

Inheritance and relationships of important agronomic traits in almond

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Abstract The inheritance of 16 important agronomic traits and its relationship were studied for four years in a population of 167 almond [*P. dulcis* (Mill.) D.A. Webb] seedlings obtained from a cross between the French selection ‘R1000’ (‘Tardy Nonpareil’ × ‘Tuono’) and the Spanish cultivar ‘Desmayo Largueta’. For some traits (blooming and leafing date) descendants segregated between the value of both progenitors, meanwhile for others the mean of the offspring was lower (bloom density, productivity and ripening date) or higher (in-shell/kernel ratio and double kernels). As expected, kernel bitterness and self-incompatibility behaved as monogenic traits. Some important correlations between traits were detected. The implications of the transmission and the correlation of these traits in the breeding programmes are discussed.

Keywords Almond · *Prunus dulcis* · Breeding · Quantitative traits · Qualitative traits · Kernel quality · Inheritance · Correlations

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Introduction

The efficiency of cross-breeding programs mainly depends on the choice of the progenitors and the knowledge on the transmission of traits we want to improve. A high efficiency is especially important in fruit breeding, almond included, due to the high cost and time consuming of breeding programs of these species.

Late blooming has been one of the most important objectives of the almond breeding programs (Kester 1965; Grasselly 1972; Vargas et al. 1984; Socias i Company et al. 1999), and its transmission studied (Kester et al. 1977a; Dicenta et al. 1993a). Blooming density and productivity are also two important traits, which were studied by Grasselly (1972), Kester and Asay (1975), Grasselly and Crossa-Raynaud (1980), Vargas et al. (1984) and Dicenta et al. (1993a). Some studies were also performed regarding the time of maturity (Grasselly 1972; Kester and Asay 1975; Dicenta et al. 1993a).

Furthermore, there are studies on transmission of some fruit and kernel traits (Grasselly 1972; Spiegel-Roy and Kochba 1974, 1981; Kester et al. 1977b; Vargas et al. 1984; Dicenta et al. 1993b). In addition, self-compatibility was studied by different authors determining its monogenic nature with a multi-allelic *S* series, and identifying the *S_f* allele as responsible for self-compatibility (Grasselly et al. 1981; Socias i Company and

Felipe 1988; Dicenta and García 1993a; Rovira et al. 1997; Bošković et al. 1999; Ortega and Dicenta 2003). Finally, kernel bitterness was characterized as a monogenic trait, the bitter genotype being recessive (Heppner 1923, 1926; Dicenta and García 1993b; Vargas et al. 2001).

On the other hand, a close relationship between traits could facilitate or hinder the breeding process, since the selection for a given trait, could favour the presence of another desirable or undesirable characteristic for this fruit tree (Dicenta and García 1992).

The objective of this work was to study the inheritance of different tree and fruit traits in an almond progeny of 167 seedlings from a cross between the French selection ‘R1000’ and the Spanish cultivar ‘Desmayo Langueta’ for four years and the most important correlations between these traits.

Material and methods

Plant material

The plant material assayed is an almond progeny of 167 seedlings from the cross ‘R1000’ × ‘Desmayo Langueta’, performed in 1996 at INRA-Avignon (France) by Mr Henri Duval. ‘Desmayo Langueta’ is a traditional Spanish cultivar, early blooming, late ripening and self-incompatible. On the other hand, ‘R1000’ is a late-blooming, mid-ripening, self-compatible selection of INRA from a cross between the North American cultivar ‘Tardy Nonpareil’ and the Italian self-compatible cultivar ‘Tuono’. In 1997 the seeds obtained were germinated and the seedlings planted (1 × 3m spacing, under drip irrigation) in the orchard at the experimental field of CEBAS-CSIC in Murcia (Spain).

Evaluation of agronomic traits

During the years 2000, 2001, 2002 and 2003 the following tree traits were studied:

- Blooming date (Julian days when 50% of flowers were opened)
- Blooming density (scored between 0 = null and 5 = maximum)

- Leafing date (Julian days when 50% of vegetative buds were sprouted) (only data of 2003 available)
- Productivity (scored between 0 = null and 5 = maximum)
- Ripening date (Julian days when 95% of fruits had their mesocarp opened)
- *S* genotypes of progenitors and descendants were identified in 2003 by *S*-allele specific PCR using the primers AmyC5R and AS1II and the cycling parameters indicated by Tamura et al. (2000).

