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Peach mendelian genetics: a short review and new results

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Summary — A short review of the knowledge on peach genetics to date is presented in the introduction. Until now, thirty-one phenotypic characters, and ten polymorphic enzymatic systems with mendelian inheritance have been described. Linkages between eight pairs of loci have been established and three genetic maps published. These maps include mainly the location of RAPD and RFLP molecular markers and cannot easily be superimposed. In addition to this review work, results of observations made on a family originated from a test cross between homozygous and heterozygous parents are given for two mendelian phenotypic characters (ie, fruit acidity and fruit shape) and for two isoenzymatic systems (ie, malate dehydrogenase and catalase). A narrow linkage (5.8 cM) was found between the locus for fruit acidity *(D/d)* and that for catalase *(CAT1-1/CAT1-2)*. The other pairs of loci segregate independently, particularly fruit shape (flat/round), and fruit acidity (sweet/acid). This contradicts a previous report of a 35 cM linkage between the loci responsible for these last pairs of characters, assumed from observations made on a small size family.

Prunus persica **= peach / mendelian genetics / linkage**

Résumé — Génétique mendélienne du pêcher. Bilan et nouveaux résultats. *Une étude bibliographique succinte faisant le point sur les connaissances en matière de génétique du pêcher est présentée en introduction. Trente-et-un caractères phénotypiques à hérédité mendélienne ont été décrits, auxquels il faut ajouter dix systèmes enzymatiques polymorphes. Des liaisons ont pu être établies entre huit couples de loci ; trois cartes génétiques de l'espèce ont été publiées, mais elles comportent essentiellement des emplacements de marqueurs moléculaires RAPD ou RFLP et sont difficilement superposables. En supplément à ce travail bibliographique, sont donnés les résultats d'observations réalisées sur une famille issue d'un test cross entre un géniteur homogyzote et un géniteur hétérozygote pour deux caractères phénotypiques mendéliens (acidité du fruit, forme du fruit) et deux systèmes iso-enzymatiques (malate déshydrogénase et catalase). Une liaison étroite (5,8 cM) entre le locus de l'acidité du fruit* (D/d) *et celui de la catalase* (CAT1-1/CAT1-2) *est mise en évidence. Les autres couples se disjoignent indépendamment. Ainsi les couples de caractères allélomorphes forme du fruit (plat/rond), acidité du fruit (doux/acide) ne sont pas liés. Ceci est en contradiction avec la liaison de 35 cM qui avait été pressentie, à partir d'observations faites sur une famille à effectif limité, entre les loci responsables de ce dernier couple de caractères.*

Prunus persica ***= pêcher / génétique mendélienne / liaison génétique***

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INTRODUCTION

To introduce the partial results presented here in the context of present knowledge of peach genetics the following review of this knowledge is necessary.

The peach, *Prunus persica* (L) Batsch, is a diploid species with 2n = 16 chromosomes. Its relatively small diploid genome is contained in 0.60 ± 0.03 pg of DNA, ie 5.8 x 10^8 nucleotide base pairs (Baird et al, 1994). It is a preferential autogamous plant which is quite suitable for genetic studies, except for its long reproductive cycle (three years on average) and for the space taken by each tree.

In this review, we examine successively the polymorphism of 'phenotypic' characters (this term is used in preference to 'morphological' which is too restrictive), of isozymes, and the linkages discovered between these two types of characters. A mention is also made of the three attempts at genetic mapping made with molecular markers in the peach.

Polymorphism of phenotypic characters

The latest review included twenty-one phenotypic characters of mendelian inheritance (Monet, 1989). The list did not include the 'Wavy leaf' character (symbols *Wa/wa*) described by Scott and Cullinan (1942). The 'Slow ripening' character discovered by Brecht et al (1984) was not included, as its heredity was not well established. Finally, we did not include the resistance to *Myzus persicae* (Massonié et al, 1984) because the first results need to be confirmed (Monet and Massonié, 1994).

Since 1988, seven new characters have been described as follows:

- 'Leaf blotch' (Okie and Reilly, 1989) consists of abnormal foliar spots which are probably the expression of a mutation the inheritance of which has not yet been established.
- 'Pillar' (Scorza et al, 1989) is an upright growth habit tree with narrow angle branches.
- 'Semi-dwarf' peach (SD 22-59) described by Gradziel and Beres (1993) resembles very much the 'A72 dwarf' studied by Monet and Salesses (1975) and might be caused by the same mutation.
- 'Evergreen' is a dominant monogenic character with the symbols *Ev/ev* (Rodriguez et al, 1994).
- 'Dwarf 3', 'Pollen sterile 2', and 'Wavy leaf 2' discovered and studied by Chaparro et al (1994), with the symbols: *Dw3/dw3*, *Ps2/ps2* and *Wa2/wa2* respectively.

