

Apricot Flower Bud Development: Main Biological, Physiological and Environmental Aspects Related to the Appearance of Anomalies

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ABSTRACT

Apricot (*Prunus armeniaca* L.) is a fruit species that, in certain cultivation area, shows several problems related to floral biology, appearance of flower bud anomalies, inconstant and extremely low yield. In this review, environmental, biological and physiological aspects affecting flower bud development are discussed and the complex phenomena of flower bud anomalies are analyzed. Three phases of the whole flower bud development periods are considered: 1) from flower bud initiation to beginning of dormancy; 2) from deep dormancy to bud swelling; 3) from beginning of flowering to petal drop. The early appearance of flower bud anomalies is related to the first growth period, involving flower bud induction, differentiation, organogenesis and beginning of dormancy, when several environmental and agronomical factors can heavily modify these processes. The second flower bud growth period is characterized by the dormancy phase followed by the resumption phase, when bud dormancy release occurs. Several types of anomalies have been observed when the buds are still dormant and also at the end of dormancy. During the third period, the development of the female and male gametophyte is completed and all organs are functional. At this time, the appearance of anomalies determines significant problems, such as morphological abnormalities of pistil, stamen, and a reduction of male and female fertility.

Keywords: adaptation, climate, flowering, heritability, necrosis, phenological stage, *Prunus armeniaca* L.

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INTRODUCTION

Apricot (*Prunus armeniaca* L.) is a stone fruit native of China that spread throughout Asia, Europe, North and South America, and Oceania. In European and Mediterranean countries production covers more than 75% of the world's supply. This fruit specie is characterized by a non-surplus yield, by a wide range of possible valorisation and by a specific adaptation to particular environmental areas due to a notable richness of local genotypes (Audergon *et al.* 2006). However, apricot shows several problems related to its floral biology being particularly subjected to irregular and/or insufficient fruit bearing. The difficulty of adaptability of several apricot cultivars to environments different from that of origin is well known (Carraut 1968; Guerriero and Bartolini 1991; Bassi *et al.* 2006). The trouble of adaptability to specific environments and abiotic stress can particularly occur when cultivars originating from continental zones are introduced into coastal areas. As a result, an erratic and poor bloom occurs with an inconstant and extremely low yield not traced strictly to genetic traits. Several

authors observed that the yield irregularities of several apricot genotypes were due to important levels of flower bud anomalies and abscission. In adversed years, some cultivars, such as 'Goldrich', 'Orange Red', 'Polonais', 'Stark Early Orange', 'Guillermo', can reach flower bud anomalies higher than 80% (Garcia *et al.* 1997; Guerriero *et al.* 2000; Martinez-Gomez *et al.* 2002).

During the whole flower bud development period, several and diversified anomalies may occur from deep dormancy to the time of blooming (Legave 1978, 1984). The influence of floral abortion on fruitfulness regularity has been demonstrated (Legave *et al.* 2006a, 2006b), but the knowledge about the mechanism and nature of anomalies are very scant. Studies conducted on anomalies determinism in apricot flower buds showed different kinds of anomalies in relation to the appearance time: early, intermediate, and late. The 'early anomalies', during the autumn season, seem to be caused by the summer drought/heat conditions that occur during flower bud differentiation; the 'intermediate anomalies', such as tissue necrosis of floral primordia, can appear in the winter as a consequence of