On the other hand, each year, at maturity state, a sample of 25 fruits was taken and stored at room temperature. The fruit and kernel traits studied in 2000, 2001, 2002, and 2003 were:

- In-shell weight (g)
- Shell hardness (scored between 1 = very soft and 5 = very hard, by cracking with a hammer).
- Kernel weight (g)
- In-shell/kernel ratio (%)
- Empty nuts (%) (nuts without kernels)
- Double kernels (%) (two deformed kernels in the same nut)
- Kernel thickness (scored 1. flat, 2. intermediate, 3. globose)
- Kernel shrivelling (scored 1. smooth, 2. intermediate, 3. wrinkle)
- Pellicle colour intensity (scored between 1 = very light brown and 5 = very dark brown)
- Kernel bitterness (by tasting some almonds by two people, classifying each genotype as sweet, slightly bitter or bitter).

Statistical analysis

Mean, minimum and maximum values of traits, were calculated for the four years of the study. Differences between years for each trait were analyzed by Duncan Multiple Range Test. The distribution of the seedling population for each trait was represented in frequency histograms, using the mean values of the four years of the study. In the case of self-compatibility and kernel bitterness, the number of individuals of each type was analysed by the test of goodness-

of-fit chi-square (χ^2), against the expected frequencies for one gene with dominance of self-compatibility and sweet flavour. Finally, correlation between traits was calculated with row data of the four years, using the Pearson correlation coefficient.

Results and discussion

Blooming date

The blooming date of the descendants spread between the earliest progenitor ('Desmayo Largueta') and the latest one ('R1000'), with a range of 32 days, considering the mean values of each descendant for the four years. Neither of the descendants was earlier than 'Desmayo Largueta' (blooming day 29) nor later than 'R1000' (blooming day 72). The population seems to follow a bimodal distribution (Fig. 1). The Duncan Test did not detect any difference between years 2000, 2001 and 2002, but in 2003 the trees bloomed later (Table 1).

Kester (1965), Grasselly (1978), and Socias i Company et al. (1999), studying some descendants of 'Tardy Nonpareil' also observed a bimodal distribution for this trait what was explained by the presence of a late blooming major gene, quantitatively modified by other minor genes. This seems to be the case of our

population, as the progenitors of 'R1000' are 'Tardy Nonpareil' and 'Tuono'. On the other hand, Ballester et al. (2001) studied a population from 'Tardy Nonpareil', identified three molecular markers associated with this "late blooming gene", and located this trait in the linkage group four of the 'Felisia' × 'Bertina' genetic map.

Despite this case of descendants of 'Tardy Nonpareil', in general, blooming date was considered as a quantitative trait by several authors (Grasselly 1972; Vargas and Romero 2001) with a high heritability (Kester et al. 1977a; Dicenta et al. 1993a, 2005a). Dicenta et al. (2005a) established that the best strategy to obtain late-blooming descendants is to cross progenitors as late-blooming as possible. When the offspring show a bimodal distribution we must select the latest-blooming, probably carrying the late-blooming allele, which could be transmitted to its descendants. Despite the fact that we did not find any descendant blooming later than the progenitors, this has indeed happened in other crosses, being used by the breeders to delay the blooming date of the descendants even more.

Blooming density and productivity

Mean values of blooming density and productivity of all the genotypes showed significant differences between the four years of the study (Table 1) the

Fig. 1 Distribution of the 167 almond seedlings of 'R1000' x 'Desmayo Largueta' for the tree traits: blooming date, blooming density, leafing date, productivity, ripening date and S genotype

