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Kernel taste inheritance in almond

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SUMMARY – Kernel taste (sweet or bitter) has been observed in 4919 seedlings, derived from 152 controlled crosses, using 61 cultivars as parents. The kernel of 4771 seedlings (96.99%) was sweet and 148 kernels (3.01%) were bitter. In 133 families (4206 seedlings), all the trees gave sweet kernels. In 19 progenies, with a total of 713 seedlings analysed, a proportion of 79.24% of sweet almonds (565 seedlings) and 20.76% of bitter almonds (148 seedlings) was recorded. This proportion is close to the expected (75% sweet and 25% bitter), as the kernel taste is considered to be controlled by a gene, sweet being dominant over bitter. The information obtained from analysing these 19 families, has allowed 18 cultivars to be classified as heterozygous. On the other hand, in 81 of the analysed crosses, at least one of the parents was heterozygous. The study of these progenies and the knowledge of the origin of some of the cultivars used as parents, has also allowed 20 cultivars to be classified as homozygous for sweetness.

Key words: Almond, breeding, progenies, cultivars, kernel taste.

RESUME – “Hérédité du goût de l'amande”. Le caractère goût de l'amande (doux, amer) a été observé sur 4919 arbres, provenant de 152 croisements contrôlés, utilisant 61 cultivars comme géniteurs. Le fruit de 4771 arbres (96,99%) est doux et celui de 148 (3,01%) amer. Dans 133 familles (4206 arbres), la totalité des arbres ont donné des amandes douces. Dans 19 familles, avec un total de 713 arbres analysés, a été enregistrée une proportion de 79,24% d'amandes douces (565 arbres) et 20,76% d'amères (148 arbres). Cette proportion est proche de celle espérée (75% douces et 25% amères), puisque le goût est considéré comme contrôlé par un seul gène avec dominance du caractère doux sur l'amer. L'information obtenue dans l'analyse de 19 familles, a permis de classer 18 cultivars comme hétérozygotes. D'autre part, dans 81 des croisements analysés, au moins, un des géniteurs était hétérozygote. L'étude de ces descendance et la connaissance de l'origine d'une part des cultivars utilisés comme géniteurs, a permis aussi de classer 20 cultivars comme homozygotes pour le caractère doux.

Mots-clés : Amandier, amélioration génétique, croisements, variétés, goût de l'amandon.

Introduction

Almond kernel taste is an important commercial trait and varies with the cultivar genotype. Differences in flavour are due to the presence of the glycoside amygdaline that gives the “bitter” principle. Low levels or the absence of amygdaline produces the “sweet” flavour. There are sweet, bitter and slightly bitter cultivars. Bitterness in almond seeds results from hydrolysis of amygdaline after crushing or chewing and it is enzymatically transformed in benzylaldehyde (which is bitter) and cyanide (which is poisonous) (Conn, 1980). Even though in some products is appreciated a light bitter taste, the bitterness is a very serious commercial problem, due to the possible toxicity. Bitterness is controlled by the genotype of the seed mother, and not by the pollen parent, as the amygdaline precursor is translocated from the mother plant to the developing seed. Thus, cultivar pollinator does not affect kernel taste. All the fruits of an almond tree are sweet or bitter, according to the genotype of the tree (Kester and Gradziel, 1996; Socias i Company, 1998).

The bitterness is a chemical defense of wild almond species, it apparently protects the seed against predation by animals. Sweet kernels which originated in these plants by mutation, led to the domestication of the almond. As a consequence of growers selection, a decrease on the frequency of alleles responsible for the bitter taste in this species has occurred (Browicz and Zohary, 1996).

Bitterness in almond is controlled by a single recessive gene with two alleles: S (sweet) dominant over s (bitter) and was first identified by Heppner (1923, 1926). This monogenic relationship has been confirmed by almond breeders and the genotype of some cultivars has been known. Most Californian and some Mediterranean almond cultivars are heterozygous for bitter (Ss) and a number of homozygous sweet (SS) have been also identified through crossing (Kester and Asay, 1975; Kester *et al.*, 1977;

Spiegel-Roy and Kochba, 1977, 1981; Grasselly and Crossa-Raynaud, 1980; El Gharbi, 1981; Vargas *et al.*, 1984; Vargas and Romero, 1988; Dicenta and García, 1992; Kester and Gradziel, 1996). Among the heterozygous cultivars (Ss), it is possible to find sweet ('Atocha', 'Marcona') or slightly bitter ('Garrigues') kernels. Dicenta and García (1992) suggest that slightly bitter forms must correspond to heterozygous trees (Ss) and occasionally the presence of the recessive allele may produce a certain degree of bitterness.