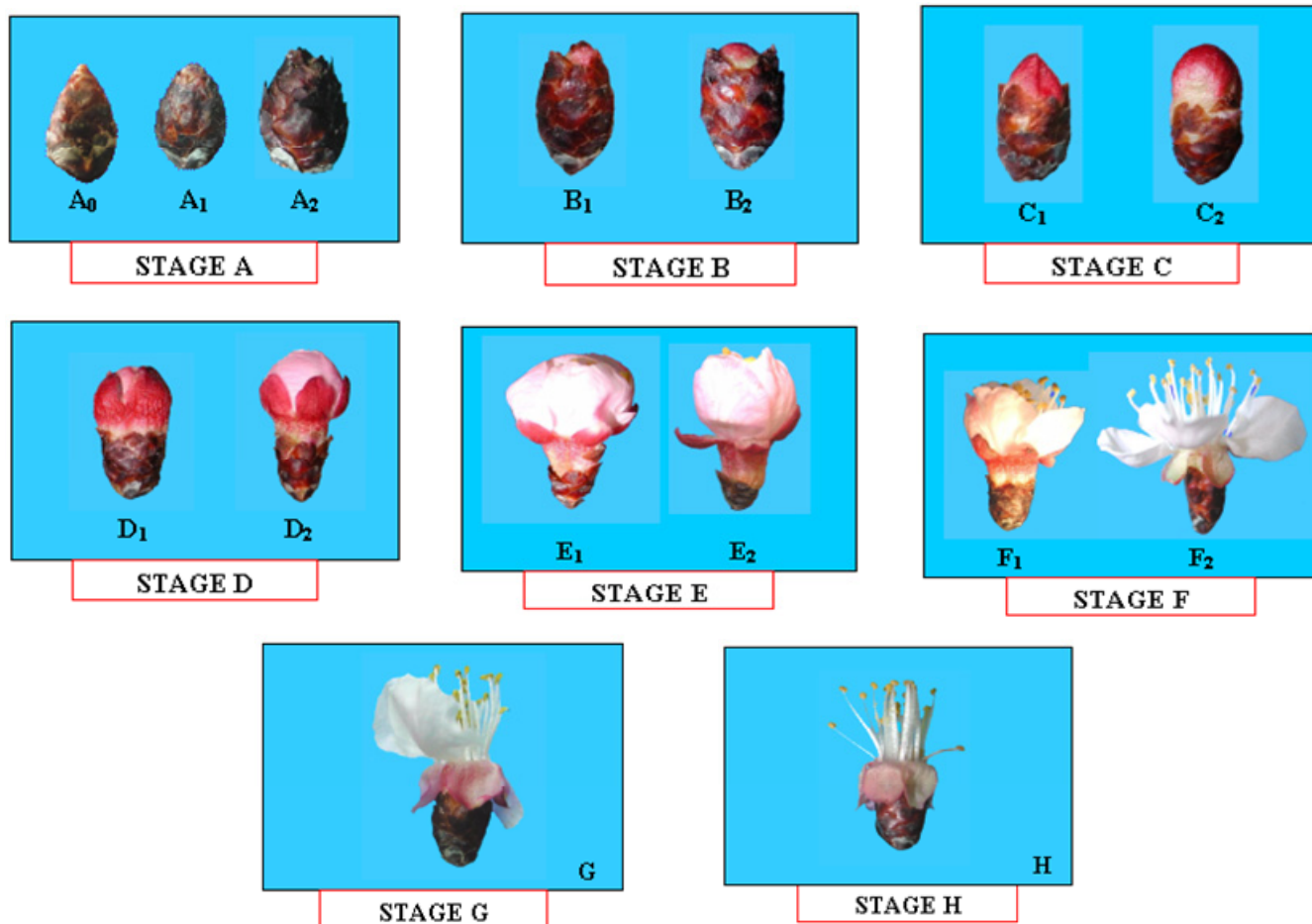


Fig. 1 Evolution of flower bud phenological stages in apricot: deep dormancy (stage A), pink sepal tips appearance (stage B), sepals clearly visible (stage C), achievement of bud swelling (stage D), petals clearly visible (stage E), anthesis (stage F), end of flowering (stage G) and petal fall (stage H). Adapted from Bartolini *et al.* (2004). Copyright permission kindly provided by Research Signpost Press, Kerala, India.

strong oscillations between minimal and maximal temperatures; the 'late anomalies', such as pistil abortion, occurring after the loss of dormancy, can be caused by late spring frost or by genetic factors (Viti and Monteleone 1991). The appearance of flower bud anomalies induces several bud drop waves at different time of the bud ontogenetic cycle. The bud drop can occur early, during the autumn-winter season, and/or late, at the reactivation of flower bud development, during the spring season. These events provide a poor yield efficiency leading to problems of economic importance.

