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Inheritance of several important agronomic traits in almond

F. Dicenta*, E. Ortega*, R. Sánchez-Pérez*, H. Duval and P. Martínez-Gómez***
*Departamento de Mejora y Patología Vegetal, Centro de Edafología y Biología Aplicada del Segura,
CSIC, P.O. Box 164, E-30100, Espinardo (Murcia), Spain
**Unité de Génétique et d'Amélioration des Fruits et Légumes, INRA, Site AGROPARC,
Domaine Saint Paul, BP91, F-84914 Avignon, Cedex 9, France
fdicenta@cebas.csic.es

SUMMARY – Four tree traits (flowering time, flowering density, productivity and ripening time) and 5 fruit traits (kernel weight, shell hardness, kernel percentage, double kernels and kernel bitterness) were studied in an almond [*P. dulcis* (Mill.) D.A. Webb] progeny of 165 seedlings, for 3 years. This progeny comes from a cross between the French selection 'R1000' ('Tardy Nonpareil' x 'Tuono') and the Spanish cultivar 'Desmayo Largueta'. In addition, incompatibility alleles were identified using a specific *S*-allele PCR. The inheritance of the quantitative and the qualitative traits in this progeny is described and the implications for the almond breeding programmes are discussed.

Key words: Almond, *Prunus dulcis*, breeding, agronomic traits, kernel quality.

RESUME – *"Hérédité de plusieurs caractères d'importance agronomique chez l'amanier". Au cours de ce travail nous avons étudié quatre caractéristiques de l'arbre (date de floraison, densité de fleurs, productivité et date de maturation) et cinq caractéristiques du fruit (poids de l'amandon, dureté de la coque, pourcentage d'amandons, et amertume de l'amandon) dans une famille de 165 descendants d'un croisement entre la variété d'amandier [*P. dulcis *(Mill.) D.A. Webb] française 'R1000' ('Tardy Nonpareil' x 'Tuono') et la variété espagnole 'Desmayo Largueta' sur 3 années. L'identification des allèles d'incompatibilité a été étudiée grâce à la technique de la PCR. L'hérédité des caractères quantitatifs et qualitatifs a été étudiée et les implications dans l'amélioration variétale de l'amandier sont discutées.*

Mots-clés : *Amandier,* Prunus dulcis*, amélioration végétale, caractéristiques agronomiques, qualité de l'amandon.*

Introduction

The efficiency of cross-breeding programs depends on the information available on the transmission of those traits whose improvement is desired (Dicenta, 1991). In almond [*P. dulcis* (Mill.) D.A. Webb], most of the important agronomic characteristics are quantitative (Grasselly, 1972; Kester and Asay, 1975; Spiegel-Roy, 1979; Grasselly and Crossa-Raynaud, 1980; Dicenta, 1991), and thus influenced by the environmental conditions.

Late flowering has been one of the most important objectives of the almond breeding programmes (Kester, 1965; Grasselly, 1972; Vargas *et al.,* 1984; Socias *et al.,* 1999), and its transmission has been studied (Kester *et al.,* 1973; 1977b; Dicenta *et al.,* 1993a). Flowering density and productivity are also two important traits, which have been studied by Grasselly (1972), Kester and Asay (1975), Grasselly and Crossa-Raynaud (1980), Vargas *et al.* (1984), and Dicenta *et al.* (1993a). However, few studies have been performed regarding the time of maturity (Grasselly, 1972; Kester and Asay, 1975; Dicenta *et al.,* 1993a). On the other hand, there are many studies regarding the transmission of the kernel traits (Grasselly, 1972; Spiegel-Roy and Kochba, 1974; 1981; Kester *et al.,* 1977a; Vargas *et al.,* 1984; Dicenta *et al.,* 1993b). In addition, kernel bitterness was characterized as a monogenic trait, the bitter genotype being recessive (Heppner, 1923; 1926, Dicenta and García 1993a; Vargas *et al.,* 2001). Finally, self-compatibility was studied by different authors, determining its monogenic nature with a multi-allelic *S* series, and identifying the S_f allele as being responsible for self-compatibility (Socías and Felipe, 1988; Dicenta and García, 1993b; Rovira *et al.,* 1997; Ortega and Dicenta, 2003).

The objective of this work was to study the inheritance of different tree and fruit traits in an almond progeny of 165 seedlings from a cross between the French selection R1000 and the Spanish cultivar 'Desmayo Largueta'.

Materials and methods

The plant material assayed was an almond progeny of 165 seedlings from the cross 'R1000' x 'Desmayo Largueta', performed in 1996 at INRA-Avignon (France) by Mr Henri Duval. 'R1000' is a self-compatible selection of INRA from a cross between the North American cultivar 'Tardy Nonpareil' and the Italian cultivar 'Tuono'. In 1997, the seeds obtained were germinated and the seedlings planted in the orchards. During the years 2000, 2001 and 2002 the following traits were studied:

(i) Flowering time (Julian days when 50% of flowers were opened).

