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Chromosomal Location of Genes Controlling Seed Proteins in Species Related to Wheat

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Summary. The seed proteins of 'Chinese Spring' wheat stocks which possess single chromosomes from other plant species related to wheat have been separated by gel electrophoresis in the presence of sodium dodecyl sulphate. Marker protein bands have been detected for both arms of barley chromosome 5, chromosome E (= 1R) and B (= 2R) of rye, chromosomes A,B (= $1C^u$) and C (= $5C^u$) of *Aegilops umbellulata* and chromosomes I and III of *Agropyron elongatum*. These studies, and previous findings, indicate that chromosome 5 of barley, chromosome 1R of rye, chromosome I of *Ag. elongatum* and possibly chromosome $1C^u$ of *Ae. umbellulata* are similar to chromosomes 1A, 1B and 1D in hexaploid wheat in that they carry genes controlling prolamins on their short arms and genes controlling high-molecular-weight (apparent molecular weight greater than 86,000) seed protein species on their long arms. These findings support the idea that all these chromosomes are derived from a common ancestral chromosome and that they have maintained their integrity since their derivation from that ancestral chromosome.

Key words: Seed proteins – Wheat – Barley – Rye – *Ae. umbellulata* – *Ag. elongatum*.

Introduction

Studies of the chromosomal location of genes controlling seed proteins in hexaploid bread wheat (*Triticum aestivum*, 2n = 42, genomic formula AABBDD) have shown that each of the genomes in hexaploid wheat possesses one chromosome (chromosome 1A, 1B and 1D) with genes controlling prolamins (alcohol-soluble proteins) on its short arm and genes controlling glutenins (alcohol-insoluble proteins) on its long arm, as well as another chromosome (chromosomes 6A, 6B and 6D) with genes controlling prolamins on its short arm (Shepherd 1968; Wrigley and Shepherd 1973; Bietz et al. 1975; Lawrence and Shepherd 1980; and this paper). These findings raise the question of whether the genes controlling seed proteins in other genomes in the tribe Triticeae have a similar chromosomal distribution. This paper provides information on the chromosomal location of genes controlling seed proteins in the genomes of rye (*Secale cereale* 2n = 14), barley (*Hordeum vulgare*, 2n = 14), *Aegilops umbellulata* (2n = 14) and *Agropyron elongatum* (2n = 14).

Except for the recent study of Brown et al. (1979), all the previous investigations of the chromosomal control of seed proteins in these genomes have used 2M urea to solubilize the proteins prior to electrophoresis in gels at pH 3.2 (Shepherd 1968; 1973 and unpublished). However, the glutenin fraction of wheat is insoluble in 2M urea and could not be investigated with this system. The glutenins, which contain protein aggregates of high molecular weight formed by the association of a number of constituent polypeptide chains, only became amenable to investigation when Bietz and Wall (1972) found that the aggregates could be broken down to their component subunits by treatment with a detergent, sodium dodecyl sulphate (SDS), which disrupts hydrophobic interactions and hydrogen bonds between proteins, and 2-mercaptoethanol (2-ME), which breaks disulphide bonds. The component subunits could then be separated by electrophoresis in polyacrylamide gels containing SDS (SDS-PAGE). The SDS-PAGE procedure has now been used to investigate the chromosomal location of additional genes controlling seed proteins in genomes distantly and closely related to those of wheat and the results are reported in this paper.

Materials and Methods

In outline, the procedure was to compare the electrophoretic banding patterns of the seed proteins of the wheat cultivar 'Chinese Spring' with the patterns of 'Chinese Spring' stocks which had, in addition, a chromosome pair (or arms) from another alien species.

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Bands present in the pattern of the addition-line stock which were not present in the pattern of 'Chinese Spring' were assumed to be controlled by genes on the 'alien' chromosome or chromosome arm present in that particular addition-line.