The present paper addresses questions about biological, physiological, environmental, and genetic determinism on the appearance of flower bud anomalies, in relation to phenological development of flower buds, from the beginning of differentiation to blooming time.

FLOWER BUD DEVELOPMENT

In apricot, morphological flower bud development was first reported by Baggiolini (1952), later integrated by sub-phases within each phenological stage (Bartolini *et al.* 2004) as reported in **Fig. 1**. Dormant buds (stages A₀, A₁, A₂) are characterised by a conic shape, rounded at the base, with the brown bud scales strictly closed (A₀) or more enlarged (A₁ and A₂) at the beginning of bud swelling (stages B₁ and B₂) the pink sepal tips appear; at stages C₁ and C₂ sepals are clearly visible; at stages D₁ and D₂ the full bud swelling happens with the appearance of the white petal tips; at stages E₁ and E₂ petals are clearly visible; at stages F₁ and F₂ the full flowering occurs; at stages G and H petal fall begins with the end of flowering.

In the following paragraphs, flower bud development is analyzed taking into account three phases (**Fig. 2**): 1) from

flower bud initiation to the beginning of dormancy (stage A₀); 2) from deep dormancy to bud swelling (stages A₁–D₂); 3) from the beginning of flowering to petal fall (stages E₁–H).

From flower bud initiation to beginning of dormancy

During this first growth period, including the time of flower bud initiation, differentiation, organogenesis and entrance in endodormancy, several environmental and agronomical factors can heavily modify the regularity of these processes resulting in early appearance of flower bud anomalies.

Concerning flower initiation, three classical steps were considered according to Bernier (1981): *induction*, with production of a 'floral stimulus' in the leaves; *translocation* of the 'floral stimulus' towards the meristems; *evocation* followed by floral morphogenesis. The flower-bearing bud development is a process requiring the transformation of an undifferentiated meristematic apex into a structure carrying flowers (**Fig. 3**). During this process, a sequence of morphological and biochemical changes occurs such as cell division, increase in carbohydrate content, and activity of some respiratory enzymes. Moreover, protein and RNA synthesis are other examples of early biochemical changes (Marcelle 1984). In particular, an increase in RNA synthesis is considered to be one of the earliest indicators of 'floral evocation' (Bernier *et al.* 1981; Buban and Faust 1982) involving the transition from vegetative to reproductive phase (Wada *et al.* 2002). In this process, flowering genes are de-repressed and alternatively genes responsible for vegetative patterns of morphogenesis are eliminated (Evans 1971).

In apricot, as well as in other deciduous fruit species, flower initiation begins during the growth season that pre-