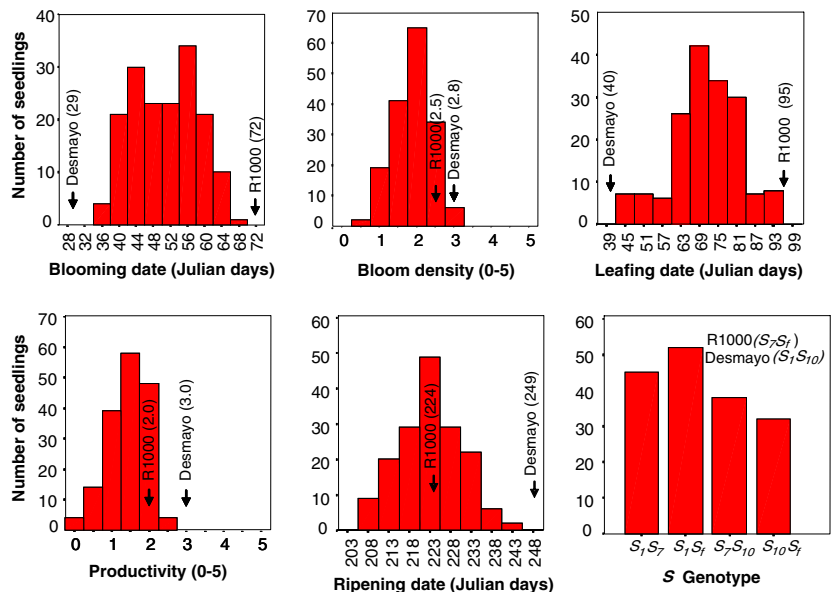


Table 1 Evaluation of quantitative traits in the 167 almond seedlings of ‘R1000’ x ‘Desmayo Largueta’

	Year				Total		
	2000	2001	2002	2003	<i>x</i>	<i>m</i>	<i>M</i>
Blooming date	46 b	46 b	46 b	62 a	50.7	35.0	67.3
Blooming density	0.9 c	2.1 b	2.5 a	2.6 a	2.0	0.8	3.2
Leafing date	–	–	–	71	70.8	45.0	95.0
Productivity	0.5 d	1.2 c	2.0 a	1.8 b	1.4	0.0	2.7
Ripening date	209 d	216 c	224 b	227 a	222.3	205.3	244.0
In-shell weight	3.3 a	3.3 a	3.2 ab	2.9 b	3.1	1.1	5.5
Shell hardness	3.4 b	3.6 ab	3.7 a	3.4 b	3.5	1.3	5.0
Kernel weight	1.0 b	1.0 b	1.0 a	1.0 b	1.0	0.6	1.6
In-shell/kernel ratio	34 a	33 a	36 a	37 a	35.4	19.7	73.0
Empty nuts	1.0 a	1.0 a	1.0 a	1.0 a	1.0	0.0	21.0
Double kernels	8.0 a	3.0 b	5.0 b	4.0 b	3.9	0.0	43.0
Kernel thickness	2.2 a	2.0 b	2.0 b	2.4 a	2.1	1.0	2.7
Kernel shrivelling	1.8 a	1.5 b	1.1 c	1.8 a	1.5	1.0	2.3
Pellicle colour	1.8 b	2.7 a	1.8 b	2.6 a	2.3	1.0	4.0

Values with different letters showed statistically significant differences between years at the 5% level according to the Duncan Test

Mean value for each year. Mean (*x*), minimum (*m*), and maximum (*M*) for the four years

third and fourth being the most productive ones. In general we have observed a normal distribution of both traits in the population (Fig. 1). The productivity was a little lower than the blooming density and we never obtained high levels, probably as a consequence of the culture conditions (narrow planting). The descendants were less floriferous (2.0 on average over the four years) and less productive (1.4 on average over the four years) than their parents (Fig. 1). The reason for obtaining these low values is a consequence of the mean value being calculated for the first years of production (when usually productivity is low) and the narrow planting.

Grasselly (1972) indicated that the most productive trees at the first blooming were also the most productive along the following years. However, Kester and Asay (1975) pointed out that the selection for blooming density and productivity should begin at the fourth or fifth year. Vargas et al. (1984) observed a good transmission of these traits in the progenies. Dicenta et al. (1993a) determined that these traits are quantitative, influenced by the year, mainly when trees are young, and with an intermediate heritability. Usually the culture conditions of the descendants in the breeding programmes are not the most appropriate ones to evaluate the productivity. However, it is true that the behaviour of each

seedling will be more or less similar to the tree in a commercial plantation, once they have been grafted on a suitable rootstock.