Proteins were extracted from single kernels by treatment with SDS and 2-ME and then electrophoresed in 8.33% acrylamide gels containing SDS (Lawrence and Shepherd 1980). The extraction procedure is expected to solubilize all of the different protein species in the grain.

The 'alien' chromosome addition lines were all derivatives of the wheat cultivar 'Chinese Spring'. The rye chromosomes (designated A to G) in the seven wheat-rye addition lines were derived from the rye cultivar 'Imperial' (see Driscoll and Sears 1971). The original seed was kindly supplied by Dr E.R. Sears. The barley chromosomes in the wheat-barley addition lines were derived from the barley cultivar 'Betzes' (Islam *et al.* 1978). The designation of each chromosome in the addition lines (1 to 7) corresponds to the standard nomenclature of barley chromosomes (Islam 1980). Seed of the wheat-barley addition lines, together with seed of a stock possessing a wheat-barley translocation chromosome, was kindly provided by Mr A.K.M.R. Islam. The wheat – *Ae. umbellulata* addition lines (designated A to G) were those produced by Kimber (1967) and Dr G. Kimber kindly provided seeds of these stocks, together with seed of *Ae. umbellulata* and the 'Chinese Spring' wheat + *Ae. umbellulata* amphiploid. The wheat – *Ag. elongatum* addition lines (designated I to VII) were produced by Dvorak and Knott (1974) and these stocks, together with seed of the 'Chinese Spring' wheat + *Ag. elongatum* amphiploid, were kindly provided by Dr G.E. Hart.

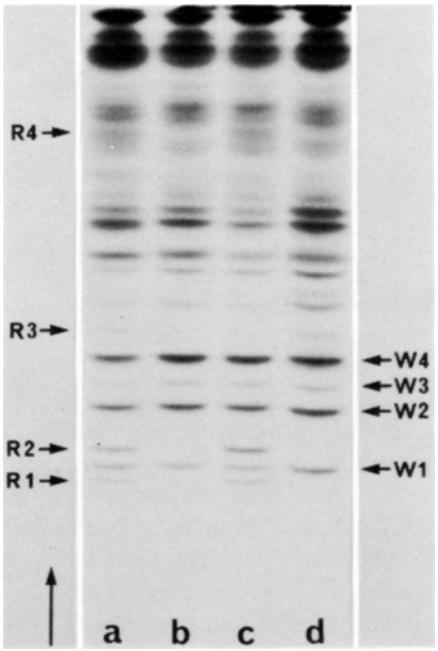

Fig. 1. SDS-PAGE patterns of total seed proteins of (a) 'Chinese Spring'-'Imperial' rye amphiploid (2n = 54) (b) 'Chinese Spring' (c) disomic addition of chromosome E (= 1R) of 'Imperial' rye to 'Chinese Spring' (d) disomic addition of chromosome B (= 2R) of 'Imperial' rye to 'Chinese Spring'

Results

The Banding Pattern of the Wheat Cultivar, 'Chinese Spring'

