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The inheritance of tetraploid wheat seed peroxidases

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Summary. Embryo and endosperm peroxidases from dry mature seeds of three subspecies of tetraploid wheat (*Triticum turgidum* L.) were subjected to genetic analysis. The inheritance of eight isozymes (embryo isozymes a_2, d_1, d_2, e and f; and endosperm isozymes b, d and 4) were studied in F_2's obtained from different wheat accessions. Simple monogenic inheritance producing three banded: one null segregation and two epistatic segregations (9:7 and 15:1) were found. In the case of isozymes b, d and 4, monogenic or epistatic segregation depended on the F_2 analyzed. Segregation data indicated that at least 9 different loci would determine the peroxidase isozymes of tetraploid wheat seed, all the loci studied containing 'null' alleles. Furthermore, several loci determining embryo peroxidases were noticed to be mutually linked. All these data are discussed in context of the inheritance of seed peroxidases in hexaploid wheat and rye.

Key words: *Triticum turgidum* – Tetraploid wheat – Peroxidases – Inheritance – Linkage

Introduction

Since electrophoretic techniques came into general use in genetic research, isozyme and storage-protein loci have formed the basis of many formal genetic studies of plants. Thus these loci constitute a high proportion of the loci of higher plant mapped in chromosomes (O'Brien 1982). The advantage of the mapping of enzyme coding genes lies in the various methods by which it can be carried out and in the interesting applications of the resulting information (Tanksley 1983), especially when crops are concerned. Moreover, genetic mapping retains its interest as higher plant chromosomes are less fully mapped than some animal and microorganism chromosomes (see O'Brien 1982). The status of research in enzyme mapping in individual plant species has recently been reviewed by Tanksley and Orton (1983).

The peroxidase system has been widely used in genetic studies (although it lacks some of the characteristics of typical isozymatic markers listed by Tanksley and Rick 1980) owing to several factors: its great variability among higher plants, the generally high number of isozymes (with the consequently high number of markers), and the good results obtained by means of relatively easy and inexpensive techniques. Peroxidases are usually characterized by a monogenic control, monomeric behaviour, and the presence of null alleles (Benito et al. 1980; Felder 1976; García et al. 1982; Sandmeier et al. 1981; Yen and Sadanaga 1977), and are described as glycoproteins and hemoproteins (Liu 1975; van Huystee and Cairns 1980). Dimeric peroxidase isozymes have been reported in *Oryza perennis* (Endo 1971), while repeated observations have been made in several plant species of 'regulatory' or epistatic genes which affect the expression of peroxidase isozymes by post-transcriptional modifications and/or preventing the appearance of some isozymes, thus affecting segregation ratios (Berg et al. 1983; Endo 1971; García et al. 1982; Pai et al. 1973; Rick et al. 1979; Sandmeier et al. 1981).

The purpose of the present paper is to analyze the genetic control and linkage relationships of peroxidase isozymes of the embryo-plus-scutellum and endosperm of tetraploid wheat (*Triticum turgidum* L.), and to contribute new markers to the as yet poorly drawn chromosome maps of tetraploid wheats. The peroxidase markers are also studied in relation to recently mapped phosphatase markers (Asíns and Pérez de la Vega 1985). The results obtained are compared with recent

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data concerning the genetics and linkage relationships of peroxidase of hexaploid wheat and rye (Benito et al. 1980; García et al. 1982). Some general conclusions are reached concerning all these materials. These conclusions may be useful in further studies in the genera *Triticum* and *Secale.*

Materials and methods

The materials used were fifteen tetraploid ($2n=4x=28$) wheat accessions (comprising thirteen of *Triticum turgidum* ssp turgidum conv. durum (Desf.) MacKey, one of *T. turgidum* ssp cartlicum (Nevski) MacKey, syn. *T. persicum* Vav. ex Zhuk., and one of *T. turgidum* ssp dicoccoides (Körn) Tell) and eleven F_2's obtained from them (Tables 1 and 2). Persicum and didoccoides wheats were used in order to obtain F_2's which segregate simultaneously for a high number of isozymes. The hexaploid wheat 'Chinese Spring' and the durum wheat 'D' were used as electrophoretic controls in gels. The polyacrylamide electrophoretic techniques used have been described by Benito and Pérez de la Vega (1979).