The complete list of these characters is given in table I.

Enzymatic polymorphism

Ten polymorphic enzymatic systems have been described in the peach as follows.

Malate dehydrogenase (EC 1.1.1.37, dimeric enzyme)

This anodal polymorphism was first underscored by Arulsekar et al (1986) on starch gel electrophoresis. The authors described three zymotypes segregating into a 1:2:1 ratio. Consequently a locus with two alleles seems to be involved, but the zymograms obtained are difficult to interpret. Even though a two-allele locus appears to be the best hypothesis, the slow band is missing in the zymotype corresponding to the slow allele, while it is present in the heterozygous form.

Durham et al (1987) noted that on the zymotype corresponding to the fast allele, two bands (2 and 3) are missing. They nevertheless concluded that the polymorphism is due to the activity of two alleles on the same locus MDH1.

Mowrey et al (1990) have an even more complex interpretation. They obtained six different zymotypes on a starch gel and suggested that such polymorphism comes from a locus MDH1 with three alleles: *MDH1-1*, *MDH1-2*, *MDH1-3* (allele 1 being rare, the most common polymorphism would come from alleles 2 and 3).

Such interpretation difficulties disappear when acrylamide gel electrophoresis is used. It offers an improved resolution but also requires a purification of the leaf extracts. In acrylamide gels, the slow band corresponding to the allele *MDH1-2*, which is not visible in starch gels, appears clearly, and so do the bands 2 and 3 of the fast allele zymotype (unpublished data). This demonstrates the existence of a MDH1 locus with two alleles: *MDH1-1/MDH1-2*.

Diaphorase (EC 1.6.4.3, monomeric enzyme)

Durham et al (1987) discovered an anodal polymorphism of diaphorase corresponding to one locus *DIA1* with two alleles *DIA1-1/DIA1-2*.

Table I. Peach mendelian characters.

Characters	*Dom*	*Rec*	*Int Dom*	*Symbols*	*Named by*	*Date*	*Comments*
Anthocyanin deficiency		Yes		*An/an*	Monet	1967	
Bushy		Yes		*Bu1/bu1* *Bu2/bu2*	Lammerts	1945	Probably monogenic
Albinism		Yes		*C/c*	Bailey and French	1933	
Cotyledon adherent		Yes		*Co/co*	Monet and Bastard	1977	
Compact tree	Yes			*Ct/ct*	Mehlenbaker and Scorza	1986	
Sweet fruit (non acid)	Yes			*D/d*	Monet	1979	
Double flower		Yes		*D1/d1*	Lammerts	1945	
Dwarf (Bonanza)		Yes		*Dw/dw*	Lammerts	1945	
Dwarf3		Yes		*Dw3/dw3*	Chaparro et al	1994	
Circular glands			Yes	*E/e*	Connors	1921	
Evergreen		Yes		*Evg/evg*	Rodriguez et al	1994	
Clingstone (canning)		Yes		*F/f/f1*	Bailey and French	1933	Allelic series?
Nectarine		Yes		*G/g*	Blake	1933	
Red leaf	Yes			*Gr/gr*	Blake	1935	
Dwarf (A72)			Yes	*N/n*	Monet and Salesses	1975	
Pillar		Yes		*Pi/pi*	Scorza et al	1989	
Weeping tree		Yes		*Pl/pl*	Monet et al	1988	
Male sterility		Yes		*Ps/ps*	Scott and Weinberger	1944	
Male sterility 2		Yes		*Ps2/ps2*	Chaparro et al	1994	
Red flower		Yes		*R/r*	Lammerts	1945	
Myzus resistance	Yes			*Rm1/rm1*	Massonié et al	1984	
Flat peach	Yes			*S/s*	Lesley	1940	
Showy flower		Yes		*Sh/sh*	Connors	1920	
Corky triangle		Yes		*T/t*	Monet and Bastard	1982	
White flower		Yes		*W/w*	Lammerts	1945	
Wavy leaf		Yes		*Wa/wa*	Scott and Cullinan	1942	
Wavy leaf 2		Yes		*Wa2/wa2*	Chaparro et al	1994	
Yellow flesh		Yes		*Y/y*	Connors	1920	
Slow ripening		Yes			Brecht et al	1984	Unnamed
Leaf blotch					Okie and Reilly	1989	Inheritance unknown
Semidwarf (SD22-59)			Yes		Gradziel and Beres	1993	Same as A72?

