6-24-1994

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ABSTRACT

A system for the application of nuclear genome symbols in the tribe Triticeae is proposed. It is based mainly on prevailing symbols. In agreement with this, the system uses individual upper case letters as symbols in the first place. Since the number of basic nuclear genomes in the Triticeae exceeds the number of single letters in the Roman alphabet, some basic genomes are designated with an upper case letter followed by a lower case letter, e.g. **Ns** for the genome of *Psathyrostachys*. Superscripts in small letters are used when modified versions of a basic genome are referred to, e.g. $\mathbf{H}^{p}$ for the genome found in *Hordeum pusillum*. Unknown or equivocally identified genomes are designated by **X** followed by a lower case letter, e.g. **Xu** for *Hordeum murinum*. Underline of the relevant genome symbol can be used to indicate the origin of the cytoplasm.

PROPOSAL

Classification of the Triticeae based on genome relationships has over the years been a matter of controversy, especially between taxonomists and cytogeneticists (Löve 1984, Baum et al. 1987, Gupta and Baum 1989, Kellogg 1989, Seberg 1989). Today there is, however, no disagreement as to the conceptual ideas of genomes *per se* as defined by several authors (Löve 1982, Alonso and Kimber 1983, Kimber and Zhao 1983, Dewey 1984). In the Triticeae the genomes of the various genera, or groups of species, are more or less similar as indicated by the variation in chromosome pairing ability at meiotic metaphase I in interspecific or intergeneric hybrids. The genomic affinities may vary from complete pairing, i.e., homology, to no pairing, i.e, non-homology, with various intergrades, i.e., homoeology.

One practical aspect which has created problems among Triticeae researchers is the designations of individual basic genomes. Traditionally, each genome has been designated with a single, upper case letter A-Z. Because of the large number of basic genomes in Triticeae, the number of letters in the Roman alphabet is insufficient for covering all basic genomes of the tribe. Further, various authors have used different symbols for the same genome and in some cases different basic genomes have been designated with the same symbol. Especially, there have been confusion between the genome designations used by scientists studying wheat and related species, and those used by researchers working with other groups in the Triticeae. Moreover, various authors have assigned the letters X and Y to the unidentified genomes of several species or unrelated groups of species. Since the knowledge of genome relationships in the tribe and the need to use intergeneric hybridization for cereal improvement are rapidly increasing, there is an increasing demand for a standardization of the genome symbols.

In this paper we propose a system of assigning basic genome symbols that may be acceptable to all scientists working with the Triticeae. Instead of proposing a

