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The genetic control of grain esterases in hexaploid wheat

2. Homoeologous loci in related species

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Summary. A comparison of EST-5 grain esterase phenotypes from wheat-alien amphiploid, addition and substitution genotypes, resolved by flat-bed isoelectric focusing identified homoeologous *Est-5* loci on chromosome 3H of *Hordeum vulgare,* $3H^{ch}$ of *H. chilense,* $3S^{b}$ of *Aegilops bicornis,* $3S^{l}$ of *Ae. sharonensis* and *Ae. longissima* and 6R of *Secale cereale* and $6R^{m}$ of *S. montanum.* The *Est-5* genes in alien species provide evidence for chromosome homoeology with wheat.

Key words: Esterase isozymes – Isoelectric focusing – Wheat – Rye – Barley – *Aegilops* – *Agropyron*

1 Introduction

Wild relatives of wheat, the so called 'alien' species are being studied increasingly as a source of agronomically important genes which can be exploited in the genetic improvement of hexaploid bread wheat *Triticum aestivum* (2n = 6x = 42). These aliens include species in the genera *Hordeum, Secale, Agropyron, Aegilops* and *Haynaldia* which, together with the other members of the *Triticeae,* are considered to have evolved from a common ancestor (Morris and Sears 1967).

The techniques available to the cytogeneticist for the transfer of alien genetic material are well established (Riley and Kimber 1966; Feldman and Sears 1981; Law 1981). The ability to develop disomic addition lines of alien chromosomes added to hexaploid wheat both provides a means of introducing alien genes into wheat and also enables the chromosomes of the alien genome to be characterised genetically. In the past, such characterisation has been largely dependent on the use of morphological markers, on tests of chromosome pairing and on the ability of the alien chromosome to genetically compensate when substituted for a wheat chromosome.

Genes controlling enzymes, however, provide convenient markers for alien genetic material. Such genes are often expressed in the background genotype of hexaploid wheat, and their products readily distinguished from those of their homoeologous wheat loci. Enzyme marker genes have been successfully used to genetically assess the additions to wheat of chromosomes of *Hordeum vulgare* cv. 'Betzes' (Hart et al. 1980; Islam et al. 1981), *Agropyron elongatum* (= *Elytrigia elongata*) (Hart and Tuleen 1983) and *Aegilops longissima* (= *T. longissimum*) (Hart and Tuleen 1984).

This paper describes the analysis of grain esterase loci homoeologous to the *Est-5* series of wheat and present in a number of alien species. The structural *Est-5* genes are located on chromosome arms 3AL, 3BL and 3DL in hexaploid wheat (Ainsworth et al. 1984).

2 Materials and methods

2.1 Alien species and wheat-alien chromosome addition and substitution lines

The following alien species obtained from the Plant Breeding Institute collection were examined: *Hordeum vulgare* cv. 'Betzes' (2n = 2x = 14, HH); *H. chilense* (2n = 2x = 14, $H^{ch}H^{ch}$); *Secale cereale* cvs. 'King II' and 'Imperial' (2n = 2x = 14, RR); *S. montanum* (2n = 2x = 14, $R^{m}R^{m}$); *Ae. bicornis* (2n = 2x = 14, $S^{b}S^{b}$); *Aegilops sharonensis* (2n = 2x = 14, $S^{l}S^{l}$); *Ae. longissima* (2n = 2x = 14, $S^{l}S^{l}$); *Ae. umbellulata* (2n = 2x = 14, UU); *Agropyron elongatum* (= *Elytrigia elongata*) (2n = 2x = 14, EE). The available wheat-alien amphiploids and chromosome addition and substitution lines which were examined are listed in Table 1.

2.2 Electrophoresis

Extracts from single grains were resolved by flat-bed isoelectric focussing (IEF) and stained for esterase activity as described previously (Ainsworth et al. 1984).