Leafing date

The leafing date of the descendants showed a normal distribution with a range of 50 days (Table 1). Most of the genotypes sprouted between the earliest progenitor (‘Desmayo Largueta’, leafing day 40) and the latest one (‘R1000’, leafing day 95) (Fig. 1). As only data for one year was available, the influence of environment on this trait was not studied.

Kester et al. (1977a) indicated a high heritability for this trait in almond progenies. Dicenta et al. (2005a) obtained a heritability of 0.69, analyzing 502 descendants of 13 families. In general, leafing date has been a trait that breeders have associated with blooming date. Indeed, almond trees normally first bloom and later leaf. Some growers think that when leafing occurs at the same time or before blooming, competition between both types of buds results in lost of blooming buds.

Ripening date

A great inter-annual variation was observed for the mean values of all the genotypes between the four

years of the study, indicating the influence of the environmental conditions in this characteristic (Table 1). It is curious, that the ripening date mean of the population was later as the seedlings aged. The ripening date showed a normal distribution between the earliest progenitor ('R1000', at day 224) and the latest ('Desmayo Langueta', at day 249) for 50% of the descendants. However, some seedlings ripened before 'R1000', even 18 days before (at day 206) (Fig. 1). Neither descendant was later than 'Desmayo Langueta'.

Grasselly (1972) and Kester and Asay (1975) established that this trait was characteristic of each cultivar, quantitative and easily transmitted to the offspring. In addition, Dicenta et al. (1993a) obtained high values of heritability for this trait, and suggested the presence of non-additive factors, which would allow breeders to hasten the ripening date, which coincides with our results. The ability to obtain earlier ripening descendants than progenitors is very interesting for breeders, as this characteristic is very important in cold areas to accelerate the harvest.

Self-compatibility

The results of PCR differentiated the self-incompatibility alleles, S_I (1.1 kb), S_7 (2.0 kb) and S_{I0} (0.6 kb), and the S_f allele (1.3 kb) in the progeny.

The S genotypes of the parents 'R1000' (S_7S_f) and 'Desmayo Langueta' ($S_I S_{I0}$) were as previously described by Ortega and Dicenta (2004) and Ortega et al. (2005), respectively. The S genotypes of the descendants were those expected from the parents and the monogenic hypothesis accepted for this trait, with a probability ≥ 0.05 . Half of the seedlings were self-compatible ($S_I S_f$ or $S_{I0} S_f$) and the other half self-incompatible ($S_I S_7$ or $S_7 S_{I0}$) (Fig. 1).

Socias i Company and Felipe (1977) studied the transmission of self-compatibility in almond progenies and pointed out the heterozygosity of the self-compatible progenitor and the dominance of self-compatibility. Dicenta and García (1993a) (by fluorescence microscopy) and Rovira et al. (1997) (by fruit set), determined that self-incompatibility is a monogenic trait with a multi-allelic S series, being the self-compatible allele (S_f) dominant over the others. Later, Bošković et al.

(1999) studied the transmission of S -alleles to the offspring by analysis of styler ribonucleases. Recently, Ortega and Dicenta (2003) using three different methods (fluorescence microscopy, styler ribonuclease assay and S -allele PCR) showed different breeding strategies to assure self-compatibility in the offspring. Nowadays, the early selection of self-compatible seedlings in the nursery before taking the plantlets to the orchard is a routine practice in our almond breeding program.

In-shell weight

Duncan test did not show important differences between years, although in 2003 the nuts were slightly smaller (Table 1) indicating a stability of this trait in our growth conditions. The variability in the descendants was very high, as we found fruits from 1 to 5 g. Some of the descendants showed nut weights similar to 'R1000' (3.5 g) and 'Desmayo Langueta' (4.0 g), although most of them had smaller nuts than 'R1000' (up to 1.1 g) and only some of the descendants showed bigger values than 'Desmayo Langueta' (up to 5.5 g) (Fig. 2).

