International Journal of Plant Developmental Biology ©2007 Global Science Books

Apricot Floral Development: Keys for a Good Yield

Nuria Alburquerque* • Jose Egea • Lorenzo Burgos

Department of Fruit Breeding. CEBAS-CSIC. Aptd. 164. 30100, Murcia, Spain

Corresponding author: * **nalbur@cebas.csic.es**

ABSTRACT

Different aspects related to floral development have a close link to fruit set failures in apricot and other fruit trees. In this work we review studies on flower bud development, pollen viability and germinability, ovule development and longevity, fertilization, as well as on molecular bases of self- and cross-(in)compatibility. A high flower buds drop and a scarce flower bud production of some apricot cultivars affect negatively fruit set. Climatic conditions during flowering influence pollen germination and pollen tubes growth. A delay in the ovule development at anthesis has been found as genotype-dependent in apricot and this trait has been related to low percentages of fertilisation. Also differences in fruit set observed between cultivars may be related to the ability of the ovules to develop and mature after anthesis. Abnormal embryo sacs or ovules have been observed in apricot at different stages of flower development, which is a direct cause of low fruit set. Different plant growth regulators can be useful to regulate different processes. The knowledge of the incompatibility phenotype for many apricot cultivars has allowed advising about the planting of single-cultivar orchards. The study of the inheritance of this and other traits in apricot and other fruit trees has allowed planning of hybridisations to minimise or eliminate the production of undesirable seedlings, increasing the efficiency of the breeding programmes. Furthermore, molecular studies and characterization of S-alleles in apricot have allowed the development of molecular markers for self-(in)compatibility, a successful tool for breeding. All together, these studies on the floral development in apricot have provided valuable information to help select the appropriate cultivars for producers and to avoid losses caused by an inadequate cultivar selection.

Keywords: flower buds, fruit set, male sterility, ovule, pistil, pollen, self-(in)compatibility, *S*-RNases

Abbreviations: BA, benzyladenine; **GA_3**, gibberellic acid; **PA**, polyamine

CONTENTS

INTRODUCTION

Apricot (*Prunus armeniaca* L.) is a very appreciated fruit for its potential health benefit due to a high content of carotenoid and phenolic compounds that are present in many cultivars (Ruiz *et al*. 2005a, 2005b). Productivity is often erratic in many apricot cultivars depending of several and frequently unclear factors. It is known that fruit set is affected by climatological events prior or during flowering (Egea 1995). The influence of weather conditions on pollination, stigma receptivity, ovule fertility, ovule longevity and fruit set have been widely studied in many apricot varieties (Burgos *et al*. 2004).

There are many factors that affect productivity before blooming. Failure in bud development, inadequate bud production and high flower bud drop have a negative influence on fruit production and yield (Legave 1978).

Different aspects of reproductive biology such as self-compatibility, pollen viability, the stage of development of the ovules at bloom or the fertilization process are implicated in a successful yield. Pollen germination is strongly influenced by environmental conditions such as high temperatures during flowering (Burgos *et al.* 2004). Yield of male-sterile apricot cultivars can be scarce due to inadequate pollen transfer from other cultivars. Male sterility is a heritable trait and can be avoided by breeders through selection of homozygous fertile parents (Burgos and Egea 2001). Delayed ovules that are not able to develop, produce low fertilization percentages of flowers in some apricot cultivars (Alburquerque *et al*. 2004b).

The presence of some plant growth regulators at specific levels prior or during flowering has been described as a positive influence on the development of reproductive organs in fruit tree flowers (Naylor 1984). Furthermore, treatments with different plant growth regulators have been applied to improve fruit set.

Traditionally the self-incompatibility has been identified as the main cause of poor crops in apricot, as in other fruit species. Nowadays, self-compatible apricot cultivars are required by farmers to avoid the use of pollinators. There are many studies about the inheritance of compatibility and consequently modern technologies have been deve-

Received: 16 April, 2007. Accepted: 5 September, 2007.

Invited Review

loped to determine the genotypes of different cultivars (Halász *et al*. 2005; Vilanova *et al*. 2005).

Studies on the flower biology may help farmers to better choose cultivars well adapted to specific climatic conditions. This review tries to give an overview of the state of the art in the research on apricot floral biology and the different aspects that can influence on the final yield.

FLOWER BUDS

Flower bud drop has been widely studied in stone fruits, because it negatively affects flower production and therefore the final number of the fruits yielded (Hendrickson and Veihmeyer 1950; Weinberger 1956; Brown 1958; Monet and Bastard 1971; Legave 1978).

Different factors may influence development and flower bud drop. So, in temperate fruits, such us peach (*Prunus persica* L. Batsch) (Erez and Lavee 1971), or apple (*Malus domestica* Borkh) (Jackson *et al*. 1983) the absence of adequate chilling or unfavourable spring temperatures have been related to reductions in growth rate and development and low yield. In sweet cherry (*Prunus avium* L.), improved flower quality and fruit set have been associated with increases in chilling requirements being satisfied (Mahmood *et al*. 2000). Limited winter chilling has also been considered a cause of flower bud drop in apricot when cv. 'Polonais' was studied (Legave 1978). However, other authors did not observe an influence of chilling on apricot flower bud drop or bud development. Viti and Monteleone (1991) indicated that the abnormalities found in flower buds of four apricot cultivars ('Polonais', 'Portici', 'Reale d'Imola' and 'Rival') can not be attributed to unsatisfied chilling requirements or late frost. Similarly, no correlation was found between lack of chilling and flower bud drop in the apricot cultivar 'Guillermo' (Alburquerque *et al.* 2003). In other crops, such as grape, high temperatures were associated with good production, since probably warm temperatures are required for flower bud initiation and development (Caprio and Quamme 1998).

Traditionally, problems in flower bud development have been associated with deficit irrigation treatments. Benzoni and Dunstone (1985) found that Jojoba plants (*Simmondsia chinensis* Link Schneid) need enough available water to complete flower bud morphogenesis. Furthermore, Benzoni *et al*. (1992) observed that the final steps of jojoba flower bud development were inhibited by water stress and that blooms were delayed.

The effects of timing and severity of postharvest water stress on productivity of different species are contradictory. So, in nectarine (*Prunus persica* L. Batsch) drought stress delayed flower bud development and flower buds with double pistils were found in the cultivar 'Snow Queen' (Naor *et al*. 2005). However, water-stressed pomelo trees (*Citrus grandis* L. Osbeck) showed an increase in the number of inflorescences, flower buds, and opened flowers, and the stress treatments had no effect on the percentage of fruit set (Nakajima *et al*. 1993). In the apricot cultivar 'Búlida' a significant decrease in yield was observed when drought stress was caused by withholding irrigation after harvest (Ruiz-Sanchez *et al*. 1999). Authors indicated that the decrease in fruit yield was due to early fruit drop.

Some works indicate that irrigation deficit may cause abnormal apricot flower bud development (Brown 1952 1953; Uriu 1964) and, therefore their drop (Hendrickson and Veihmeyer 1950). However, Ruiz-Sánchez *et al*. (1999) found no differences in flower bud drop, which was high in all irrigation situations, or flower quality between water stress treatments during two consecutive years. Furthermore, when different irrigation doses and treatments were applied to one apricot cultivar there was no influence on flower bud drop and large flower bud drops were recorded in all treatments (Alburquerque *et al*. 2003).

A strong influence of apricot genotypes on flower bud drop has been reported by different authors. Cultivars 'Bergeron', 'Badami', 'Royal' and 'Stark Early Orange' showed a higher percentage of damages or flower buds drop than 'Priana', 'Colomer' 'Polonais' and 'Canino' (Legave *et al.* 1982). When nine apricot cultivars were studied (Alburquerque *et al*. 2004a) flower bud drop percentages were lower in the earliest flowering cultivars than in the rest, where more than 50% of flower buds drop was recorded, as average, in a three-year study (**Table 1**).

The type of shoot has a strong influence on bud drop and flower damage in apricot. Legave *et al*. (1982) recorded higher percentages of flower buds or young flower drop as well as damaged buds or flowers on long shoots than on spurs in 'Polonais'. Similar results were found for long shoots in 'Guillermo' (Alburquerque *et al*. 2003) due to heavy bud drop (more than 90%) and a high number of malformed flower buds. Therefore, long shoots should be eliminated by pruning to save trees resources used in unproductive branches.