Table 1. Genome symbols in the Triticeae

Genus or Species	Previous designation	Reference	Suggested designation	Reference
Agropyron	P	Löve 1984	**P**	
Heteranthelium	Q	Löve 1984	**Q**	
Crithopsis	K	Löve 1984	**K**	
Taeniatherum	T	Löve 1984	**Ta**[1]	
Hordeum vulgare	I	Löve 1984	**I**	
H. bulbosum	H	Löve 1984	**I**	Dewey 1984
H. marinum	H	Löve 1984	**Xa**[2]	Bothmer et al. 1986
H. murinum	H	Löve 1984	**Xu**	Bothmer et al. 1987, 1988a,b
other *Hordeum* species	H	Löve 1984	**H**	
Hordelymus	HT	Löve 1984	**XoXr**[3]	Bothmer et al. 1994
Festucopsis	G	Löve 1984	**L**[4]	
Peridictyon sanctum	(in *Festucopsis*)	Löve 1984	**Xp**[4]	Seberg et al. 1991
Australopyrum	W	Löve 1984	**W**	
Pseudoroegneria	S	Löve 1984	**St**[1]	
P. pertenuis	SP	Löve 1984	**StP**	Wang et al. 1986; Assadi
P. deweyi	SP	Jensen et al. 1992		
P. geniculata ssp. scythica	SS	Löve 1984	$\mathbf{E^eSt}$	Liu & Wang 1993b
Psathyrostachys	N	Löve 1984	**Ns**	
Thinopyrum bessarabicum	J	Löve 1984	$\mathbf{E^b}$[6]	Wang 1985
T. junceiforme	JJ	Löve 1984	$\mathbf{E^bE^e}$	Liu & Wang 1992
T. sartorii	JJ	Löve 1984	$\mathbf{E^bE^e}$	Liu & Wang 1992
T. distichum	JJ	Löve 1984	$\mathbf{E^bE^e}$	Liu & Wang 1993a
T. junceum	JJJ	Löve 1984	$\mathbf{E^bE^bE^e}$	Liu & Wang 1993a
Lophopyrum elongatum	E	Löve 1984	$\mathbf{E^e}$[6]	Wang 1985
L. caespitosum	EE	Löve 1984	$\mathbf{E^eSt}$	Liu & Wang 1989, 1993b
L. curvifolium	EE	Löve 1984	$\mathbf{E^bE^b}$	Liu & Wang 1993a
L. nodosum	EE	Löve 1984	$\mathbf{E^eSt}$	Liu & Wang 1993b
L. scirpeum	EE	Löve 1984	$\mathbf{E^eE^e}$	Liu & Wang 1993a
Trichopyrum	ES	Löve 1984	$\mathbf{E^eSt}$	
T. intermedium	EES		$\mathbf{E^eE^eSt}$	Liu & Wang 1993b
			$\mathbf{E^bE^eSt}$	Xu & Conner 1994
Elymus sibiricus	SH	Löve 1984	**StH**	
E. caucasiucus	SH	Löve 1984	**StY**[5]	Jensen & Wang 1991
E. drobovii	SH	Löve 1984	**StHY**	Dewey 1980
E. batalinii	SH	Löve 1984	**StPY**	Jensen 1990
E. scabrus	SH	Löve 1984	**StWY**	Torabinejad & Mueller 1993
E. transhyrcanus			**StStH**	Dewey 1972
Kengyilia	(included in *Elymus*)	Löve 1984	**StPY**	Yen & Yang 1990
Leymus	JN	Löve 1984	**NsXm**[7]	Zhang & Dvorak 1990
				Wang & Jensen 1994
Elytrigia	SX	Löve 1984		
E. repens			**StStH**[8]	Assadi & Runemark 1994
				Vershinin et al. 1994
Psammopyrum	GJ	Löve 1984	**LE**	
Pascopyrum	SHJN	Löve 1984	**StHNsXm**[7]	Zhang & Dvorak 1990
Crithodium	A	Löve 1984		
~ *Triticum monococcum*			$\mathbf{A^m}$	Dvorak et al. 1993
~ *T. urartu*			$\mathbf{A^u}$	Dvorak et al. 1993
Sitopsis	B		**S**	Kimber & Tsunewaki 1988
Aegilops speltoides			**S**	
Ae. bicorn			$\mathbf{S^b}$	