In the case of hard-shelled almonds, in-shell weight is not an important trait for the breeder, as this trait mainly depends on the shell and not on the kernel. Kester et al. (1977b) and Spiegel-Roy and Kochba (1981) obtained slightly high heritability for this trait. Later, Dicenta et al. (1993b) obtained a high heritability for this trait, although observed a slight effect of the year, due to the known influence of productivity on fruit size (Hill et al. 1987). Arteaga and Socias i Company (2001) obtained a heritability very low (0.2) for this trait.

Shell hardness and in-shell/kernel ratio

Duncan test showed small inter-annual differences for shell hardness and for in-shell/kernel ratio (Table 1). More than half of the descendants showed similar shell hardness (scored 4.5) as the parents 'Desmayo Langueta' (4.1) and 'R1000' (4.2). However, some of them had harder shells, but mainly softer shells (Fig. 2). The variability within the population for in-shell/kernel ratio was

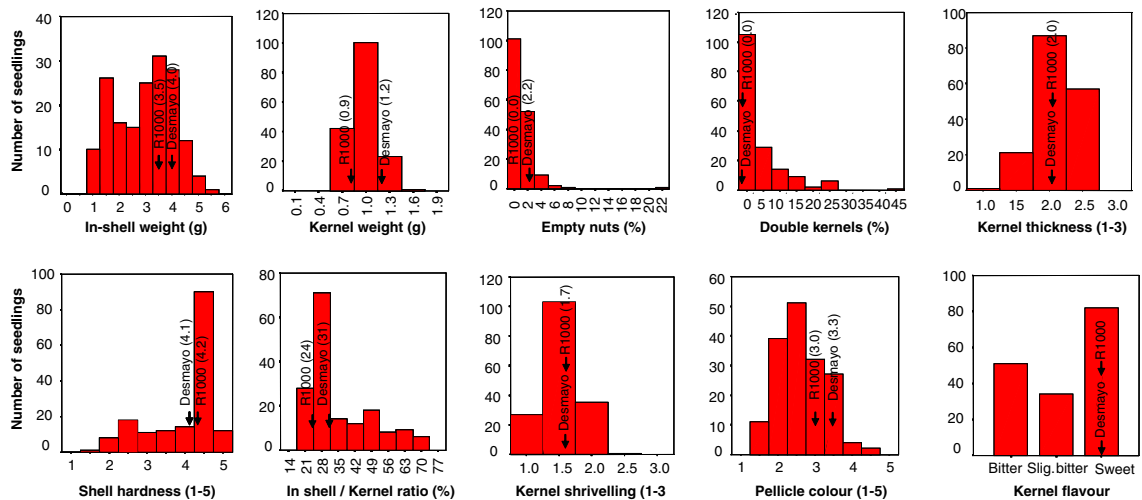


Fig. 2 Distribution of the 167 almond seedlings of ‘R1000’ x ‘Desmayo Langueta’ for the fruit traits: in-shell weight, shell hardness, kernel weight, in-shell/kernel ratio, empty

nuts, double kernels, kernel thickness, kernel shrivelling, pellicle colour and kernel flavour

very high (between 20 and 73%) (Table 1). In spite of most of the descendants falling between ‘R1000’ (24%) and ‘Desmayo Langueta’ (31%), some of them showed lower but mainly higher percentages (Fig. 2).

Grasselly (1972) and Grasselly and Crossa-Raynaud (1980) indicated that the inheritance of shell hardness was controlled by major genes, hard shell being dominant, although when cultivars with intermediate shell hardness were crossed the inheritance was more complex. Kester et al. (1977b) and Dicenta et al. (1993b) proposed that shell hardness and in-shell/kernel ratio were quantitative traits, with an intermediate heritability. Arteaga and Socias i Company (2001) obtained the lowest heritability (around 0.3) for shell hardness. Our results seem to indicate that these traits are more complex than previously proposed by Grasselly (1972) and Grasselly and Crossa-Raynaud (1980). As we have seen in the results, many descendants had soft shell, which suggests to us that both progenitors are heterozygous for this trait, being soft shell recessive. This high amount of soft shell descendants is inconvenient for Spanish breeders, as the Spanish industry is adapted to hard shell almonds. For this reason, right now, the only way to obtain more quantities of hard shell

seedlings is to increase the number of the descendants.

