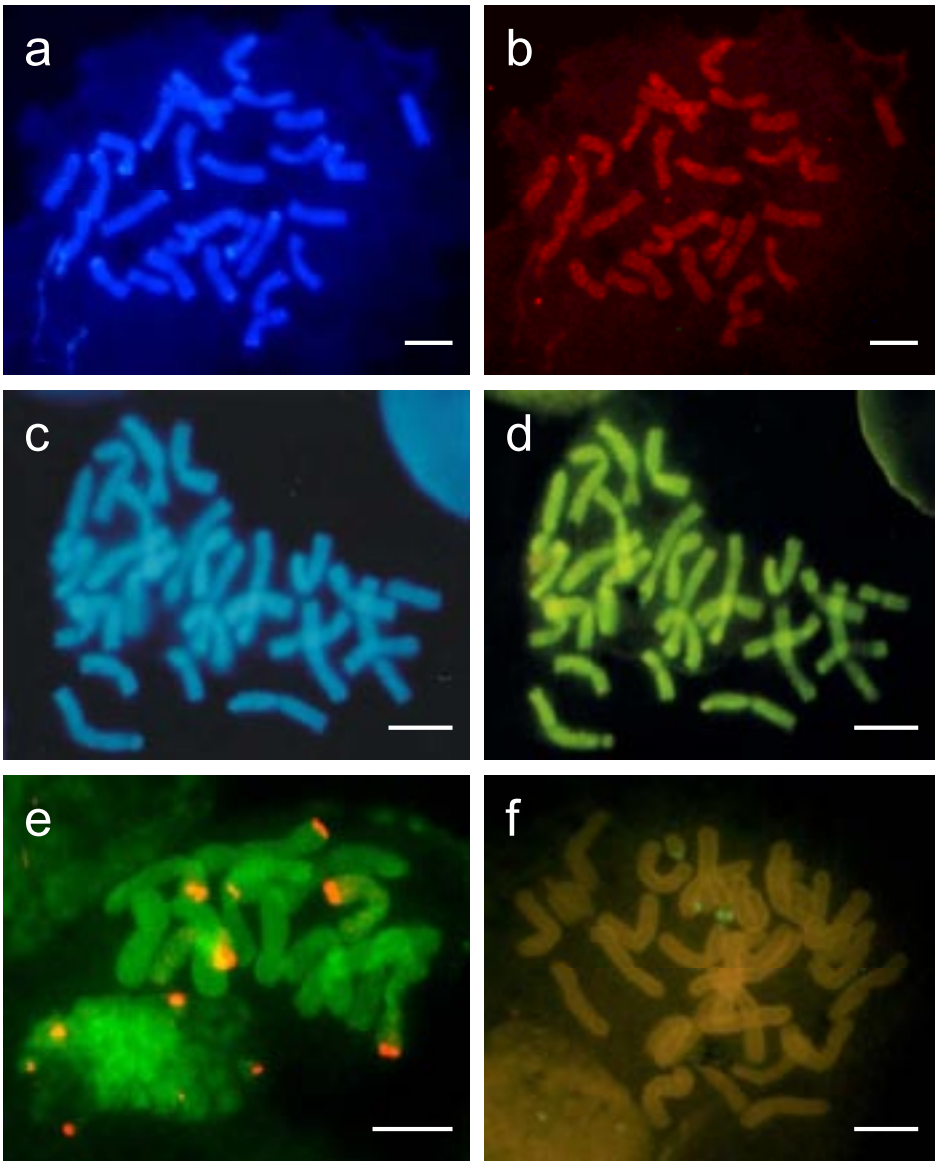

Figure 1. **(a)** Mitotic metaphase from root-tip of *Leymus cinereus* plant (2*n* = 28, tetraploid) showing DAPI-stained chromosomes. Intense DAPI bands at sub-telomeric regions of most chromosome arms are common characteristics of *Leymus* species; **(b)** The same metaphase cell as in (a) after fluorescent *in situ* hybridization (FISH) with red fluorescently rhodamine-labeled clone pLmIs44. The probe hybridization sites are distributed along chromosome arms of all chromosomes except at centromeres, telomeres and NORs; **(c)** Mitotic metaphase from root-tip of *Leymus mollis* plant (2*n* = 28, tetraploid) showing DAPI-stained chromosomes; **(d)** The same metaphase cell as in (c) after fluorescent *in situ* hybridization with green fluorescently FITC-labeled clone pLmIs51. The hybridization sites are dispersed on all chromosomes similarly to that of pLmIs44 in (b) although they are more evenly distributed along the chromosome arms; **(e)** Mitotic metaphase from root-tip of a *Psathyrostachys* plant (2*n* = 14, diploid) after fluorescent *in situ* hybridization with green fluorescently FITC-labeled total genomic DNA from *L. mollis* and red fluorescently rhodamine-labeled ribosomal DNA clone pTa71. The total genomic probe hybridizes evenly to the whole *Psathyrostachys* genome, to all chromosomal regions as expected. The major rDNA sites correspond to the NORs and they occur in three pairs mostly at sub-telomeric regions typical of *P. fragilis*; **(f)** Mitotic metaphase from root-tip of a tetraploid *Elymus* plant after fluorescent *in situ* hybridization with red rhodamine-labeled clone pLmIs44 under exactly the same condition as with (b) and green FITC-labeled ribosomal DNA clone pTa71. The N^s-genome specific clone pLmIs44 does not hybridize at all to *Elymus*, whereas the rDNA sites are positively localized on the chromosomes. Scale bar represents 5 μm