Several crosses were carried out and F_1 individuals were selfed, the mature dry seed thus obtained being divided before electrophoresis into two parts: embryo + scutellum (E + S) and endosperm (Ed).

Hypotheses about peroxidase isozyme genetic control were at first based on previous peroxidase inheritance data for hexaploid wheat (Benito et al. 1980) and rye (García et al. 1982). The hypotheses tested were: firstly, each band in the zymogram is determined by a single locus with an active and a null allele; secondly, when a segregation differed significantly from the 3:1 one, a multilocus control was tested; and thirdly, when no individuals simultaneously lacking two segregating bands were noticed, the allelism hypothesis was tested (i.e. isozymes a_2 and e).

The isozyme nomenclature used for cathodal peroxidase designation in this study follows that described by Benito et al. (1980), while that used for the loci is adapted from Hart's (1983), both for hexaploid wheat. The nomenclature of alkaline phosphatases and electrophoretical procedures are those described by Asíns and Pérez de la Vega (1985). Allard's (1956) maximum likelihood equations were used to estimate the genetic distance between loci, their standard errors and the heterogeneity among common-isozyme segregation.

Results

Table 1 shows the accessions used together with the peroxidase patterns for both seed parts: embryo + scutellum (E + S) and endosperm (Ed). No variability was observed in the peroxidase pattern among seeds from any single accession. Isozymes e and d_1 appear faintly in some accessions (e.g., Petrel and Cocorit, respectively) and their presence is sometimes difficult to determine in F_2's of Pingüino × Petrel and Cocirit × Stork crosses; they are therefore not recorded for these F_2's.

The segregations (Table 2) generally fit the two-allele single-locus segregation, there being present at each locus an active-dominant allele and a null-recessive one. However, in some crosses certain isozymes fit epistatic ratios (9:7 or 15:1): whereas isozyme d otherwise fits the 3 : 1 ratio in 1112 × 3417 it fits 15 : 1;

Table 1. Isozyme peroxidase patterns of *T. turgidum* accessions

Accessions	Embryo + scutellum					Endosperm			Source[b]
	a_2 1.00[a]	d_1 0.82	d_2 0.68	e 0.54	f 0.36	b 0.89	d 0.75	4 0.61	
Cocorit	+[c]	+−	−	−	−	+	−	−	E.T.C.
D	+	−	+	−	−	+	+	+	E.T.C.
G.B.	+	−	+	−	−	+	+	+	E.T.C.
Petrel	+	−	+	+−	−	−	+	+	E.T.C.
Pingüino	−	−	++	+	−	+	+	+	E.T.C.
Senatore Capelli (S.C.)	+	−	+	−	−	+	+	+	E.T.C.
Stork	+	−	+	−	−	+	+	+	E.T.C.
1112	+	+	−	−	−	−	−	−	C.N.R.
1450	+	+	−	−	−	+	+	+	C.N.R.
3078	−	−	+	+	+	+	+	+	C.N.R.
3417[d]	−	−	−	+	+	+	+	+	C.N.R.
8804[d]	+	+	−	+	+	+	+	+	A.K.U.
40219	−	−	++	+	−	+	+	+	E.T.L.
64120	+	−	+	−	−	+	−	−	E.T.L.
64137	+	−	+	−	−	+	−	−	E.T.L.

[a] Relative mobility
[b] E.T.C. = Escuela Técnica Superior I. Agrónomos, Córdoba, Spain; CNR. = Laboratorio del Germoplasma, C.N.R., Bari, Italy; A.K.U. = Germ-Plasm Inst., Agriculture, Kyoto Univ., Japan; E.T.L. = Escuela Téc. Agrícola, Lérida, Spain
[c] + = Isozyme present, − = isozyme absent, +− = faint isozyme, ++ = very intense isozyme
[d] 3417 is *T. persicum;* 8804 is *T. turgidum* spp dicoccoides

