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The chromosomal locations of leaf peroxidase genes in hexaploid wheat, rye and barley

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Summary. Eight leaf peroxidase isozymes were distinguished by IEF in 'Chinese Spring'. Two genes which control the production of three of these isozymes were located on chromosome arms 1BS and 1DS by nullisomic analysis. These loci probably form part of a homoeoallelic series and have been designated *Per-B1* and *Per-D1* respectively. Analysis of chromosome 1B short arm terminal deletion stocks indicated that the *Per-B1* locus is located between the nucleolar organiser region and another isozyme marker, *Hk-B1*. Two variant leaf peroxidase phenotypes were distinguished in a small sample of hexaploid wheat varieties. Analysis of wheat-alien addition and substitution lines identified homoeologous loci in rye (*Per-R1*) and barley (*Per-H1*).

Key words: Hexaploid wheat – Rye – Barley – Leaf peroxidase – Isozymes – Isoelectric focusing

1 Introduction

The physiological role of plant peroxidases (E.C. 1.11.1.7.), which use peroxide to oxidize a variety of hydrogen donors, is poorly understood. In wheat, peroxidase levels have been associated with genetic dwarfing (Cunningham et al. 1975; Singh et al. 1979), grain weight (Singhal et al. 1979), the colour quality of pasta products (Kobrehel et al. 1972) and disease resistance (Johnson and Cunningham 1972).

In wheat grains, structural genes controlling endosperm peroxidases have been identified on chromosome arms 4BL, 7AS and 7DS by PAGE analysis of aneuploid genotypes of 'Chinese Spring', (Kobrehel and Feillet 1975; Benito and Perez de la Vega 1979) and those controlling the embryo plus scutellum isozymes have been identified on chromosome arms 3BL, 3DS and 3DL (Benito and Perez de la Vega 1979). Chromosome arms 1BS and 1DS were implicated in the production of leaf peroxidases by May et al. (1973).

Peroxidase isozymes are frequently organ or tissue specific (Asins et al. 1982). The aim of the present study is to investigate the genetic control of leaf peroxidases in hexaploid wheat (*Triticum aestivum*).

2 Material and methods

2.1 Aneuploid lines

The nullisomic-tetrasomic and ditelosomic lines of 'Chinese Spring' (CS) developed by E.R. Sears were employed to establish the chromosomal control of leaf peroxidase isozymes. Where critical chromosomes were identified, the relevant ditelosomic lines were employed (CSDT1AS, CSDT1AL, CSDT1BS, CSDT1BL, CSDT1DL).

2.2 Species and varieties

Diploids (2n = 2x = 14): *Triticum monococcum, Aegilops squarrosa.* Tetraploid (2n = 4x = 28): *T. durum* cv. 'Cando'. Hexaploids (2n = 6x = 42): *T. aestivum* cvs. 'Atlas', 'Bersée', 'Bezostaya 1', 'Bounty', 'Cappelle-Desprez', 'Cheyenne', 'Champlein', 'Chinese Spring', 'Ciano 67', 'Hybride du Joncquois', 'Hahn 'S'', 'Hobbit', 'Hobbit 'S'', 'Holdfast', 'Hope', 'Jitpur', 'Koga II', 'Lutescens 62', 'Mara', 'Minister Dwarf', 'Poros', 'Red Chief', 'Sicco', 'Synthetic' (amphidiploid of *T. dicoccum* × *Ae. squarrosa;* McFadden and Sears 1946), 'Timstein', 'Veery 'S'', 'Vilmorin 27', 'VPM', 1BS satellite deletion line (Payne et al. 1984), Bersée/Sappo (B/S) 1BS deletion line (Jackson, unpublished), *T. macha, T. spelta.*

2.3 Inter-varietal chromosome substitution lines

The group 1 substitutions of CS ('Synthetic'), developed by C. N. Law and A. J. Worland, were employed to identify the chromosomal control of novel isozymes present in 'Synthetic'.