pattern of hybridization on chromosomes (Figure 1b as opposed to the more uniform pattern by the sequence pLmIs51 in Figure 1d and by total genomic *Leymus* DNA in Figure 1e). This sequence pLmIs44 is also the most specific to *Leymus*, i.e. it is not detected in other *Triticeae* genera under high stringency of hybridization (Anamthawat-Jónsson 2001). No FISH hybridization signal can be detected in *Elymus* for example (Figure 1f). This seems to suggest that the sequence may have been evolved recently within *Leymus*, by means of retrotransposable dispersion or other molecular events. The dispersion over whole chromosomes may as well still be in progress, possibly along with the polyploidization process.

Transposable elements are now known to have contributed significantly to plant gene and genome evolution, which can possibly lead to speciation following reproductive isolation or formation of polyploidy species. Genome-wide comparative analysis of the transposable elements in the related species *Arabidopsis thaliana* and *Brassica oleracea* shows that a significant amount of both *copia*-like and *gypsy*-like LTR-transposons are *B. oleracea* genome-specific and have recent origin (Zhang & Wessler 2004). Recent molecular and cytogenetic experiments have shown that different types of retroelements in barley, or even different domains within elements, do not show the same distribution over the genome (Vicient *et al.* 1999; Kalendar *et al.* 2004). It can be postulated that the *Leymus*-specific sequences isolated here have evolved and dispersed within the *Leymus* genomes at different rates, and the sequence pLmIs44 is probably the youngest of them all.

FISH mapping of *Leymus*-specific sequences has also shown that the sequences are dispersed over all genomes/haplomes of *Leymus* species investigated. No discrimination can be seen between homoeologous chromosomes in the proposed N^sX^m genomes for *Leymus* as proposed by Wang *et al.* (1994), even under the most stringent hybridization conditions. The pattern of hybridization is the same on all chromosomes whether or not it is the spotted pattern of pLmIs44 on *L. cinareus* (Figure 1b) or the more even pattern of pLmIs51 on *L. mollis* (Figure 1d). These sequences also hybridize to all chromosomes of *Psathyrostachys* the same way as with *Leymus* (FISH results not shown here). The only interpretation possible is that all the genomes/haplomes of *Leymus* are molecularly the same as the N^s-genome of *Psathyrostachys*. The genome designation for *Leymus* should therefore be $(N^s)n$.