The banding pattern obtained with crude extracts of the total seed proteins of the wheat cultivar 'Chinese Spring' is shown in Fig. 1b. The four slowest-moving bands in this pattern (bands W1, W2, W3 and W4) represent glutenin protein subunits (Bietz et al. 1975; Lawrence and Shepherd 1980), and they are commonly referred to as the high-molecular-weight (HMW) glutenin subunits, since larger protein molecules usually migrate at a slower rate than smaller molecules in SDS gels (e.g., Weber and Osborn 1969; Dunker and Rueckert 1969). Bands W1 and W4 are controlled by genes on the long arm of chromosomes 1D and bands W2 and W3 by genes on the long arm of chromosome 1B (Bietz et al. 1975; Lawrence and Shepherd 1980). Some other wheat cultivars also possess a single band either sligtly faster or slightly slower in mobility than band W1 of 'Chinese Spring'. These bands are known to be controlled by a gene(s) on chromosome 1A (Lawrence and Shepherd 1980), but, in this previous study, the arm location was not determined. Indirect evidence on the arm location of this gene has now been obtained from seed of a stock of the wheat cultivar 'Federation', kindly provided by Dr R.A. McIntosh, University of Sydney, which was heterozygous for a telocentric chromosome, 1AL. Federation possesses a HMW glutenin subunit with the same mobility as a band in the cultivar 'Hope', and, since this band in 'Hope' is known to be controlled by chromosome 1A (Lawrence and Shepherd 1980), it is likely that the band in 'Federation' is also controlled by chromosome 1A. A plant heterozygous for 1AL and the complete 1A was selected and crossed as female to 'Chinese Spring'. Twenty-one of the resulting progeny kernels were tested on SDS gels and they all possessed the glutenin subunit band thought to be controlled by chromosome 1A of 'Federation'. Thus, it is likely that this band is controlled by a gene(s) on the long arm of chromosome 1A, since, if the gene(s) was located on the short arm of 1A, 50% of the progeny kernels would be expected to lack the 1A glutenin band.

Those bands in the 'Chinese Spring' pattern that are faster-moving than band W4 (see Fig. 1b) are considered to be mainly prolamin proteins. As shown in Fig. 1, these bands are not as well resolved as the slow-moving glutenin subunits, partly because there are so many bands. Therefore, SDS-PAGE is most useful for analysing the HMW glutenin subunits in wheat and the equivalent slow-moving proteins of species related to wheat. On the other hand, the prolamins in these species are most conveniently studied by extraction with 2M urea and separation by electrophoresis in gel systems lacking SDS.

Banding Patterns of Wheat-Rye Addition Lines

The banding pattern of a 'Chinese Spring' – 'Imperial' rye amphiploid (2n = 54), which was deficient for a pair of rye chromosomes, is shown in Fig. 1a. It possesses four bands (R1, R2, R3 and R4) in addition to those normally present in the pattern of 'Chinese Spring' (Fig. 1b). Bands R1, R2 and R4 are controlled by genes on rye chromosome E, since they are present in the pattern of addition line E (Fig. 1c). Tests of a stock possessing a ditelocentric addition of the long arm of rye chromosome E and a stock possessing a translocation chromosome involving the short arm of rye E, have shown that bands R1 and R2 are controlled by genes on the long arm of E and band R4 by a gene(s) on the short arm. Band R4 is likely to be a prolamin because Shepherd (1968) has shown that the short arm of rye E carries genes controlling prolamins. Rye chromsome E will compensate genetically for the absence of wheat chromosome 1D or 1B (Shepherd 1973) and is now referred to as rye chromosome 1R to indicate its homoeology with the group 1 wheat chromosomes. Band R3 is controlled by a gene(s) on rye chromosome B, since this band is present in the pattern of addition line B (Fig. 1d). In addition to band R3, rye chromosome B also controls a second band whose mobility is almost identical to that of 'Chinese Spring' band W4, but its presence is much less distinct in destained gels (Fig. 1d). The arm location of the genes controlling these bands has not been determined. Rye chromosome B has been shown to be homoeologous with group 2 chromosomes in wheat (Sears 1968) and is now referred to as chromosome 2R. In the previous investigation by Shepherd (1968) using 2M urea as the protein extractant followed by electrophoresis at pH 3.2 in starch gels, the rye bands detected in the amphiploid were all found to be controlled by genes on the short arm of rye chromsome E. Therefore those protein species that constitute bands R1, R2 and R3 may not be soluble in 2M urea, at least when they occur in a wheat kernel: alternatively, these protein species could be soluble in 2M urea, but were not identified in the starch gels either because they have the same mobility as wheat bands or because they are too large to enter the gel.

Banding Patterns of Wheat-Barley Addition Lines

The banding pattern of the barley cultivar 'Betzes' (2n = 14) shows a single slow-moving band of similar mobility to the HMW wheat glutenin subunits in addition to a number of fast-moving bands (Fig. 2a).