3 Results and discussion

3.1 Barley (Hordeum)

3.1.1 'Chinese Spring'-Hordeum vulgare *cv. 'Betzes' addition lines. H. vulgare* cv. 'Betzes' expresses relatively

Table 1. Wheat-alien genotypes screened for grain esterase phenotypes

Alien chromosome donor species	Hexaploid wheat recipient variety	Wheat-alien genotypes	Original source of material
Hordeum vulgare cv. 'Betzes'	'Chinese Spring'	Additions: A, B, C, D, E, F	Islam et al. (1975)
H. chilense	'Chinese Spring'	Amphiploid Additions: A, B, C, D, E, F	Chapman and Miller (1978) Miller et al. (1982b)
Secale cereale cv. 'King II'	'Holdfast'	Amphiploid Additions: 1R, 2R, 4R, 5R, 6R, Additions: 6RS, 6RL, 7R Substitutions: 6R (6A), 6R (6B), 6R (6D)	Riley and Chapman (1958) Riley (1965)
S. cereale cv. 'King II'	'Chinese Spring'	Amphiploid Additions: 1R, 2R, 3R, 4R, 5R, 6R, 7R	Miller (1973)
S. cereale cv. 'Imperial'	'Chinese Spring'	Additions: 1R, 2R, 3R, 4R, 5R, 6R, 7R	Driscoll and Sears (1971)
S. montanum	'Chinese Spring'	Amphiploid Additions: $1R^m$, $2R^m$, $4R^m$, $5R^m$, $6R^m$ Substitutions: $6R^m$ (6A), $6R^m$ (6D)	Miller (1973) Miller and Reader, unpublished
Aegilops bicornis	'Holdfast'	Addition: $3S^b$, $7S^b$ Substitutions: $3S^b$ (3A)	Riley, Chapman and Miller, unpublished
Ae. sharonensis	'Chinese Spring'	Amphiploid Addition: $4S^l$ Substitution Additions: 1, 9, 91, 18, 41	 Miller et al. (1982a) Miller (1983)
Ae. longissima	'Chinese Spring'	Amphiploid Additions: A, B, C, D, E, F, G	Feldman (1975)
Ae. umbellulata	'Chinese Spring'	Amphiploid Additions: A, B, C, D, F, G	Kimber (1967)
Agropyron elongatum	'Chinese Spring'	Amphiploid Additions: I, II, III, IV, V, VI, VII	Dvořák and Knott (1974)

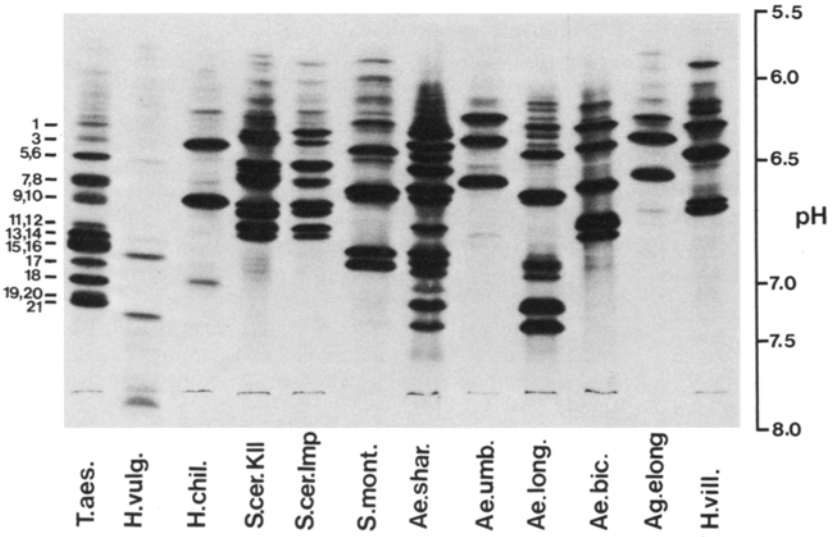

Fig. 1. Grain esterase (EST-5) phenotypes of wheat and its related species. T. aes = *Triticum aestivum* cv. 'Chinese Spring'; H. vulg = *Hordeum vulgare* cv. 'Betzes'; H. chil = *H. chilense;* S. cer K II = *Secale cereale* cv. 'King II'; S cer Imp = *S. cereale* cv. 'Imperial'; S. mont = *S. montanum;* Ae. shar = *Aegilops sharonensis;* Ae. umb = *Ae. umbellulata;* Ae. long = *Ae. longissima;* Ae. bic = *Ae. bicornis;* Ag. elong = *Agropyron elongatum;* H. vill = *Haynaldia villosa.* CS isozymes are numbered as described in Ainsworth et al. (1984)

few grain esterases in comparison to the zymograms of the other diploid species examined (Fig. 1). All but the three most alkaline isozymes are weakly expressed. In an analysis of the CS-Betzes additions, two of these isozymes were expressed in the zymogram of addition F, though very weakly (not shown). The barley chromosome in addition F, has been designated as barley chromosome 3 (Islam 1980) and shares homoeology with the chromosomes of wheat group 3 (Islam et al. 1981). This indicates that a locus (or loci) homoeo-

