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The inheritance of seed peroxidases of wheat and rye: further data

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Summary. Further data on the inheritance of seed peroxidases of hexaploid wheat (*Triticum aestivum* L.) and rye (*Secale cereale* L.) have been obtained from the genetic analysis of several progenies of both species. Additional data on the inheritance and the chromosomal location and linkage have been obtained for peroxidases of wheat embryo and rye endosperm. The general presence of null alleles in peroxidase loci has been confirmed in both species. In addition to simple monogenic inheritance, epistatic segregations have been observed in both species. These epistatic segregations again suggest the presence of "regulatory" genes controlling the expression of individual peroxidases in both species and also the existence of several duplicate homoeologous genes in wheat. Known linkage relationships have been confirmed and new ones are indicated. Loci for embryo wheat peroxidases seem to be in chromosomes of the homoeology group 3. The rye endosperm ones should be in chromosome 7R, although it is hypothesized that a duplication of gene EPer1 is located in chromosomes 4R and 7R.

Key words: Triticum – Secale – Wheat – Rye – Peroxidases – Inheritance

Introduction

The peroxidase isozyme system has been widely used in genetic studies of higher plants because it supplies a high number of genetic markers, owing to the generally high number of isozymes of this system, its great variability and the good results obtained with relatively easy techniques. Peroxidases are generally characterized by a monomeric behaviour and the presence of null alleles. They have been described as glycoproteins and hemoproteins (Gaspar et al. 1982). Peroxidase isozymes were firstly reported to be under monogenic control in seed of hexaploid wheat (Benito et al. 1980) and rye (García et al. 1982), except rye endosperm isozyme 4 which was also under the control of a "regulatory" gene. Epistatic or "regulatory" genes have been repeatedly reported in several plant species, either affecting genetic segregations or the timing or level of expression of peroxidase isozymes (Asíns and Pérez de la Vega 1985 in *Triticum turgidum;* Berg et al. 1983 in *Petunia* ssp.; Endo 1981 and Pai et al. 1973 in *Oryza sativa* and *O. perennis;* García et al. 1982 in *Secale cereale;* Rick et al. 1979 in *Lycopersicon pimpinellifolium;* Sandmeier et al. 1981 in *Penisetum americanum*). Benito and Pérez de la Vega (1979) located the genes related to embryo-plus-scutellum peroxidases of hexaploid wheat *T. aestivum* in chromosomes of homoeology group 2. García et al. (1982) showed that most of the loci related to endosperm peroxidases of rye are in the same linkage group. Later on Salinas and Benito (1984) located these loci in chromosome 7R, and the locus related with peroxidase 1 (*EPer1*) in chromosome 4R.

The purpose of this paper is to contribute further data on the genetic control of seed peroxidases of hexaploid wheat and rye and simultaneously to locate and to map new markers in the wheat and rye chromosomes by means of linkage studies.

Materials and methods

The wheat materials used were seven cultivars of hexaploid wheat (*Triticum aestivum* L., $2n=6x=42$) and F_2s., obtained from them (Table 5). Rye materials (*Secale cereale* $2n=14$) were inbred lines kindly provided by Prof. J. Sybenga and plants from the cultivar JNK which has a high rate of self-com-

patibility. In wheat, several crosses were carried out and F_1 individuals were selfed to obtain the F_2s; in rye several progenies (like F_2s) from selfed heterozygous plants or from crosses were scored.

Mature dry seeds were divided before electrophoresis into two parts: embryo and scutellum, and the endosperm. Each individual part was crushed and the enzymes were extracted by adding 5 µl (embryos) or 50 µl (endosperm) of sodium acetate 0.1 *M*, pH 7.2, for 1 h 30 min at 0 °C. After that, paper wicks (Watman 3M) 7×2 mm were soaked with the crude extract and then inserted in 180×260×2 mm polyacrylamide gels. Buffer, gel casting and electrophoretic conditions have been described by Benito and Pérez de la Vega (1979). *Secale vavilovii* and the cultivar Chinese Spring of hexaploid wheat were used as control in gels. After electrophoresis, the gels were immersed in 5% w/v aluminium lactate for 10 min at 40 °C, washed in distilled water and stained by the pyrocathecol method: 100 ml per gel of fresh pyrocathecol stain were made by mixing and stirring for 5 h in the dark 3 g of pyrocathecol, 0.15 g of boric acid, 1.5 g of Cl_2Ca, 0.2 g of $Na_2EDTA\ 2H_2O$ and 2 g of Tris. Dark bands usually appeared in gels after a few minutes.