Table 2. Single locus segregation of tetraploid wheat seed peroxidase isozymes

Isozyme	Organ	Cross	F_2 offsprings[a]		$\chi^2_{(1)}$ values	
			+	–	3:1	Epistatic
a_2	E+S	Pingüino×Petrel	72	32	1.85	
		Pingüino×D	75	27	0.12	
		1112×3417[b]	113	42	0.36	
		3417×D	61	17	0.43	
		40219×S.C.	42	10	0.92	
			363	128	0.30	
d_1	E+S	1450×64120	88	40	2.67	
		G.B.×8804[c]	93	31	0.00	
			181	71	1.35	
		1112×3417	70	85	73.60***	
d_2	E+S	1450×64120	97	31	0.04	
		3417×3078	17	7	0.22	
		3417×D	54	24	1.39	
		G.B.×8804	85	39	2.75	
		Cocorit×Stork	32	7	1.03	
			285	108	1.29	
e	E+S	Pingüino×D	74	28	0.32	
		1112×3417	119	36	0.27	
		3417×D	57	21	0.15	
		G.B.×8804	99	25	1.54	
		40219×S.C.	37	15	0.41	
			386	125	0.07	
f	E+S	1112×3417	111	44	0.95	
		3417×D	55	23	0.84	
			166	67	1.75	9:7
		G.B.×8804	64	60	36.17***	1.08
b	Ed	Pingüino×Petrel	84	20	1.85	
		1112×3417	102	49	4.47*	
		40219×Petrel	105	39	0.33	
			291	108	0.91	
d	Ed	1450×64120	98	37	0.42	
		G.B.×64137	79	25	0.05	
		Cocorit×Stork	28	11	0.21	
			205	73	0.24	15:1
		1112×3417	146	5		2.23
						9:7
4	Ed	Cocorit×Stork	24	15	3.77	0.44
		1450×64120	88	47	6.94**	4.38*
		G.B.×64137	58	46	20.51***	0.01
			170	108	28.44***	2.71
		1112×3417	120	31	1.61	

[a] Isozyme present, +, or absent, –; [b] *T. persicum;* [c] *T. turgidum* spp dicoccoides
Significance levels in this and following tables: *** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$

and isozyme f gives 3 : 1 in all cases except GB×8804, where the ratio is 9 : 7.

The results of a two-locus segregation for peroxidase isozymes are shown in Table 3, the data for isozyme d_1 in 1112×3417 being excluded because its highly significant deviation from 3 : 1 and epistatic segregations. All progenies and their summation (when no heterogeneity was found among them) were tested for their fit to the independence hypothesis. If this χ^2 was significant, the linkage χ^2 was calculated. Since individuals lacking both a_2 and e isozymes were observed the allelism hypothesis was tested, and subsequently rejected

Table 3. Two-locus segregation for the detection of linkage

Isozyme	Cross	F_2 offspring[a]				χ^2 values			Distance
		+ +	+ –	– +	– –	9:3:3:1	Others	Linkage	
a_2-d_2	3417[b]×D	42	19	12	5	1.86			
a_2-e	Pingüino×D	47	28	27	0	15.62**			
	40219×S.C.	27	15	10	0	6.26			
	1112×3417	77	36	42	0	18.29***			
	3417×D	40	21	17	0	8.38*			
		191	100	96	0	45.40***		45.26***	0.00±5.09
a_2-f	1112×3417	74	39	37	5	9.83*			
	3417×D	38	23	17	0	10.84*			
		112	62	54	5	19.16***		17.40***	26.94±6.06
a_2-b	Pingüino×Petrel	58	14	26	6	3.76			
	1112×3417	71	39	31	10	6.63			
		129	53	57	16	3.78	45:3:15:1		
a_2-d	1112×3417	107	3	39	2		2.78		
a_2-4	1112×3417	90	20	30	11	3.10			
d_1-d_2	1450×64120	63	25	34	6	5.83			
	G.B.×8804	66	27	19	12	3.91			
		129	52	53	18	2.65			
d_1-e	G.B.×8804	79	14	20	11	6.72	27:21:9:7		
d_1-f	G.B.×8804	63	30	1	30		40.41***	39.33***	2.77±2.02
d_1-d	1450×64120	63	25	30	10	3.17			
d_1-4[d]	1450×64120	60	28	28	12	5.33	11.17*		
d_2-e	3417×D	42	12	15	9	4.07			
	G.B.×8804[c]	60	25	39	0	19.91***		15.62***	0.00±8.98
d_2-f	3417×D	40	14	15	9	3.87			
	G.B.×8804	37	48	27	12		11.21*	7.38**	15.95±16.36
d_2-d	Cocorit×Stork	23	9	5	2	1.25			
	1450×64120	67	30	26	5	3.14			
		90	39	31	7	3.19			
d_2-4[d]	Cocorit×Stork	21	11	3	4	5.44			
	1450×64120	59	38	26	5		10.18*		
e-f	1112×3417	104	15	7	29	65.30***			
	3417×D	55	2	0	21	81.68***			
		159	17	7	50	139.30***		137.52***	10.63±2.09
	G.B.×8804	64	35	0	25		30.44***	27.82***	5.04±4.25
e-b	1112×3417	76	39	26	10	5.20			
e-4	1112×3417	87	28	33	3	5.28			
f-b	1112×3417	68	39	34	10	8.60*	45:3:15:1	2.75	
f-d	1112×3417	102	5	44	0		5.12		
f-4	1112×3417	82	25	38	6	5.06			
b-d	1112×3417	99	3	47	2		6.54		
b-4	1112×3417	80	22	40	9	6.54	27:21:9:7		
d-4	Cocorit×Stork	24	4	0	11		25.66***		
	1450×64120	88	10	0	37		94.08***		
	G.B.×64137	58	21	0	25		40.54***		
		170	35	0	73		157.09***	154.14***	0.00±0.97
								45:15:3:1	
	1112×3417	120	26	0	5		14.32***	10.48***	–

