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A guide to the homoeology of chromosomes within the *Triticeae*

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Summary. A method of assessing chromosome homoeologies within the genomes of the *Triticeae* which does not require the ultimate test of substitution of the chromosomes into wheat is presented. This takes the form of a table listing key characters that are associated with specific homoeologous groups. These characters include marker genes, chromosome morphology, and plant morphologies of wheat-alien chromosome addition and wheat tetrasomic lines.

Key words: Homoeology – *Triticeae* – Alien chromosome addition

Introduction

The genera and species of the tribe *Triticeae* contain many different genomes, which are, in all probability, derived by divergence from a single ancestral genome. Consequently, each chromosome of each genome is expected to have an equivalent (homoeologous) chromosome in every other genome. Despite the considerable divergence that has occurred, many chromosomes still retain similar genetic material as indicated by homoeoallelic series of genes, in particular those which code for enzyme production (McIntosh 1986). Individual chromosomes from several genomes have been isolated as additions or substitutions into wheat, many of which are listed by Driscoll (1983).

The 21 chromosomes of the three genomes (A, B and D) of hexaploid wheat (*Triticum aestivum*, $2n=6x=42$) have been assigned to seven homoeologous groups (Sears 1954; Okamoto 1962). Each group contains one chromosome from each genome; thus homoeologous group 1 is comprised of chromosomes 1A, 1B and 1D, group 2 of 2A, 2B, 2D and so on. Assignment of homoeology of the chromosomes of the other ('alien') genomes with wheat chromosomes allows them to be given a similar nomenclature; for example the chromosomes of the R genome of *Secale* are designated 1R, 2R, 3R, 4R, 5R, 6R, and 7R (Miller 1984).

Knowledge of the homoeology of alien chromosomes to wheat chromosomes is of great value if genes from alien genomes are to be transferred to wheat. This paper aims to serve as a guide for determining the homoeology of chromosomes within the *Triticeae*.

Assessment of homoeology

The ability of an 'alien' chromosome, when substituted into wheat, to adequately compensate for the loss of the wheat chromosome is generally accepted as the critical test of homoeology. The production of such substitution lines is, however, a lengthy process, especially if no prior indication of homoeology is available (Gale and Miller 1987). The presence of marker genes, which produce easily recognizable phenotypes such as tissue pigmentation or specific proteins, can provide a more rapid indication of homoeology (Miller et al. 1985).

The addition of an extra pair of chromosomes to the normal hexaploid complement of wheat often changes the plant phenotype. In general, the changes in phenotype of an addition or tetrasomic line depend more on the homoeologous group of the extra chromosome pair than on the genome from which it is derived. Similarities in plant morphology of different 'alien' chromosome addition lines to wheat and wheat tetrasomic lines can therefore also be an indication of homoeology.

A guide to homoeology

The characters normally associated with particular homoeologous groups are listed in Table 1. The presence

Table 1. Key characters and their homoeologous chromosome location for use in determining the homoeology of chromosomes in the *Triticeae*

Character		Homoeologous group						
		1	2	3	4	5	6	7
Marker genes:								
Black glume	*Bg*	S						
Purple coleoptile	*Rc*							S
Purple culm	*Pc*							S
Red grain	*R*			+*				
Brittle rachis				+				
Enzymes:								
Acid phosphatase	*Acph-1*				+			
Aliphatic alcohol dehydrogenase	*Adh-1*				+			
Amino peptidase	*Amp-1*						S	
α-amylase	*α-Amy-1*						L	
	α-Amy-2							L
β-amylase	*β-Amy-1*				+			
	β-Amy-2					L		
Endopeptidase	*Ep-1*							L
Esterase	*Est-1*			S				
	Est-4						L	
	Est-5			L				
Glucose phosphate isomerase	*Gpi-1*	S						
Malate dehydrogenase	*Mdh-1*	L						
Phosphodiesterase	*Pde-1*			S				
Phosphoglucomutase	*Pgm-1*				+			
Shikimate dehydrogenase	*Skdh-1*					S		
Superoxide dismutase	*Sod-1*		L					
Triosephosphate isomerase	*Tpi-1*			S				
	Tpi-2					L		
Storage proteins:								
Glutenins	*Glu-1*	L						
'Triplet'	*Tri-1*	S						
Other proteins:								
Lectins	*Lec-1*	L						
Chromosome morphology:								
Satellite/nucleolus organiser region		S				S	S	
Heterobrachial with secondary constriction in long arm						+		
Addition/tetrasomic line plant morphology:								
Short stature		L		L		L		
Tall stature							+	
Thin culms			L					L
Thick culms						L		
Narrow leaves			+					+
Broad leaves								
Small spikes		+		+				
Tapered spikes								+
Dense spikes				+				
Lax spikes								
Narrow spikes								+
Broad clavate spikes						L		
Sterile top (about ⅓) of spike					+			
Rounded glumes							L	
Narrow glumes			L					
Tough glumes			+					
Round grains							L	
Narrow grains			L					
Wrinkled grains								+
Coarse textured grains						L		

(continued overleaf)

Table 1 (continued)

Character	Homoeologous group						
	1	2	3	4	5	6	7
Vitreous grains		+					
Short awns		L					
Erect habit				+			
2-D (fan shaped) juvenile habit						L	
Increased susceptibility to powdery mildew (*Erysiphe graminis*)					L		

+ = arm location not identified; S = short arm; L = long arm; * = group 6 in *Secale* R genome

of the key characters listed should be assessed in order to determine the homoeology of the unidentified extra chromosomes carried by a line.