Table 1. Genome symbols in the Triticeae

Genus or Species	Previous designation	Reference	Suggested designation	Reference
Ae. longissimum			S^{l}	
Ae. sharonensis			S^{l}	
Ae. searsii			S^{s}	
Orrhopygium	C	Löve 1984		
Aegilops caudata			C	
Patropyrum	D	Löve 1984		
Aegilops tauschii			D	
Comopyrum	M	Löve 1984		
Aegilops comosa			M	
Amblyopyrum	Z	Löve 1984		
Aegilops mutica			T	Kimber & Tsunewaki 1988
Chennapyrum	L	Löve 1984		
Aegilops uniaristata			N	Kimber & Tsunewaki 1988
Kiharapyrum	U	Löve 1984		
Aegilops umbellutata			U	
Secale	R	Löve 1984	R	
Dasypyrum	V	Löve 1984	V	
Eremopyrum	F	Löve 1984	F, Xe^{9}	Frederiksen & Bothmer 1989
Henrardia	O	Löve 1984	O	
Gigachilon	AB	Löve 1984	AB	Kimber & Tsunewaki 1988
Triticum durum	AB	Löve 1984	$A^{u}B$	Dvorak et al. 1993
T. timopheevii	AB	Löve 1984	$A^{u}G^{1}$	Dvorak et al. 1993
T. zhukovskyi	AAB	Löve 1984	$A^{m}A^{u}G^{1}$	Dvorak et al. 1993
Triticum aestivum	ABD	Löve 1984	$A^{u}BD$	
*T. ventricosum**	DM	Löve 1984	DN	Kimber & Tsunewaki 1988
*T. recta **	MMU	Löve 1984	UMN	Kimber & Tsunewaki 1988
			UMX	Yen & Kimber 1992
T. syriacum			DMS	Kimber & Tsunewaki 1988
			$D^{c}S^{s}X$	Zhang & Dvorak 1992
Aegilemma	BU	Löve 1984	US	Kimber & Tsunewaki 1988
Aegilops variabilis			US^{1}	Zhang et al. 1992
Cylindropyrum	CD	Löve 1984	CD	
Aegilops cylindrica			CD	
Aegilopodes	CU	Löve 1984	UC	Kimber & Tsunewaki 1988
Aegilops triuncialis			UC	
Gastropyrum	DM	Löve 1984	DM	
Aegilops crassa (4x)			$D^{c}Xc$	Zhang & Dvorak 1992
Ae. crassa (6x)			$DD^{c}Xc$	Zhang & Dvorak 1992
Aegilonearum	DMU	Löve 1984		
Aegiops juvenale			$D^{c}ZcU$	McNeil et al. 1994
Aegilops	MU	Löve 1984	UM	Kimber & Tsunewaki 1988
Aegilops ovata			UM	
Ae. biuncialis			UM	
Ae. columnaris			UM	
Ae. triaristata			UMN	

*included in *Gastropyrum* by Löve (1984).
**inclucded in *Aegilops* by Löve (1984).
[1] to [9] see comments.

completely new system, the suggested system builds on the most prevalent, presently used designations. Only when there is an overlap or a controversy between various systems do we suggest new symbols or change of symbols. The symbols proposed (Table 1) are basically those used by Löve (1984) in his classification with minor modifications (e.g. Kimber and Tsunewaki 1988). Löve's system is based on the prerequisite that a genus should consist species of the same genome constitution. His system of nomenclature is not endorsed here for a formal taxonomic classification system of the Triticeae. We use it merely as a framework for listing different basic genomes and combinations of genomes.

We propose the following basic rules for the designations of genome symbols in the Triticeae:

1. Genome symbols should be written in **bold face**.
2. Different basic genomes in Triticeae (with x=7), defined as having less than 50% of complete meiotic pairing, i.e. c 0.5, in a diploid hybrid in the absence of the Ph or other pairing promoter/suppressor gene effect, should be designated with different symbols.
3. Single upper case letters of the Roman alphabet (A-Z) should, as far as possible, be used as symbols for basic genomes (see Table 1).
4. Since all upper case letters of the alphabet are now occupied, additional basic genomes should be designated by an upper case letter followed by a lower case letter.
5. The genome designation of a polyploid taxon should be given as a combination of the symbols of the constituent basic diploid genomes.
6. Unknown or unverified genomes should be designated with the letter **X** followed by a lower case letter (e.g., **Xu** for *Hordeum murinum*). When a genome has been sufficiently identified as distinct from all other established basic genomes, it should be given a permanent basic genome symbol.
7. The letter **Y** has previously been used to designate unknown genomes. However, it has been extensively used as the designation of one basic genome present in some species of the polyploid genus *Elymus*. The diploid donor species for **Y** has not yet been identified. We propose that the designation **Y** is retained for this basic genome.
8. Modified versions of a basic genome should be designated by superscripts in small letters indicative of the species carrying such modified genomes. Further modifications may be indicated by superscripted numeric numbers.
9. When previously unrecogized basic genomes are identified, genome symbols should be assigned in accordance with this system.
10. A genome symbol may be underlined to indicate the origin of the cytoplasm of an alloploid species.
11. From this date (1996) on, the designations given in Table 1 should have priority over younger ones.