Table 2. Summary of the different nomenclatures used to describe the CS/*H. vulgare* cv. 'Betzes' additions

Additions (initial designation[a])	Barley chromosome present[b]	Designation by homoeology with wheat
A	4	4H
B	7	5H
C	6	6H
D	1	7H
E	2	2H
F	3	3H
G	5	1H

[a] Islam et al. (1978)
[b] Islam (1980); Islam et al. (1981)

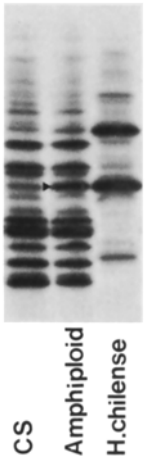

Fig. 2. Est-5 phenotypes of 'Chinese Spring' (CS), *Hordeum chilense* and the *H. chilense*-CS amphiploid. The arrow designates an isozyme from *H. chilense* expressed in the amphidiploid

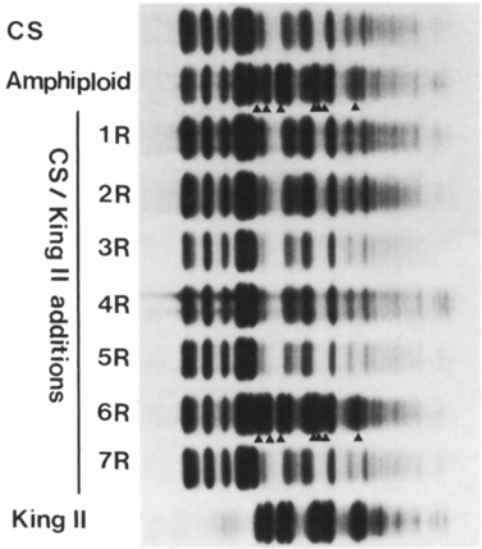

Fig. 3. EST-5 phenotypes of the CS-*Secale cereale* cv. 'King II' additions and CS-*S. cereale* cv. 'King II' amphiploid. *Arrows* indicate the expression of rye isozymes in a wheat background

logous to *Est-5* and designated *Est-5H*, occurs on this chromosome. The finding of *Est-H5* on chromosome 3 reinforces the evidence for this homoeology. Chromosome 3 is now also designated 3H on the basis of homoeology with wheat. This classification has been completed for the other Betzes addition chromosomes (see Table 2). Both arms of 3H are now marked, by *Est-H5* on 3HL and *Tpi-H1* on 3HS (Pietro and Hart 1985). The observation by Hart et al. (1980) that barley esterases could be observed in extracts from seven day old leaves from addition F probably relates to products of a gene homoeologous to the *Est-1* set in wheat, present on the short arms of the group 3 chromosomes (Barber et al. 1968, 1969; Bergman 1972). The *Est-5* genes, which are only active in grains, are located on the long arms of the group 3 chromosomes (Ainsworth et al. 1984).

Addition D carries barley chromosome 1(7H) (Islam et al. 1981) which is homoeologous with group 7 of wheat (Table 2). The esterases encoded by this barley chromosome may be the products of a locus homoeoallelic to the *Est-3* series in wheat whose loci have been identified on the short arms of chromosomes 7A (Ainsworth et al. 1984), 7B and 7D (Jaaska 1980) and which are active in coleoptiles and probably also in immature grains.

3.1.2 'Chinese Spring'-H. chilense *addition lines.* The grain esterase phenotype of *H. chilense* includes four main isozymes, one of which is clearly expressed in the *H. chilense*-CS amphiploid (Fig. 2). This isozyme is expressed by addition D (not shown), suggesting homoeology of this chromosome to group 3.