2.4 Alien chromosome addition and substitution lines

Three alien chromosome addition series were examined for leaf peroxidases: 'Chinese Spring'/*S. cereale* cv. 'King II' (Chapman et al. 1974), CS/*Hordeum vulgare* cv. 'Betzes' (Islam et al. 1978), CS/*H. chilense* (Miller et al. 1982). The three group 7 CS/H^{ch}7 substitutions (Miller, unpublished) were also examined.

2.5 Enzyme extraction

Flag leaf tissue (120 mg) was ground in a chilled mortar and pestle with 350 µl of 0.05 M Na_2HPO_4 buffer (pH7.0) at 4°C containing 0.01 M dithiothreitol together with 14 mg of insoluble polyvinyl-pyrollidone. The macerate was centrifuged at 20,000×g for 20 min and the supernatant used immediately for isoelectric focusing.

2.6 Isoelectric focusing

Peroxidase isozymes were separated by flat-bed isoelectric focusing (IEF) using Ampholine PAG plates, pH 3.5–9.5 (LKB). Gels were prefocused for 30 min before applying 20 µl sample extracts absorbed in 5×10 mm filter-paper wicks and placed 20 mm from the cathode, directly onto the gel surface. The sample wicks were removed after 30 min focusing at a constant power of 1.2 W cm^{-1} width of gel. IEF was terminated after a further 2 h. pH gradients were obtained, prior to staining, by taking pH readings at 5 mm intervals, across the gel surface.

Gels were stained for peroxidase activity according to Kobrehel and Feillet (1975).

3 Results

3.1 Deletion mapping

3.1.1 Nullisomic-tetrasomic analysis. In extracts obtained from flag leaves of 'Chinese Spring', eight peroxidase isozymes with isoelectric points (pIs) between pH 5.0 and pH 8.0 can be consistently distinguished (Fig. 1). Several isozymes, with pIs greater than pH 8.5, which appear similar to grain peroxidases, are poorly resolved and are not considered below.

Analysis of CS nullisomic-tetrasomic lines for chromosome groups 1 to 7 implicated chromosomes 1B and 1D in the control of the production of leaf peroxidases (Fig. 1). Nullisomy for 1B results in the absence of isozyme band 5. Nullisomy for 1D results in the absence of bands 6 and 7. The remaining five isozymes are not removed by nullisomy for any chromosome. Bands 1, 2, 3 and 8 were inconsistently expressed and are weak or absent in extracts from young flag-leaves.

3.1.2 Ditelosomic analysis. Analysis of the available CS group 1 ditelosomics further located the control of band 5 to the short arm of chromosome 1B and bands 6 and 7 to the short arm of 1D: the zymogram of CSDT1BS was identical to the euploid zymogram,

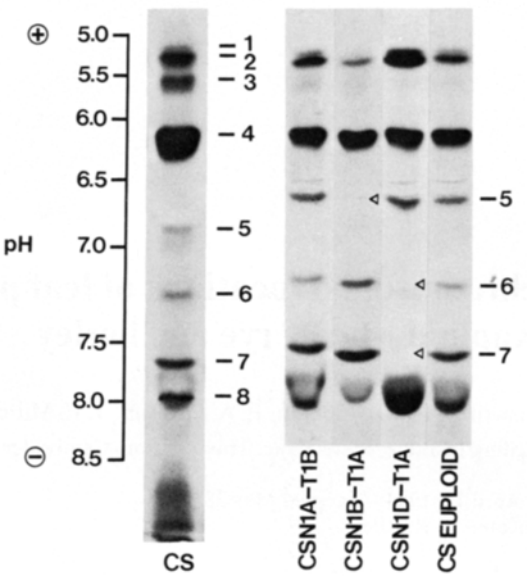

Fig. 1. The leaf peroxidase isozymes of 'Chinese Spring' wheat and three chromosome group 1 nullisomic-tetrasomic (CSN-T) genotypes in 'Chinese Spring'. *Arrows* indicate the absence of *CS* bands

while those of CSDT1BL and CSDT1DL lacked the respective 1B and 1D isozymes.