Comments (cf. Table 1)

1. The symbols **S, T, N** and **G** have been used in two different senses (cf. Love 1984, Kimber and Tsunewaki 1988). Therefore, the three former symbols are replaced by the symbols **St, Ta,** and **Ns**, to designate the genomes of species of the genera *Pseudoroegneria, Taeniatherum* and *Psathyrostachys*, respectively. For **G**, see comment 4 below.
2. The genomes of *Hordeum marinum* and *H. murinum* are given the symbols **Xa** and **Xu**, respectively, to indicate that they are different enough from **H** to deserve different basic genome symbols, but still being imperfectly known.
3. The two genomes in *Hordelymus* have not been unequivocally identified, thus they are temporarily assigned the symbols **Xo** and **Xr**.
4. Since the new genus *Peridictyon* split from *Festucopsis* by Seberg et al. (1991) has not been studied by chromosome pairing, the genome is assigned **Xp** for now. *Festucopsis* is not the donor of the **G** genome in *Triticum timopheevi*; therefore, the genome symbol of *Festucopsis* is changed to **L**.
5. **Y** is retained as the symbol for a basic genome of an unidentified diploid species that contributed a genome to some species of the polyploid genus *Elymus*.
6. The **E** genome is present in *Thinopyrum, Lophopyrum*, and *Trichopyrum* (Liu and Wang 1992, 1993a, 1993b) in combination with **J** and **St**. Because **J** is closely related to **E** (Wang 1985) and **E** has been extensively used by wheat workers (Dvorak 1980), we propose the change of **J** to **E**. Most existing evidence (for reservation, see Jauhar 1990) from diploid c values, the triploid trivalent frequency, triploid x values, the multivalent frequency in amphidiploids, and *in situ* hybridization results indicates that **J** and **E** are closer to each other than the genomes of *Hordeum vulgare* and *H. bulbosum*. Because the genomes in these two *Hordeum* species have the same basic genome symbol, we must also use a single basic genome symbol for *Thinopyrum bessarabicum* and *Lophopyrum elongatum*.
7. Because the presence of **J**(=**E**) in *Leymus* and *Pascopyrum* is in doubt (Zhang and Dvorak 1991,

Wang and Jensen 1994), it is proposed to replace **JNs** with **NsXm** until **Xm** is experimentally identified.

8. Newer results indicate that the formerly unknown X genome in *Elytrigia repens* is actually an **H** genome (Assadi and Runemark 1995, Vershinin et al. 1994). The genome combination of *E. repens* is thus **StStH** and is identical to a group of species in *Elymus*.

9. The genus *Eremopyrum* probably comprises two different genomes (Sakamoto 1979). They are assigned the symbols **F** and **Xe**.

LITERATURE CITED

Alonso, L.C. and Kimber, G. 1983. A study of genomic relationships in wheat based on telocentric chromosome pairing. Z. Pflanzenzuchtg. 90:23-31.

Assadi, M. 1995. Meiotic configuration and chromosome number in some Iranian species of *Elymus* L. and *Agropyron* Gaertner (Poaceae: Triticeae). Bot. J. Linn. Soc. 117:159-168.

Assadi, M. and Runemark, H. 1995. Hybridization, genomic constitution and generic delimitation in *Elymus* s. l. (Poaceae, Triticeae). Pl. Syst. Evol. 194:189-205

Baum, B.R., Estes, J.R., and Gupta, P.K. 1987. Assessment of the genomic system of classification in the Triticeae. Am. J. Bot. 74:1388-1395.