The isozyme nomenclature used for cathodal peroxidase isozyme designation follows Benito et al. (1980) and García et al. (1982) for wheat and rye, respectively; that used for the loci was adapted from Asíns and Pérez de la Vega (1985) and Schlegel et al. (1986). Table 1 shows the nomenclature relationships between isozymes and the old and new designation. The maximum likelihood method was used to estimate genetic distance between loci, their standard errors and the heterogeneity among common-isozyme segregation (Allard 1956).

Table 1. Wheat and rye peroxidase nomenclature used in previous works. See "Materials and methods". Ed: endosperm; E+S: embryo plus scutellum

		Isozyme	Loci		Chromosomal location
T. aestivum	Ed	a	*CPX-A*	or *Per-1*	7DS
		b–c	*CPX-B*	or *Per-2*	4BL
		d	*CPX-D*	or *PerA-3*	7AS
				PerB-3	?
	E+S	m		*Per-5*	3DS
		a_1	*CPX-A*$_1$	or *Per-6*	3BL
		a_2	*CPX-A*$_2$	or *Per-7*	3DL
		d_1	*CPX-D*$_1$	or *Per-9*	?
		d_2	*CPX-D*$_2$	or *Per-10*	3BL
		e	*CPX-E*	or *Per-11*	3DL
		f	*CPX-F*	or *Per-12*	3DL
S. cereale	Ed	1	*CPX-1*	or *EPer-1*	4R
		2	*CPX-2*	or *EPer-2*	7R
		3	*CPX-3*	or *EPer-3*	7R
		4	*CPX-4*	or *EPer-4*	7R
		5	*CPX-5*	or *EPer-5*	7R?
		6	*CPX-6*	or *EPer-6*	7R?

Results

Several rye progenies from crosses or self-pollinated plants were scored for endosperm peroxidase segregations (Table 2). Since one of our aims was to complete the data on peroxidase genetics, a particular search for plants with isozyme 1 was made. Most of the progenies supported the hypothesis of a single locus with an active allele and a null allele controlling the expression of each isozyme, because they segregated 3:1 or 1:1 (presence: absence of isozyme). However, isozyme 3 was an exception because in half of the progenies it fitted a two locus 9:7 segregation. When the heterogeneity X^2 test of a given set of progenies segregating for each isozyme was not significant at the 5% level, all the progeny data were grouped and tested for their fit to the expected segregation. All the sets showed no significant deviations from expectations (Table 3).

Table 4 shows the results of two locus segregations in rye. All the progenies of each pair of loci, and the sum of those with the same segregation, were tested for their fit to the independence hypothesis. When X^2 was significant, the linkage hypothesis was tested. Most of the linkage X^2 for individual progenies and all of them

Table 2. Rye endosperm peroxidase segregations

Cross or self-pollination	Isozymes present									
	1	2	3	1–2	1–3	1–5	2–3	1–2–3	None	Total
71D⊗[a]		11			23			28		62
69D⊗		14			19		1	40		74
((108F×408X)1)⊗					67				26	93
((108F×408X)8)⊗					110				53	163
((9A×372X)7)⊗			48						33	81
((9A×372X)32)⊗			45						34	79
72D×G(72)4					28		30			58
Fe 1⊗	16				25				8	49
Fe 4⊗				12					7	19
Fe 10⊗						77			33	110
423Z×116F					9			9		18

[a] ⊗ : self-pollination

Table 3. Single locus segregation of rye endosperm peroxidases. +: isozyme present; −: isozyme absent

Isozyme	Progeny	+	−	$\chi^2$3:1	$\chi^2$1:1	$\chi^2$9:7
1	71D⊗	51	11	1.74		
	69D⊗	59	15	0.88		
	((108X×408X)8)⊗	110	53	4.91*		
	Fe 1⊗	41	8	1.97		
	Fe 4⊗	12	7	1.42		
	Fe 10⊗	77	33	1.47		
		350	127	0.67		
	72D×G(72)4	28	30		0.07	
2	71D⊗	39	23	4.84*		
	69D⊗	55	19	0.02		
	Fe 4⊗	12	7	1.42		
		106	49	3.61		
	72D×G(72)4	30	28		0.07	
	423Z×116F	9	9		0.00	
		39	37		0.05	
3	71D⊗	51	11	1.74		
	69D⊗	60	14	1.46		
	((108F×408X)8)⊗	110	53	4.91*		
		221	78	0.20		
	Fe 1⊗	25	24			0.54
	((9A×372X)7)⊗	48	33			0.30
	((9A×372X)32)⊗	45	34			0.02
		118	91			0.01
5	Fe 10⊗	77	33	1.47		

* $P<0.05$; ** $P<0.01$; *** $P<0.001$

for the summations were significant. When the genetic distances were estimated, the results showed that all loci behaved as closely linked. In fact, the estimations of distances, either from single progenies or from the joint estimation in each set of progenies, were always close to zero and their standard errors were of the same magnitude or higher than the estimated distance; therefore we accepted the arbitrary distance of 1 Morgan and its standard error in each set of data.