[a] Isozyme present, +, or absent, –; [b] *T. persicum;* [c] *T. turgidum* spp dicoccoides; [d] Isozyme '4' differs significantly from 3:1 and 9:7 segregation in 1450×64120 F_2

Table 4. Two-locus segregation for peroxidase (Per) and alkaline phophatase (Phos) isozymes of tetraploid wheat seed

Isozymes		Cross	F_2 offspring				χ^2 values	
			++	+−	−+	−−	9:3:3:1	29:27:9:7
Per-Phos								
b	3	40219 × Petrel	82	23	24	15	2.72	
b	4	40219 × Petrel	82	23	24	15	2.72	
b	7[a]	40219 × Petrel	58	47	24	15		0.86
e	3	40219 × S.C.	26	10	9	3	0.15	
e	7	40219 × S.C.	25	11	9	3	0.59	

[a] Phosphatase isozyme '7' segragates 9:7

as the χ^2 value was 137.79 ($P<0.001$). Furthermore, accession 8802 simultaneously present both isozymes.

The results of two-locus segregations have been grouped in two different ways, as two different linkage relationships were observed depending on the subspecies crossed. Thus, in durum × durum or durum × persicum crosses, the loci determining a_2, e and f are linked, while those determining d and 4 also appear to be linked, these loci behaved independently in relation to all other isozyme loci (Table 3); but in durum × dicoccoide crosses the locus for isozyme d_2 behaved as linked with loci determining isozymes e and f, while isozymes d_1 and f appear to be related, perhaps through linkage between the locus for d_1 and the epistatic locus that modifies the segregation of isozyme f. Embryo isozymes are not linked with endosperm isozymes.

The two-locus segregation for peroxidases and endosperm alkaline phosphatases was observed in some F_2's segregating for both kinds of isozymes. All the isozyme pairs tested behaved independently (Table 4).

Discussion

The results suggest a similar general monogenic control and monomeric behaviour for *T. turgidum* peroxidase isozymes as was previously indicated for *T. aestivum* (Benito et al. 1980) and other higher plant species (Felder 1976; García et al. 1982; Sandmeier et al. 1981; Yen and Sadanaga 1977). Likewise, null alleles seem to occur generally, so each structural locus should have two allelic alternatives; one responsible for the active isozyme and one – the null allele – producing null expression. Exceptions to monogenic determination are isozyme d, which segregated 15 : 1 in some crosses (Table 2), and isozymes f and 4, which segregated 9 : 7 in some crosses (Table 2).