To determine the chromosomal location of genes controlling seed proteins in barley, six stocks were tested initially, each of which possessed an individual pair of chromosomes from the barley cultivar 'Betzes' (chromosomes 1, 2, 3, 4, 6 and 7) added to 'Chinese Spring' wheat. However, the banding pattern of each of these stocks was identical to that of 'Chinese Spring' (Fig. 2b). Chromosome 5 of 'Betzes' barley was not available in a simple addition line because this chromosome causes complete sterility when added alone to wheat (Islam et al. 1978). However, a plant was obtained that possessed a single dose of both chromosomes 5 and 6 of barley added to 'Chinese Spring' and this plant was partly fertile when pollinated with 'Chinese Spring'. Some of the progeny kernels from this cross were found to possess several barley protein bands in addition to the wheat bands (see Fig. 2c), indicating that barley bands B1, B2 and B3 are controlled by genes on barley chromosome 5. The arm location of these genes was determined by testing a stock that possessed a translocation chromosome involving the whole of the short arm of barley chromosome 5 (as indicated by N-banding) joined to an arm of an unidentified wheat chromosome (Islam 1980). This stock possessed barley bands B2 and B3, but not band B1, indicating that the genes controlling B2 and B3 are located on the short arm of chromsome 5 and that the gene(s) controlling B1 is located on the long arm of chromosome 5. Since the genes controlling prolamins (hordeins) in barley are known to be located on the short arm of barley chromosome 5 (see Shewry et al. 1980), barley bands B2 and B3 are considered to be barley prolamins.

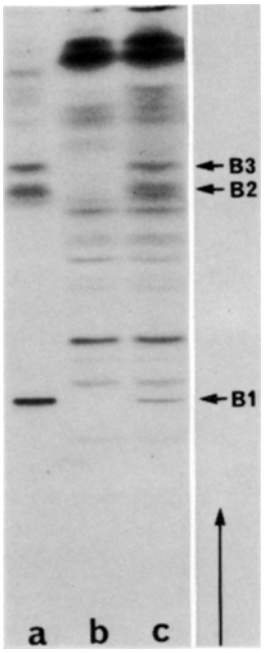

Fig. 2. SDS-PAGE patterns of total seed proteins of (a) 'Betzes' barley (b) 'Chinese Spring' (c) 'Chinese Spring' stock possessing a monosomic addition of chromosome 5 of 'Betzes'

Banding Patterns of Wheat – Ac. umbellulata Addition Lines

The banding pattern of the 'Chinese Spring' – *Ae. umbellulata* amphiploid (2n = 56) (Fig. 3a) possesses five bands (U1, U2, U3, U4 and U5) not present in the pattern of 'Chinese Spring' wheat (Fig. 3c). The pattern of an *Ae. umbellulata* (genome C^u) accession (2n = 14) is also shown (Fig. 3b). Although this accession is not the one used to produce the amphiploid there is close agreement between its bands and the extra bands present in the amphiploid with the exception of band U4. Bands U1, U2 and U4 are controlled by genes on *Ae. umbellulata* chromosome B since they are present only in the pattern of addition line B (Fig. 3d). Shepherd (1973) has shown that chromosome B carries genes controlling prolamin proteins (arm location not determined) and that this chromosome is homoeologous with group 1 wheat chromosomes. For this reason, chromosome B is now referred to as chromosome $1C^u$. The arm locations of the genes controlling bands U1, U2 and U4 have not been determined, but, if the same gene arrangement as has been found in the homoeologous group 1 chromosomes applies, it can be predicted that bands U1 and U2 will be controlled by genes on the long arm of $1C^u$ and that band U4 will be controlled by a gene(s) on the short arm. Although chromosome $1C^u$ was associated with only three bands in the present study, Brown et al. (1979) detected seven proteins controlled by $1C^u$ using two-dimensional gel electrophoresis.