3.2 Rye (Secale)

3.2.1 'Chinese Spring'-Secale cereale *cv. 'King II' addition lines.* Of the nine major isozymes expressed by *S. cereale* cv. 'King II', which occupy a pH range coincident with the more acidic region of the CS zymogram, all are expressed in the CS-*S. cereale* cv. 'King II' amphiploid (Fig. 3). Addition lines are available for all seven rye chromosomes. All the major rye esterase isozymes are expressed in the 6R addition (Fig. 3) which is indicative of the presence of a homoeologous *Est-5* locus, *Est-R5.*

3.2.2 'Holdfast'-S. cereale *cv. 'King II' addition and substitution lines.* Analysis of the grain esterase phenotypes of the six available 'Holdfast'-*S. cereale* cv. 'King II' additions identified the homoeologous *Est-R5* locus in both the complete 6R and the 6RL telocentric additions (Fig. 4). However, in contrast to the CS-'King II' 6R addition, where all nine King II isozymes are expressed, only two isozymes are expressed in these

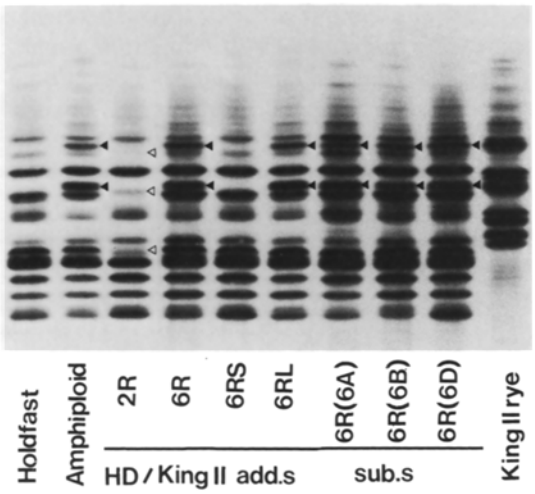

Fig. 4. EST-5 phenotypes of some 'Holdfast'-*S. cereale* cv. 'King II' additions and substitution lines and the 'Holdfast'-*S. cereale* cv. 'King II' amphiploid. *Arrows* indicate the expression of rye isozymes in a wheat background (◄) and the absence of wheat isozymes encoded by *Est-D5* on chromosome 3D (◁)

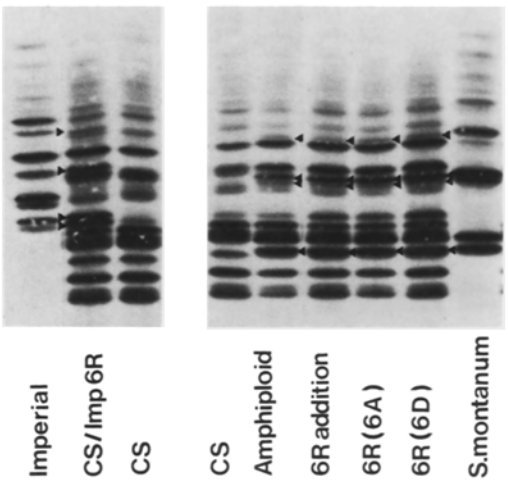

Fig. 5. EST-5 phenotypes of CS-*S. cereale* cv. 'Imperial' and CS/*S. montanum* genotypes. Arrows indicate rye isozymes expressed in a wheat background

additions. This is similarly the case in the phenotype of the 'Holdfast'-*S. cereale* cv. King II amphiploid (Fig. 4).

The most likely explanation for the lack of expression of these rye esterases, including the group of the four most alkaline isozymes, is that the original 'King II' parent used to produce the 'Holdfast'-based amphiploid and the additions was different from that presently available and used to produce the CS-King II lines. It is possible that, as rye is an outbreeder, the stocks of 'King II' may have been segregating for the *Est-R5* locus, the null form being used to produce the 'Holdfast'-'King II' addition set. This is lent plausibility by the fact that the addition series in 'Holdfast' (Riley and Chapman 1958) was produced earlier than the series in CS (Chapman et al. 1974), which might account for the absence of the null esterase allele in the stocks of 'King II' available now.

The presence of such a null allele at the *Est-R5* locus is not surprising. It is likely that the *Est-R5* locus is compound, in common with the *Est-5* loci in wheat, for which both completely null alleles (affecting the products of all the subunits making up the compound locus) and partial null alleles (affecting only some of the products) are relatively common (Ainsworth et al. 1984). In addition, rye varieties have been shown to be very heterogeneous in their esterase isozyme phenotypes (Cooke and Ainsworth, in preparation).