Scarce flower bud production is indicative of poor productivity. The production of flower buds has been represented by flower bud density (number of flower buds per branch section). In peach, nectarine (Okie and Werner 1996) and apricot (Alburquerque *et al*. 2004a) flower bud density is highly genotype-dependent. Generally, early blooming apricots ('Palstein', 'Priana' and 'Beliana') showed the highest flower bud density, the best fruit set percentages and also the highest average productivity in a warm area during three consecutive years (**Table 1**).

Knowledge on the biological behaviour of flower buds provides important information, since floral biology may have a strong influence on the final crop.

POLLEN

Pollen viability plays an important role in the fertilization process. Apricot pollen shows a high percentage of viability and a high number of germinated pollen grains that reach the ovary and the ovule (**Fig. 1**) in a wide range of temperatures (Vachun 1981; Egea *et al*. 1992) and the amount of produced pollen, for most apricot cultivars tested, was enough for a correct pollination (Egea and Burgos 1993).

The effect of withholding irrigation on pollen quality was evaluated during two postharvest periods in drip-irrigated 'Búlida' trees. The water stress treatment consisted

Table 1 Parameters of flower biology in nine apricot cultivars.[a]

Cultivar	% Flower buds drop	Flower bud density (№ buds/cm^2)	% Fruit set	Productivity (№ fruits/№ flower buds)
'Palstein'	52.78 ± 3.43	180.32 ± 10.20	53.77 ± 2.09	25.87 ± 2.42
'Bebeco'	49.41 ± 5.61	175.37 ± 31.55	36.37 ± 5.70	18.60 ± 6.35
'Goldrich'	72.23 ± 4.35	165.65 ± 13.80	12.08 ± 2.16	2.87 ± 1.30
'Beliana'	41.81 ± 6.03	145.42 ± 17.56	63.50 ± 3.30	45.23 ± 8.08
'Priana'	50.53 ± 5.40	133.92 ± 11.94	56.40 ± 2.91	39.93 ± 13.50
'Bergeron'	38.40 ± 4.84	112.16 ± 10.95	14.50 ± 3.08	9.53 ± 4.54
'Colorao'	11.29 ± 2.52	109.96 ± 21.31	7.95 ± 1.06	6.80 ± 1.93
'Pepito'	63.37 ± 3.26	71.34 ± 9.52	13.16 ± 2.33	5.20 ± 2.11
'Guillermo'	60.29 ± 2.86	62.71 ± 7.03	23.43 ± 1.35	11.40 ± 1.86

[a] Data elaborated from results published by Alburquerque *et al*. 2004a
Data are means ± standard errors

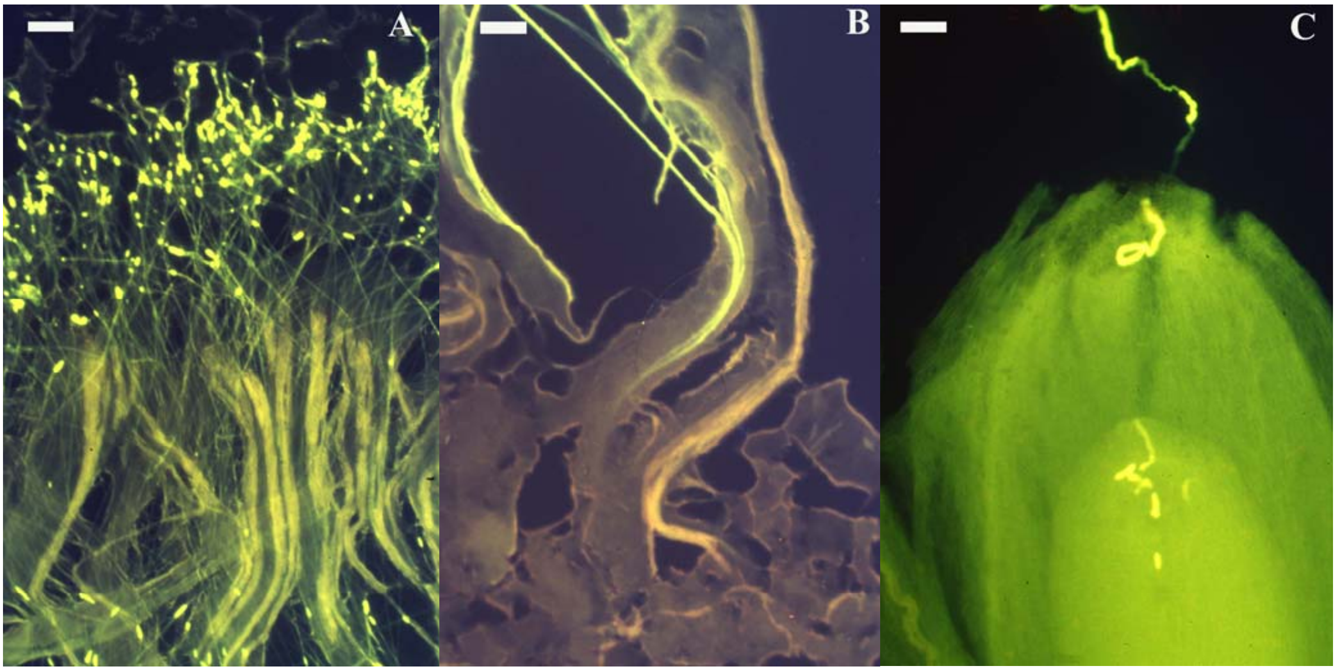

Fig. 1 Pollen germination in pistils of the apricot cultivar 'Pepito del Rubio'. Pollen tube germination on the stigma (**A**). Pollen tube growth in the style reaching the ovary (**B**) and detail of a pollen tube entering the ovule (**C**). Samples were processed 72 hours after pollination under controlled conditions of 20ºC. Bars represent 50 µm in (**A**) and (**B**) and 10 µm in (**C**).

in withholding irrigation during 1.5 months immediately after harvest and was found to induce a decrease in pollen germination (Ruiz-Sanchez *et al.* 1999).

Climatic conditions during flowering influence pollen germination and pollen tube growth in different fruit trees such as apricot, apple or pear (*Pyrus communis*) (Burgos *et al.* 2004). Recently, the influence of temperature on sweet cherry pollen germination was evaluated. High temperatures reduced pollen germination only one day after anthesis (Hedhly *et al.* 2003). When several sweet cherry genotypes ('Bing', 'Stark Hardy Giant', 'Van', 'Hedelfingen', 'Blanca de Provenza', 'Burlat', 'Reverchon' 'Talaguera Brillante' and 'Ambrunés') were tested, a different behaviour of the pollen tube growth was found depending on the female cultivar (Hedhly *et al.* 2005a). Furthermore, in that work a significant temperature-genotype interaction affecting the number of pollen tubes reaching the base of the style was reported. In the sweet cherry cultivars 'Sunburst' and 'Cristobalina' increases in temperature reduced pollen germination, but accelerated pollen tube growth. However, pollen tube response was genotype dependent and the number of pollen tubes reaching the base of the style was reduced at 30ºC for 'Sunburst' and at 10ºC for 'Cristobalina', a cultivar native to Southeastern Spain and adapted to warm conditions (Hedhly *et al.* 2004).

In the peach cultivar 'Hakuho' a negative effect of constant high temperatures (above 25ºC) on pollen germination was observed. However, the pollen tube growth in the pistil was faster than at 15 or 20ºC (Kozai *et al.* 2004). Accordingly, pollen germination and pollen tube growth kinetics was accelerated when temperature was increased from 10ºC to 20ºC and 30ºC, and a higher number of pollen tubes were found at the base of the style in the peach cultivars 'Rose Diamond', 'Pavía Amarilla de Tolosa' and 'Moret' (Hedhly *et al.* 2005b).

Male sterility is defined as the failure of plants to produce functional anthers, pollen or male gametes (Kaul 1988). When apricot pollen fertility was studied in many cultivars, only three male sterile cultivars ('Arrogante', 'Colorao de Moxó' and 'Colorao') were described (García *et al.* 1988; Burgos 1991). Also the cultivar 'Trevatt Blue' showed anthers containing degenerated microspores, with some failure in tapetal breakdown, which was related to its low fruit set (Lillecrapp *et al.* 1999).

