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Ibf-1 (Iodine binding factor), a highly variable marker system in the *Triticeae*

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Summary. Isoelectric focusing of extracts from the endosperm of mature grains of hexaploid wheat and related species was used to study the genetic control of 'Iodine binding factor' (IBF). Ten IBF bands were present in "Chinese Spring" ("CS") and analysis of the nullisomic-tetrasomic and ditelosomic lines of "CS" showed nine of them to be controlled by genes on the long arms of the homoeologous group 5 chromosomes. Five alleles were detected at *Ibf-A1* locus, four at *Ibf-B1* and four at *Ibf-D1* among a sample of 46 wheat genotypes. Homoeoloci were found on chromosome 5R of *Secale cereale*, 5E of *Agropyron elongatum*, 5U of *Aegilops umbellulata*, $5Ag^{i}$ of *Agropyron intermedium*, $5S^{1}$ and $4S^{1}$ of *Aegilops sharonensis* and 4H of *Hordeum vulgare*.

Key words: Iodine binding factor (*Ibf*) – Isoelectric focusing – *Triticeae*

Introduction

The genes controlling protein production in wheat, *Triticum aestivum* ($2n=6x=42$), have value as markers in both basic and applied genetic investigations and in practical breeding programmes (Hart 1979, 1983; Ainsworth and Gale 1987), and in recent years there has been considerable progress in the identification and chromosomal localization of both new storage protein and isozyme gene systems. Although many marker systems have been studied in the *Triticeae* (Hart and Gale 1986) allelic variation, which is essential for application as genetic markers, has been demonstrated at only a few loci. For more extensive use, many more systems, ideally with considerable intra- and interspecific polymorphism, are needed.

Iodine binding factor (IBF) is a new marker system discovered recently in this laboratory. This paper describes the chromosome location of the controlling genes and some allelic variants found in hexaploid wheat and at homoeoloci in related alien species.

Materials and methods

Genotypes

Aneuploid lines. All the available compensating nullisomic-tetrasomic lines and the three available group 5 ditelosomic lines of "CS" developed by Sears (1954, 1966a, b) were examined.

Genotypes. Forty-seven hexaploid wheat genotypes, selected because of their use in various ongoing cytogenetic investigations in this laboratory, were surveyed for IBF variation (Table 2).

Intervarietal chromosome substitution lines. Several intervarietal chromosome substitution series were employed to identify the chromosomal control of bands not present in "CS": "CS" ("Hope") developed by E. R. Sears (University of Missouri); "CS" ("Cheyenne") by R. Morris (University of Nebraska); and "Capelle-Desprez" ("Mara"), "Hobbit 'S'" (*T. macha*, PBI line 1), "Bersee" ("Koga II"), "CS" ("Cappelle-Desprez"), "CS" ("Synthetic") and "CS" ("Ciano 67") all by C. N. Law and A. J. Worland at the Institute of Plant Science Research, Cambridge.

Alien-wheat chromosome addition and substitution lines. Seven alien-wheat addition series were examined: "CS"/*Hordeum vulgare* cv. "Betzes" (Islam et al. 1975), "CS"/*Secale cereale* cv. "King II" (Miller 1973), "CS"/*S. cereale* cv. "Imperial" (Driscoll and Sears 1971), "CS"/*Agropyron elongatum* (Dvorak and Knott 1974), "CS"/*Aegilops umbellulata* (Kimber 1967), "Vilmorin 27"/*Agropyron intermedium* developed by Y. Cauderon and "CS"/*Aegilops sharonensis* lines (Miller et al. 1982).

Enzyme analysis

Extraction. The endosperm half of a mature dry grain was crushed in a microhammer mill and incubated in 70 µl of 20% sucrose solution containing 0.01 *M* dithiothreitol at room tem-