It is unlikely that the products of *Est-R5* are partially suppressed by the wheat genome to give the 'Holdfast'-'King II' phenotype because the CS-'King II' *Est-R5* phenotype is complete.

Analysis of the 'Holdfast'-'King II' additions also reveals the absence of CS isozymes 3, (7, 8) and (13, 14, 15) from the phenotype of the 2R addition (Fig. 4). These isozymes are the total products of the *Est-5* locus on chromosome 3D, *Est-D5*. A null allele, *Est-D5b,* in the phenotype of which the same isozymes are absent, is carried by *Triticum macha* (Ainsworth et al. 1984). It is likely a deletion for the *Est-D5* locus has arisen spontaneously in the 'Holdfast' 2R addition line as its presence has not been shown in the other 'Holdfast'-'King II' additions or other stocks of 'Holdfast'.

Substitution of chromosome 6R of the 'Holdfast'-'King II' additions for each of chromosomes 6A, 6B and 6D of 'Holdfast' again allows expression of the partially null rye *Est-R5* phenotype. No wheat isozymes are removed since the *Est-5* genes are located on the group 3 chromosomes.

3.2.3 'Chinese Spring'-S. cereale *cv. 'Imperial' addition lines.* A homeologous grain esterase locus was identified in the CS-'Imperial' 6R addition (Fig. 5 a). A number, but not all, of the rye isozymes are expressed, perhaps for similar reasons to those put forward for the 'Holdfast'-'King II' genotypes.

The esterase phenotypes of 'Imperial' and 'King II' are very similar, differing only in that 'King II' contains an isozyme in the mid-pI region which is not expressed by 'Imperial' (Fig. 1).

3.2.4 'Chinese Spring'-S. montanum *additions and substitution lines.* Analysis of the CS-*S. montanum* additions identified the homoeologous locus, *Est-R^{m}5,* on chromosome 6R^m in the 6R^m addition and the 6R^m(6A) and 6R^m(6D) substitutions (Fig. 5 b). The rye isozymes, where they do not co-focus with wheat isozymes, are expressed in the wheat background.

A previous study on the grain esterases encoded by rye additions identified esterase loci on chromo-

some 6R of 'King II', 'Imperial' and 'Dakold', although the chromosome arm responsible was not identified (Artemova 1982).

The finding that both the *Est-R5* and *Est-R^{m}5* genes are carried on the long arm of 6R and 6R^m conflicts with the evidence that the wheat and other alien *Est-5* genes are carried on the long arms of group 3 chromosomes. The evidence for homoeology between 6R and wheat group 6 is considerable, and includes the ability of 6R to substitute for the wheat group 6 chromosomes (Riley 1965; Jenkins 1966), the presence of corroded genes, *Co*, on 6BS and 6RS (Miller 1984) and a glutamate oxaloacetate transaminase gene. *Got-R2* (Tang and Hart 1975).

However, evidence for some homoeology between 6R and the wheat group 3 chromosomes extends beyond *Est-5*, and includes the presence of genes for red grain colour, *sphaerococcum* grain shape and phosphogluconate dehydrogenase, *PgdR2* (Rao and Rao 1980) on both 6R and wheat group 3 (Miller 1984). No interchange involving 3R and 6R relative to wheat has been reported; however, the presence of a chromosomal rearrangement seems likely.

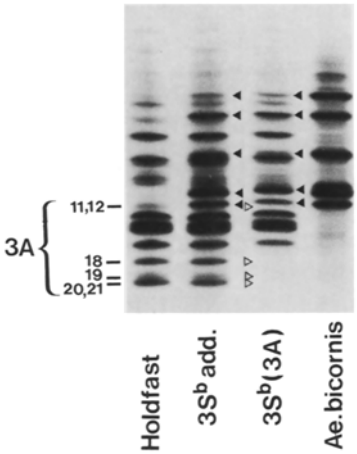

Fig. 6. EST-6 phenotpyes of the Holdfast-*Aegilops bicornis* 3S^b addition and 3S^b (3A) substitution lines. *Arrows* indicate the presence of isozymes from *Ae. bicornis* expressed in wheat (▲) and the absence of *Est-D5* wheat isozymes (△)

Analysis of esterase from leaves and roots identified both chromosomes 3R and 6R as being responsible for the production of rye esterases (Bergman and Maan 1973; Barber et al. 1968). The genes involved are likely to have been homoeologous to the *Est-1* loci located on chromosome arms 3AS, 3BS and 3DS (Barber et al. 1969) and *Est-4* loci located on chromosome arms 6AL, 6BL and 6DL (May et al. 1973; Nakai 1976; Jaaska 1980).