3.1.3 Chromosome 1B deletion analysis. Two genotypes which carry terminal deletions of parts of the short arm of chromosome 1B were examined. The '1BS satellite deletion' line is a spontaneous deletion which was identified in one grain amongst 360 offspring from a tri-parental cross (Payne et al. 1984). The deletion involves that part of the short arm distal to the nucleolar organiser, the break point being within the organiser. Of the markers on 1BS, the ω-gliadin locus, *Gli-B1*, (Payne et al. 1984) and the glucose phosphate isomerase locus, *Gpi-B1* (A. J. S. Chojecki, personal communication), are absent whilst the hexokinase locus, *Hk-B1* is present (Ainsworth 1983). This genotype expressed a normal peroxidase phenotype including band 5, indicating that *Per-B1* is located proximally to the nucleolar organiser (*Nor1*).

The second deletion examined, the B/S deletion which arose spontaneously in the progeny of a cross between 'Bersée' and 'Sappo', involves a larger part of the short arm of chromosome 1B than does the 1BS satellite deletion. Karyotype analysis shows about two thirds of the arm to be absent; the deleted segment included *Gli-B1*, *Gpi-B1* and *Nor1* but not *Hk-B1* which was expressed. The leaf peroxidase zymogram of this deletion line lacked band 5 encoded by the locus *Per-B1*. This locus must therefore be proximal to *Nor1*, but distal to *Hk-B1*, and be physically located in the middle third of the arm, i.e. between *Nor1* (two thirds

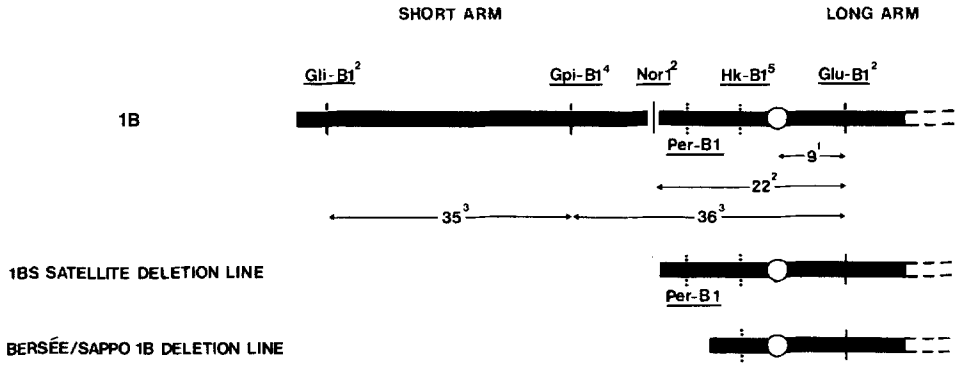

Fig. 2. The location of *Per-B1* on chromosome 1B by deletion mapping. (Map distances expressed as % recombination). [1]Payne et al. (1982). [2]Payne et al. (1984). [3]Map distances between *Gli-D1, Gpi-D1* and *Glu-D1* on chromosome 1D (Chojecki et al. 1983). [4]Chojecki, personal communication. [5]Ainsworth (1983)

of the short arm from the centromere; Riley et al. 1958) and the B/S deletion breakpoint (one third of the short arm from the centromere) (Fig. 2).

3.2 Locus and allele nomenclature

3.2.1 Loci. Enzyme loci are allocated locus symbols according to the "Recommended Rules for Gene Symbolisation in Wheat" (see McIntosh 1973). Non-allelic loci with phenotypically similar effects are designated by a sequential series where the gene symbol is immediately followed by an Arabic numeral e.g. *Per1* and *Per2* would specify two non-allelic peroxidase loci. However, where two or more loci are considered to be homoeoallelic, the set of loci is designated by the basic gene symbol followed by a hyphen and then an Arabic numeral, e.g. the first set of peroxidase loci to be described would be *Per-1*. The individual homoeoallelic loci making up the set are referred to by the homoeologous set symbol with the number preceded by the genome letter, e.g., the locus in the D genome in the *Per-1* set would be referred to as *Per-D1*.

Loci identified on alien chromosomes which are considered to be homoeoallelic with genes in wheat are referred to by the wheat homoeologous set symbol with the set number preceded by the symbol for the alien genome. For example, a locus on chromosome 1 of barley (*Hordeum vulgare*), homoeoallelic to the *Per-1* loci in wheat would be referred to by *Per-H^{v}1*.