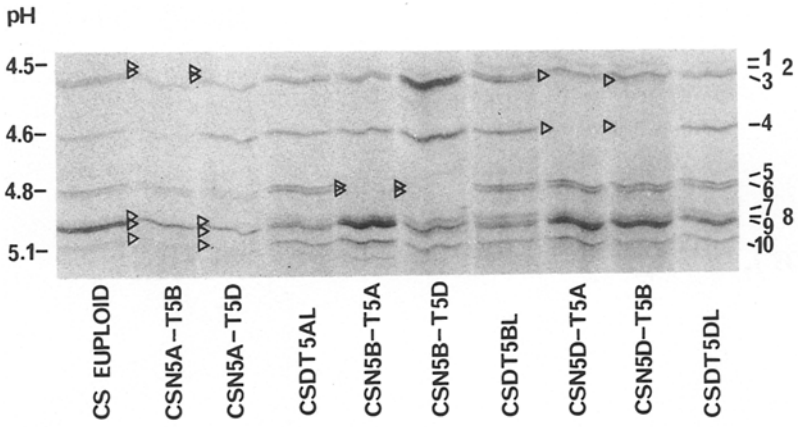

Fig. 1. The IBF phenotypes of the "Chinese Spring" group 5 nullisomic-tetrasomic and ditelosomic lines. Note: *Arrows* indicate the absence of "CS" bands

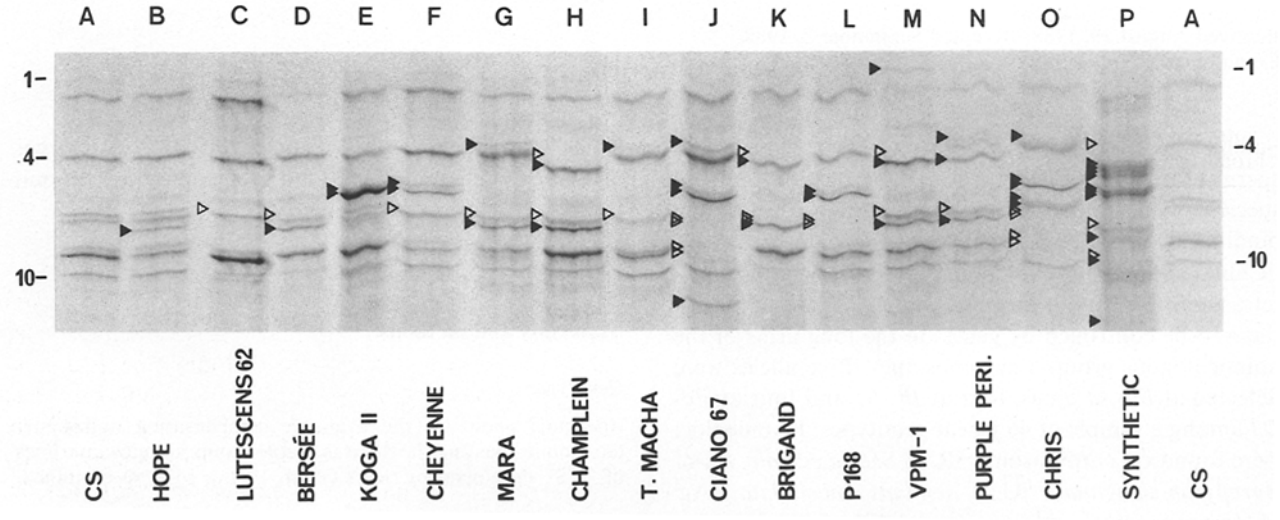

Fig. 2. The 16 IBF phenotypes found among 46 varieties. Note: ▶, Novel bands, ▷ absence of "CS" bands

perature for 1 h. Prior to application to the gel, the extract was centrifuged briefly.

Electrophoresis. Isoelectric focusing was carried out on 0.26 mm thick, 12 cm wide polyacrylamide gels containing 2% (w/v) ampholyte (Pharmalyte 4.2–4.9, Pharmalyte 4.5–5.4 and Isolyte 4–6 in the ratio 1:1:1). For anolyte and catholyte, 0.04 *M* L-glutamic acid and 0.1 *M* NaOH were used, respectively. Constant power of 1 W/cm length was applied up to a maximum voltage of 2,500 V and cooling at 5°C. The gel was prefocused for 25 min and small paper wicks (5 × 8 mm) were soaked with 20 µl of supernatant and placed on the surface of the gel about 0.5 cm from the cathode. The sample wicks were left on the gel for 30 min and then removed. Focusing was continued for another 1.5 h.

Visualisation. IBF bands were visualized by incubation in a solution of 1.5×10^{-3} *M* iodine, 3.5×10^{-3} *M* potassium iodide, 3% acetic acid and 0.2% starch (Merck) in the dark at room temperature. Brown bands appeared after about 1 h; however, incubation was continued overnight to obtain a clear background.