(ii) Flowering density (scored between 0 = null and 5 = maximum).

(iii) Productivity (scored between 0 = null and 5 = maximum).

(iv) Ripening time (Julian days when 95% of mesocarps were opened).

(v) Kernel weight (g).

(vi) Shell hardness (scored between 1 = very soft and 5 = very hard).

(vii) Kernel percentage (% kernel/nut).

(viii) Double kernels (%).

(ix) Kernel bitterness (1 = sweet, 2 = slightly bitter and 3 = bitter).

In addition, incompatibility alleles were identified using an *S*-allele specific PCR (Tamura *et al.,* 2000).

Means of the 3 years were calculated to represent the results of quantitative traits. In the case of qualitative traits (bitterness and self-compatibility), the genotype of each individual was determined using data of at least 1 year.

Results and discussion

The distribution of the seedling population for each trait is shown in Fig. 1.

Flowering time

The flowering time of the descendants showed a distribution between the earlier progenitor ('Desmayo Largueta') and the later one ('R1000'), with a range of 28 days. None of the descendants was earlier than 'Desmayo Largueta' (flowering at day 29) nor later than 'R1000' (flowering at day 66). The population seems to follow a bimodal distribution.

In general, flowering time is considered as a quantitative trait (Grasselly, 1972; Vargas *et al.,* 1984) with a high heritability (Kester *et al.,* 1973, 1977b; Dicenta *et al.,* 1993a). However, when studying some descendants of 'Tardy Nonpareil', other authors (Kester, 1965; Grasselly, 1978; Socías *et al.,* 1999) observed a bimodal distribution for this trait. This distribution was explained by the presence of a late-flowering major gene, which could be modified quantitatively by other minor genes. This seems to be the case for our population, taking into account the origin of 'R1000' ('Tardy Nonpareil' x 'Tuono').

Flowering density and productivity

In general, the descendants were less floriferous (1.8) and productive (1.2) than their parents. These extremely low values are a consequence of being the means of the first years of production and, probably, the difficult culture conditions of the descendants in the breeding programmes.