3.3 Aegilops *species*

3.3.1 'Holdfast'-Ae. bicornis *addition and substitution lines.* All the major esterases from *Ae. bicornis* were expressed in both the 3S^b addition and the 3S^b(3A) substitution (Fig. 6). In the substitution, the esterases encoded by the *Est-A5* locus on chromosome 3A were absent. No esterase isozymes from *Ae. bicornis* were apparent in the 7S^b addition.

The identification of the homoeologous *Est-5* locus, *Est-S^{b}5* on chromosome 3S^b of *Ae. bicornis* adds to previous evidence of homoeology with wheat group 3 as does its ability to substitute for wheat group 3 chromosomes and the presence of genes encoding red grains. Chromosome 3S^b also carries the brittle rachis gene.

3.3.2 'Chinese Spring'-Ae. sharonensis *addition lines.* Only one of the seven possible CS-*Ae. sharonensis* additions is available because of preferential transmission of this chromosome, 4S^l (Miller et al. 1982). Addition lines of the remaining *Ae. sharonensis* chromosomes added to a 4S^l(4D) substitution have subsequently been produced (Miller 1983).

Two of the ten or so *Ae. sharonensis* grain esterase isozymes are expressed in the CS-*Ae. sharonensis* amphiploid, those being two of the three most alkaline isozymes in the *Ae. sharonensis* zymogram (Fig. 7 a). The same two isozymes, though not expressed in the 4S^l addition, are expressed in line 18 which includes 4S^l and another *Ae. sharonensis* chromosome (Fig. 7), which may be 3S^l, and also has a brittle rachis.

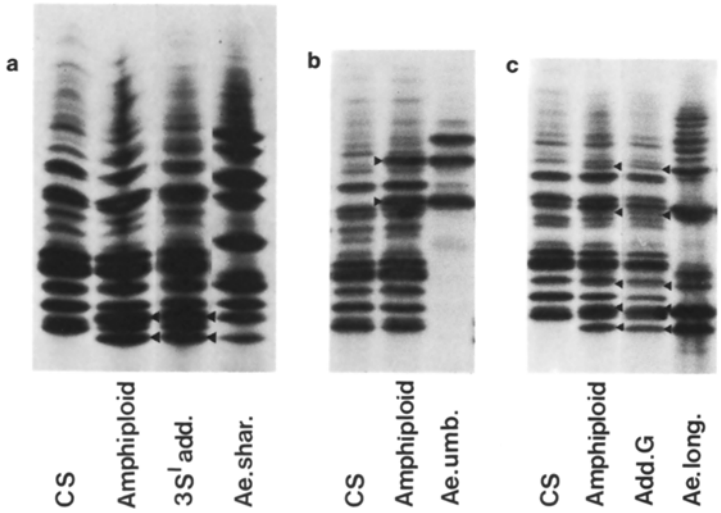

Fig. 7. EST-5 phenotypes of **a:** CS-*Ae. sharonensis*, **b:** CS-*Ae. umbellulata* and **c:** CS-*Ae. longissima* genotypes. *Arrows* indicate the expression of *Aegilops* esterase isozymes in a wheat background

3.3.3 'Chinese Spring'-Ae. longissima *addition lines.* At least five of the *Ae. longissima* esterase isozymes are expressed in both the CS-*Ae. longissima* amphiploid and addition G (Fig. 7c). The presence of the esterase locus *Est-S^{l}5* indicates homoeology with wheat group 3. Previous evidence for homoeology with wheat group 3 is provided by the presence of esterase, triosephosphate isomerase and glutamate oxalocacetate transaminase loci, *Est-S^{l}1, Tpi-S^{l}1* and *Got-S^{l}3* (Hart and Tuleen 1984). Addition G is also characterised by the 'neckbreak' brittle rachis character.