Results

Nullisomic Analysis

Extracts of "CS" showed ten IBF bands with isoelectric points (pI) ranging from pH 4.5–5.1 (Fig. 1). Nullisomic-tetrasomic analysis demonstrated that nine of these bands were controlled by genes on the group 5 chromosomes: Nullisomy for chromosome 5A (CSN5A-T5B and CSN5A-T5D) resulted in the absence of bands 1, 2, 7, 9 and 10; for chromosome 5B (CSN5B-T5A and CSN5B-T5B), the removal of bands 5 and 6; and for chromosome 5D (CSN5D-T5A and CSN5D-T5B), the removal of bands 3 and 4. Band 8 was not removed in the absence of any single chromosome. The three group 5 ditelosomic lines (CSDT5AL, CSDT5BL and CSDT5DL) exhibited an identical zymogram with that of euploid "CS", indicating that the genes encoding these bands must be on the long arms of their respective chromosomes.

Table 1. IBF band phenotype variation in 48 varieties of hexaploid wheat

Phenotype	Bands																										
	1a	1	2	3	4a	4	4b	4c	4d	4e	4f	5c	5a	5b	5d	5e	5	6	6a	6b	7	8	9	9a	10	10a	10b
A		+	+	+		+											+	+			+	+	+		+		
B		+	+	+		+											+	+	+		+	+	+		+		
C		+	+	+		+												+			+	+	+		+		
D		+	+	+		+												+	+		+	+	+		+		
E		+	+	+		+							+	+			+	+			+	+	+		+		
F		+	+	+		+							+	+				+			+	+	+		+		
G		+	+	+	+	+												+	+		+	+	+		+		
H		+	+	+		+												+	+		+	+	+		+		
I		+	+	+	+	+												+			+	+	+		+		
J		+	+	+	+	+							+	+											+	+	
K		+	+	+			+												+		+	+	+		+		
L		+	+	+		+							+	+							+	+	+		+		
M	+	+	+	+			+											+	+		+	+	+		+		
N		+	+	+	+	+	+											+	+		+	+	+		+		
O		+	+	+	+	+							+	+	+	+									+		
P		+	+	+				+	+	+	+	+	+	+				+		+			+	+	+		+
Controlled by chromosome 5:	?	A	A	D	?	D	D	?	B	?	B	B	A	A	?	?	B	B	A	D	A	?	A	A	A	?	B

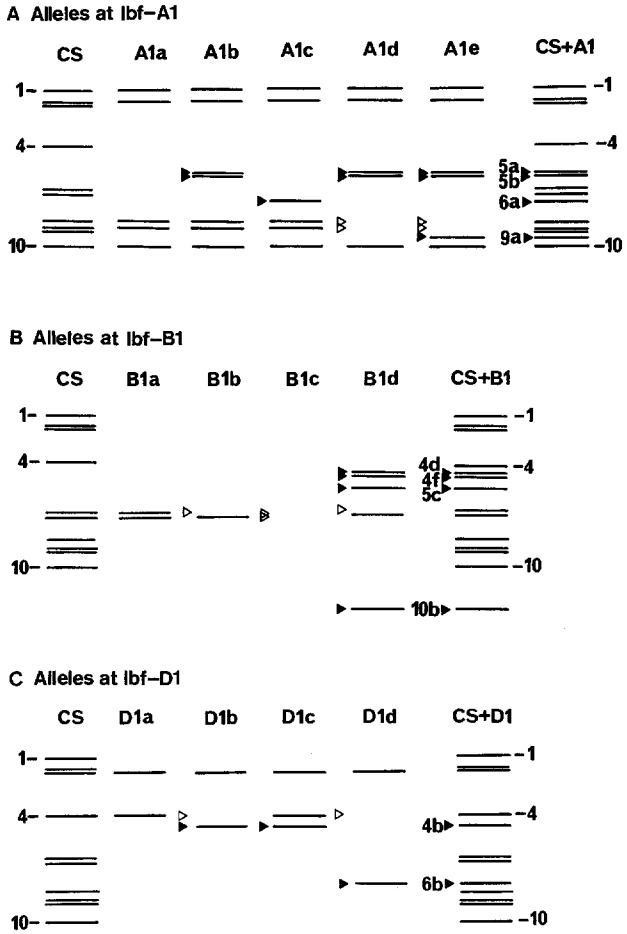

Fig. 3A–C. Alleles at: **A** *Ibf-A1*; **B** *Ibf-B1*; **C** *Ibf-D1*. Note: The columns marked CS+A1 etc. show the positions of all novel bands controlled by each locus relative to those of "CS"