The wheat cultivars and their embryo peroxidase patterns are shown in Table 5. They showed embryo peroxidase patterns not previously described (Benito et al. 1980), which allowed us to study new linkage relationships between loci for embryo peroxidases. However, they did not show any endosperm isozyme additional to those reported by Benito et al. (1980), therefore endosperm results have been not included. The segregations observed fitted either the two-allele single-locus segregation (active-dominant versus null-recessive) or two-locus epistatic segregations (9:7 or 15:1). Segregation of isozyme d_2 of C×CK has not been included in Table 6 because the peculiarly low staining of this isozyme in that cross sometimes made it difficult to determine its presence in gels. Two-locus segregation results (Table 7) were obtained in a similar way to those for rye. These results showed linkage relationships between loci controlling isozymes a_2, d_1 and d_2. The estimation of the recombination frequency between a_2 and d_1 was close to 11% (10.88 ± 1.52) from the joint esti-

Table 4. Two locus segregation of rye endosperm peroxidases

Isozymes	Cross	++	+−	−+	−−		$\chi^2$9:3:3:1	$\chi^2$1:1:1:1	$\chi^2$27:21:9:7	χ^2 Linkage	Distance[a]
1–2	71D⊗	28	23	11	0	R[b]	16.39***			9.76**	
	69D⊗	40	19	15	0	R	6.67				1.00±1.12
		68	42	26	0		20.13***			15.13***	
	Fe 4⊗	12	0	0	7	C	35.74***			32.90***	
	72D×G(72)4	0	28	30	0	R		58.14***		58.00***	
1–3	71D⊗	51	0	0	11	C	43.81***			40.33***	
	69D⊗	59	0	1	14	C	52.04***			49.70***	
	((108F×408X)8)⊗	110	0	0	53	C	224.70***			214.88***	
		220	0	1	78		314.36***			313.85***	1.00±0.56
	Fe 1⊗	25	16	0	8	C			9.10*	6.59**	
2–3	71D⊗	28	11	23	0	R	16.39***			9.81**	
	69D⊗	41	14	19	0	R	6.53			5.05*	
		69	25	42	0		19.92***			14.23***	1.00±8.57
1–5	Fe 10⊗	77	0	0	33	C	144.22***			141.28***	1.00±0.95

* $P<0.05$ ** $P<0.01$ *** $P<0.001$

[a] Distances and standard errors for each isozyme pair have been jointly calculated from all the progenies segregating for each pair (Allard 1956)

[b] R=repulsion; C=coupling

mation with the three progenies; the values obtained between a_2 and d_2 were close to 15% (Table 7). Unfortunately it was not possible to estimate the distance between d_1 and d_2 because the number of individuals of the progenies was too low to obtain significative information from their segregations (9:7/3:1 and 9:7/15:1). The same applied to individual segregations B × CT and C × A for a_2–d_2, although it was possible to obtain a joint estimation for the pair B×CP and B×CT (14.99 ± 7.67).

Discussion

Previous work has suggested that null alleles are generally present in all rye and wheat peroxidase loci, and that the expression of individual peroxidase isozymes of both rye and wheat could be under the control of different non-allelic genes. Benito and Pérez de la Vega (1979) pointed out that at least isozyme e of hexaploid wheat embryo could be controlled by two structural

Table 5. Isozyme peroxidase patterns of *T. aestivum* cultivars

Cultivar		Isozymes				
		a_2 1.00[a]	d_1 0.82	d_2 0.68	e 0.54	f 0.36
A	Anza	–	–	+	+	+
B	Banks	+	+	–	+	+
CP	Capitol	–	–	+	+	+
CT	Castan	–	–	+	+	+
C	Condor	+	+	–	+	+
CK	Cook	+	–	+	+	–
M	Línea M	+	–	–	+	+

[a] Relative mobility

Table 6. F_2 segregation of wheat embryo peroxidases. A: Anza; B: Banks; CP: Capitol; CT: Castan; C: Condor; CK: Cook; M: Linea M