Burgos and Ledbbeter (1994) proposed a preliminary model for the inheritance of male sterility in apricot after observing a relatively high number of male-sterile trees in progenies from controlled hybridisations among fertile cultivars in apricot. This trait is controlled by one recessive gene, which was confirmed in a later work (Burgos and Egea 2001). Other mode of inheritance of male-sterility has been described in several fruit trees (Yamamoto *et al.* 1997; Besnard *et al.* 2000; Yaegaki *et al.* 2003) based in cytoplasmic genes interacting with nuclear genes (gene-cytoplasmic type).

Nowadays, monoculture apricot production seems to be the best option for farmers and cultivars that do not need cross-pollination are chosen. In the case of male-sterile cultivars, yield could be restricted because their production depends on an adequate pollen transfer from other cultivars. This trait can be avoided by breeders through selection of homozygous fertile parents. Also, the information about the inheritance of male sterility has been used to develop molecular markers that will allow detection and elimination of male-sterile plants at the seedling stage (Badenes *et al.* 2000).

OVULES

The stage of development of the ovule at anthesis (just when the flower opens) and its influence on the reproductive process until fruit set have been studied in different species and important differences have been found between them. Thus, in sweet cherry (Eaton 1962; Stösser and Anvari 1982), sour cherry (Stösser and Anvari 1982; Furukawa and Bukovac 1989) or plum (Thompson and Liu 1972) a well developed embryo sac at anthesis was found. However in other *Prunus* species, such as almond (Pimienta and Polito 1983) or apricot (Eaton and Jamont 1964; Toyama 1980; Egea and Burgos 1994; Lillecrapp *et al.* 1999; Alburquerque *et al.* 2002a) a genotype-dependent delay in ovule development has been described.

Frequently, over-maturity of the megagametophyte has been considered a cause of poor fruit set (Eaton 1962; Marro 1976; Stösser and Anvari 1982). However, the delay in embryo sac development at anthesis has also been related to low percentages of fertilisation in apple (Sato *et al.* 1988) and fructification in pear (Jaumien 1968; Herrero 1983), sour cherry (Furukawa and Bukovac 1989) or apricot (Lillecrapp *et al.* 1999). The influence of the cultivar on the developmental stage of the ovules was greater than the year in nine apricot cultivars studied (Alburquerque *et al.* 2002a). In those cultivars with low chilling requirements, more than 50% of functional ovules were recorded. However, late-blooming cultivars, with high chilling requirements, had most of their ovules non functional at anthesis and often showed a low fruit set. In a later work, approximately 50% of apricot ovules were found at very immature stages 5 and 6 days after anthesis, which seems to indicate that ovules stopped their development at early maturation steps (Alburquerque *et al.* 2004b). These suggest that a certain degree of ovule development at anthesis is required for a successful fertilisation. Work by other authors supports this hypothesis and an incapacity of immature ovules to attract pollen tubes has been described (Cerovic and Micic 1999; Shimizu and Okada 2000). Different signals provided by the ovary and the ovule are necessary to orient and direct pollen tube growth to the right course (Herrero 2001), and particular secretions from ovary cells, along the pollen tube pathway, are required for the pollen tube to proceed towards the embryo sac (Herrero 2000). Furthermore, changes in the megagametophyte seem to play an important role in the entry of pollen tubes into the ovule. In cotton (*Gossypium hirstium*), the structure and composition of synergid cells change between pollination and the arrival of pollen tubes (Jensen *et al.* 1983), which enter the ovule through the synergid, causing its degeneration. In *Arabidopsis thaliana* it has been suggested that the egg and synergid cells are necessary to attract the male gametophyte toward the ovule. Also, non-functional or abnormal embryo sacs or ovules with delayed embryo sac development were unable to attract pollen tubes (Ray *et al.* 1997). Pollen tubes lost their way before entering the micropylar channel, which suggests that a functional and well-developed megagametophyte is responsible for pollen tube attraction.

The fertilization process of apricot ovules is poorly understood. The biochemical and genetic events that are implicated or the hormonal changes that occurs during this process have not been deeply studied. There are some works related to changes of starch contents in apricot flowers or in ovules. The high values of photoassimilates stored at anthesis in the flowers decreased whereas the ovary size increased (Rodrigo *et al.* 2000). When the ovules were observed, primary ovule growth was inversely related to starch content and independent of the pollination (Rodrigo and Herrero 1998). The results of these works suggest a self-supported development of the ovary on its own carbohydrate content.

Different development anomalies of the embryo sac have been observed at different stages of flower development in different species, including apricot (**Table 2**). Twin nucellus or shortened integuments was the most frequent malformation observed in several apricot cultivars at anthesis. The frequency of malformed apricot ovules was higher when they were analysed few days after anthesis than at full bloom (Burgos and Egea 1993; Burgos *et al.* 1995). In later works, ovules without megasporocyte and with a failure of elongation of the embryo sacs several days after anthesis were classified as malformed (Alburquerque *et al.* 2000) and the presence of ovules without mother cell and embryo sacs were higher than the degenerated ovules at six days from anthesis (Alburquerque *et al.* 2004b).

From the extensive studies carried on, it can be concluded that the frequency of malformed ovules from anthesis to ten days after anthesis in apricot is a trait with a strong genotype influence.

INFLUENCE OF PLANT GROWTH REGULATORS

Plants produce hormones that play a regulatory role in growth, development and reproduction process. Different plant growth regulators can be useful to regulate bud development, initiation or termination of bud dormancy, promotion or delay of flowering, thinning of flowers, fruit set and fruit development, etc. (Naylor 1984).

Promalin® is a mixture of the cytokinins 6-benzyladenine (BA) and gibberellins GA_4 and GA_7, which has been applied to different fruit trees to improve fruit set and also the fruit quality (Rai and Bist 1991; Son and Kuden 2005).

The effect of different gibberellins was observed on flower bud development in peach (Reinoso *et al.* 2002). The treatment with the gibberellin 16,17-dihydro GA5 was the best and more consistent for enhancing flower bud development. Gibberellic acid (GA_3) applied at late developmental

Table 2 Percentages of malformed ovules or aborted ovaries found in different fruit tree crops.

Specie/cultivar	%	Examined ovules	Type of malformation	Reference
Pear/ 'Decana del Comizio'	25	500	Embryo sacs with necrosis, ovules with two embryo sacs	Bini 1972; Jaumien 1968
Avocado/ 'Fuerte'	20.7	692	Twin ovules and embryo sacs, extra-ovary ovules, intra-ovary abnormal positions, additional nuclei and immature ovules	Tomer *et al.* 1976
Avocado/ 'Ettiger'	40	1.400		
Avocado/ 'Hass'	15.6	416		
Avocado/ 'Tova'	15.3	431		
Olive/ 'Manzanillo	12	158	Ovules with a small cavity at the ovule micropylar end	Rallo *et al.* 1981
Olive/ 'Rubra'	10	134		
Olive/ 'Swan Hill'	84	289		
Apple/ 'Golden Delicious'	24	50	Two or less completely developed embryo sacs	Forino *et al.* 1987
Apple/ 'Starkrimson'	23	62		
Sweet cherry/ 'Windsor'	4.8	21	Degenerated embryo sacs	Eaton 1959
Almond/ 'Nonpareil'	-	-	Delayed ovule development	Pimienta and Polito 1982, 1983
Banana/ 'Chinese Cavendish'	-	-	Protusion of the nucellus and nucellar cap through the micropyle	Fortescue and Turner 2005
Banana/ 'Hsien Jen Chaio'	-	-		
Apricot/ 'Moniquí'	0	80	Twin nucellus or shortened integuments, which leave part of the nucellus in contact with the ovary wall	Egea and Burgos 1994
Apricot/ 'Pepito del Cura'	0	40		
Apricot/ 'Gitano'	1.25	80		
Apricot/ 'Velazquez fino'	1.5	80		
Apricot/ 'Pepito del Rubio'	2.5	80		
Apricot/ 'Velazquez tardío'	0	40		
Apricot/ 'Carrascal'	0	80		
Apricot/ 'Candelo'	1.25	80		
Apricot/ 'Velazquez fino'*	18.5	302	"	Burgos *et al.* 1995
Apricot/ 'Gitano'*	24.3	321		
Apricot/ 'Moniquí Fino'*	18.8	341	"	Burgos and Egea 1993
Apricot/ 'Palstein'*	1	20	Ovules without megasporocyte or no elongated embryo sacs	Alburquerque *et al.* 2000
Apricot/ 'Goldrich'*	2	20		