3.2.2 Alleles. Alleles are named by suffixing the locus symbol with lower-case Roman letters. 'Chinese Spring' is always assigned the *'a'* allele and variants are identified by *'b'*, *'c'* etc., e.g. the allele at the *Per-D1* locus carried by CS is *Per-D1a*.

3.2.3 Peroxidase loci. Previous work has implicated the involvement of the chromosomes of homoeologous chromosome groups, 3, 4 and 7 in the control of the production of grain peroxidases in wheat and group 1 in the control of leaf peroxidases. These reports are summarised in Table 1.

It is proposed to assign the loci on 1BS and 1DS described here, which are presumed to be homoeoallelic, the symbols of *Per-B1* and *Per-D1* respectively.

Table 1. Peroxidase loci in wheat

Chromosome arm(s)	Tissue	Set and homoeoallelic loci	Non-allelic loci[a]	Reference
1BS, 1DS	Leaves	*Per-1: Per-B1, Per-D1*	–	This paper; May et al. (1973)
7AS, 7DS	Endosperm		–	Kobrehel and Feillet (1975);
			CPX-A, CPX-D (*Per3, Per1*)	Benito et al. (1980)
4BL	Endosperm		–	Kobrehel and Feillet (1975);
			CPX-B (*Per2*)	Benito et al. (1980)
3BL, 3DL, 3DS	Embryo, Scutellum		$CPX-A_1$, $CPX-D_2$ $CPX-A_2$ CPX-E, CPX-F	Benito and Perez de la Vega (1979)

[a] Gene symbols assigned in original references and rationalised by Hart (1982) in parentheses

3.3 *Allelic variation*

Two variant leaf peroxidase phenotypes were identified amongst the 34 hexaploid genotypes examined (Fig. 3). A novel band (8a) was present in the zymogram of 'Synthetic', on the cathodal side of band 8 (Fig. 3). By employing the group 1 CS ('Synthetic') inter-varietal chromosome substitution lines, band 8a was shown to be controlled by chromosome 1D of 'Synthetic'. The variant allele at the *Per-D1* locus in 'Synthetic' has been designated *Per-D1b*. Two additional bands (1a, 1b) were present in the zymogram of 'Ciano 67', on the anodal side of band 1. The chromosome responsible for the production of this band has not been established.

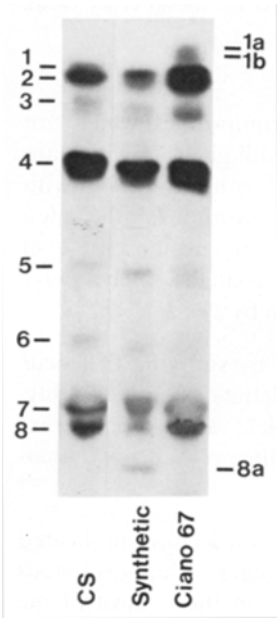

Fig. 3. Leaf peroxidase zymograms of 'Chinese Spring' and two hexaploid genotypes exhibiting variation in isozyme pattern

3.4 *Alien homoeoalleles*

3.4.1 Rye. The leaf peroxidase zymogram of *Secale cereale* cv. 'King II' differed from the CS type by the presence of a novel band located between the positions of CS bands 7 and 8 and by the absence of CS bands (2, 5, 7 and 8). By analysis of the CS/'KingII' addition series, a homoeologous locus, *Per-R1,* was identified on the rye 'King II' 1R chromosome. This finding lends support to previous evidence for the group 1 homoeology which was established on the basis of the ability to substitute for the group 1 homoeologues of wheat (Shepherd 1973), the presence of seed protein loci (Lawrence and Shepherd 1981) and a glucose phosphate isomerase locus, *Gpi-R1* (Chojecki and Gale 1982).