Notes on the key characters

1 Morphology of chromosomes. There is considerable variation within the *Triticeae* for chromosome morphology. However, this is usually of little use in determining homoeology as the differences between genomes are so great, for example the genomes of the genus *Aegilops* (Chennaveeraiah 1960). The nucleolus organizer regions (NORs) which are frequently associated with a visible satellite are of value as these are normally found only on chromosomes from three homoeologous groups. However, the appearance of these satellites of the chromosomes of some genomes is suppressed in the presence of some other genomes (Martini et al. 1982; Cermeño et al. 1984; Lacadena et al. 1984). It may, therefore, be necessary to use other techniques such as in situ hybridization of rDNA to show their presence (Miller et al. 1980).

The chromosomes of homoeologous group 5 are often heterobrachial and as univalents at meiosis show a distinct secondary constriction in their long arms (Sears 1954; Miller 1984).

2 Plant morphology of addition and tetrasomic lines. It must be emphasised that many of the characters listed in this section of Table 1 do not occur singly, but in combinations that give a distinctive overall plant morphology characteristic of a particular homoeologous group. For example: – homoeologous group 2 lines generally have thin culms, narrow leaves, narrow spikes with narrow tough glumes carrying short awns and have narrow vitreous grains (Sears 1954; Miller 1984). Group 5 lines have short thick culms, broad leaves, broad clavate spikes and large coarse textured grains; they also frequently show increased susceptibility to powdery mildew, *Erisyphe graminis* and yellow rust, *Puccinia graminis* (Sears 1954; Pink et al. 1983; Gale and Miller 1987). Plant morphology is dependent on the wheat background to which the pair of chromosomes is added. Comparisons are, therefore, best made between lines with identical or similar backgrounds.

3 Marker genes. The number of marker genes has increased considerably with the development of electrophoretic techniques for locating genes for specific enzymes and seed storage proteins, and more will undoubtedly become available. Only those marker genes present on homoeologues of at least two genomes have been included in Table 1. The enzyme and storage protein genes included are those which can be readily identified and have been unequivocally located to specific chromosomes. Other protein marker genes such as those for the enzymes glutamic oxaloacetic transaminase, hexokinase and peroxidase, and the gliadin storage proteins can also be used to support the assessment of homoeology. Full details of these genes and references to their designations and locations are given by McIntosh (1983, 1986) and Hart and Gale (1987).

Discussion

It is essential to remember that no single character can be relied upon as an indicator of homoeology. Some characters may regularly be controlled by genes on chromosomes of more than one homoeologous group, and not all homoeologues necessarily carry genes which produce a particular character. An indication of the homoeology of a chromosome will therefore be provided by the group in Table 1 to which the largest number of its characters can be matched.

Chromosomal rearrangements such as translocations and inversions can make determination of the exact homoeology of some chromosomes impossible. The R genome of *S. cereale*, for example, carries a reciprocal translocation between chromosomes 4R and 7R relative to wheat (Koller and Zeller 1976). In the case of chromosomes exhibiting homoeology to more than one group we suggest they are given the homoeolo-

gous designation of the group to which they show the greatest homoeology. Robertsonian translocations produced by centromeric breakage and fusion resulting from misdivision of univalents at meiosis (Sears 1973) also frequently occur between 'alien' chromosomes during the production of 'alien' addition lines (Miller 1984). These translocated chromosomes may show characters normally attributed to chromosomes of two homoeologous groups. Chromosome arm location of the key characters, where possible, is given and in many cases this should enable the components of translocations to be identified. Translocated chromosomes arising from centric fusion and thereby consisting of complete arms of non-homoeologous chromosomes should be given a dual designation as proposed by Koebner and Miller (1986), where the homoeology of their components can be established.

Identification of further marker genes particularly those coding for specific proteins will allow more precise assessments of homoeology and may be of particular value for chromosome arms which at present carry few identified markers. The identification of restriction fragment length polymorphisms (Botstein et al. 1980) may in the future also provide a valuable series of markers.

Conclusions

The homoeology of 'alien' chromosomes to those of the wheat genomes is best determined by their ability to compensate successfully for the loss of a wheat chromosomes when substituted into wheat. However, an assessment of homoeology can be obtained by the study of homoeoallelic genes and by the comparison of the plant morphologies of 'alien' chromosome addition lines and wheat tetrasomic lines. The availability in tabular form of key marker gene and morphological characters should serve as a useful guide in determining the homoeology of chromosomes in the genomes of the *Triticeae*.

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