*Ovules collected from the day of anthesis to several days later stages also hastened floral bud development and shortened the time to bloom. Also gibberellins may inhibit flowering in fruit trees. It is thought that these plant regulators, produced by seeds in developing fruits, move from fruits to nearby nodes and, there, they inhibit development of new flower primordia (Webster and Spencer 2000). The application of exogenous GA_3 can be used as an indirect thinning method, reducing thinning costs, since during flower bud induction may affect the floral process and partially reduce flowering in different species such as Japanese plum (*Prunus salicina* Lindl. cvs. 'Black Diamond' and 'Black Gold') (González-Rossia *et al.* 2006), the 'Springlady' peach and the 'Zincal 5' nectarine (González-Rossia *et al.* 2007) or the 'Patterson' apricot (Southwick *et al.* 1995). Additionally, gibberellin application combined with high temperatures has been found to induce early embryo sac degeneration in the sweet cherry cv. 'Satohnishiki' (Beppu *et al.* 2001).

Blooming time is very important to avoid risk of frost damage. Delayed blooming times have been produced by using plant growth regulators (Dennis 1976; Sedgley 1990). In a recent work, the application of gibberellic acid and ethephon at high concentrations delayed full bloom and reduced percentages of opened flowers and fruit set in the apricot cv. 'Shahroudi' (Moghadam and Mokhtarian 2006).

Polyamines (PAs) are involved in stimulation of cell division, regulation of rhizogenesis, embryogenesis, floral induction and differentiation of floral organs (Evans and Malmberg 1989; Martin-Tanguy 1996; Kakkar *et al.* 2000). Exogenous application of putrescine extended ovule longevity and the effective pollination period in pear (Crisosto *et al.* 1988, 1992). PAs has been suggested to stimulate fruit set and the initial phase of fruit development for several fruits, such as apple (Costa and Bagni 1983; Biasi *et al.* 1991), pear (Crisosto *et al.* 1986, 1988) and olive (*Olea europaea* L.) (Rugini and Mencuccini 1985), among others. Kushad and Orvos (1990) found that the main percentage of the total PA content was localized in the reproductive organs, and there were changes in conjugated and free PAs related to *Citrus* flower growth. Pritsa and Voyiatzis (2004) studied the fluctuations of free and conjugated spermidine and spermine in different organs of two olive cultivars, finding a relationship between PA fluctuations and developmental processes such as floral differentiation, shoot growth, anthesis, fertilisation and fruit growth.

In apricot polyamine levels varied differently with ovary development depending on the cultivar (Alburquerque *et al.* 2006). The exogenous application of putrescine to 'Bergeron' flowers, which had delayed ovules at anthesis, increased the percentage of functional ovules. These results support that exogenous polyamine application may hasten ovary and ovule development.

SELF-(IN)COMPATIBILITY

Incompatibility is the inability of a fertile seeded-plant to produce zygotes after self- or cross-pollination (self- or cross-incompatibility). This reaction is an active, regulated constraint of pollen tube growth where, depending on the species and the system operating, the process may be blocked at the initial steps of pollen hydration and germination on the stigma (Dickinson 1995), during pollen tube growth in the style (Matton *et al.* 1994) or further down in the ovary (Sage *et al.* 1994).

Recognising and rejecting their own pollen before fertilisation allows self-incompatible plants to promote outcrossing and improve genetic variability, which is considered to play an important role in the evolutionary success of the angiosperms. Outcrossing establishes a regulated degree of heterozygosity in the population.

Although, traditionally, the European group of apricot (within which the apricots grown in Europe, North America, South Africa and Australia are included) has been described as self-compatible (Mehlenbacher *et al.* 1991), in the last two decades many widely-cultivated apricot cultivars have been described as self-incompatible (see review by Burgos *et al.* 2004). In fruit trees, incompatibility complicates horticultural practices because self-incompatible clones require the addition of pollinators and the yield depends on abundant pollen transfer among the trees.

Most of the new apricot selections are self-compatible. However, in breeding programmes some self- incompatible parentals from the USA have been used to introduce virus resistance. Characterization for this trait in the progenies generated may allow detection of self-incompatible plants at the seedling stage and reduce cost considerably. Also, this information can help to avoid cross-incompatibility, which appears due to a short genetic base and reduced number of parentals used in crosses.

Genetic control

In *Prunus*, the incompatibility system operating in most of the studied species is controlled by one gene with several different alleles. Pollen is rejected when its *S*-allele is present in the genotype of the style (**Fig. 2A, 2B**) and may growth if the *S*-alleles are different (**Fig. 2C**). Hence, an incompatibility reaction will occur between two plants if their genotypes at the *S* locus do not differ in at least one allele (Heslop-Harrison 1975).

Sweet cherry was the first *Prunus* species where this model was described (Crane and Brown 1937). The same mechanism has been demonstrated in almond (Dicenta and García 1993) and apricot (Burgos *et al.* 1997). However, a different mode of inheritance was found in Japanese plum, for which it has been proposed that two genes with epistatic relationships control the trait (Arora and Singh 1990).

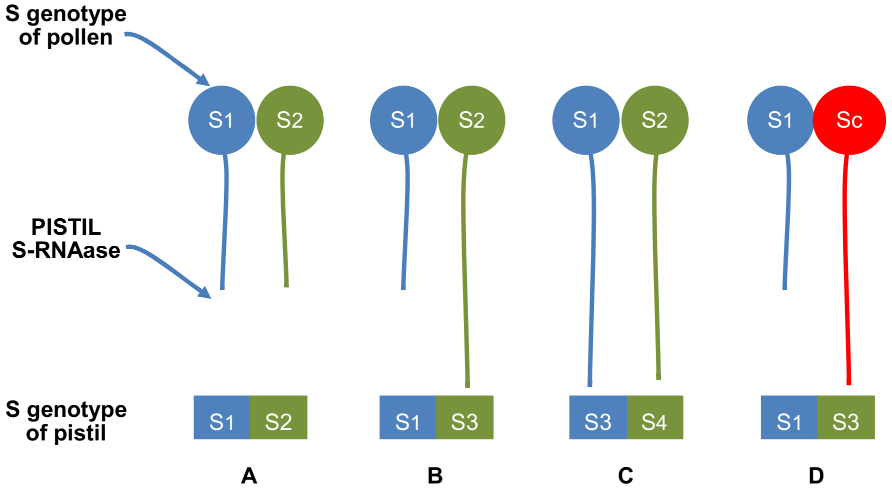

Fig. 2 Representation of the self-(in)compatibility system in apricot. After self-pollination pollen tube growth is arrested in the style (**A**). After cross-pollination only pollen tubes with S-alleles of different genotype that is found in the style, will grow (**B**) and (**C**). During a self-compatibility reaction, pollen tubes with the Sc genotype will grow in any pistil (**D**).

In apricot, alleles for self-compatibility would allow pollen tube growth in any style (**Fig. 2D**). Self-incompatibility alleles would stop pollen tube growth if the same allele was present in the pistil and the pollen grain (Burgos *et al.* 1997). Therefore, cross-incompatibility will occur if two cultivars do not differ in at least one S allele. Two groups of cross-incompatible cultivars have been described after controlled pollinations. One of them includes three Hungarian apricot cultivars (Nyéki and Szabó 1995) and the other the North American cultivars 'Lambertin', 'Goldrich' and 'Hargrand' (Egea and Burgos 1996).