The varieties 'Veery 'S'' and 'Hahn 'S'' each carry a 1B/1R translocation. Band 5, encoded by *Per-B1,* is absent from the zymograms of 'Veery 'S'' and 'Hahn 'S'' and the novel band from rye is present in both. This clearly shows that the 1B/1R translocation chromosome includes the segment of chromosome 1R which carries the *Per-R1* locus and excludes the segment of 1B carrying the *Per-B1* locus, thus reinforcing the assumption of homoeology between the two loci. The positions of the breakpoints themselves are not known but N-banding (Jewell 1979, 1981) and C-banding (Seal and Bennett 1982) studies of 'Aurora', a variety carrying the same translocation, have indicated that a whole arm exchange is involved.

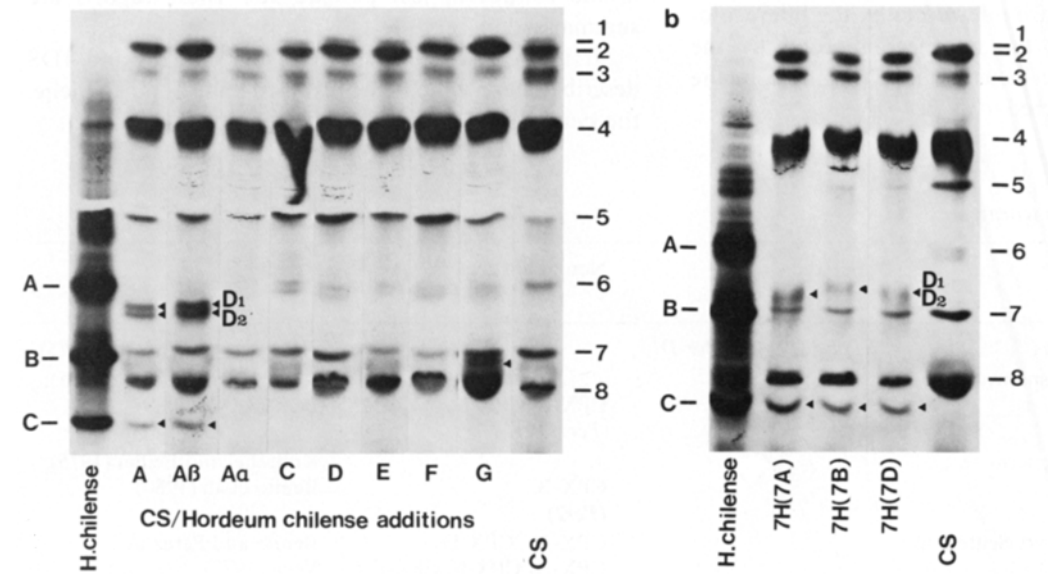

Fig. 4. Leaf peroxidase zymograms of the available 'Chinese Spring'/*Hordeum chilense* additions (**a**) and group 7 substitutions (**b**). *Arrows* indicate the presence of *H. chilense* bands *B* and *C*, and bands D_1 and D_2

3.4.2 Barley. The zymogram of *Hordeum chilense* differs markedly from that of CS, and includes three strong novel bands (A, B and C) in the alkaline region (Fig. 4). The locus *Per-H^{ch}1,* encoding *H. chilense* band B, was identified on the CS/*H. chilense* addition G chromosome, which has previously been shown to display homoeology with chromosomes of wheat group 1 on the basis of the presence of a high molecular weight glutenin locus (Miller et al. 1982) and a glucose phosphate isomerase locus, *Gpi-H^{ch}1* (Chojecki and Gale 1982).

A second peroxidase locus is displayed by the CS/*H. chilense* addition chromosome A and by one of the two telocentric additions for this chromosome (Addition A_β, Fig. 4a). The *H. chilense* band C is evident in these genotypes together with two additional bands (D_1 and D_2) which are not present in either CS or *H. chilense* (Fig. 4). The *H. chilense* chromosome in addition A is homoeologous to wheat group 7 on the basis of plant morphology and the ability to substitute for the wheat group 7 chromosomes. Bands C, D_1 and D_2 are also expressed in the substitutions of chromosome $7H^{ch}$ for wheat chromosomes 7A, 7B and 7D (Fig. 4b). This second leaf peroxidase locus, encoding bands C, D_1 and D_2 may well be homoeoallelic to the *Per1* and *Per3* loci on chromosomes 7A and 7D which encode grain peroxidases (Kobrehel and Feillet 1975). Grain peroxidase isozymes have alkaline pIs (greater than 8.5) and it is likely that band C of *H. chilense* (pI 8.3) is a grain isozyme.