The ratio for isozyme d is 15 banded : 1 null in the F_2 from 1112 (durum) × 3417 (persicum), while it is 3 : 1 for durum × durum crosses. The 15 : 1 segregation must be due to the existence of two independent loci, probably located in homoeologous chromosome pairs, coding homoeologous proteins with the same electrophoretic migration. Thus, the parental genotypes of 1112 × 3417 would be *Per-A3*^{n} *Per-A3*^{n} *Per-B3*^{n} *Per-B3*^{n} and *Per-A3 Per-A3 Per-B3 Per-B3*, respectively; *Per-A3* and *Per-B3* being the active alleles of A and B genomes, and *Per-A3*^{n} and *Per-B3*^{n} their null alternatives. On the other hand, the genotypes of durum parentals would be *Per-A3 Per-A3 Per-B3*^{n} *Per-B3*^{n} (active alleles probably being present in genome A, as it will be further discussed) and *Per-A3*^{n} *Per-A3*^{n} *Per-B3*^{n} *Per-B3*^{n}, respectively, for accessions with and without isozyme d.

This hypothesis of homoeologous location is supported by other studies concerning the location of isozyme loci, where homoeologous protein loci are reported to be located in homoeologous chromosomes (Benito and Pérez de la Vega 1979; Hart 1983). It is further supported by the fact of isozyme e of *T. aestivum* (which is present in all hexaploid cultivars so far analyzed) being determined by at least one pair of loci situated in different pairs of chromosomes (Benito and Pérez de la Vega 1979). Isozyme d may, therefore, be produced in *T. turgidum* by two loci, one probably located in chromosome 7A, where isozyme d of *T. aestivum* is situated (Benito and Pérez de la Vega 1979) and one on the homoeologous chromosome of the B genome.

In two F_2's isozyme f segregated 3 : 1, but gives a 9 : 7 ratio in the F_2 from GB × 8804. Therefore, it can be deduced the necessity of a dominant allele in an independent locus (*rPer-12*) for the expression of the active allele that determines isozyme f.

Isozyme 4 also segregates 3 : 1 and 9 : 7, so an independent locus (*rPer-4*) in which a dominant allele determines the expression of the active *Per-4* allele may also be possible. Although no endosperm showed 4 without d, some had d without 4. Two hypotheses could explain this: i) two closely linked structural loci (*Per-3*

and *Per-4*) determine respectively d and 4, with an additional independent epistatic locus acting on 4; ii) isozyme 4 is a posttranslational modification of d, and this modification is determined by a dominant allele in an independent locus (*mPer-3?*). Both hypotheses have been previously pointed out. For example, García et al. (1982) described a rye endosperm peroxidase that segregated 3:1 and 9:7, the expression of which was determined by an epistatic gene; while Sandmeier et al. (1981) also described a peroxidase isozyme that segregated 3:1 and 9:7 in pearl millet. On the other hand, Rick et al. (1979), with regard to *Lycopersicon pimpinellifolium,* described a gene that post-translationally modified the products of an independent peroxidase locus to yield two electrophoretically separable isozymes.

According to the results of the present study, to the previous nomenclature of wheat isozymes (Hart 1983) and to the peroxidases previously reported in hexaploid wheat (Benito et al. 1980), we propose the following nomenclature for the loci determining cathodal peroxidases of tetraploid wheat, *T. turgidum* L.

Isozyme	Locus	Active allele	Null allele	Others
b	*Per-2*	*Per-2*	$Per\text{-}2^n$	
d	*Per-A3*	*Per-A3*	$Per\text{-}A3^n$	*mPer-3?*
	Per-B3	*Per-B3*	$Per\text{-}B3^n$	
4	*Per-4*	*Per-4*	$Per\text{-}4^n$	*rPer-4*
a_2	*Per-7*	*Per-7*	$Per\text{-}7^n$	
d_1	*Per-9*	*Per-9*	$Per\text{-}9^n$	
d_2	*Per-10*	*Per-10*	$Per\text{-}10^n$	
e	*Per-11*	*Per-11*	$Per\text{-}11^n$	
f	*Per-12*	*Per-12*	$Per\text{-}12^n$	*rPer-12*

There may exist an additional locus, *Per-6,* which determines the E+S isozyme a_1 which migrates with Rm 1.14.

The mapping of tetraploid wheat peroxidases can not be definitive because different subspecies may have different recombination frequencies, and perhaps different locations for some genes. Furthermore, not every possible combination of segregating isozymes has been studied, and the high error of estimation can give rise to fictitious distances. Figure 1 shows the tentative maps deduced from this study.