The guidelines for nomenclature of biochemical loci indicates that only a single locus symbol should be assigned to complex band patterns shown to be controlled by a single chromosome, unless segregational evidence indicates otherwise (Hart and Gale 1986). The *Ibf-1* band patterns of 40 F2 progeny of "CS" × "Synthetic" were analysed and no intrachromosomal recombinants were observed for the patterns assigned with the alleles *Ibf-Bla* and *Ibf-Bld*. This limited evidence is consistent with the conclusion that the *Ibf-1* set are carried a single loci in each genome. These were designated *Ibf-A1*, *Ibf-B1* and *Ibf-D1*, respectively.

As no hybrid bands were observed, it is concluded that IBF is monomeric.

Varietal variation

Among the 46 genotypes surveyed for IBF, 16 patterns were detected (types A–P) (Table 1 and Fig. 2). Types A, B, C, D, E, F, H and J were represented by 3, 2, 3, 12, 6, 3, 7 and 2 varieties, respectively, and each of the other phenotypes was represented by only a single genotype. In all, 27 IBF bands were identified, the 10 "CS" bands together with 17 novel bands.

The genetic control of the 17 bands not present in "CS" was investigated by analysis of intervarietal chromosome substitution lines. This allowed the identification of five alleles at *Ibf-A1*, four at *Ibf-B1* and four at *Ibf-D1* locus.

Ibf-A1 variants

The five *Ibf-A1* alleles coded for nine different IBF bands, of which four, 5a, 5b, 6a and 9a, were not found in "CS" (Fig. 3A and Table 2):

Table 2. IBF-1 allelic variation in 48 varieties of hexaploid wheat

Type	Variety	Genotype													
		IBF-A1					IBF-B1				IBF-D1				
		a	b	c	d	e	a	b	c	d	a	b	c	d	
1	CS, C306, SD2	+					+				+				
2	Highbury, Wembley, Lutescens, *T. macha*	+						+			+				
3	Timstein, Sappo, SD1, Koga II, Thatcher, Carmen		+				+				+				
4	Cheyenne, Atlas 66, Favorit		+				+				+				
5	P168		+						+		+				
6	Hope, Tom Thumb			+			+				+				
7	Bersee, Bezostaya I, Huntsman, Sicco, Little Joss, Capitole, Hobbit 'S', Poros, Vilmorin 27, Spica, Sava, Minister Dwarf, Mara			+				+			+				
8	Champlein, Desprez 80, Bounty, Cappelle-Desprez, Rendevous, Maris Ranger, Sportman, VPM-1			+				+				+			
9	Purple Pericarp			+				+					+		
10	Brigand			+					+			+			
11	Chris				+			+			+				
12	Ciano 67, Azteca				+				+		+				
13	Synthetic					+				+					+

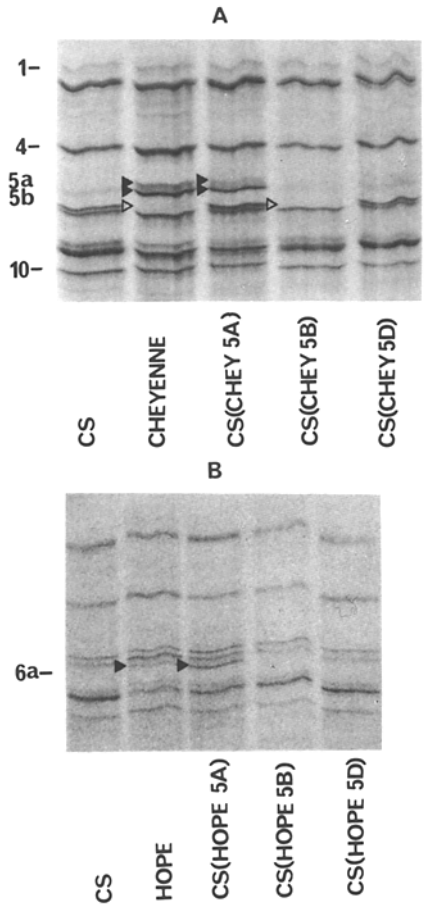

Fig. 4A and B. IBF phenotypes of group 5 inter-varietal chromosome substitution lines: **A** "CS" ("Cheyenne"); **B** "CS" ("Hope")

Ibf-A1a. The allele present in "CS" and in four other varieties.