H. vulgare cv. 'Betzes' (not shown) encodes a similar peroxidase zymogram to *H. chilense.* Two bands, which appear identical to bands D_1 and D_2, are also present in the group 7 addition (Addition D) of CS/'Betzes' but are not evident in 'Betzes' itself.

4 Discussion

The two wheat leaf peroxidase loci described here, *Per-B1* and *Per-D1,* on the short arms of chromosomes 1B and 1D, comprise a probably homoeologous and further set of peroxidase loci to the loci controlling grain peroxidases. A previous study by May et al. (1973) also implicated chromosome arms 1BS and 1DS in the control of the production of leaf peroxidases and it is likely that the same three isozymes were identified although pIs were not given.

The leaf peroxidase system in wheat and its related species appears to show a high degree of conservation. Of the eight bands present in the CS zymogram, five are not removed by nullisomy for any chromosome and it is likely that these consist of isozymes with similar pIs, encoded by more than one structural gene on different homoeologues. Indeed, the zymograms of *Triticum monococcum* (AA), *T. durum* (AABB) and *Aegilops squarrosa* (DD) all include band 4, emphasising the degree of conservation of the loci between genomes. In addition, there is little allelic variation evident amongst the sample of hexaploid genotypes examined. It is possible, therefore, that there is a locus on chromosome 1A but that its products co-focus with products of *Per-B1* or *Per-D1.*

The expression of bands D_1 and D_2, encoded by the peroxidase locus on the group 7 homoeologues of *H. chilense* and *H. vulgare* cv. 'Betzes' and which are not apparent in the zymograms of barley or wheat, only being expressed by chromosome 7H when in a wheat background genotype, would appear to indicate that products of this locus undergo modification by the wheat genome such that an alteration in isoelectric point occurs. Plant peroxidases are generally monomeric (Garcia et al. 1982) although exceptions exist, such as the dimeric rice peroxidases (Endo 1981). In view of the lack of evidence for peroxidase dimers in wheat, dimerisation would seem to be a less likely explanation for the presence of bands D_1 and D_2 than post-translational modification. Post-translational modification of peroxidase isozymes has been implicated in *Lycopersicon* (Rick et al. 1979) and *Petunia* (Berg and Wijsman 1981).

Analysis of the presence of leaf peroxidase and hexokinase loci in 1BS deletion stocks enabled *Per-B1* to be located genetically on 1BS. Genotypes carrying chromosomal rearrangements such as deletions and translocations provide a convenient method of ordering enzyme marker genes on a chromosome and may enable genetic chromosome maps to be equated with physical maps. Conversely, marker genes provide a means of determining the positions of the breakpoints in structural chromosome rearrangements. For example, Payne et al. (1984) who analysed a genotype carrying a deletion for the short-arm satellite of chromosome 1B which includes a locus encoding gliadins, *Gli-B1* and a glucose phosphate isomerase locus, *Gpi-B1,* showed that although the satellite region only comprises about one third of the arm (Riley et al. 1958), the ribosomal RNA genes, *Nor1,* map only 13cM from the centromere, indicating a low level of recombination in the segment proximal to *Nor1.*

The leaf peroxidase system is not particularly suitable as a biochemical marker system for wheat and related species because of the degree of isozyme conservation between genomes and varieties and the possible overlap with grain endosperm isozymes encoded by different homoeoallelic series of loci. However, the leaf peroxidase loci add another biochemical marker to the three other series of biochemical marker loci which have been identified on the short arms of the group 1 chromosomes of wheat (*Gpi-1, Hk-1* and *Gli-1*), and the

four which have been identified on the long arms (lipopurothionins, *Pur-1,* Fernandez de Caleya et al. 1976; malate dehydrogenase, *Mdh-1,* Benito and Salinas 1983; glutenin subunits, *Glu-1,* Payne et al. 1982 and lectins, Stinissen et al. 1983).

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