It is possible that *Leymus* derived from *Psathyrostachys* by simple chromosome doubling (autopolyploidy), or through intergeneric hybridization (allopolyploidy). Polyploid cytotypes of *Psathyrostachys* exist and autosyndetic multivalents seem to be common in *Leymus* (see discussion in Anamthawat-Jónsson & Bödvarsdóttir 2001). The N^s-genomes in *Leymus* may have come through hybridization of different *Psathyrostachys* species and/or with *Leymus*, making *Leymus* segmental allopolyploid as often anticipated. FISH mapping of 18S-26S ribosomal genes has indicated that the octoploid *L. arenarius* probably derived from hybridization between two tetraploid *Leymus* species, one of whom being *L. racemosus* (Anamthawat-Jónsson & Bödvarsdóttir 2001). X^m-genome could also be an ancestor of *Leymus* or taken part in the allopolyploidy. Rapid genomic changes might have taken place, like the spread of dispersed repetitive DNA to new genomes since polyploidy formation in cotton (Zhao *et al.* 1998), preferential sequence elimination in wide hybrids involving wheat (Ozkan *et al.* 2001), disappearance of parental RFLP fragments and appearance of novel fragments in *Triticeae* allopolyploids (Han *et al.* 2003), and rapid amplification of transposable elements contributing significantly to genome expansion in *Brassica* (Zhang & Wessler 2004). Perhaps a major genome replacement has occurred in *Leymus* allopolyploidization resulting in the dominance of N^s-genome, making *Leymus* essentially autopolyploid.

Whatever events that may have occurred in the *Leymus* genome evolution the genus is now molecularly autopolyploid. Southern genomic hybridization experiments confirm that there is nothing else in *Leymus* but N^s-genomic DNA (example shown in Figure 2). Total genomic DNA from *L. mollis* was used as labeled probe to hybridize to *Dra*I restricted genomic DNA from *Leymus* and *Psathyrostachys* species (Figure 2a), using ECL non-radioactive method of labeling and hybridization (Pharmacia-Biotech, Denmark), under high (ca. 90%) hybridization stringency to ensure species-specificity of the genomic probing (as in Anamthawat-Jónsson *et al.* 1990). The blot was reprobed with the same labeled total genomic DNA of *L. mollis* (Figure 2b), this time in the presence of unlabelled and sheared genomic DNA from *P. huashanica*, about 100 times the probe amount, with an aim to further enhance the specificity of the *Leymus* probe. The results show