IBf-A1b. In the presence of this allele, all the "CS" bands and two novel ones, 5a and 5b, are produced. *Ibf-A1b* was carried by 12 varieties and confirmed by analysis of the "CS" ("Cappelle-Desprez"), "Bersee" ("Koga II") and "CS" ("Cheyenne") (Fig. 4A) group 5 chromosome substitutions.

Ibf-A1c. This allele encodes all the "CS" bands and one novel band, 6a. Analysis of "CS" ("Hope") (Fig. 4B) and "Hobbit 'S'" (*T. macha*) group 5 chromosome substitutions indicated that these bands were encoded by a gene on the 5A chromosome. Over half of the 46 genotypes surveyed possessed this allele (Table 2).

Ibf-A1d. This allele, carried by three varieties, produces a phenotype which lacks two of the "CS" bands controlled by chromosome 5A (7 and 9) and has two additional bands, 5a and 5b, which are indicated in the phenotype of *Ibf-A1b*.

Ibf-A1e. This allele is present only in "Synthetic". It resembles *Ibf-A1d*, except for the presence of an extra band 9a (Fig. 5A).

Ibf-B1 variants

The four *Ibf-B1* alleles encoded six different IBF bands, of which four, 4d, 4f, 5c and 10b,were not found in "CS" (Fig. 3B and Table 2).

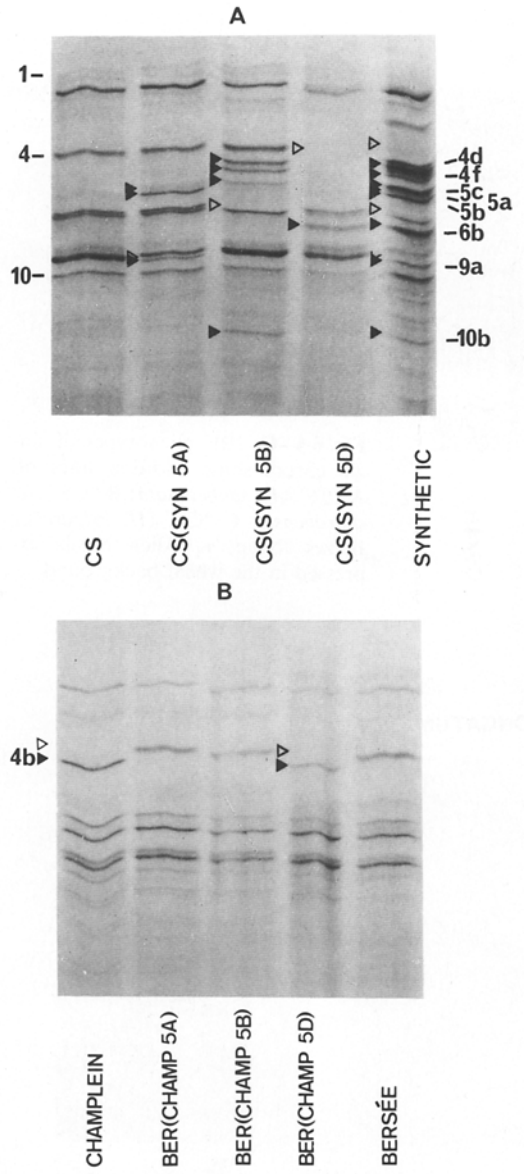

Fig. 5 A and B. IBF phenotypes of group 5 inter-varietal chromosome substitution lines: **A** "CS" ("Synthetic"); **B** "CS" ("Bersee")

Ibf-B1a. The allele present in "CS" and in ten other varieties.

Ibf-B1b. This allele, carried by 30 varieties, differs from *Ibf-B1a* in that band 5 is absent as demonstrated in "CS" ("Cheyenne" 5B) substitution (Fig. 4A).