3.3.4 'Chinese Spring'-Ae. umbellulata *addition lines.* The three major esterase isozymes from *Ae. umbellulata* are expressed in the CS-*Ae. umbellulata* amphiploid (Fig. 7b). None of the six CS-*Ae. umbellulata* additions was found to exhibit *Ae. umbellulata* esterase isozymes. It therefore appears likely that the *Ae. umbellulata* chromosome carrying the grain esterase gene is not represented in any of the six additions. Four of the addition chromosomes, 1U, 2U, 5U and 7U, have been identified and assigned homoeology with wheat by substitution (Chapman et al. 1975) and analysis of biochemical markers (Brown et al. 1979; Lawrence and Shepherd 1981; Koebner and Shepherd 1982). The fifth is thought to be homoeologous with group 4. The sixth addition shows some homoeology with group 6 (Shepherd 1973) and the missing chromosome is probably the group 3 homoeologue.

3.4 'Chinese Spring'-Agropyron elongatum *addition lines.* The CS-*Ag. elongatum* amphiploid expresses several grain esterase isozymes which are not present in the CS zymogram (Fig. 8). However, these isozymes do not correspond to the esterases of the accession of *Ag. elongatum* available here (Fig. 8). This accession is not that used by Dvořák and Knott (1974) to produce the initial amphiploid.

None of these additional esterase isozymes were observed in the esterase phenotypes of the CS-*Ag. elongatum* additions I–VII. Hart and Tuleen (1983) characterised these additions with several biochemical markers and showed that chromosomes 1E, 4E, 6E and 7E only are represented, the other three additions involving translocations. The remaining three additions, 2E, 3E and 5E have since been developed (Dvořák 1980; Hart and Tuleen 1983). The 3E addition encodes *Est-1* isozymes (Hart and Tuleen 1983) and therefore possibly also carries the *Est-E5* locus.

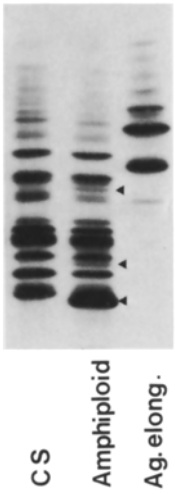

Fig. 8. EST-5 phenotpye of the CS-*Agropyron elongatum* amphiploid. *Arrows* indicate esterases from *Ag. elongatum*

Table 3. The chromosomal locations of homoeologous *Est-5* loci identified in alien species

Species	Locus	Chromosome
Hordeum vulgare cv. 'Betzes'	*Est-H5*	3H
H. chilense	*Est-H^{ch}5*	3H^{ch}
Secale cereale cv. 'King II'	*Est-R5*	6RL
cv. 'Imperial'	*Est-R5*	6R
S. montanum	*Est-R^{m}5*	6R^m
Aegilops bicornis	*Est-S^{b}5*	3S^b
Ae. sharonensis	*Est-S^{l}5*	3S^l
Ae. longissima	*Est-S^{l}5*	3S^l

4 Conclusions

This analysis has identified homoeoallelic *Est-5* loci in a range of barley, rye and *Aegilops* species (Table 3). The chromosome locations of the *Est-5* loci provide additional evidence for homoeology between chromosomes of group 3 of hexaploid wheat and chromosomes 3H (addition F) of *H. vulgare,* and 3H^{ch} (addition D) of *H. chilense,* 6R and 6R^m of rye, and 3S^l and 3S^b of the genus *Aegilops.*

The grain esterase phenotypes of all the alien species studied were markedly different from those of the hexaploid wheat varieties examined. In all cases where a wheat-alien amphiploid was available, some alien esterase isozymes were expressed and were detectable in the wheat genetic background. The *Est-5* system therefore provides a useful marker system for the detection of wheat-alien hybrids.

The *Est-5* phenotypes expressed by the wheat-alien genotypes examined here provide no evidence for the EST-5 isozymes being polymeric. Hybrid bands with pIs differing from the EST-5 isozymes of the wheat and alien parents were not observed in hybrid genotypes. This is in contrast to the EST-1 isozymes which have been shown to be dimeric (Barber et al. 1968, 1969; Jaaska 1980).

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