Kernel weight

Mean value of kernel weight of all the genotypes was 1 g in the four years of the study (Table 1), also indicating the stability of this trait in our growth conditions. Most of the descendants showed kernel weights between ‘R1000’ (0.9 g) and ‘Desmayo Langueta’ (1.2 g), although some of them had smaller kernels than ‘R1000’ (up to 0.6 g) and bigger than ‘Desmayo Langueta’ (up to 1.6 g) (Fig. 2). We have also observed a normal distribution of this trait in the population (Fig. 2).

Kester et al. (1977b) and Spiegel-Roy and Kochba (1981) obtained a heritability of 0.64 and 0.45 respectively, for this trait. On the other hand, Dicenta et al. (1993b) obtained a higher heritability (0.78) for this trait, although they observed a slight effect of the year, which the authors related to the influence of productivity on kernel size (Hill et al. 1987). This could be one of the reasons of the smaller or larger kernels than progenitors in some of our descendants. Results indicate that if the breeder wants big-kernelled seedlings (around 1.5 g) he should avoid progenitors of small kernel size.

Empty nuts

Mean value of empty nuts was only of 1% during the four years of the study (Table 1). Percentage of empty nuts of progenitors was very low (between 0% in ‘R1000’ and 3% in ‘Desmayo Largueta’). In this sense, most of the descendants showed values within this range, although some of them showed higher percentage of this defect, up to 21% (Fig. 2).

Empty nuts results agree with previous found by Dicenta et al. (1993a) who indicated the very small annual variation of this trait. However, Kester et al. (1977b) observed the high influence of the environment in the expression of this trait. Even though this is an important trait for the breeder, is not very frequent in the descendants, since this defect is not usually present in the progenitors.

Double kernels

Despite the fact that neither of progenitors, in our local conditions, has double kernels some of the descendants showed this defect, up to 43% in some cases (Table 1, Fig. 2). Duncan test revealed some differences between the four years, and mean value of population ranged from 3% to 8% (Table 1).

The influence of the environment on the production of double kernels is well known (Grasselly 1972; Spiegel-Roy and Kochba 1974; Kester and Asay 1975; Spiegel-Roy 1979). Egea and Burgos (1995) determined that low temperatures during the previous months to bloom, favour the development of double kernels in some cultivars. Grasselly and Crossa-Raynaud (1980) described an important relationship between progenitors and the offspring for this trait. On the other hand, Spiegel-Roy and Kochba (1974), Kester et al. (1977b), Dicenta et al. (1993b) and Arteaga and Socias i Company (2001) reported that it was a quantitative trait, with a complex inheritance and a heritability difficult to estimate, mainly due to the environmental effect. Spiegel-Roy and Kochba (1981), Vargas et al. (1984) and Dicenta et al. (1993b) observed some dominance, the descendants showing a higher percentage of double

kernels than the parents. Our results seem to support this hypothesis. Finally, this defect has been observed (with more or less intensity) in the breeding programmes because most breeders have used Tuono, a self-compatible cultivar with a high percentage of double kernels, being therefore transmitted to the descendants.

Kernel thickness

Mean value of this trait varied from 2.0 and 2.4 in the four years of the study (Table 1). Kernel thickness was similar (2.0) in both progenitors (‘R1000’ and ‘Desmayo Largueta’) and numerous descendants showed this intermediate value. However, some of the descendants had flat kernels (1.0) or thicker ones (2.7) (Fig. 2).

With reference to kernel thickness, the breeder looks for intermediate kernels, although sometimes it is necessary to have flat or thicker kernels for some specific purposes in the industry.

Kernel shrivelling

A significant variation was observed in this trait between the four years of the study with shrivelling values ranging from 1.1 to 1.8 (Table 1). Kernel shrivelling was 1.7 in ‘Desmayo Largueta’ and ‘R1000’. Shrivelling values of descendant were similar to parents in most cases. However, a reduced number of seedlings showed lesser (around 1.0) and higher (around 2.3) values for this seed trait (Fig. 2). We have also observed a normal distribution of this trait in the population.