Ibf-B1c. A null allele, lacking both "CS" *Ibf-B1a* bands (5 and 6) was present in four varieties.

Ibf-B1d. This allele is found only in "Synthetic". It encodes five IBF bands, only one of which, band 6, was found in "CS" together with four novel bands, 4d, 4f, 5c and 10b (Fig. 5A).

Ibf-D1 variants

The four *Ibf-D1* alleles identified on chromosome 5D encoded for four different bands, 3, 4, 4b and 6c (Fig. 3C):

Ibf-D1a. The "CS" allele, also present in 33 other varieties.

Ibf-D1b. In the presence of this allele, band 4 is replaced by a novel band, 4b. This was confirmed by the analysis of the "Bersee" ("Champlein") (Fig. 5B) and "CS" ("Cappelle-Desprez") group 5 substitutions.

Ibf-D1c. This allele encodes bands 3, 4 and 4b. The designation is based on the assumption that the bands in the central region (see "Purple Pericarp" in Fig. 2) are identical with bands 4 and 4b that are shown elsewhere to be controlled by *Ibf-D1*.

Ibf-D1d. This allele is present only in "Synthetic". It encodes for band 3 and a novel band, 6c (Fig. 5A).

Based on this analysis, the 16 IBF patterns can be shown to be the result of 13 defined alleles (Table 2). Seven additional bands could not be allocated to specific chromosomes. Intervarietal chromosomal substitution series were not available for locating the chromosomal control of bands 1a, 5d and 5e (Table 1). However, although "Ciano 67" possesses bands 4a and 10a (absent in "CS"), no "CS" ("Ciano 67") substitution line expresses these bands. Similarly, bands 4c and 4e, present in "Synthetic" but not in "CS", were not present in any "CS" ("Synthetic") substitution lines.

Chromosomal location of Ibf-1 genes in species related to wheat

The amphiploids of "CS"/*Ae. umbellulata*, "CS"/*Secale cereale* cv. "Imperial", "CS"/*S. cereale* cv. "King II", "CS"/*Ag. elongatum* and TAF ("Vilmorin"/*Ag. intermedium*) all express IBF bands not present in their wheat parents, and these bands are all also expressed in the addition lines carrying the respective group 5 chromosomes (Figs. 6 and 7). Thus the homoeoloci *Ibf-U1*, *Ibf-R1*, *Ibf-E1* and *Ibf-Ag^{i}1* are all located on group 5 chromosomes, as in wheat. In the case of *Ibf-R1* and *Ibf-E1*, telocentric additions of the alien chromosomes allow the arm location of these genes to be determined. *Ibf-R1* is not expressed in "CS"/*S. cereale* 5RS addition (Fig. 7B), while *Ibf-E1* is expressed in "CS"/*Ag. elongatum* 5EL but not in "CS"/*Ag. elongatum* 5ES (Fig. 7C). Thus, these genes are present on the long arms of their respective chromosomes, as in wheat.