Band U5 is controlled by a gene(s) on *Ae. umbellulata* chromosome A (arm location not determined) since this band is present in the pattern of addition line A (Fig. 3f). This band may be a prolamin since Shepherd (1973) had shown earlier that chromosome A possesses a gene(s) controlling prolamins. There is some evidence that chromosome A is homoeologous with group 6 chromosomes in wheat (Athwal and Kimber 1972); this relationship is not unexpected as chromosomes 6A, 6B and 6D in wheat each carry genes controlling prolamins (Shepherd 1968; Wrigley and Shepherd 1973).

Finally, band U3 is controlled by a gene(s) on chromosome C of *Ae. umbellulata* (arm location not determined) because it is present in the pattern of addition line C (Fig. 3e). Since chromosome C of *Ae. umbellulata* is homoeologous with group 5 chromosomes in wheat, it is now referred to as chromosome $5C^u$ (Chapman and Riley 1970).

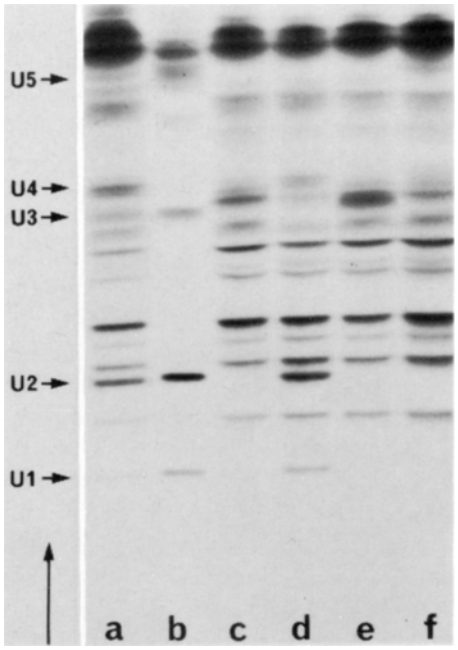

Fig. 3. SDS-PAGE patterns of total seed proteins of (a) 'Chinese Spring' – *Ae. umbellulata* amphiploid (2n = 56) (b) *Ae. umbellulata* (2n = 14) (c) 'Chinese Spring' (d) disomic addition of chromosome B (= $1C^u$) of *Ae. umbellulata* to 'Chinese Spring' (e) disomic addition of chromosome C (= $5C^u$) of *Ae. umbellulata* to 'Chinese Spring' (f) disomic addition of chromosome A of *Ae. umbellulata* to 'Chinese Spring'

Banding Patterns of Wheat – Ag. elongatum Addition Lines

The banding pattern of the 'Chinese Spring' – *Ag. elongatum* amphiploid (2n = 56) (Fig. 4a) possesses three bands

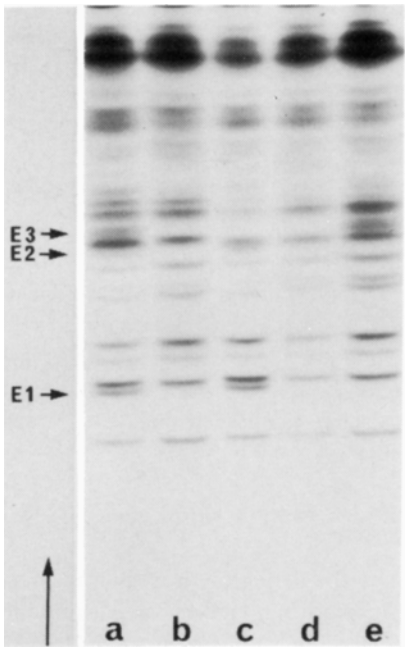

Fig. 4. SDS-PAGE patterns of total seed proteins of (a) 'Chinese Spring' – *Ag. elongatum* amphiploid (2n = 56) (b) 'Chinese Spring' (c) disomic addition of chromosome I of *Ag. elongatum* to 'Chinese Spring' (d) disomic addition of the short arm of chromosome I of *Ag. elongatum* to ' Chinese Spring' (e) disomic addition of chromosome III of *Ag. elongatum* to 'Chinese Spring'