Dom = Dominant; Rec = recessive; Int Dom = intermediate dominance.

Peroxydase (EC 1.11.1.7, monomeric enzyme)

Durham et al (1987) found a cathodal polymorphism corresponding to one locus with the two alleles: *PER1-1* and *PER1-2*.

Esterase (EC 3.1.1.2, monomeric enzyme)

Messeguer et al (1987) obtained three zymotypes the inheritance of which has not been established but which correspond, in the simplest interpretation of the zymogram, to the expression of one locus EST1 with two alleles *EST1-1*, *EST1-2*.

Isocitrate dehydrogenase (EC 1.1.1.42, monomeric enzyme)

Messeguer et al (1987) obtained three zymotypes the mode of inheritance of which has not been established, but which probably correspond to the expression of one locus IDH2 with two alleles. According to the authors, the presence of an even more anodal activity, though not interpretable, justifies the index 2.

However Mowrey et al (1990) did not observe such anodal activity. They consider that the three zymotypes correspond to the activity of one locus IDH1 with two alleles, *IDH1-2* and *IDH1-3*; *IDH1-*

1 being reserved for an allele present in some species related to the peach *(P amygdalus)*. To simplify the symbolism while remaining within the peach species, we will adopt the symbols *IDH1-1* and *IDH1-2*.

Acid phosphatase (EC 3.1.3.2, monomeric enzyme)

Messeguer et al (1987) obtained zymograms showing two different zymotypes from protein leaf extracts. Though the genetic study of the zymotype inheritance has not been carried out, the most simple interpretation is that involving one locus with two alleles: *APS1-1*, *APS1-2*.

Shikimate dehydrogenase (EC 1.1.1.25, monomeric enzyme)

Mowrey et al (1990) obtained two zymotypes: one with a fast band related to the homozygous genotype, and another with two bands for the heterozygous genotype. After crossing a homozygous with a heterozygous individual, they observed a 1:1 disjunction in the hybrid family. The two alleles were symbolized as *SDH1-2* and *SDH1-3*, the symbol *SDH1-1* being reserved for an allele present in species related to the peach and the almond. In order to simplify the symbolism and remain in the peach species, we will adopt, as for isocitrate dehydrogenase, the symbols *SDH1-1* and *SDH1-2* instead of *SDH1-2* and *SDH1-3*.

α-Amylase (EC 3.2.1.1, monomeric enzyme)

Monet and Gibault (1991) demonstrated that α-amylase was polymorphic in the peach, and the three zymotypes present (one slow band, one fast band and two bands) correspond to the expression of one locus with two alleles: *AMY1-1* and *AMY1-2*.

Catalase (EC1.11.1.6, tetrameric enzyme)

Werner (1992) observed three zymotypes for the catalase: one slow band, one fast band and five bands. The five band zymotype is explained by the tetrameric nature of the enzyme, as there are five possible combinations of the polypeptides produced by two alleles in heterozygous individuals. The symbols suggested for the two alleles are *CAT1-1* and *CAT1-2*.

Alcohol dehydrogenase (EC 1.1.1.1, dimeric enzyme)

Monet et al (1994) demonstrated that ADH is polymorphic in the peach and that the zymograms observed represented the activity of three loci, one of which (the one coding for the slowest isozyme) has two alleles. The zymotype interpretation is complicated by the presence of bands issued from the formation of intergenic heterodimers. The two alleles involved in the polymorphism were symbolized as *ADH3-1* and *ADH3-2*.

Table II. Polymorphic isozymes of the peach.

Enzymes	*Quaternary structure*	*Allele symbols at the polymorphic locus*	*Discovered by*	*Date*	*Comment*
Malate dehydrogenase	Dimeric	*MDH1.1/MDH1.2*	Arulsekar et al	1986	
Diaphorase	Monomeric	*DIA1.1/DIA1.2*	Durham et al	1987	
Peroxydase	Monomeric	*PER1.1/PER1.2*	Durham et al	1987	Cathodal
Esterase	Monomeric	*EST1.1/EST1.2*	Messeguer et al	1987	
Isocitrate dehydrogenase	Monomeric	*IDH1.1/IDH1.2*	Messeguer et al	1987	
Acid phosphatase	Monomeric	*APS1.1/APS1.2*	Messeguer et al	1987	
Shikimate dehydrogenase	Monomeric	*SDH1.1/SDH1.2*	Mowrey et al	1990	
α-Amylase	Monomeric	*AMY1.1/AMY1.2*	Monet et al	1991	
Catalase	Tetrameric	*CAT1.1/CAT1.2*	Werner	1992	
Alcohol dehydrogenase	Dimeric	*ADH3.1/ADH3.2*	Monet et al	1994	Interallelic heterodimer

All the results on the peach enzymatic polymorphism are presented in table II.