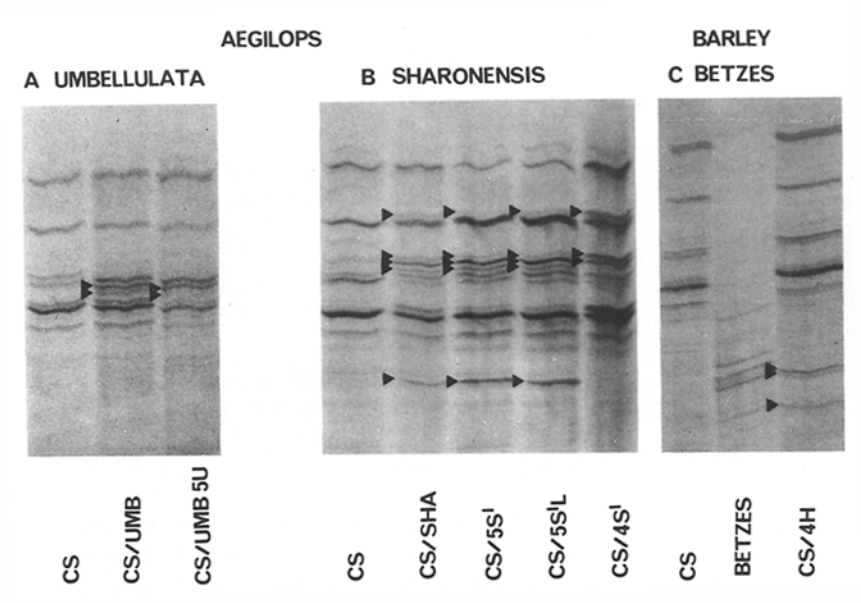

Fig. 6A–C. IBF phenotypes of single chromosome addition lines of: **A** "CS"/*Ae. umbellulata*; **B** "CS"/*Ae. sharonensis*; **C** "CS" (*H. vulgare* cv Betzes. Note: ▸, Alien bands expressed in the wheat background

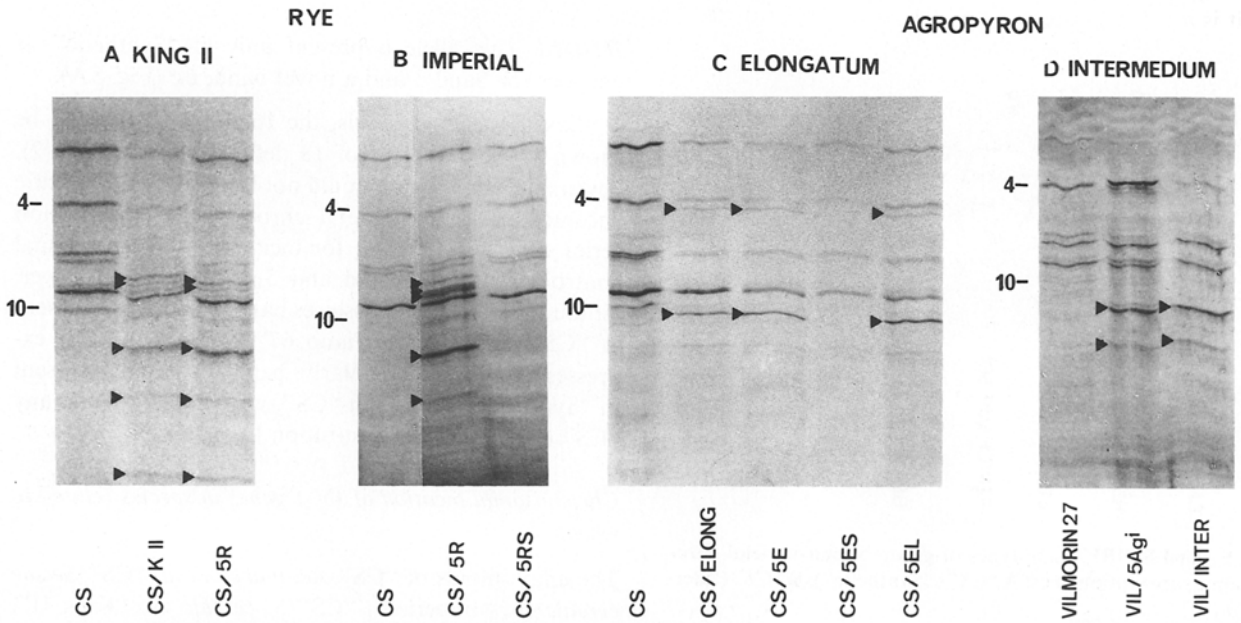

Fig. 7A–C. IBF phenotypes of single chromosome addition lines of: **A** "CS"/*S. secale* cv King II; **B** "CS"/*S. secale* cv Imperial; and **C** "Vilmorin 27"/*Ag. intermedium*

Occasionally when alien chromosomes are added to a wheat background, the staining intensities of some wheat proteins or isozymes are reduced dramatically, presumably because of altered competition for available substrate. For IBF, this occurred in the "CS"/*Ae. umbellulata* (band 5, Fig. 6A) and "CS"/*S. cereale* cv. "King II" (bands 5 and 6, Fig. 7A) additions.

The "CS"/*Ae. sharonensis* amphiploid expresses five IBF bands not present in "CS". The "CS"/*Ae. sharonensis* 4S^1 expresses three of these bands with more acidic pIs, while the "CS"/*Ae. sharonensis* 5S^1 and 5S^{1}L expresses all five bands. As all "CS"/*Ae. sharonensis* addition lines carry the 4S^1 "cuckoo" chromosome (Finch et al. 1984), it is concluded that the two more basic *Ae. sharonensis* bands are encoded by gene(s) on chromosome 5S^{1}L (Fig. 6B). This gene is probably an *Ibf-1* homoeolocus, and can be designated *Ibf-S^{1}1*. The group 4 gene is given the temporary designation *IbfS^{1}1*.