Usually, in breeding programmes only sweet types are used. Three possible crosses (SS × SS, SS × Ss and Ss × Ss) between sweet kernel genotypes (SS or Ss) produce 100% progeny having sweet almonds, but when both parents are heterozygous (Ss), presumably about 25% of the seedlings will have bitter kernel. Crosses between sweet (SS or Ss) and bitter (ss), can give the 100% or about the 50% of the seedlings with sweet kernel. A bitter (ss) × bitter (ss) cross produces progenies with only bitter almonds.

In this paper, the results of a large number of controlled crosses made between sweet genotypes since 1975 at IRTA's almond breeding programme are presented and the genotypes of some cultivars are deduced.

Materials and methods

The kernel taste has been observed in 4919 seedlings, derived from 152 controlled crosses, made at IRTA Mas Bové during the period 1975-1993, using 61 sweet cultivars (SS or Ss) as parents. The observations were carried out in different years between 1979 and 1998.

The trait was recorded only as sweet or bitter kernel. The slightly bitter kernel were classified as sweet kernels, like in the market. It is not easy to determine exactly types producing "slightly" bitter kernels.

Results and discussion

The kernels of 4771 seedlings (96.99%) were sweet and of 148 seedlings (3.01%) were bitter. In 133 families (4206 seedlings), all the trees gave sweet kernels and in 19 progenies (713 seedlings) there were seedlings with sweet kernels and seedlings with bitter kernels. In this last progenies with some bitter kernel seedlings, a proportion of 79.24% of sweet almonds (565 seedlings) and 20.76% of bitter almonds (148 seedlings) was recorded (Table 1). This percentage is close to the expected (75% sweet and 25% bitter).

Classification as heterozygous

In Table 2 (made from Table 1), the 16 parents used in the 19 progenies which gave some seedlings with bitter kernels are shown. Obviously, if the two parents used in one cross are sweet and there are some bitter almond in the progeny, the two parents will be heterozygous (Ss) for this kernel trait. Therefore, this 16 parents can be considered heterozygous.

As 'Ferragnes' is homozygous (Grasselly and Crossa-Raynaud, 1980; Dicenta and García, 1992), genotype which was confirmed and the selections ('Ferragnes' × 'Filippo Ceo')092, ('Ferragnes' × 'Troito')13 and ('Ferragnes' × 'Troito')30 are heterozygous, the cultivars 'Filippo Ceo' and 'Troito' will be also heterozygous.

Table 5 lists the 18 cultivars and selections classified as heterozygous. In earlier work (Vargas and Romero, 1988), 5 of these cultivars were classified already as heterozygous ('Desmayo Largueta', 'Gabaix', 'Mena d'en Musté', 'Texas' and 'Tuono'). In addition, Dicenta and García (1992) reported as heterozygous to 'Genco' and 'Tuono', Spiegel-Roy and Kochba (1977) to 'Marcona' and Kester and Asay (1975) to 'Texas'.

Table 1. Progenies with some seedlings with bitter kernels

Cross [†]	Number seedlings			% Seedlings	
	Total	Sweet	Bitter	Sweet	Bitter
'Desmayo Langueta' 'Mena d'en Musté'	1	0	1	0.00	100.00
'Falsa Barese' 'Desmayo Langueta'	50	40	10	80.00	20.00
'Falsa Barese' 'Marcona'	168	135	33	80.36	19.64
'FGFP092' [†] 'Marcona'	52	41	11	78.85	21.15
'FGTR13' [†] 'Desmayo Langueta'	19	12	7	63.16	36.84
'FGTR13' [†] 'Marcona'	12	11	1	91.67	8.33
'FGTR30' [†] 'Marcona'	8	7	1	87.50	12.50
'FLTU18' [†] 'Desmayo Langueta'	3	2	1	66.67	33.33
'FLTU18' [†] 'Marcona'	44	35	9	79.55	20.45
'Genco' 'Desmayo Langueta'	9	7	2	77.78	22.22
'Genco' 'Marcona'	20	15	5	75.00	25.00
'Marcona' 'Carriset'	12	9	3	75.00	25.00
'Marcona' 'Esperanza Forta'	9	4	5	44.44	55.55
'Marcona' 'Mas Bové -1'	10	8	2	80.00	20.00
'Stelliete' 'Marcona'	67	57	10	85.07	14.93
'Texas' 'Gabaix'	43	33	10	76.74	23.26
'Tuono' 'Desmayo Langueta'	98	78	20	79.59	20.41
'Tuono' 'Marcona'	45	38	7	84.44	15.56
'Tuono' 'Mena d'en Musté'	43	33	10	76.74	23.26
Total	713	565	148	79.24	20.76

[†]'FGFP092' = ('Ferragnes' 'Filippo Ceo')092, 'FGTR13' = ('Ferragnes' 'Troito')13, 'FGTR30' = ('Ferragnes' 'Troito')30, 'FLTU18' = ('Ferralise' 'Tuono')18.