(E1, E2 and E3) in addition to those present in 'Chinese Spring' (Fig. 4b). Bands E1 and E2 are controlled by genes on the long arm of *Ag. elongatum* chromosome I, since they are present in the pattern of a 'Chinese Spring' addition line possessing a complete chromosome I of *Ag. elongatum* (Fig. 4c), but are not present in the pattern of the addition line possessing just the short arm of this chromosome (Fig. 4d). Shepherd (unpublished), using 2M-urea extracts and protein separation in starch gels at pH 3.2, has shown that the short arm of chromosome 1 carries genes controlling prolamins. Therefore, chromosome I of *Ag. elongatum* carries genes controlling seed proteins on both arms, similar to the group 1 chromosomes of hexaploid wheat. Chromosome I of *Ag. elongatum* will compensate genetically for the absence of chromosome 1A (Dvorak and Knott 1974) so that all the evidence presently available suggests that chromosome I of *Ag. elongatum* is homoeologous with group 1 wheat chromosomes. Band E3 is controlled by a gene(s) on chromosome III of *Ag. elongatum* (arm location not determined) since this band is present in the pattern of addition line III (Fig. 4e). Chromosome III of *Ag. elongatum* is homoeologous with the group 4 chromosomes of wheat (Dvorak and Sosulski 1974).

Discussion

Protein Nomenclature

There is a problem with protein nomenclature when discussing the results of gel electrophoresis studies of seed proteins in wheat and its relatives, because the solvents used to extract the proteins prior to electrophoresis are not those that traditionally have been used to fractionate the seed proteins.

Osborne (1907) divided the proteins of the wheat kernel into four solubility classes: the albumins, soluble in water; the globulins, soluble in dilute salt solutions, but insoluble in water; the gliadins, soluble in 70 to 90% ethanol and the glutenins, insoluble in neutral aqueous solutions, saline solutions, or alcohol. The generic names prolamin and glutelin are substituted for gliadin and glutenin respectively when referring to the equivalent protein fractions from other cereal grains (Osborne 1924). In wheat, the gliadins (= prolamins) and glutenins are the major fractions, each containing about 40 to 45% of the total seed protein. The albumins and globulins each contain about 5 to 10% of seed proteins (Osborne 1907).

In the initial electrophoretic studies of the seed proteins of wheat and its relatives, 2M urea was used as the protein solvent and it was assumed to solubilize the albumin, globulin and prolamin fractions, but not the glutelin fraction. When the 2M urea-soluble proteins of the wheat kernel were electrophoresed in gels at pH 3.2, a few fast-moving protein species were detected, plus a large group of slow-moving protein species. The fast-moving protein species were assumed to be mostly albumins and globulins, whereas the large group of slow-moving proteins were assumed to be mostly prolamins (Shepherd 1968). In the following discussion, the term prolamin is used for those seed proteins that are soluble in 2M urea and which are electrophoretically slow-moving in gels at pH 3.2.

When the dissociating agents SDS and 2-ME are used to extract the proteins, all the protein fractions are expected to be solubilized. When electrophoresed in gels containing SDS the protein species can be classified on the basis of their apparent molecular weights since these can be inferred directly from mobility in SDS gels (e.g. Weber and Osborn 1969; Dunker and Rueckert 1969).

Therefore, for the purposes of the present discussion, it is convenient to classify the proteins into just two groups, with the division point between the groups occurring at band W4 in the 'Chinese Spring' pattern (see Fig. 1), which Bietz et al. (1975) have estimated to have an apparent molecular weight of 86000. Bands with the same or slower mobility than band W4 will be referred to as HMW protein species and bands with a faster mobility as low-molecular-weight (LMW) protein species. Under this classification the HMW protein species in hexaploid wheat are all HMW glutenin subunits, whereas the LMW protein species will be mostly prolamins, but will also include the albumins, globulins and LMW glutenin subunits.