Isozyme	Cross	+	–	$\chi^2$3:1	$\chi^2$9:7	$\chi^2$15:1
a_2	B×CP	434	160	1.19		
	B×CT	54	24	1.38		
	C×A	102	33	0.02		
		590	217	1.54		
d_1	B×CP	348	246		1.32	
	B×CT	36	42		3.23	
		384	288		0.22	
	C×A	104	31	0.30		
	C×CK	101	5			0.42
	M×C	246	16			0.01
		347	21			0.19
d_2	B×CP	549	45			1.78
	B×CT	71	7			0.99
		620	52			2.54
	C×A	80	55		0.50	
f	C×CK	79	27	0.01		

Table 7. Two locus segregation of wheat embryo peroxidase isozymes. A: Anza; B: Banks; CP: Capitol; CT: Castan; C: Condor; CK: Cook; M: Linea M

Isozyme	Cross	++	+–	–+	––	$\chi^2$9:3:3:1	$\chi^2$27:21:9:7	$\chi^2$45:3:15:1	χ^2(9:7) (15:1)	χ^2 Linkage	Distance
a_2–d_1	B×CP	322	122	26	134		168.61***			166.10***	9.82 ± 2.03
	B×CT	30	24	6	18		13.12**			8.51**	23.59 ± 7.89
		352	136	32	152		174.11***			171.86***	
	C×A	97	5	7	26	71.95***				71.63***	9.51 ± 2.60
											10.88 ± 1.52[a]
a_2–d_2	B×CP	390	44	159	1			21.41***		18.44***	14.29 ± 8.09
	B×CT	47	7	24	0			7.19		4.82*	N.C.[b]
		437	51	183	1			27.46***		22.89***	14.99 ± 7.67
	C×A	48	54	32	1		56.31***			55.79***	N.C.
d_1–d_2	B×CP	311	37	238	8				16.77***	13.68***	N.C.
	B×CT	29	7	42	0				15.46**	12.37***	N.C.
	C×A	50	54	30	1		22.20***			21.40***	N.C.
d_1–f	C×CK	76	25	3	2			0.88			

[a] Joint estimation from the three crosses
[b] *N.C.*: not calculated
* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

loci. Asíns and Pérez de la Vega (1985) observed null alleles and epistatic segregations (9:7 and 15:1), to be general in some isozymes of both embryo and endosperm of tetraploid wheat. García et al. (1982) likewise described null alleles and epistatic segregations for isozyme 4 of endosperm in rye. The results now presented support these findings as follows.

(1) All segregations of both wheat and rye suggest active-dominant and null-recessive alleles are present at each segregating structural locus.

(2) There seem to be "regulatory" transacting genes controlling specific peroxidase isozyme expression in both rye and wheat. Thus, the 9:7 segregation observed for rye endosperm isozyme 3 could be attributed to the simultaneous segregation of independent structural and "regulatory" genes, the presence of the dominant allele (*Rp3*) in the "regulatory" locus being needed either for the synthesis or for the activity of the isozyme. This should also be true for 9:7 segregations in wheat. The action of these "regulatory" genes which prevent the expression of peroxidase isozymes seems specific, since they restrain the expression of a given isozyme without affecting others. So, for instance, in wheat F_2 C×A (Table 6) the segregation of isozyme d_2 is affected (9:7) while isozymes a_2 and d_1 do not deviate from the single-locus segregation. Additional examples can be observed in Tables 3 and 6 and in previous work (García et al. 1982; Asíns and Pérez de la Vega 1985).

(3) In wheat 15:1 segregations of d_1 and d_2 isozymes fit the hypothesis of two structural and independent genes, probably located in homoeologous chromosome pairs (Hart 1983), coding homoeologous proteins with the same electrophoretic migration. Additional evidence supports the presence of homoeologous peroxidase genes in *T. aestivum,* besides the 15:1 segregations now reported. Diploid and tetraploid *Triticum* species, including the putative progenitors of hexaploid wheat, simultaneously show several of the isozymes observed in *T. aestivum* and sometimes as many as in hexaploid wheat. Some migrate like isozymes located in chromosome 3D of the cultivar Chinese Spring of hexaploid wheat, despite their lacking the D genome (Asíns and Carbonell 1986). Linkage relationships, which will be further discussed, seem to indicate that peroxidase genes of wheat embryo are located in chromosomes of the homoeology group 3.