Table 2. Parents used in progenies with some seedlings with bitter kernels

Parent (mother or father) [†]	Number crosses	Number seedlings		
		Total	Sweet	Bitter
'Carriset'	1	12	9	3
'Desmayo Langueta'	6	180	139	41
'Esperanza Forta'	1	9	4	5
'Falsa Barese'	2	218	175	43
'FGFP092' [†]	1	52	41	11
'FGTR13' [†]	2	31	23	8
'FGTR30' [†]	1	8	7	1
'FLTU18' [†]	2	47	37	10
'Gabaix'	1	43	33	10
'Genco'	2	29	22	7
'Marcona'	11	447	360	87
'Mas Bové -1'	1	10	8	2
'Mena d'en Musté'	2	44	33	11
'Stelliete'	1	67	57	10
'Texas'	1	43	33	10
'Tuono'	3	186	149	37

[†]'FGFP092' = ('Ferragnes' 'Filippo Ceo')092, 'FGTR13' = ('Ferragnes' 'Troito')13, 'FGTR30' = ('Ferragnes' 'Troito')30, 'FLTU18' = ('Ferralise' 'Tuono')18.

Classification as homozygous

In 81 of the 152 analysed crosses, at least one of the parents was heterozygous. In one cross, when one of the parents is heterozygous (Ss), it is necessary that the other parent would be homozygous (SS), to obtain all seedlings with sweet kernel.

In Table 3, 53 crosses made using some of the 18 heterozygous cultivars and giving progenies with all sweet kernelled seedlings are shown.

Table 3. Crosses made with one heterozygous parent (Ss) and with all the seedlings analysed with sweet kernel

Crosses [†]	Number seedlings	Crosses [†]	Number seedlings
'4-665' 'Stelliette'	13	'FGFP092' [†] 'Glorieta'	5
Total '4-665'	13	'FGTR13' [†] 'Glorieta'	12
'A-202' 'FGFP092' [†]	4	'FGTR30' [†] 'Glorieta'	27
'A-202' 'FGTR30' [†]	5	'FLTU18' [†] 'Glorieta'	5
'A-202' 'Marcona'	10	'Stelliette' 'Glorieta'	36
'A-202' 'Stelliette'	6	Total 'Glorieta'	85
Total 'A-202'	25	'Lauranne' 'D. Langueta' [†]	68
'A-226' 'Marcona'	16	'Lauranne' 'Marcona'	136
Total 'A-226'	16	Total 'Lauranne'	204
'FGTR13' [†] 'Anxaneta'	39	'FGTR13' [†] 'Masbovera'	6
'FGTR30' [†] 'Anxaneta'	27	'FGTR30' [†] 'Masbovera'	2
'FLTU18' [†] 'Anxaneta'	42	'FLTU18' [†] 'Masbovera'	22
'Anxaneta' 'Tuono'	3	'Genco' 'Masbovera'	88
Total 'Anxaneta'	111	'Stelliette' 'Masbovera'	44
'Cristomorto' 'D. Langueta' [†]	34	'Masbovera' 'Tuono'	3
'Cristomorto' 'Esp. Forta' [†]	49	Total 'Masbovera'	165
'Cristomorto' 'Gabaix'	96	'Marcona' 'Pla. Elche'	17
'Cristomorto' 'Marcona'	79	Total 'Planeta de Elche'	17
'Cristomorto' 'M. Musté' [†]	38	'Primorskiy' 'Marcona'	96
'Cristomorto' 'Texas'	15	'Primorskiy' 'M. Musté'	8
'Cristomorto' 'Tuono'	22	Total 'Primorskiy'	104
Total 'Cristomorto'	333	'FGFP092' [†] 'Ramillete'	1
'Ferragnes' 'D. Langueta' [†]	309	'FGTR13' [†] 'Ramillete'	40
'Ferragnes' 'Esp. Forta'	20	'Falsa Barese' 'Ramillete'	20
'Ferragnes' 'Marcona'	216	'Genco' 'Ramillete'	13
'Ferragnes' 'M. Musté' [†]	61	'Ramillete' 'D. Langueta' [†]	10
'Ferragnes' 'Tuono'	167	'Ramillete' 'M. Musté' [†]	10
Total 'Ferragnes'	773	Total 'Ramillete'	94
'Stelliette' 'Francolí'	2	'T. Verdiere' [†] 'Marcona'	7
'Francolí' 'FGTR30' [†]	41	'T. Verdiere' [†] 'M. Musté' [†]	17
'Francolí' 'D. Langueta' [†]	1	Total 'Tardive de la Verdiere'	24
Total 'Francolí'	44		
'Garbi' 'FGTR30' [†]	4		
'Garbi' 'D. Langueta' [†]	15		
'Garbi' 'Marcona'	4		
'Garbi' 'Stelliette'	37		
Total 'Garbi'	60		