Bothmer, R. von, Flink, J., and Landström, T. 1986. Meiosis in interspecific *Hordeum* hybrids. I. Diploid combinations. Can. J. Genet. Cytol. 28:525-535.

Bothmer, R. von, Flink, J., and Landström, T. 1987. Meiosis in interspecific *Hordeum* hybrids. I. Triploid combinations. Evol. Trends Plants 1:41-51.

Bothmer, R. von, Flink, J., and Landström, T. 1988a. Meiosis in interspecific *Hordeum* hybrids. I. Tetraploid (2x X 6x) combinations. Hereditas 108:141-148.

Bothmer, R. von, Flink, J., and Landström, T. 1988b. Meiosis in interspecific *Hordeum* hybrids. I. Tetraploid (4x X 4x) combinations. Genome 30:479-485.

Bothmer, R. von, Lu, B.R. and Linde-Laursen, I. 1994. Intergeneric hybridization and C-banding patterns in *Hordelymus* (Triticeae, Poaceae). Pl. Syst. Evol. 189:259-266.

Dewey, D.R. 1972. The origin of *Agropyron leptorum*. Am. J. Bot. 59:836-842.

Dewey, D.R. 1980. Cytogenetics of *Agropyron drobovii* and five of its interspecific hybrids. Bot. Gaz. 141:469-478.

Dewey, D.R. 1984. The genomic system of classification as a guide to intergeneric hybridization with perennial Triticeae. *In*: J.P. Gustafsson (ed.) Gene Manipulation in Plant Improvement. Plenum, N.Y., pp.209-279.

Dvorak, J. 1980. Homoeology between *Agropyron elongatum* chromosomes and *Triticum aestivum* chromosomes. Can. J. Genet. Cytol. 22:237-259.

Dvorak, J., di Terlizzi, P., Zhang, H-B., and Resta, P. 1993. The evolution of polyploid wheat: identification of the A genome donor species. Genome 36:21-31.

Frederiksen, S. 1991. Taxonomic studies in *Eremopyrum* (Poaceae). Nord. J. Bot. 11:271-285.

Gupta, P.K. and Baum, B.R. 1989. Stable classification and nomenclature in the Triticeae: desirability, limitation and prospects. Euphytica 41:191-197.

Jauhar, P.P. 1990. Multidisciplinary approach to genome analysis in the diploid species *Thinopyrum bessarabicum* and *Th. elongatum (Lophopyrum elongatum)* of the Triticeae. Theor. Appl. Genet. 80:523-536.

Jensen, K.B. 1990. Cytology and Taxonomy of *Elymus kengii*, *E. grandiglumis*, *E. alatavicus* and *E. batalinii* (Triticeae: Poaceae). Genome 33:563-570.

Jensen, K.B. and Wang R.R-C. 1991. Cytogenetics of *Elymus caucasicus* (Koch) Tzvelev and *E. longearistatus* (Boiss.) Tzvelev (Poaceae: Triticeae). Genome 34:860-867.

Jensen, K. B., S. L. Hatch, and J. Wipff. 1992. Cytogenetics and morphology of *Pseudoroegneria deweyi* (Poaceae: Triticeae), a new species from the Soviet Union. Can. J. Bot. 70:900-909.

Kellogg, E.A. 1989. Comments on genomic genera in the Triticeae (Poaceae). Am. J. Bot. 76:796-805.

Kimber, G. and Tsunewaki, K. 1988. Genome symbols and plasma types in the wheat group. *In*: T.E. Miller and R.M.D. Koebner (eds.) Proc. 7th Int. Wheat Symp., Cambridge 1987, pp. 1209-1211.

Kimber, G. and Zhao, Y.H. 1983. The D genome of the Triticeae. Am J. Genet. Cytol. 25:581-589.

Liu, Z-W. and Wang R.R-C. 1989. Genome analysis of *Thinopyrum caespitosum*. Genome 32:141-145.