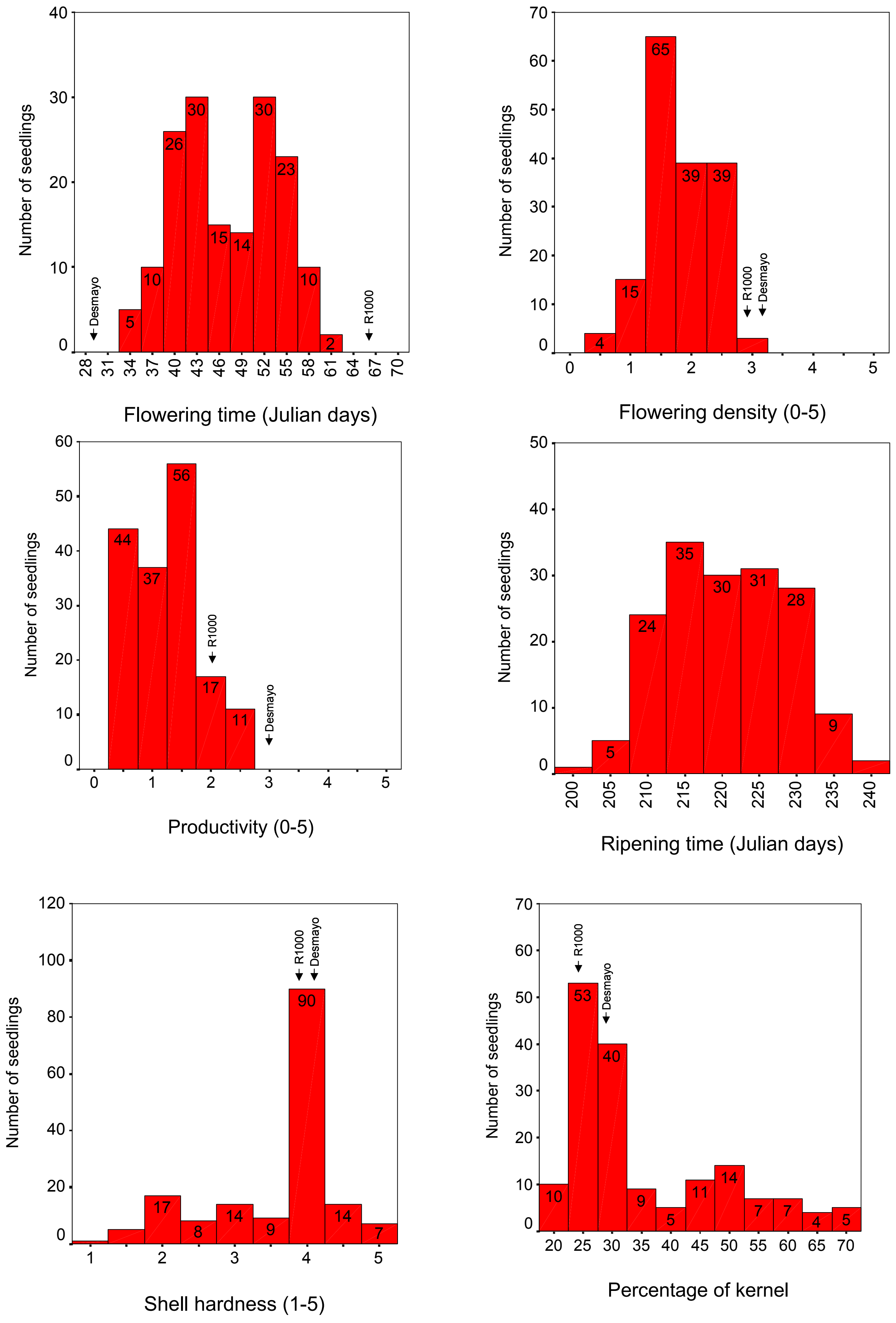

Fig. 1. Distribution of the 165 seedlings of 'R1000' x 'Desmayo Largueta', for 10 different traits.

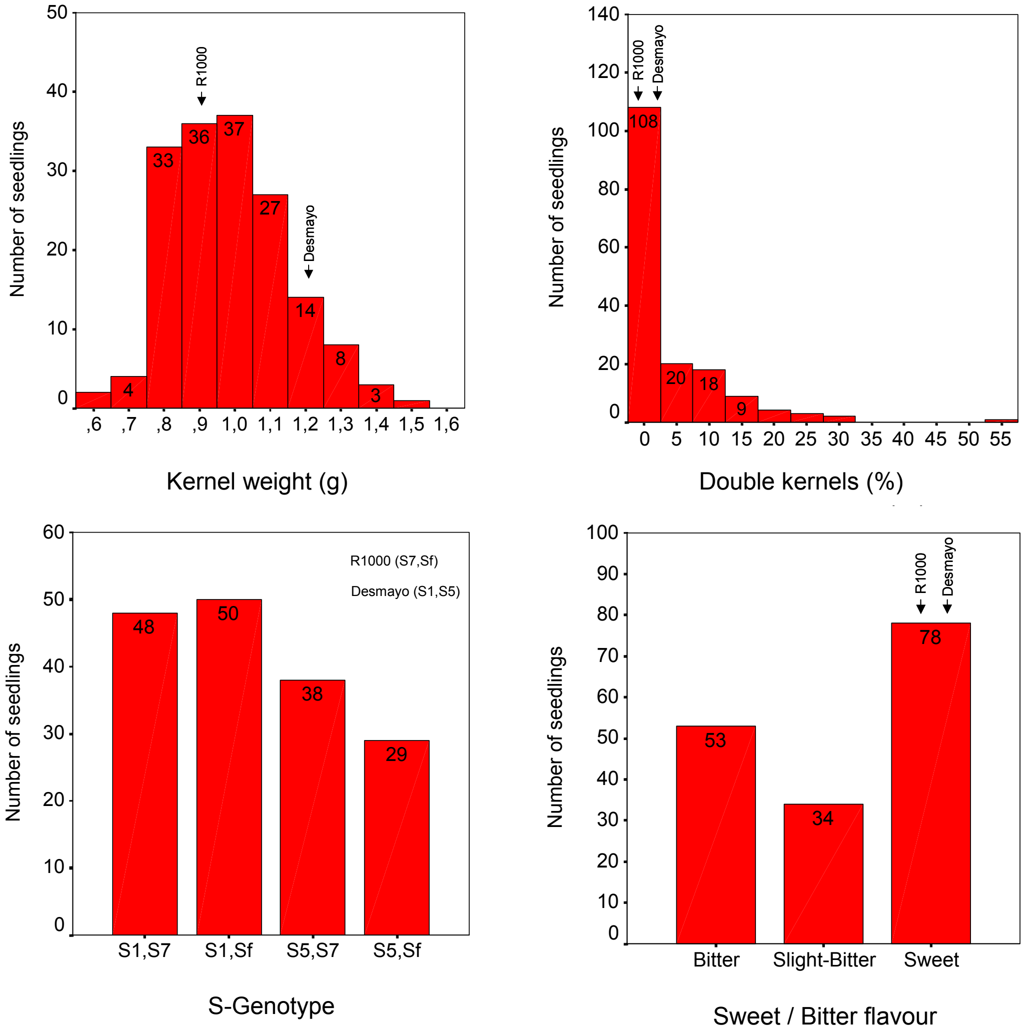

Fig. 1 (cont.). Distribution of the 165 seedlings of 'R1000' x 'Desmayo Largueta', for 10 different traits.