Chromosomal Distribution of Genes Controlling Seed Proteins in Different Genomes

Using the nomenclature just outlined, the chromosomal distribution of the genes controlling seed proteins in rye, barley, *Ae. umbellulata* and *Ag. elongatum* can be compared to that found in the three genomes of hexaploid wheat. One obvious similarity is that each of the four diploid species possesses a chromosome that appears to correspond to the group 1 chromosomes in wheat, which carry genes controlling prolamins on their short arms and genes controlling HMW proteins on their long arms. Thus, rye chromosome E (= 1R), barley chromosome 5 and *Ag. elongatum* chromosome I all possess genes controlling prolamins on their short arms and a gene or genes controlling HMW proteins on their long arms. *Ae. umbellulata* chromosome B (= $1C^u$) carries genes controlling prolamins as well as genes controlling HMW proteins but it has not been determined whether these genes are located on different arms. When present in 'Chinese Spring' the prolamin proteins controlled by rye chromosome 1R, barley chromosome 5 and *Ae. umbellulata* chromosome $1C^u$ can apparently also be detected in SDS gels as LMW proteins. Since rye chromosome E (= 1R), *Ae. umbellulata* chromosome B (= $1C^u$) and *Ag. elongatum* chromosome I have been shown to be homoeologous with the group 1 chromosomes of wheat (Shepherd 1973; Dvorak and Knott 1974) it would seem likely that barley chromosome 5 also is homoeologous with group 1 wheat chromosomes.

Besides the genes controlling seed proteins located on group 1 chromosomes, wheat also possesses additional

genes controlling prolamins that are located on the group 6 chromosomes. However, so far, genes corresponding to those on group 6 chromosomes of wheat have apparently only been identified in *Ae. umbellulata*. Thus, with *Ae. umbellulata*, genes controlling prolamin proteins have been located on chromosomes A and B (= $1C^u$) (Shepherd 1973) and Shepherd has suggested that the prolamins controlled by chromosome A may correspond to the prolamins controlled by the group 6 chromosomes in wheat.

It is not unexpected that the distribution of genes controlling seed proteins in *Ae. umbellulata* should be similar to that in the A, B and D genomes of hexaploid wheat, because the D genome is known to have come from *Ae. squarrosa* and, although the origin of the B genome is uncertain, it too is thought to be derived from an *Aegilops* species. The origin of the A genome has been assigned to *Triticum boeoticum* (see review by Sears 1974).

With *Ag. elongatum* the prolamins that could be detected in the 'Chinese Spring' – *Ag. elongatum* amphiploid following extraction with 2M urea and electrophoresis at pH 3.2 were all found to be controlled by *Ag. elongatum* chromosome I (Shepherd unpublished). In the present study chromosome III was found to control a LMW protein band, but it is unlikely that this band corresponds to the wheat prolamins controlled by genes on group 6 chromosomes of wheat because chromosome III of *Ag. elongatum* is homoeologous with group 4 chromosomes of wheat (Dvorak and Sosulski 1974). In wheat a LMW band controlled by chromosome 4D has been identified that has a mobility in SDS gels similar to the mobility of the band controlled by chromosome III of *Ag. elongatum* (Bietz et al. 1975; Joppa et al. 1978).

In the case of barley and rye, no prolamins have been identified so far that are controlled by genes corresponding to those on group 6 chromosomes of wheat. Thus, the genes controlling all of the seed proteins in barley are apparently located on a single chromosome of barley, chromosome 5 (see Shewry et al. 1980; and this paper). In rye, the prolamin proteins identified by gel electrophoresis at pH 3.2, in the absence of SDS, are all controlled by genes on chromosome E (= 1R) (Shepherd and Jennings 1971). The rye protein bands controlled by chromosome B are unlikely to correspond to the wheat prolamins controlled by group 6 wheat chromosomes since the mobility of these rye bands in SDS gels is distinctly slower than the LMW bands assumed to be wheat prolamins (Fig. 1) and because rye chromosome B is homoeologous with group 2 wheat chromosomes (Sears 1968).