[†]'D. Langueta' = 'Desmayo Langueta', 'Esp. Forta' = 'Esperanza Forta', 'FGFP092' = ('Ferragnes' 'Filippo Ceo')092, 'FGTR13' = ('Ferragnes' 'Troito')13, 'FGTR30' = ('Ferragnes' 'Troito')30, 'FLTU18' = ('Ferralise' 'Tuono')18, 'M. Musté' = 'Mena d'en Musté', 'Pla. Elche' = 'Planeta de Elche', 'T. Verdiere' = 'Tardive de la Verdiere'

From this Table 3, 15 cultivars could be classified as homozygous (SS). Some of these results can be confirmed with observations about the origin of 3 cultivars ('Anxaneta', 'Glorieta' and 'Masbovera') and 3 selections ('4-665', 'A-202' and 'A-226') given in Table 4. This Table 4 gives also information to classify as homozygous one cultivar ('Tarragonés') and four selections ('A-209', 'A-220', 'A-232' and 'A-60').

Table 4. Origin of some parents used in the crosses

Genitor	Origin		Genotype expected
'4-665'	'Primorskiy' (SS)	'Cristomorto' (SS)	SS
'A-202'	'Primorskiy' (SS)	'Cristomorto' (SS)	SS
'A-209'	'Primorskiy' (SS)	'Cristomorto' (SS)	SS
'A-220'	'Cristomorto' (SS)	'Primorskiy' (SS)	SS
'A-226'	'Cristomorto' (SS)	'Primorskiy' (SS)	SS
'A-232'	'Cristomorto' (SS)	'Primorskiy' (SS)	SS
'A-60'	'Cristomorto' (SS)	'Tardive de la Verdier' (SS)	SS
'Anxaneta'	'Primorskiy' (SS)	'Cristomorto' (SS)	SS
'Glorieta'	'Primorskiy' (SS)	'Cristomorto' (SS)	SS
'Masbovera'	'Primorskiy' (SS)	'Cristomorto' (SS)	SS
'Tarragonés'	'Cristomorto' (SS)	'Primorskiy' (SS)	SS

This study has allowed to classify 20 cultivars as homozygous for sweetness (Table 5). Grasselly and Crossa-Raynaud (1980) classified as homozygous to 'Ferragnes' and, wrongly, as heterozygous to 'Cristomorto' (in one progeny only two bitter almonds were obtained). Dicenta and García (1992) classified as homozygous 'Ferragnes' and 'Ramillete' in agreement with this work.

Table 5. Heterozygous (Ss) and homozygous (SS) cultivars for kernel taste

Heterozygous (Ss)		Homozygous (SS)	
Cultivars and selections [†]	Origin	Cultivars and selections [†]	Origin
'Carriset'	Spain	'4-665'	Spain
'Desmayo Langueta'	Spain	'A-202'	Spain
'Esperanza Forta'	Spain	'A-209'	Spain
'Falsa Barese'	Italy	'A-220'	Spain
'FGFP092' [†]	Italy	'A-226'	Spain
'FGTR13' [†]	Greece	'A-232'	Spain
'FGTR30' [†]	Greece	'A-60'	Spain
'Filippo Ceo'	Italy	'Anxaneta'	Spain
'FLTU18' [†]	France	'Cristomorto'	Italy
'Gabaix'	Spain	'Ferragnes'	France
'Genco'	Italy	'Francolí'	Spain
'Marcona'	Spain	'Garbi'	Spain
'Mas Bové-1'	Spain	'Glorieta'	Spain
'Mena d'en Musté'	Spain	'Lauranne'	France
'Stelliette'	France	'Masbovera'	Spain
'Texas'	USA	'Planeta de Elche'	Spain
'Troito'	Greece	'Primorskiy'	Ukraine
'Tuono'	Italy	'Ramillete'	Spain
		'Tardive de la Verdier'	France
		'Tarragonés'	Spain

[†]'FGFP092' = ('Ferragnes' 'Filippo Ceo')092, 'FGTR13' = ('Ferragnes' 'Troito')13, 'FGTR30' = ('Ferragnes' 'Troito')30, 'FLTU18' = ('Ferragne' 'Tuono')18.

Conclusions

The study of the progenies and the knowledge of the pedigree of some of the cultivars used as parents, has allowed to classify 18 cultivars and selections as heterozygous (Ss) and 20 as homozygous (SS) for the sweetness of the kernel.

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