Molecular aspects of incompatibility

Within the Rosaceae, a correlation between known genotypes for self-(in)compatibility and bands resulting from electrophoresis of stylar extracts has been found in Japanese pear (Sassa *et al.* 1992; Hiratsuka *et al.* 2001) where the proteins have been characterised as glycoproteins with RNase activity (Hiratsuka 1992; Sassa *et al.* 1993; Hiratsuka *et al.* 1995; Hiratsuka and Okada 1995). Similar results have been found in apple (Sassa *et al.* 1994), and European and Chinese pears (Tomimoto *et al.* 1996).

In *Prunus*, similar studies have been carried out in sweet cherry (Mau *et al.* 1982; Boskovic and Tobutt 1996; Boskovic and Tobutt 2001) and almond (Boskovic *et al.* 1997; Tao *et al.* 1997; Certal *et al.* 2002). In our laboratory, a good correlation was established between RNases from stylar extracts and the available information on (in)compatibility genotypes of different apricot cultivars. It was also demonstrated that these proteins were inherited as if they were the products of the *S* gene (Burgos *et al.* 1998) and this methodology was used to genotype unknown cultivars and selections from the breeding programme (Alburquerque *et al.* 2002b).

A further step in the molecular research on *S*-alleles in fruit trees was the use of a combination of *S*-allele-specific primers, designed from non-conserved sequences from each allele in apple, and the digestion of PCR products with *S*-allele-specific restriction enzymes (Janssens *et al.* 1995). Results from this approach to the identification of *S*-alleles correlated perfectly with information on genotypes from phenotypic and RNases analyses and it is a rapid and useful method for determination of the genotype of different apple cultivars (Sakurai *et al.* 1997, 2000). In apple 15 different *S*-alleles have been identified using this methodology (Broothaerts 2003).

The same strategy, with or without modifications, has been used to design specific primers for *S*-alleles in almond (Tamura *et al.* 2000; Channuntapipat *et al.* 2003), pear (Zuccherelli *et al.* 2002), sweet cherry (Tao *et al.* 1999; Yamane *et al.* 2000; Wiersma *et al.* 2001; Sonneveld *et al.* 2001) and Japanese apricot (Yaegaki *et al.* 2001).

The applicability of the *S*-gene-specific consensus PCR primers designed from sweet cherry sequences was tested in apricot (Halász *et al.* 2005). Cherry consensus primers amplified 11 out of 16 possible alleles.

In apricot, the alleles S_1, S_2 and S_4 have been sequenced completely (Romero *et al.* 2004) and were found to be highly haplotype-specific. Additionally, the *S-RNases* were expressed only in style tissues but not in pollen or leaves whereas the F-box allelic variants (probably the pollen determinants) were only expressed in pollen. All these results support these genes as candidates for the pistil and pollen determinants of genetic incompatibility in apricot. A further step in this research allowed the design of primers from these sequences in order to amplify different *S*-alleles in apricot. Combining two sets of consensus primers to amplify fragments containing the first and the second *S-RNase* introns all *S*-alleles could be distinguished (Vilanova *et al.* 2005), including the self-compatibility allele that has been found in all self-compatible apricot cultivars tested to date (Alburquerque *et al.* 2002b) including self-compatible Iranian cultivars (Hajilou *et al.* 2006).

A recent study goes further inside the molecular characteristics of the self-compatibility allele and found that whereas the *Sc-RNase* is unaltered, an insertion was found in the *SFBc* gene, resulting in the expression of a truncated protein. Additionally, the allele S_2 from the cultivar Canino (S_2Sc) was found, by PCR analysis of its progenies, to overcome also the incompatibility barrier. However, differences were not found with the wild allele at the S locus and therefore other factors, independent from this locus, are also required for gametophytic self-incompatibility in apricot (Vilanova *et al.* 2006).

ACKNOWLEDGEMENTS

This work has been financed by the project 'Mejora Genética del Albaricoquero' (AGL 2004-04126-CO2-01) from the 'Plan Nacional de I+D' of the Spanish Ministry of Education and Science. N. Alburquerque is a researcher under a 'Juan de la Cierva' postdoctoral contract.

REFERENCES

Alburquerque N, Burgos L, Egea J (2000) Consequences to fertilization of the developmental stage of apricot ovules at anthesis. *Journal of Horticultural Science and Biotechnology* **75**, 662-666

Alburquerque N, Burgos L, Egea J (2002a) Variability in the developmental stage of apricot ovules at anthesis and its relationship with fruit set. *Annals of Applied Biology* **141**, 147-152

Alburquerque N, Burgos L, Egea J (2003) Apricot flower bud development and abscission related to chilling, irrigation and type of shoots. *Scientia Horticulturae* **98**, 265-276

Alburquerque N, Burgos L, Egea J (2004a) Influence of flower bud density, flower bud drop and fruit set on apricot productivity. *Scientia Horticulturae* **102**, 397-406

Alburquerque N, Burgos L, Sedgley M, Egea J (2004b) Contributing to the knowledge of the fertilisation process in four apricot cultivars. *Scientia Horticulturae* **102**, 387-396

Alburquerque N, Egea J, Burgos L, Martinez-Romero D, Valero D, Serrano M (2006) The influence of polyamines on apricot ovary development and fruit set. *Annals of Applied Biology* **149**, 27-33

Alburquerque N, Egea J, Pérez-Tornero O, Burgos L (2002b) Genotyping apricot cultivars for self-(in)compatibility by means of RNases associated with *S* alleles. *Plant Breeding* **121**, 343-347

Arora RL, Singh R (1990) Genetics of incompatibility in plum (*Prunus Salicina* Lindl). *Indian Journal of Horticulture* **47**, 1-11

Badenes ML, Hurtado MA, Sanz F, Archelos DM, Burgos L, Egea J (2000) Searching for molecular markers linked to male sterility and self-compatibility in apricot. *Plant Breeding* **119**, 157-160

Benzoni A, Dunstone RL (1985) A possible role for abscisic acid in controlling dormancy in Jojoba flower buds. *Australian Journal of Plant Physiology* **12**, 463-470

Benzoni A, Palzkill DA, Nelson JM (1992) Flower bud dormancy, ABA concentration, and survival during frost of jojoba genotypes under water stress. *Journal of the American Society for Horticultural Science* **117**, 976-980

Beppu K, Suehara T, Kataoka I (2001) Embryo sac development and fruit set of 'Satohnishiki' sweet cherry as affected by temperature, GA$_3$ and Paclobutrazol. *Journal of the Japanese Society for Horticultural Science* **70**, 157-162

Besnard G, Khadari B, Villemur P, Berville A (2000) Cytoplasmic male sterility in the olive (*Olea europaea* L.). *Theoretical and Applied Genetics* **100**, 1018-1024

Biasi R, Costa G, Bagni N (1991) Polyamine metabolism as related to fruit-set and growth. *Plant Physiology and Biochemistry* **29**, 497-506

Bini G (1972) Ulteriori osservazioni su alcuni aspetti della biologia fiorale e di fruttificazione della cultivar di pero 'Decana del Comizio'. *Rivista Ortoflorofrutticoltura Italiana* **56**, 299-307

Boskovic R, Tobutt KR (1996) Correlation of stylar ribonuclease zymograms with incompatibility alleles in sweet cherry. *Euphytica* **90**, 245-250

Boskovic R, Tobutt KR (2001) Genotyping cherry cultivars assigned to incompatibility groups, by analysing stylar ribonucleases. *Theoretical and Applied Genetics* **103**, 475-485

Boskovic R, Tobutt KR, Batlle I, Duval H (1997) Correlation of ribonuclease zymograms and incompatibility genotypes in almond. *Euphytica* **97**, 167-176

Broothaerts W (2003) New findings in apple S-genotype analysis resolve previous confusion and request the re-numbering of some S-alleles. *Theoretical and Applied Genetics* **106**, 703-714

Brown DS (1952) Relation on irrigation practice to the differentiation and development of apricot flower buds. *Proceedings of the American Society for Horticultural Science* **114**, 95-102

Brown DS (1953) The effects of irrigation on flower bud development and fruiting in the apricot. *Proceedings of the American Society for Horticultural Science* **61**, 119-124

Brown DS (1958) The relation of temperature to the flower bud drop of peaches. *Proceedings of the American Society for Horticultural Science* **71**, 77-87

Burgos L (1991) Biología floral de variedades de albaricoquero (*Prunus armeniaca* L.). PhD Thesis, CEBAS-CSIC, 260 pp