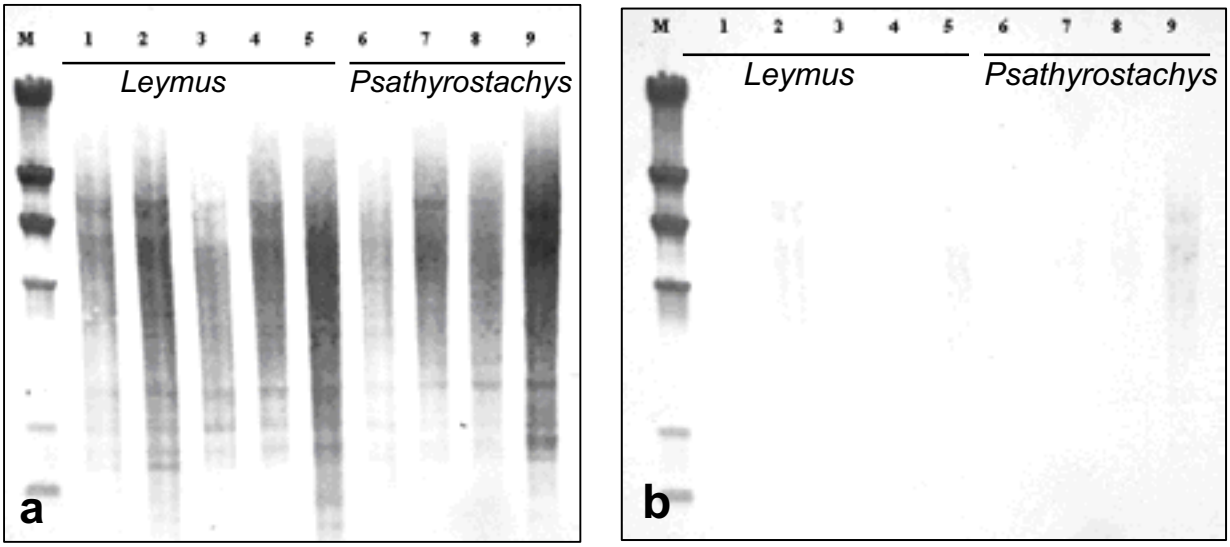

Figure 2. **(a)**: Luminograph showing Southern genomic hybridization using ECL labeled total genomic DNA from *Leymus mollis* as probe, under high (about 90%) hybridization stringency, to *Dra*I restricted total genomic DNA from (1) *Leymus arenarius*, (2) *L. mollis*, (3) *L. racemosus*, (4) *L. karelinii*, (5) *L. angustus*, (6) *Psathyrostachys juncea*, (7) *P. lanuginosa* (8), *P. fragilis* and (9) *P. huashanica*. The amount of DNA loaded in gel is about 1 μg per lane, except lanes 2, 5 and 9 where the DNA amount is higher. In both *Leymus* and *Psathyrostachys* (all lanes, except the marker lane), the intensity of hybridization signal is relative to the DNA amount. **(b)**: Luminograph of the same Southern blot as in (a) after hybridization with the same labeled *L. mollis* probe but with unlabelled blocking DNA from *P. huashanica*, 100× the probe amount. No hybridization signal can be seen on this blot. Lane M (far left) is *Hin*dIII lambda size marker showing from bottom 2.0, 2.3, 4.4, 6.6 and 9.4 kb

that the *Leymus* probe without blocking (Figure 2a) hybridized to all *Leymus* and *Psathyrostachys* species and the signal intensity is proportional to DNA amount loaded in the gel. Fluorescently labeled total genomic DNA from *Leymus* also hybridized to all chromosomes of *Psathyrostachys* (Figure 1e), and vice versa (results not shown here). The fact that *Leymus* probe hybridized strongly to both *Leymus* and *Psathyrostachys* indicates that the two genera are not different in terms of genome homology. Furthermore, when the blot was blocked with *Psathyrostachys* (Figure 2b), there was no hybridization at all with the *Leymus* probe. The blocking effect, together with high stringency, resulted in almost empty blots. These results show conclusively that the genomes of *Leymus* and *Psathyrostachys* are molecular identical.

Future work: Phylogenetic analysis of *Leymus* and taxonomic implications

The N^s-genome specific sequences are not only abundant in the species containing the basic N^s-genome (i.e. *Leymus* and *Psathyrostachys*), they are also polymorphic in their sequences. The polymorphisms can be captured simply as RFLPs (restriction fragment length polymorphisms) and analysed phylogenetically. As the stringency of hybridization is lowered, cross-hybridization can be detected over a broad range of species and genera of the *Triticeae*, and their RFLPs can often reveal genetic distance from the N^s-species. We have included in the study more than 30 species and accessions of known, or suspected, to have the N^s-genome. Preliminary results have shown that, as expected, the N^s-genome is clearly differentiated from all other genomes examined. This N^s-genome cluster includes all species of *Leymus*, *Psathyrostachys*, *Hordelymus* and *Hystrix* (one species). Furthermore, the N^s-genome cluster appears to divide into two major subgroups: one containing Eurasian *Leymus* species and the other comprising the rest, i.e. North American and Asiatic *Leymus*, *Psathyrostachys* and other N^s-species. The detailed molecular and phylogenetic study of N^s-genome specific sequences is believed to be an important

foundation for taxonomic revision of *Leymus* and its related genera of the *Triticeae*.

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