Hordeum vulgare cv. "Betzes" expresses seven IBF bands. Analysis of the six available additions of "Betzes" chromosomes to "CS" shows that addition 4H expresses the three most alkaline barley bands (Fig. 6C), while the other addition lines, including 5H, produced the same zymogram as that of "CS". This locus is given the temporary designation, *IbfH1*.

Discussion

The *Ibf-1* system provides valuable marker genes for the group 5 chromosomes of the *Triticeae*. Based on the evidence derived from the genotypes sampled here, *Ibf-1* is more polymorphic than any isozyme system thus far reported in wheat. Indeed the level of variability is similar to that of the storage protein locus, *Glu-1* (Payne and Lawrence 1983) and also has a simple and rapid visualisation procedure.

The precise identity of IBF, beyond the suggestion that it is a protein which binds iodine, remains unclear. When gels are stained with 'Coomassie blue' the IBF bands appear among other water-soluble grain proteins. These bands are, however, preferentially picked out when the iodine-starch staining method is employed. Thus IBF may only be a temporary designation, to be replaced by a more informative name and symbol at some later date.

The identity of IBF with lypoxygenase (LPX) must be considered, as there are several coincidences between these systems. Apart from the same location on groups 4 and 5 in the *Triticeae* (Hart and Langston 1977), LPX is also visualized with an iodine-based stain. Unfortunately it has not yet been possible to stain LPX in our IEF gels. On starch gels, however, IBF is not visualized when linoleic acid is omitted from the LPX staining procedure (G. E. Hart, personal communication).

The value of *Ibf-1* in genetic studies and breeding will not be known until the genes have been mapped with respect to important characters. An easily analysed marker linked to *Kr1* and *Kr2*, the genes on chromosomes 5AL and 5BL determining crossabilities to rye and other alien species (Sitch et al. 1985), would be extremely valuable in cytogenetic research. Similarly, a marker linked to *Vrn1*, *Vrn2* and *Vrn3*, the series of major genes controlling vernalization response on chromosomes 5AL, 5BL and 5DL (Law et al. 1976), would be a value in the production of genetic stocks in which the genes are to be assembled, either in isogenic lines or in combination with other adaptive genes. Such a marker would also find application in screening breeder's progenies from spring × winter wheat hybrids. The value of *Ibf-B1* as a marker for the presence or absence of 5BL in studies were the *Ph1* locus is removed by nullisomy to induce chromosome pairing between wheat and alien genomes has already been demonstrated in this laboratory.

The multi-banded monomeric band pattern of IBF may indicate control by small multigene families, or the result of post-translational or post-transcriptional modification. The multiple isozymes controlled by *α-Amy-1* and *α-Amy-2* (Gale et al. 1983) are associated with approximately equivalent numbers of members of small multi-gene families (Lazarus et al. 1985). Conversely, however, the multiple isozyme patterns of *β-Amy-1* (Ainsworth et al. 1983) are produced by very few, and probably only one gene copy at each locus (Sharp et al. 1988) followed by post-translational modification.

A possible indication that *Ibf-1* may be in the former category can be seen from a consideration of the IBF phenotype of Sears "Synthetic" (McFadden and Sears 1964; Sears 1976) and diploid and tetraploid genotypes similar to those used to construct the synthetic hexaploid. The 22 bands which comprise the "Synthetic" zymogram closely correspond to the sum of the bands in the parents (not shown). One reason for the discrepancy in band numbers in modern hexaploids and the reconstructed primitive form could be that some of the *Ibf-1* gene copies may have been silenced. The *Glu-A1-2* locus on chromosome 1A, which controls production of the y-type HMW glutenin subunits (Forde et al. 1985), is an example of such a case. Although the gene operates in diploid and tetraploid wheats (Waines and Payne 1987; Levy et al. 1988), it has not yet been found unsilenced in hexaploid varieties (Payne et al. 1981). The resolution of this problem will ultimately require precise molecular analysis.

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