Linkages

Because of the long cycle of the peach sexual reproduction, linkage studies are scarce. The observations gathered were made on families which were not especially created for linkage studies. This is still true for the establishment of genetic maps using molecular markers. Therefore, there has been no systematic study of the different possible associations, although scattered results are now being put together.

All these results, as well as some cases of independent disjunctions observed on other families (partly unpublished due to their secondary interest), are presented in table III.

Genetic mapping and molecular markers

Three genetic maps of the peach species have been published:

Chaparro et al (1994) built their map using RAPD markers. The map includes 15 groups of linkage homologous two by two (except for the last one which is alone) and covers 396 cM. 83 RAPD markers, four phenotypic characters (double flower *Dl*, pillar tree habit *Br* = *Pi*, purple leaf *Gr* and nectarine *G*) and the isoenzymatic locus for catalase (CAT1), are located on the map.

Dirlewanger and Bodo (1994) developed a linkage map consisting of eight linkage groups (corresponding to the eight basic peach chromosomes) and covering 350 cM. This map includes 52 RAPD markers and one phenotypic character (weeping habit *We* = *Pl*).

Rajapakse et al (1995) built a map consisting of eight linkage groups and covering 332 cM. Forty six RFLP markers, 12 RAPD and three phenotypic markers (double flower *Dl*, pillar tree habit *Pi* and flesh colour *Y*) are located on the map.

The three maps are difficult to compare, as they are made with different molecular markers and their size was not measured on the same basis (the first one includes homologous linkage groups, the second one does not). The only common feature between the first and third maps, located on the first linkage group, are the two phenotypic characters: double flower *(Dl)* and pillar tree habit *(Pi)*.

Rapid progress in establishing the peach genetic map will only be obtained if common molecular markers are adopted, to be used as anchors for the various incomplete maps which will precede the definitive one. The location of phenotypic markers on the final map, remains dependent on the creation of families in which these characters are in disjunction. This is a time-consuming process, but in the meantime, each partial result is interesting and contributes to the progress of the map. Here we present a few results obtained from a cross initially made for creating varieties of flat nectarines (platerines).

MATERIALS AND METHODS

Plant material

This study was done on a family originated from a cross between an unnamed flat nectarine S5524 and the round nectarine cv Fantasia. The hybridization made in 1989 produced 468 seeds containing immature embryos which required in vitro culture. Ninety-two plants were rescued, overwintered in a greenhouse and later planted outdoors in the orchard in 1990. The first fruit yield was obtained in 1992. The two mendelian phenotypic characters which were in disjunction in this family were fruit shape (flat and round) and fruit taste (acid or non acid). The fruit taste is easily identified by simple tasting, or, if in doubt, by measuring titratable acidity of the juice which is always superior to 100 milliequivalents per litre for acid fruits. For these two mendelian characters, the parent S5524 is heterozygous with the genetic symbols *S/s, D/d* and the parent Fantasia is homozygous recessive: *s/s, d/d.*

Isoenzyme study

The search for enzyme polymorphism was carried out on leaf protein extracts. Young leaves were harvested in April and May at the tip of actively growing shoots. They were immediately lyophilized and stored at –80 °C.

The protein extraction method was described by Monet and Gibault (1991), and the electrophoresis technique by Monet et al (1994).

The enzymatic systems found to be in disjunction in the family were the malate dehydrogenase (MDH) and the catalase (CAT). For the latter, a very long migration time (18 h) was necessary, because of the large size of the molecule, to separate the five bands of the heterozygous form. The specific revelation staining methods were those described by Vallejos (1983) for both MDH and CAT.

Table III. Couples of independent (I) or linked (L) loci in the peach.