Liu, Z-W. and Wang, R.R-C. 1992. Genome analysis of *Thinopyrum junceiforme* and *T. sartorii*. Genome 35:758-764.

Liu, Z-W. and Wang R.R-C. 1993a. Genome constitutions of *Thinopyrum curvifolium, T. scirpeum, T. distichum*, and *T. junceum* (Triticeae: Gramineae). Genome 36:641-651.

Liu, Z-W. and Wang R.R-C. 1993b. Genome analysis of *Elytrigia caespitosa, Lophopyrum nodosum, Pseudoroegneria geniculata ssp. scythica*, and *Thinopyrum intermedium*. Genome 36:102-111.

Löve, A. 1982. Genomic evolution in the wheatgrasses. Biol. Zentralbl. 101:191-212.

Löve, A. 1984. Conspectus of the Triticeae. Feddes Repert. 95:425-521.

McNeil, D., Lagudah, E.S., Hohmann, U., and Appels, R. 1994. Amplification of DNA sequences in wheat and its relatives: the Dgas44 and R350 families of repetitive sequences. Genome 37:320-327.

Sakamoto, S. 1979. Genetic relationships among four species of the genus *Eremopyrum* in the tribe Triticeae, Gramineae. Mem. Coll. Agr. Kyoto Univ. 114:1-27.

Seberg, O. 1989. Genome analysis, phylogeny and classification. Pl. Syst. Evol. 166:159-171.

Seberg, O., Frederiksen, S., Baden, C., and Linde-Laursen, I. 1991. *Peridictyon*, a new genus from the Balkan peninsula, and its relationships with *Festucopsis* (Poaceae). Willdenowia 21:87-104.

Torabinejad, J. and Mueller, R.J. 1993. Genome analysis of intergeneric hybrids of apomictic and sexual Australian *Elymus* species with wheat, barley and rye: implications for the transfer of apomixis to cereals. Theor. Appl. Genet. 86:288-294.

Vershinin, A., Svitashev, S., Gummesson, P.-O., Salomon, B., Bothmer, R. von,

and Bryngelsson, T. 1994. Characterization of a family of tandemly repeated DNA sequences in the Triticeae. Theor. Appl. Genet. 89:217-225.

Wang, R.R-C. 1985. Genome analysis of *Thinopyrum bessarabicum* and *T. elongatum*. Can. J. Genet. Cytol. 27:722-728.

Wang, R.R-C. and Jensen, K. B. 1994. Absence of the J genome in *Leymus* species (Poaceae: Triticeae): evidence from DNA hybridization and meiotic pairing. Genome 37:231-235.

Wang, R.R-C., Dewey, D.R., and Hsiao, C. 1986. Genome analysis of the tetraploid *Pseudoroegneria tauri*. Crop Sci. 26:723-727.

Xu, J. and Conner, R.L. 1994. Intravarietal variation in satellites and C-banded chromosomes of *Agropyron intermedium* ssp. *trichophorum* cv. Greenleaf. Genome 37:305-310.

Yen, Y. and Kimber, G. 1992. Genomic relationships of N-genome *Triticum* species. Genome 35:962-966.

Yen, C. and Yang, J.L. 1990. *Kengyilia gobicola*, a new taxon from west China. Can. J. Bot. 68:1894-1897.

Zhang, H-B. and Dvorak, J. 1991. The genome origin of tetraploid species of *Leymus* (Poaceae: Triticeae) inferred from variation in repeated nucleotide sequences. Am. J. Bot. 78:871-884.

Zhang, H-B. and Dvorak, J. 1992. The genome origin and evolution of hexaploid *Triticum crassum* and *Triticum syriacum* determined from variation in repeated nucleotide sequences. Genome 35:806-814.

Zhang, H-B., Dvorak, J., and Waines, J.G. 1992. Diploid ancestry and evolution of *Triticum kotschyi* and *T. peregrinum* examined using variation in repeated nucleotide sequences. Genome 35:182-191.