Burgos L, Alburquerque N, Egea J (2004) Review. Flower biology in apricot and its implications for breeding. *Spanish Journal of Agricultural Research* **2**, 227-241

Burgos L, Berenguer T, Egea J (1995) Embryo-sac development in pollinated and non-pollinated flowers of two apricot cultivars. *Journal of Horticultural Science* **70**, 35-39

Burgos L, Egea J (1993) Apricot embryo-sac development in relation to fruit set. *Journal of Horticultural Science* **68**, 203-208

Burgos L, Egea J (2001) Inheritance of male sterility in apricot. *International Journal of Horticultural Science* **7**, 12-14

Burgos L, Ledbetter CA (1994) Observations on inheritance of male sterility in apricot. *HortScience* **29**, 127

Burgos L, Ledbetter CA, Pérez-Tornero O, Ortín-Párraga F, Egea J (1997) Inheritance of sexual incompatibility in apricot. *Plant Breeding* **116**, 383-386

Burgos L, Pérez-Tornero O, Ballester J, Olmos E (1998) Detection and inheritance of stylar ribonucleases associated with incompatibility alleles in apricot. *Sexual Plant Reproduction* **11**, 153-158

Caprio JM, Quamme HA (1998) Weather conditions associated with apple production in the Okanagan Valley of British Columbia. *Canadian Journal of Plant Science* **79**, 129-137

Cerovic R, Micic N (1999) Functionality of embryo sacs as related to their viability and fertilization success in sour cherry. *Scientia Horticulturae* **79**, 227-235

Certal AC, Almeida RB, Boskovic R, Oliveira MM, Feijó JA (2002) Structural and molecular analysis of self-incompatibility in almond (*Prunus dulcis*). *Sexual Plant Reproduction* **15**, 13-20

Channuntapipat C, Wirthensohn M, Ramesh SA, Batlle I, Arús P, Sedgley M (2003) Identification of incompatibility genotypes in almond (*Prunus dulcis* Mill.) using specific primers based on the introns of the *S*-alleles. *Plant Breeding* **122**, 164-168

Costa G, Bagni N (1983) Effects of polyamines on fruit-set of apple. *HortScience* **18**, 59-61

Crane MB, Brown AG (1937) Incompatibility and sterility in the sweet cherry (*Prunus avium* L.). *Journal of Pomology* **15**, 86-116

Crisosto CH, Lombard PB, Richardson DG, Tetley R (1992) Putrescine extends effective pollination period in comice pear (*Pyrus communis* L.) irrespective of post-anthesis ethylene levels. *Scientia Horticulturae* **49**, 211-221

Crisosto CH, Lombard PB, Sugar D, Polito VS (1988) Putrescine influences ovule senescence, fertilization time, and fruit set in 'Comice' pear. *Journal of the American Society for Horticultural Science* **113**, 708-712

Crisosto CH, Lombard PB, Richardson DG, Tetley R, Vasilakakis MD (1986) Effect of ethylene inhibitors on fruit set, ovule longevity and polyamine levels in 'Comice' pear. *Acta Horticulturae* **179**, 229-236

Dennis FG (1976) Trials of ethephon and other growth-regulators for delaying bloom in tree fruits. *Journal of the American Society for Horticultural Science* **101**, 241-245

Dicenta F, García JE (1993) Inheritance of self-compatibility in almond. *Heredity* **70**, 313-317

Dickinson HG (1995) Dry stigmas, water and self-incompatibility in *Brassica*. *Sexual Plant Reproduction* **8**, 1-10

Eaton GW (1959) A study of the megagametophyte in *Prunus avium* and its relation to fruit setting. *Canadian Journal of Plant Science* **39**, 466-476

Eaton GW (1962) Further studies on sweet cherry embryo sacs in relation to fruit setting. *Reports of the Ontario Horticultural Experimental Station* 26-38

Eaton GW, Jamont AM (1964) Embryo sac development in the apricot, *Prunus armeniaca* L. cv. 'Constant'. *Journal of the American Society for Horticultural Science* **86**, 95-101

Egea J (1995) El ciclo anual en frutales de zona templada. Factores de fructificación. *Fruticultura Profesional* **73**, 34-39

Egea J, Burgos L (1993) Producción de polen y autopolinización en albaricoquero (*Prunus armeniaca* L.). In : Audergon JM (Ed) Programme de recherche Agrimed. Deuxième rencontres sur l'abricotier Avignon (France), 27-31 May, 1991. Commission des Communautés Européennes Montfavet, pp 21-29

Egea J, Burgos L (1994) Year-to-year variation in the developmental stage of the embryo sac at anthesis in flowers of apricot (*Prunus armeniaca* L.). *Journal of Horticultural Science* **69**, 315-318

Egea J, Burgos L (1996) Detecting cross-incompatibility of three North American apricot cultivars and establishing the first incompatibility group in apricot. *Journal of the American Society for Horticultural Science* **121**, 1002-1005

Egea J, Burgos L, Zoroa N, Egea L (1992) Influence of temperature on the *in vitro* germination of pollen of apricot (*Prunus armeniaca* L.). *Journal of Horticultural Science* **67**, 247-250

Erez A, Lavee S (1971) Effect of climatic conditions on dormancy development of peach buds. 1. Temperature. *Journal of the American Society for Horticultural Science* **96**, 711-714

Evans PT, Malmberg RL (1989) Do polyamines have roles in plant development? *Annual Review of Plant Physiology and Plant Molecular Biology* **40**, 235-269

Forino LMC, Tagliasacchi S, Avanzi S (1987) Embryo-sacs frequency in ovules of abscission affected fruits in *Malus domestica* Borkh. *Advances in Horticultural Science* **1**, 65-67

Fortescue JA, Turner DW (2005) The association between low temperatures and anatomical changes in preanthetic ovules of *Musa* (Musaceae). *Scientia Horticulturae* **104**, 433-444

Furukawa Y, Bukovac MJ (1989) Embryo sac development in sour cherry during the pollination period as related to fruit set. *HortScience* **24**, 1005-1008

García JE, Egea J, Egea L, Berenguer T (1988) The floral biology of certain apricot cultivars in Murcia. *Advances in Horticultural Science* **2**, 84-87

Gonzalez-Rossia D, Juan M, Reig C, Agusti M (2006) The inhibition of flowering by means of gibberellic acid application reduces the cost of hand thinning in Japanese plums (*Prunus salicina* Lindl.). *Scientia Horticulturae* **110**, 319-323

Gonzalez-Rossia D, Reig C, Juan M, Agusti M (2007) Horticultural factors regulating effectiveness of GA3 inhibiting flowering in peaches and nectarine (*Prunus persica* L. Batsch). *Scientia Horticulturae* **111**, 352-357

Hajilou J, Grigorian V, Mohammadi SA, Nazemmieh A, Romero C, Vilanova S (2006) Self- and cross-(in)compatibility between important apricot cultivars in northwest Iran. *Journal of Horticultural Science and Biotechnology* **81**, 513-517

Halász J, Hegedús A, Hermán R, Stefanovits-Bányai E, Pedryc A (2005) New self-incompatibility alleles in apricot (*Prunus armeniaca* L.) revealed by stylar ribonuclease assay and *S*-PCR analysis. *Euphytica* **145**, 57-66

Hedhly A, Hormaza JI, Herrera M (2004) Effect of temperature on pollen tube kinetics and dynamics in sweet cherry, *Prunus avium* (Rosaceae). *American Journal of Botany* **91**, 558-564

Hedhly A, Hormaza JI, Herrero M (2003) The effect of temperature on stigmatic receptivity in sweet cherry (*Prunus avium* L.). *Plant, Cell and Environment* **26**, 1673-1680

Hedhly A, Hormaza JI, Herrero M (2005a) Influence of genotype-temperature interaction on pollen performance. *Journal of Evolutionary Biology* **18**, 1494-1502

Hedhly A, Hormaza JI, Herrero M (2005b) The effect of temperature on pollen germination, pollen tube growth, and stigmatic receptivity in peach. *Plant Biology* **7**, 476-483

Hendrickson AH, Veihmeyer FJ (1950) Irrigation experiment with apricots. *Proceedings of the American Society for Horticultural Science* **55**, 1-10