CAT1																								▨
AMY1																							▨	
MDH1																						▨		
Wavy leaf2																					▨			
Male sterility2																				▨				
Dwarf3																			▨		L=0.4cM			
Pillar																		▨						I
Weeping tree																	▨			L=15cM		I		
Myzus resistance																▨	I							
Corky triangle															▨	I								
Sweet fruit														▨										
Anthocyanin def													▨											
Double flower												▨						L=12cM	I					
White flower											▨						L=33cM			L=25cM		I		I
Red flower										▨		I												
Dwarf Bonanza									▨	I	I						I	I		I				
Male sterility								▨	I		I			I			I					I		I
Flat peach							▨	I						L=35cM?										
Red leaf						▨					I						I	I						
Clingstone					▨			I					I											
Nectarine				▨				I		I		I			I		I	I	I					
Eglandular			▨		I			I																
Showy flower		▨	I	I	I			I					I	I	L=45cM	I	I					I	L=2cM	I
Yellow flesh	▨	I	I	I	I		I	I				I		I	I	I	I	I				L=26cM	I	I
	Yellow flesh	Showy flower	Eglandular	Nectarine	Clingstone	Red leaf	Flat peach	Male sterility	Dwarf Bonanza	Red Flower	White flower	Double flower	Anthocyanin def	Sweet fruit	Corky triangle	Myzus resistance	Weeping tree	Pillar	Dwarf 3	Male sterility2	Wavy leaf 2	MDH1	AMY1	CAT1

The parent S5524 was heterozygous for the two enzymatic systems with the genetic symbols, *MDH1-1/MDH1-2*, *CAT1-1/CAT1-2*, while Fantasia was homozygous, symbols *MDH1-2/MDH1-2*, *CAT1-2/CAT1-2*.

In fact the cross S5524 x Fantasia represents a test cross for the two phenotypic characters and the two enzymatic systems.

Statistic analysis

The linkage value is estimated according to the method of maximum likelihood using the formula (a+d)(1/p)+(b+c)(1/1–p), where p is the estimated distance in cM, a and b the frequencies of recombined phenotypes in the test cross family, b and c the frequencies of parental phenotypes (Allard, 1956).

RESULTS

Five trees died prior to fruit observation and one was an impurity (a peach with fuzzy skin). The genetic study was therefore done on 86 trees.

Table IV presents the frequencies of the two classes of individuals for each character MDH, CAT, fruit shape (round/flat) and fruit taste (acid/non acid).

The observed values must be compared for each character to the theoretical frequency of 43 relative to a 1:1 disjunction. In each case they have a high probability of being in agreement with this hypothesis; the family studied is not therefore a biased sample.

Table V shows the results of the statistical analysis carried out to detect linkages for the different associations between any pair of these characters.

In comparison with the theoretical proportions 1:1:1:1 typical of an independent disjunction (the theoretical value of each case is 21.5), all the observed disjunctions may be regarded as independent except for the CAT1/acid fruit association which does not follow this pattern. The loci for CAT1 and acid fruit are therefore linked with an estimated distance of 5.8 cM.

CONCLUSION

The present knowledge on peach genetics is still small although not negligible compared to that acquired on other woody fruit trees. Obstacles to its rapid progression are of several types:

– rarity of mutant forms; the use of induced gametic mutagenesis should be envisaged in the future to fill this gap;

Table IV. Observed segregations for characters in disjunction ie malate dehydrogenase (MDH), catalase (CAT), fruit acidity and fruit shape.

Locus	♀ *genotype*	♂ *genotype*	*Observed segregation*		*Total*	χ^2	*Prob*
MDH-1	1/2	2/2	38 (2/2)	48 (1/2)	86	1.16	0.3–0.2
CAT-1	1/2	2/2	40 (2/2)	46 (1/2)	86	0.40	0.7–0.5
D (fruit taste)	D/d	d/d	41 (d/d)	45 (D/d)	86	0.18	0.3–0.2
S (fruit shape)	S/s	s/s	38 (s/s)	48 (S/s)	86	1.16	0.3–0.2

Table V. Detected linkages in the different associations between any two of the four characters.

Joint segregation of:	χ^2	*Probabiity*	*Distance in cM*
MDH-1/CAT-1	2.37	0.50	–
MDH-1/D	1.34	0.80–0.70	–
MDH-1/S	3.01	0.50–0.30	–
CAT-1/D	67.7	< 0.001	5.8
CAT-1/S	2.08	0.70–0.50	–
D/S	2.73	0.50–0.30	–

- length of time required to create a family in which new characters are in disjunction;
- lack of coordination in the choice of molecular markers; the establishment of genetic maps should not be done without adopting a minimum number of common markers.

The new results presented in this paper are:

- a relatively narrow linkage between the catalase locus CAT1 and the fruit acidity locus, which means that selection for fruit acidity could be achieved with the help of this marker;
- an independent disjunction between the pairs of loci MDH1-CAT1, MDH1 – fruit acidity, MDH1 – flat fruit shape, CAT1 – flat fruit shape and fruit acidity – flat fruit shape. This last disjunction is in contradiction with the results previously published based on a too small family of 23 plants (Monet et al, 1985). There is probably no linkage between the two characters.

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