Our results of kernel shrivelling agree with the intermediate heritability described for this trait by Dicenta et al. (1993b) and Arteaga and Socias i Company (2001). Kester and Asay (1975) also affirmed that some variation in this trait occurs with environmental conditions, mainly due to the availability of water for the tree.

Pellicle colour

Mean values of descendants showed significant differences between the four years, with values between 1.8 and 2.7 (Table 1). Pellicle colour intensity was similar in both progenitors, 3.0 in

'R1000' and 3.3 in 'Desmayo Langueta'. However, the descendants ranged between 1.0 and 4.0 (Fig. 2). The population had a normal distribution, but many descendants had lighter pellicle colour than the progenitors.

As Spiegel-Roy (1979) indicated pellicle colour is a quantitative trait. Although Kester and Asay (1975) and Spiegel-Roy and Kochba (1981) obtained a high heritability of this trait, frequently it was not significant. Dicenta et al. (1993b) and Arteaga and Socias i Company (2001) found a low and significant heritability for pellicle colour. Our results agree with previous found by Kester et al. (1977b) indicating the high influence of the environment in the expression of this trait. Although the breeder looks for light pellicle colour kernels, we have to think that once the almonds are cracked, they tend to get darker. Furthermore, for many purposes the pellicle is previously removed.

Kernel bitterness

Despite both progenitors are sweet-kernelled, 31% of descendants were bitter-kernelled, and the rest sweet-kernelled (49%) or slightly bitter-kernelled (20%) (Fig. 2). This has revealed that both progenitors were heterozygous for this trait, with the bitter flavour recessive. The observed frequencies fit the expected ones (with a probability ≥ 0.05), being bitterness a monogenic trait and the sweet allele dominant.

Almond bitterness was first studied by Heppner (1923, 1926) who established that it was a monogenic trait, with the bitter flavour recessive, and the heterozygous genotype the most frequent. Spiegel-Roy and Kochba (1974) suggested

a complex inheritance. However, Dicenta and García (1993b) and Vargas et al. (2001) studying a high number of families, supported the hypothesis of Heppner and classified numerous sweet cultivars as heterozygous or homozygous. In addition, Dicenta and García (1993b) proposed some strategies to avoid bitter-kernelled descendants in the breeding programs, which were experimentally verified later (Dicenta et al. 2007). Despite of the high number of seedlings, our results deviated slightly from the expected, with a higher number of bitter-kernelled descendants. The slightly bitter descendants cannot be explained by this monogenic theory, so other factors could be affecting the expression of this trait. Before designing crosses, the breeder must know the genotype of the progenitors in order to avoid the presence of bitter seedlings in the offspring.

Correlations between agronomic traits

No correlations were found between most agronomic traits in almond. Only in some cases these correlations were significant with values of the Pearson Correlation Coefficient (r) higher than 0.5, important from the point of view of almond breeding (Table 2).

Blooming date/leafing date

We have observed a positive and significant correlation (0.84) between these traits. Kester et al. (1977a) studying 1,000 descendants belonging to 21 crosses (intra and inter-specific) obtained a smaller correlation (0.34). Vargas and Romero (1984) studied 602 descendants and obtained also

Table 2 Pearson correlation coefficients between different agronomic traits in the 167 almond seedlings of 'R1000' x 'Desmayo Langueta'

Agronomic trait	Pearson correlation coefficient
Blooming date/leafing date	0.84**
Blooming date/blooming density	0.15**
Blooming date/productivity	ns
Blooming date/ripening date	ns
Blooming density/productivity	0.64**
Shell hardness/Kernel weight	ns
Shell hardness/in shell weight	0.70**
In-shell/kernel ratio/kernel weight	ns
In-shell/kernel ratio/in shell weight	-0.82**
In-shell/kernel ratio/shell hardness	-0.84**

** Significant level at 1%

ns = no significant

a smaller correlation (0.56). Dicenta et al. (2005a), studying 502 descendants belonging to 13 families, obtained a correlation coefficient between 0.74 and 0.25 (depending on each family), and even in two families they found no significant correlation. Apparently, blooming and leafing dates depend on the chilling requirements of the plant, therefore they should be related, but this relationship is not so close. Some genotypes bloom and leaf, or leaf then bloom, or they do both at the same time. This is characteristic of each genotype and can be observed in the cultivated varieties. Despite the fact that some authors have used the leafing date of descendants to predict their blooming date, Dicenta et al. (2005a) showed that this correlation is not useful when we try to find a correlation between the first leafing time of each descendant for its first blooming time (some years later) with early selections purposes.