Grasselly (1972) indicated that the most productive trees at the first flowering were also the most productive over the following years. However, Kester and Asay (1975) pointed out that the selection for these traits 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.

Ripening time

The ripening time was extended between the earlier progenitor ('R1000', at day 218) and the later one ('Desmayo Largueta', at day 240) for most of the descendants. However, an important number of the seedlings ripened before 'R1000', some of them nearly 20 days before (at day 199). This fact is very interesting for breeders, as it allows descendants having earlier ripening than their parents to be obtained.

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.

Shell hardness and kernel percentage

Regarding shell hardness, more than half of the descendants showed the same shell hardness (scored 4) as the parents. However, some of them had harder shells, or, particularly, softer shells. Similarly, the kernel percentage ranged between 'R1000' (24%) and 'Desmayo Largueta' (28%) for most of the descendants, although some of them showed lower and, mainly, higher (up to 71%) percentages.

Grasselly (1972) and Grasselly and Crossa-Raynaud (1980) established that the inheritance of shell hardness was controlled by major genes, the hard shell being dominant. According to these authors, this simple determinism postulated for soft and hard shells would become complicated when cultivars with an intermediate shell hardness are crossed, since other minor genes could be involved. According to Kester *et al.* (1977a) and Dicenta *et al.* (1993b), these traits are quantitative, with an intermediate heritability, lower than that obtained by Spiegel-Roy and Kochba (1981). Our results seems to indicate that these traits are more complex than previously proposed by Grasselly.

Kernel weight

Most of the descendants showed kernel weights between those of 'R1000' (0.9 g) and 'Desmayo Largueta' (1.2 g), although some of them had kernels smaller than 'R1000' (as low as 0.6 g) or bigger than 'Desmayo Largueta' (up to 1.5 g).

Kester *et al.* (1977a) and Spiegel-Roy and Kochba (1981) obtained slightly high heritabilities for this trait. Later, Dicenta *et al.* (1993b) obtained high heritabilities for this trait, although they observed a slight effect of the year, due to the known influence of productivity on kernel size (Hill *et al.,* 1987). This could be one of the reasons why the kernels were smaller or larger than those of the progenitors in some of our descendants.

Double kernels

Neither of the progenitors had double kernels, and most of the descendants behaved like this, although some of them showed this defect, reaching 55% of double kernels in some cases.

The influence of the environment on the production of double kernels is well known (Kester and Asay, 1975; Spiegel-Roy, 1979), low temperatures during flowering being one of the reasons (Grasselly, 1972; Spiegel-Roy and Kochba, 1974). Grasselly and Crossa-Raynaud (1980) described an important relationship between progenitors and offspring for this trait. On the other hand, Spiegel-Roy and Kochba (1974), Kester *et al.* (1977a), and Dicenta *et al.* (1993b) 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.

Kernel bitterness

Despite both progenitors being sweet-kernelled, more than 30% of descendants were bitter-kernelled, and the rest sweet-kernelled (47%) or slightly bitter-kernelled (20%).

Heppner (1923, 1926) established that bitterness was a monogenic trait, the bitter flavour being recessive, and the heterozygous genotype the most frequent. Spiegel-Roy and Kochba (1974) suggested a complex inheritance. However, Dicenta and García (1993a) 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. Dicenta and García (1993a) proposed some strategies to avoid bitter-kernelled descendants in the breeding programs, which were tested experimentally later. Despite the high number of seedlings, our results deviated slightly from the expected, with a higher number of bitter-kernelled descendants.

Self-compatibility

The *S* genotypes of the descendants were those expected from the parents ('Desmayo Largueta' (S_1S_5) and 'R1000' (S_7S_f)). Half of the seedlings were self-compatible (S_1S_f or S_5S_f) and the other half self-incompatible (S_1S_7 or S_5S_7).

In 1972, Grasselly and Olivier carried out crosses to obtain self-compatible descendants (Grasselly and Olivier, 1976). However, the first study on the transmission of self-compatibility in almond progenies was that of Socias i Company and Felipe (1977), who pointed out the heterozygosity of the self-compatible progenitor and the dominance of self-compatibility. Dicenta and García (1993b) (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, the self-compatible allele (S_f) being dominant over the others. Later, Bosković *et al.* (1999) studied the transmission of *S*-alleles to the offspring by analysis of stylar ribonucleases. Recently, Ortega and Dicenta (2003), using three different methods (fluorescence microscopy, stylar ribonuclease assay, and *S*-allele PCR), showed different breeding strategies capable of ensuring self-compatibility in the offspring.

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