Herrero M (1983) Factors affecting fruit set in 'Agua de Aranjuez' pear. *Acta Horticulturae* **139**, 91-96

Herrero M (2000) Changes in the ovary related to pollen tube guidance. *Annals of Botany* **85**, 79-85

Herrero M (2001) Ovary signals for directional pollen tube growth. *Sexual Plant Reproduction* **14**, 3-7

Heslop-Harrison J (1975) Incompatibility and the pollen-stigma interaction. *Annual Review of Plant Physiology* **26**, 403-425

Hiratsuka S (1992) Characterization of an S-allele associated protein in Japanese pear. *Euphytica* **62**, 103-110

Hiratsuka S, Okada Y (1995) Some properties of a stylar protein associated with self-incompatibility genotype of Japanese pear. *Acta Horticulturae* **392**, 257-264

Hiratsuka S, Okada Y, Kawai Y, Tamura F, Tanabe K (1995) Stylar basic proteins corresponding to 5 self-incompatibility alleles of Japanese pears. *Journal of the Japanese Society for Horticultural Science* **64**, 471-478

Hiratsuka S, Zhang SL, Nakagawa E, Kawai Y (2001) Selective inhibition of the growth of incompatible pollen tubes by S-protein in the Japanese pear. *Sexual Plant Reproduction* **13**, 209-215

Jackson JE, Hamer PJC, Wickenden MF (1983) Effects of early spring temperatures on the set of fruits of Cox's Orange Pippin apple and year-to-year variation in its yields. *Acta Horticulturae* **139**, 75-82

Janssens GA, Goderis IJ, Broekaert WF, Broothaerts W (1995) A molecular method for S-allele identification in apple based on allele-specific PCR. *Theoretical and Applied Genetics* **91**, 691-698

Jaumien F (1968) The causes of poor bearing of pear trees of the variety 'Doyenne du Comice'. *Acta Agrobotanica* **XXI**, 75-106

Jensen WA, Ashton ME, Beasley CA (1983) Pollen tube-embryo sac interacttion in cotton. In: Mulcahy DL, Ottaviano E (Eds) *Pollen: Biology and Implications for Plant Breeding*, Elsevier Science Publishing, New York, pp 67-72

Kakkar RK, Nagar PK, Ahuja PS, Rai VK (2000) Polyamines and plant morphogenesis. *Biologia Plantarum* **43**, 1-11

Kaul MHL (1988) Male sterility in higher plants. In: *Monographs on Theorical and Applied Genetics* 10, Springer-Verlag, Berlin, 1005 pp

Kozai N, Beppu K, Mochioka R, Boonprakob U, Subhadrabandhu S, Kataoka I (2004) Adverse effects of high temperature on the development of reproductive organs in 'Hakuho' peach trees. *Journal of Horticultural Science and Biotechnology* **79**, 533-537

Kushad MM, Orvos AR, Yelenosk YG (1990) Relative changes in polyamines during citrus flower development. *HortScience* **25**, 946-948

Legave JM (1978) Essai d'interprétation de neécroses florales avant la floraison chez l'abricotier en relation avec une étude des besoins en froid des bougeons pour la leveé de dormance. *Annales de l'Amelioration des Plantes* **28**, 593-607

Legave JM, García G, Marco F (1982) Some descriptive aspects of drops process of flower buds, or young flowers observed on apricot tree in south of France. *Acta Horticulturae* **121**, 75-83

Lillecrapp AM, Wallwork MA, Sedgley M (1999) Female and male sterility cause low fruit set in a clone of the 'Trevatt' variety of apricot (*Prunus armeniaca*). *Scientia Horticulturae* **82**, 255-263

Mahmood K, Carew JG, Hadley P, Battey NH (2000) The effect of chilling and post-chilling temperatures on growth and flowering of sweet cherry (*Prunus avium* L.). *Journal of Horticultural Science and Biotechnology* **75**, 598-601

Marro M (1976) Richerche sulla evoluzione del sacco embrionaie del melo 'Richard' nel corso della fioritura. *Rivista Ortoflorofrutticoltura Italiana* **60**, 185-198

Martin-Tanguy J (1996) Flowering, polyamines, inhibitors of polyamines and ethylene biosynthesis. *Flower Newsletters* **21**, 10-20

Matton DP, Nass N, Clarke AE, Newbigin E (1994) Self-Incompatibility: How plants avoid illegitimate offspring. *Proceedings of the National Academy of Sciences USA* **91**, 1992-1997

Mau SL, Raff J, Clarke AE (1982) Isolation and partial characterization of components of *Prunus avium* L. styles, including an antigenic glycoprotein associated with a self-incompatibility genotype. *Planta* **156**, 505-516

Mehlenbacher SA, Cociu V, Hough LF (1991) Apricots (*Prunus*). In: Moore JN, Ballington JR (Eds) *Genetic Resources of Temperate Fruit and Nut Crops*, International Society for Horticultural Science, Wageningen, pp 65-107

Moghsdam EG, Mokhtarian A (2006) Delaying apricot (cv. Shahroudi) flower induction by growth regulators application. *Journal of Applied Sciences* **6**, 266-269

Monet R, Bastard Y (1971) Effets d'une température modérément élevée: 25ºC, sur les bourgeons floraux du pêcher. *Physiologie Végétal* **9**, 209-226

Nakajima Y, Susanto S, Hasegawa K (1993) Influence of water-stress in autumn on flower induction and fruiting in young pomelo trees (*Citrus grandis* (L) Osbeck). *Journal of the Japanese Society for Horticultural Science* **62**, 15-20

Naor A, Stern R, Peres M, Greenblat Y, Gal Y, Flaishman MA (2005) Timing and severity of postharvest water stress affect following-year productivity and fruit quality of field-grown 'Snow Queen' nectarine. *Journal of the American Society for Horticultural Science* **130**, 806-812

Naylor AW (1984) Funtion of hormones at the organ level of organization. In: Scott TK (Ed) *Hormonal Regulation of Development II*, Springer-Verlag, Berlin, pp 172-174

Nyéki J, Szabó Z (1995) Cross-incompatibility in stone fruits. *Horticultural Science* **28**, 23-31

Okie WR, Werner DJ (1996) Genetic influence on flower bud density in peach and nectarine exceeds that of environment. *HortScience* **31**, 1010-1012

Pimienta E, Polito VS (1982) Ovule abortion in 'Nonpareil' almond (*Prunus dulcis* [Mill.] D.A. Webb). *American Journal of Botany* **69**, 913-920

Pimienta E, Polito VS (1983) Embryo sac development in almond (*Prunus dulcis* [Mill.] D.A. Webb) as affected by cross-, self- and non-pollination. *Annals of Botany* **51**, 469-479

Pritsa TS, Voyiatzis DG (2004) Seasonal changes in polyamine content of vegetative and reproductive olive organs in relation to floral initiation, anthesis, and fruit development. *Australian Journal of Agricultural Research* **55**, 1039-1046

Rallo L, Martin GC, Lavee S (1981) Relationship between abnormal embryo sac development and fruitfulness in olive. *Journal of the American Society for Horticultural Science* **106**, 813-817

Rai N, Bist LD (1991) Effects of promalin, sadh and chlormequat on tree growth, flowering, fruit-set, yield and fruit-quality of gola pear. *Journal of Horticultural Science* **66**, 443-447

Ray S, Park SS, Ray A (1997) Pollen tube guidance by the female gametophyte. *Development* **124**, 2489-2498

Reinoso H, Luna V, Daurfa C, Pharis R, Bottini R (2002) Dormancy in peach (*Prunus persica*) flower buds. VI. Effects of gibberellins and an acylcyclohexanedione (trinexapac-ethyl) on bud morphogenesis in field experiments with orchard trees and on cuttings. *Canadian Journal of Botany* **80**, 664-674

Rodrigo J, Herrero M (1998) Influence of intraovular reserves on ovule fate in apricot (*Prunus armeniaca* L.). *Sexual Plant Reproduction* **11**, 86-93

Rodrigo J, Hormaza JI, Herrero M (2000) Ovary starch reserves and flower development in apricot (*Prunus armeniaca* L.). *Physiologia Plantarum* **108**, 35-41