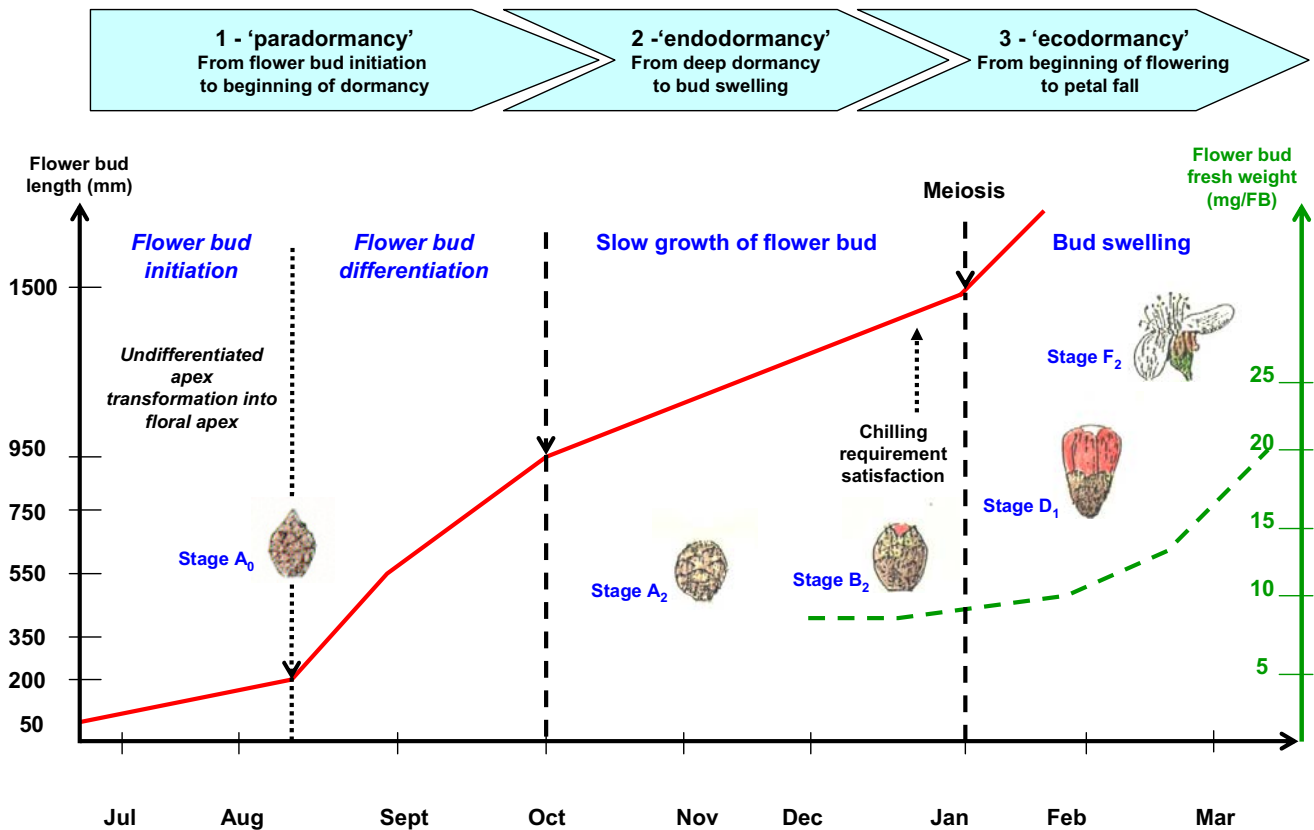


Fig. 2 Schematic representation of apricot flower bud growth during the annual cycle (by Legave 1975, modified). 1) Paradormancy: from flower bud initiation to beginning of dormancy; 2) Endodormancy: from deep dormancy to bud swelling; 3) Ecodormancy: from beginning of flowering to petal fall. Solid and dotted lines represent the flower bud length (μm) and the flower bud fresh weight (mg/FB), respectively. Evolution of the main phenological stages of flower buds are illustrated.

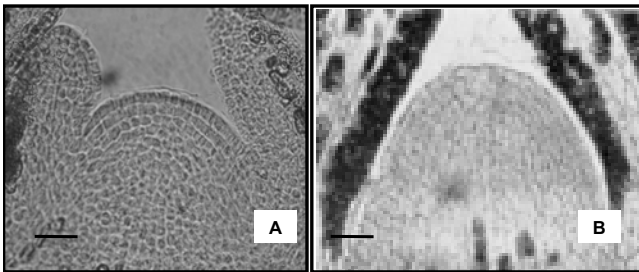


Fig. 3 Undifferentiated meristematic apex, rounded shape, during the 'induction' phase (A, x 400; scale bar 50 μm); differentiated meristematic apex, raised shape, after floral 'evocation' phase (B, x 400; scale bar 50 μm).

cedes anthesis (summer-autumn) up to the completion in the weeks immediately before bloom. The time and the length of flower differentiation are not easy to detect also within the same genotype, because this phase takes place gradually at different times in different parts of the canopy. During the vegetative period, various growth waves due to the rhythmic shoot elongation determine different types of buds from the base to the top of the annual long shoot (Costes *et al.* 1995). Generative buds and flowers on the first growth wave have the greatest degree of development, while the second and third growth waves determine the lowest degree of differentiation (Duric *et al.* 1999).