In summary, therefore, it would seem that the ancestral Triticeae genome possessed a chromosome with genes controlling prolamins on its short arm and genes controlling HMW seed proteins on its long arm and that chromosomes 1A, 1B and 1D of hexaploid wheat, together with chromosomes 1R of rye, 5 of barley, $1C^u$ of *Ae. umbellulata* and I of *Ag. elongatum* are each derived from this ancestral chromosome and, furthermore, have maintained their integrity since their derivation from that ancestral chromosome. Recently, Hart (1979) reviewed the known chromosomal locations of a large number of isozyme structural genes in the genomes of hexaploid wheat and in the genomes of rye, barley and *Ag. elongatum*. He concluded that the ancestral Triticeae gene synteny relationships are largely conserved in the genomes that exist today. This conclusion is supported by the finding that genomes from five different genera in the Triticeae each possess a chromosome with genes controlling different types of seed proteins located on opposite arms.

It does appear, however, that during the evolution of the Triticeae there has been a change in the number of genes controlling prolamins and/or in their distribution among the chromosomes. Thus, the genes controlling the prolamins in barley, rye and *Ag. elongatum* seem to be located on a single chromosome of each of these genomes, whereas in the *Triticum* and *Aegilops* genomes, genes controlling prolamins are located on two chromosomes. Finally, additional evolutionary changes in particular genomes may be indicated by the detection in SDS gels of LMW proteins controlled by chromosome B (= 2R) of rye, chromosome C (= $5C^u$) of *Ae. umbellulata* and chromosome III of *Ag. elongatum*, since, at present, there is no evidence to suggest that proteins corresponding to these are common to all genera of the Triticeae.

Besides providing information about the evolution of the Triticeae, the genes controlling seed proteins in wheat and its relatives are also of practical value, since, as genetic markers for chromosomes and chromosome arms, they can be used in two ways to facilitate the transfer of alien genetic material into wheat. First, these markers can indicate which chromosomes of wheat and the alien species might be related and a segment of alien genetic material is more likely to be successfully incorporated into wheat if it replaces a wheat segment that carries a related set of genes. Second, genetic markers can greatly facilitate the actual transfer of alien material into wheat. For example, the above findings have been used to obtain translocation chromosomes in which the long arm of rye chromosome 1R is joined to the short arms of chromosomes 1B and 1D of wheat. Double monosomics possessing chromosomes 1B and 1R (or 1D and 1R) as univalents were self-fertilized. Individual progeny kernels were cut into three parts and the part containing the embryo was put aside for growing into a plant if required. One part of the endosperm was screened using 2M-urea starch gels at pH 3.2 for the presence or absence of prolamins controlled by genes located on chromosome arms 1BS and 1RS (or 1DS and 1RS). When a kernel possessed bands controlled by 1BS (or 1DS) and lacked the bands controlled by 1RS, the third part of the kernel was examined by SDS-PAGE for

the presence or absence of the HMW protein species controlled by genes on the chromosone arms 1BL and 1RL (or 1DL and 1RL). By this means two kernels were selected which apparently possessed the 1BS and 1RL arms, but not the 1BL and 1RS arms, and three kernels were selected which apparently possessed the 1DS and 1RL arms, but not the 1DL and 1RS arms. Subsequent cytological tests of these stocks, and their progeny, showed that one of the first two stocks did in fact possess a 1DS – 1RL translocation chromosome and that one of the other three stocks possessed a 1DS – 1RL translocation chromosome. The reciprocal translocation chromosomes, namely 1BL – 1RS and 1DL – 1RS, were obtained in a previous study by one of us (K.W. Shepherd).

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