Romero C, Vilanova S, Burgos L, Martínez-Calvo J, Vicente M, Llácer G (2004) Analysis of the *S*-locus estructure in *Prunus armeniaca* L. Identification of *S*-haplotype specific *S-RNase* and *F-box* genes. *Plant Molecular Biology* **56**, 145-157

Rugini E, Mencuccini M (1985) Increased yield in the olive with putrescine treatment. *HortScience* **20**, 102-103

Ruiz-Sanchez MC, Egea J, Galego R, Torrecillas A (1999) Floral biology of 'Bulida' apricot trees subjected to postharvest drought stress. *Annals of Applied Biology* **135**, 523-528

Ruiz D, Egea J, Gil MI, Tomas-Barberan FA (2005a) Characterization and quantitation of phenolic compounds in new apricot (*Prunus armeniaca* L.) varieties. *Journal of Agricultural and Food Chemistry* **53**, 9544-9552

Ruiz D, Egea J, Tomas-Barberan FA, Gil MI (2005b) Carotenoids from new apricot (*Prunus armeniaca* L.) varieties and their relationship with flesh and skin color. *Journal of Agricultural and Food Chemistry* **53**, 6368-6374

Sage TL, Bertin RI, Williams EG (1994) Ovarian and other late-acting self-incompatibility systems. In: Williams EG, Clarke AE, Knox RB (Eds) *Genetic Control of Self-Incompatibility and Reproductive Development in Flowering Plants*, Kluwer, Dordrecht, pp 116-140

Sakurai K, Brown SK, Weeden NF (1997) Determining the self-incompatibility alleles of Japanese apple cultivars. *HortScience* **32**, 1258-1259

Sakurai K, Brown SK, Weeden NF (2000) Self-incompatibility alleles of apple cultivars and advanced selections. *HortScience* **35**, 116-119

Sassa H, Hirano H, Ikehashi H (1992) Self-incompatibility-related RNases in styles of Japanese pear (*Pyrus serotina* Rehd). *Plant and Cell Physiology* **33**, 811-814

Sassa H, Hirano H, Ikehashi H (1993) Identification and characterization of stylar glycoproteins associated with self-incompatibility genes of Japanese pear, *Pyrus serotina* Redh. *Molecular and General Genetics* **241**, 17-25

Sassa H, Mase N, Hirano H, Ikehashi H (1994) Identification of self-incompatibility-related glycoproteins in styles of apple (*Malus* x *domestica*). *Theoretical and Applied Genetics* **89**, 201-205

Sato M, Kanbe K, Nakagawa S, Yuda E, Fukunaga S (1988) Studies on development of the embryo sac and its abnormality in the triploid apple cultivar 'Mutsu'. *Journal of the Japanese Society for Horticultural Science* **57**, 366-372

Sedgley M (1990) Flowering of deciduous perennial fruit crops. *Hortic. Rev.* **12**, 223-264

Shimizu KK, Okada K (2000) Attractive and repulsive interactions between female and male gametophytes in *Arabidopsis* pollen tube guidance. *Development* **127**, 4511-4518

Son L, Kuden AB (2005) Dormex and Promalin affects fruit set and earliness of apricot (*Prunus armeniaca*) and plum (*Prunus domestica*) cultivars. *New Zealand Journal of Crop and Horticultural Science* **33**, 59-64

Sonneveld T, Robbins TP, Boskovic R, Tobutt KR (2001) Cloning of six cherry self-incompatibility alleles and development of allele-specific PCR detection. *Theoretical and Applied Genetics* **102**, 1046-1055

Southwick SM, Yeager JT, Zhou H (1995) Flowering and fruiting in Patterson apricot (*Prunus armeniaca*) in response to postharvest application of gibberellic-acid. *Scientia Horticulturae* **60**, 267-277

Stösser R, Anvari SF (1982) On the senescence of ovules in cherries. *Scientia Horticulturae* **16**, 29-38

Tamura M, Ushijima K, Sassa H, Hirano H, Tao R, Gradziel TM (2000) Identification of self-incompatibility genotypes of almond by allele-specific PCR analysis. *Theoretical and Applied Genetics* **101**, 344-349

Tao R, Yamane H, Sassa H, Mori H, Gradziel TM, Dandekar AM (1997) Identification of stylar RNases associated with gametophytic self-incompatibility in almond (*Prunus dulcis*). *Plant and Cell Physiology* **38**, 304-311

Tao R, Yamane H, Sugiura A, Murayama H, Sassa H, Mori H (1999) Molecular typing of S-alleles through identification, characterization and cDNA cloning for S-RNases in sweet cherry. *Journal of the American Society for Horticultural Science* **124**, 224-233

Thompson MM, Liu LJ (1972) Pollination and erratic bearing in 'Italian' prune. *Journal of the American Society for Horticultural Science* **97**, 489-491

Tomer E, Gottreich M, Gazit S (1976) Defective ovules in avocado cultivars. *Journal of the American Society for Horticultural Science* **101**, 620-623

Tomimoto Y, Nakazaki T, Ikehashi H, Ueno H, Hayashi R (1996) Analysis of self-incompatibility-related ribonucleases (*S*-RNases) in two species of pears, *Pyrus communis* and *Pyrus ussuriensis*. *Scientia Horticulturae* **66**, 159-167

Toyama TK (1980) The pollen receptivity period and its relation to fruit setting in the stone fruits. *Fruit Varieties Journal* **34**, 2-4

Uriu K (1964) Effect of post-harvest soil moisture depletion on subsequent yield of apricots. *Proceedings of the American Society for Horticultural Science* **84**, 93-97

Vachun Z (1981) Etude de quelques proprietes morphologiques et physiologiques du pollen d'abricotier. Germination et croissance des tubes polliniques a basses temperatures. *Acta Horticulturae* **85**, 387-417

Vilanova S, Badenes ML, Burgos L, Martinez-Calvo J, Llacer G, Romero C (2006) Self-compatibility of two apricot selections is associated with two pollen-part mutations of different nature. *Plant Physiology* **142**, 629-641

Vilanova S, Romero C, Burgos L, Llácer G, Badenes ML (2005) Identification of self-(in)compatibility alleles in apricot (Prunus armeniaca L.) by PCR and sequencing analysis. *Journal of the American Society for Horticultural Science* **130**, 893-898

Viti R, Monteleone P (1991) Observations on flower bud growth in some low yield varieties of apricot. *Acta Horticulturae* **293**, 319-326

Webster AD, Spencer JE (2000) Fruit thinning plums and apricots. *Plant Growth Regulation* **31**, 101-112

Weinberger JH (1956) Prolonged dormancy trouble in peaches in the southeast in relation to winter temperatures. *Proceedings of the American Society for Horticultural Science* **67**, 107-112

Wiersma PA, Wu Z, Zhou L, Hampson C, Kappel F (2001) Identification of new self-incompatibility alleles in sweet cherry (*Prunus avium* L.) and clarification of incompatibility groups by PCR and sequencing analysis. *Theoretical and Applied Genetics* **102**, 700-708

Yaegaki H, Miyake M, Haji T, Yamaguchi M (2003) Inheritance of male sterility in Japanese apricot (*Prunus mume*). *HortScience* **38**, 1422-1423

Yaegaki H, Shimada T, Moriguchi T, Hayama H, Haji T, Yamaguchi M (2001) Molecular characterization of *S*-RNase genes and S-genotypes in the Japanese apricot (*Prunus mume* Sieb. et Zucc.). *Sexual Plant Reproduction* **13**, 251-257

Yamamoto M, Matsumoto R, Okudai N, Yamada Y (1997) Aborted anthers of *Citrus* result from gene-cytoplasmic male sterility. *Scientia Horticulturae* **70**, 9-14

Yamane H, Tao R, Murayama H, Sugiura A (2000) Determining the S-genotypes of several sweet cherry cultivars based on PCR-RFLP analysis. *Journal of Horticultural Science and Biotechnology* **75**, 562-567

Zuccherelli S, Tassinari P, Broothaerts W, Tartarini S, Dondini L, Sansavini S (2002) *S*-allele characterization in self-incompatible pear (*Pyrus communis* L.). *Sexual Plant Reproduction* **15**, 153-158