Since hexaploid wheat has three homoeologous pairs of genomes it could have been expected to have as many as three active pairs of structural genes coding for equal or similar migrating isozymes. This is not the case because in almost all of the homozygous wheat cultivars so far studied most, if not all, of the isozymes are coded by a single structural gene pair (Asíns and Pérez de la Vega 1985; Benito et al. 1980; present work). Thus, during the evolution of wheat species and artificial selection, several loci may have become fixed for null alleles, which are frequent in all cereal species, including rye. Several factors may have contributed to the increase in the rate of fixation of null alleles: the autogamous mating system of wheat species, the retention of cultivars from a few or one individual during breeding and the possibility of losing the activity of some peroxidase gene without harming the species. As Li (1982) stated, silencing of duplicate genes can occur rather quickly if there is no advantage in maintaining duplicate expression. Null alleles are only frequent in higher plants in isozymatic systems which lack specificity (as esterases and peroxidases). Any isozyme could carry out most or all the metabolic steps requiring that kind of enzyme (e.g. a peroxidase). Indications of the non-harmful loss of peroxidase isozymes are found in both line 1112 of *T. turgidum,* in which no peroxidase isozyme in the mature-dry endosperm was observed (Asíns and Pérez de la Vega 1985), and in rye seeds with only a single isozyme in the embryo or none in the endosperm (García, unpublished data). An example of quick null allele fixation, perhaps due to change during breeding, is the cultivar Condor. It has isozyme d_1; some seeds have active alleles in only one genome pair while others have active alleles in two, as indicated by segregations 3:1 and 15:1 in different F_2s obtained from single parental plants of Condor (Table 6).

The two-locus segregation data on rye (Table 4) showed a close genetic linkage among all the peroxidase loci analysed. This result agrees with previous linkage results (García et al. 1982), except for isozyme 1 which was considered genetically independent from the others because neither of the two progenies studied showed a significant X^2 deviation from the independence (9:3:3:1) hypothesis. Later, Salinas and Benito (1984) located locus *EPer1* in chromosome 4R and *EPer3* in 7R. Therefore, the linkage between locus *EPer1* and loci *EPer2, EPer3* and *EPer5* observed in our results is striking, since it indicates that all rye endosperm peroxidase loci should be in the same linkage group and closely linked. If the data on JNK26 and E×V 1 progenies (García et al. 1982) are pooled with our data to estimate a common linkage distance, there is a highly significant heterogeneity X^2 value. This supports the idea that independence and linkage can occur, depending upon the progeny scored. Taking all the evidence into consideration, we propose the hypothesis that isozyme 1 is related to two different structural loci (probably an interchromosomal duplication) located in chromosomes 4R and 7R. Depending on whether the locus in 4R is homozygous for null alleles and that in 7R is active-null heterozygous or vice versa, the segregation would show linkage or independence, respectively. The critical result according to this hypothesis would be to find a 15:1 segregation for isozyme 1. Unfortunately, since isozyme

1 is not common in our rye materials, we have not found this, as yet.

The results on embryo wheat peroxidases showed that genes for isozymes a_2, d_1 and d_2 are linked. The genes for isozymes d_2 (*Per-B10*) and f (*Per-D12*) were located in the long arms of chromosomes 3B and 3D of Chinese Spring wheat, respectively (Benito and Pérez de la Vega 1979). The gene for a_2 (*Per-D7*) was assigned to the long arm of 3D because of genetic linkage with *Per-D12* (Benito et al. 1980). In tetraploid wheats, which lack genome D, genes for isozymes a_2, d_1, d_2 and f behaved as if linked (Asíns and Pérez de la Vega 1985). Thus, on the basis of the genetic linkage data now obtained in hexaploid wheat and the evidence of duplicated genes controlling isozymes d_1 and d_2 (segregations 15 : 1), we tentatively assigned peroxidase structural genes to the long arms of chromosomes 3D for a_2 (*Per-D7*), d_1 (*Per-D9*) and d_2 (*Per-D10*), and 3B for d_1 (*Per-B9*) and d_2 (*Per-B10*). If the gene for isozyme f is in chromosome 3D or 3B in C×CK, it should be located far enough from *Per-9* to behaved independently. The conclusion is that peroxidases of wheat (homoeologous proteins) with equal or similar migrations are coded by genes in homoeologous chromosomes, like other wheat isozymatic systems (Hart 1983).

To sum up, we have afforded further data about seed peroxidases of rye and wheat, but we are still far from obtaining a complete picture of their genetics, for instance, on the nature of the "regulators" affecting their expression. Therefore, further studies to test the unresolved hypotheses will be needed.

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