Blooming date/blooming density/productivity

Our results show that there is no important correlation between blooming date and productivity (flowers or fruits).

Dicenta and García (1992) studied 2,483 seedlings belonging to 51 families, observing low or no significant correlation between blooming date and productivity. However, Kester (1965) found a negative significant correlation (-0.28 to -0.72) between these two traits, mainly in the ‘Tardy Nonpareil’ seedlings. On the other hand, he did not find significant correlations between blooming date and blooming density, although he suggested that late blooming descendants were slightly the less floriferous. Grasselly (1972) did not find, in general, any correlation between these two traits, except in the descendants of ‘Tardy Nonpareil’, in which he observed a correlation between late blooming/low blooming density/low productivity (Grasselly 1978). Later, Grasselly and Olivier (1985) broke this correlation when they crossed ‘Tardy Nonpareil’ descendants. In fact, the selection ‘R1000’ (descendant of ‘Tardy Nonpareil’) could be one of these cases, as we have not found this correlation. Furthermore, our results show that it is possible to obtain extra-late blooming and high productivity selections as we can see in our new releases from the Almond Breeding

Program developed in the CEBAS-CSIC in Murcia, Spain.

Blooming date/ripening date

We have not observed any correlation between blooming and ripening date in the offspring, so they are independent traits.

This independence can be observed in the well-known varieties ‘Ramillete’ (early blooming/early ripening), ‘Desmayo Largueta’ (early blooming/late ripening), Antoñeta (late blooming/early ripening) and Wawona (late blooming/late ripening). This will enable the breeder to obtain new late blooming and early ripening genotypes that will be grown in the interior cold areas. Dicenta and García (1992) found slightly low positive and significant correlation coefficient between these two traits what could indicate certain tendency of the late blooming trees to ripen later.

Blooming density/Productivity

Correlation coefficient between these two traits was intermediate and significant (0.64), indicating that the most floriferous descendants are also the most productive ones.

This correlation depends on the fruit set, that is also a consequence of numerous factors such as an efficient pollination, flower fertility and the maximum number of fruits that a tree can bear (Dicenta et al. 2005b; Socias i Company et al. 2004, 2005). Kester and Griggs (1959) also found a positive correlation between the number of flowers and productivity, suggesting that to obtain high productivity it was necessary to have a high blooming density. Dicenta and García (1992) obtained correlation coefficients between 0.53 and 0.89 (depending on the year) with a mean value of 0.77, similar to our results. On the other hand, Egea et al. (1986) showed that when the number of blossoms of a high blooming density variety (‘Marcona’) was half reduced, it did not affect the productivity that was still quite high. In general, blooming density is a reliable indicator of the productivity. Only in special conditions (bad weather, no pollinators or floral defects) this correlation could disappear. So we propose that

high blooming density is an important tool to select the descendants.

In-shell/kernel ratio/in shell weight/kernel weight/shell hardness

Correlation coefficients have shown that in-shell/kernel ratio does not mainly depend on the kernel weight (that it is not so variable) but it does on the in-shell weight (−0.82). Moreover, in-shell/kernel ratio is also inversely correlated with shell hardness (−0.84).

Dicenta and García (1992) obtained correlation coefficients between 0.07 (in shell-kernel ratio/kernel weight) and −0.72 (in shell-kernel ratio/in shell weight) similar to our results. These results have an important conclusion. The hardness of the shells (soft-shell or hard-shell) does not affect the weight of kernel and so the final production of the orchard. The harvest depends on the number of kernels produced and their weight, which is independent of the in shell-kernel ratio, hardness or in shell weight.

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