The linkage maps (Fig. 1) for cathodal peroxidases of tetraploid wheats are in agreement with the data provided by Benito and Pérez de la Vega (1979) and Benito et al. (1980) for chromosomal location and segregation in *T. aestivum* cv. 'Chinese Spring'. Isozymes e and f of *T. aestivum* were located in chromosome arm 3Dq and isozyme d_2 in 3Bq, though, a_2 and f were linked, while d_2 and f behaved independently. As in the results given by García et al. (1982) for rye, the endosperm and embryo isozymes were independent (in *T. aestivum* isozyme d was located in 7Ap, b being probably situated in 4Bq). The homoeologous isozymes of *T. turgidum* should therefore be coded by loci in the homoeologous chromosomes of A or B genomes, yet, with the exception of isozyme d in the persicum accession, only one of the pairs of chromosomes carried both allelic alternatives (active and null), the other one being a homoeologous pair fixed for null alleles. Two facts bear out these hypotheses: firstly, with few exceptions similarly migrating isozymes occur in phylogenetically related diploid, tetraploid and hexaploid species of *Triticum* and *Aegilops* (Asíns 1983). Thus, for instance, no new isozyme has been reported in *T. turgidum* E+S respect those from *T. aestivum.* Secondly, as is mentioned above, in hexaploid wheat, isozyme e is located in two different pairs of chromosomes.

The different behaviour in dicoccoides or durum-persicum wheats of isozyme d_2 with regard to e and f may be connected with a translocation.

A remarkable result is that all seed peroxidase loci analysed possess null alleles although their presence in peroxidase loci seems to be general. This has been pointed out repeatedly (Cleeg and Allard 1973; Smith 1972, in *Avena;* Rick and Fobes 1975 in *Lycopersicon;* Second 1982 in *Oryza;* Sandmaier et al. 1981 in *Pennisetum;* García et al. 1982; Pérez de la Vega and Allard 1984, in *Secale;* Benito et al 1980 in *Triticum*). Therefore, as García et al. (1982) also stated, we conclude that such an abundance of null alleles would seem to be peculiar to certain isozymatic systems, and not be the results of experimental manipulation. There is, perhaps, some connection with the lack of specificity for peroxidases. Consequently, if any isozyme could carry out most – if not all – of the metabolic steps

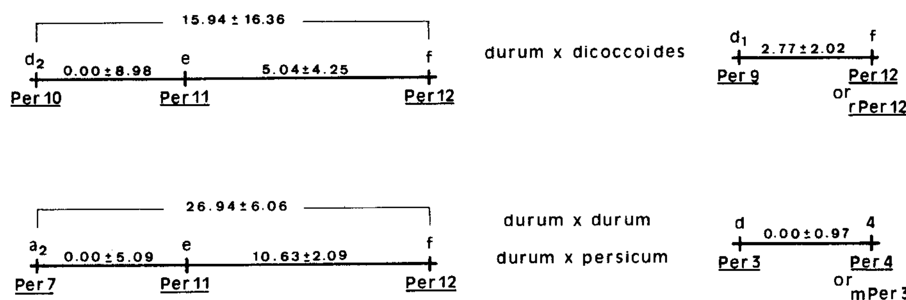

Fig. 1. Linkage maps of tetraploid wheat seed peroxidase loci. Values indicate the distances and their standard errors. Loci for isozymes 'd' and '4' seem also to be linked in *durum* × *dicoccoides* but the distance has not been calculated

requiring a peroxidase, then one or more loci could be fixed for null alleles without lethality. This statement is supported by the fact that null alleles occur quite frequently in other generally reported non-specific isozymatic systems, such as esterases and phosphatases (Allard and Khaler 1971; Asíns and Pérez de la Vega 1985; Schmidt-Stohn and Wehling 1983).

The independent segregation observed among peroxidase loci and endosperm alkaline phosphatases loci also agrees with earlier data. According to Salinas et al. (1981), wheat phosphatase isozymes are situated in homoeologous group 4 and, while some phosphatase isozymes are related to chromosome arm 4Bp, the locus for isozyme b must be in chromosome arm 4Bq.

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