Several factors influence the evolution of the differentiation process, and the degree of flower bud differentiation which can vary from year to year. The environmental factors, such as temperature, solar radiation, and water availability, cultural practices, orchard management, identified as important triggers in floral initiation (Bridget *et al.* 2001), subsequently will be examined. The occurrence of high and frost temperatures can adversely affect the beginning and

the evolution of flower bud differentiation and the bud quality. In peach (*Prunus persica* L., cultivar 'Lavinia') floral bud initiation can be severely affected by late spring frosts causing an advance in the beginning of the evocation process, as a physiological consequence of the subsequent fruit set drop (Andreini and Bartolini, in press). High summer temperatures were found to reflect in the time that the meristem became generative, affecting a later flower initiation in apple, with a decline of cluster quality (Zhu *et al.* 1997). In apricot, different periods of water stress affect the development of the flower buds: the differentiation time was delayed, the development was slowed, and the number of flower buds was lower (Brown 1960). Brown and Abi-Fadel (1953) found that the apricot flower buds from irrigated trees reached more advanced stages sooner than buds from non-irrigated plots. However, when water was again provided, development was hastened (Albuquerque *et al.* 2003).

In apricot, certain cultural practices (i.e. time and type of pruning, training system, fertilization, irrigation, and chemical treatments) can influence subsequent flower bud formation and vegetative re-growth (Xiloyannis *et al.* 1999). In particular, different light levels available within the canopy throughout the growing season, and a lower interception of photosynthetically active radiation (PAR) such as that occurring at the base of a Y training system negatively affect the earliest floral morphogenesis phases (Nuzzo *et al.* 1999). These authors found that in shaded zones of the canopy ($\text{PAR} = 1116\text{-}450 \mu\text{molm}^{-2}\text{s}^{-1}$) there were fewer spurs and fruiting shoots per unit of branch length with a decrease of 50% of differentiated floral buds with respect to exposed zones ($\text{PAR} = 1600\text{-}1200 \mu\text{molm}^{-2}\text{s}^{-1}$). The low PAR available could be responsible for the different nutritional status of flower buds on the shaded part of the canopy which showed the lowest soluble carbohydrates and starch levels at the time when crucial events of floral morphogenesis take place. Moreover, flowers in shaded zones of the canopy showed an anomalous gynoecium structure with an in-

creased percentage of underdeveloped pistils and consequently, no ability to set fruit. However, Ruiz *et al.* (2005), shading all or parts of the trees during the dormant season, found a reduction of flower bud abscission; these authors hypothesized that this result could be due to a decreased level of gibberellin resulting from a reduction of temperature in the shaded trees. Concerning the different times of summer pruning, it has been observed that later cuts were correlated with a late flower bud differentiation inducing a delay of the flowering (Burtoiou *et al.* 2006). Damage to the canopy in autumn or early defoliation had an important influence on flower bud differentiation with a subsequent appearance of floral anomalies and high percentages of abscised buds (Martinez-Gomez *et al.* 2002). Exogenous applications of gibberellic acid (GA₁, GA₄ and GA₃), used to improve the fruit thinning, seem to reduce the number of potential floral buds, inhibiting the transition of meristematic apices from the vegetative to floral stage, when applied before floral differentiation (Oliveira and Browning 1993; Southwick and Yeager 1995). On the other hand, GA treatments at the concentration of 500 ppm did not induce any difficulties in the differentiation process when the chemical was sprayed at a more advanced stage of bud differentiation (Clanet and Borsani 1972). However, a relationship between gibberellin treatments (GA₃ from 100 to 500 ppm) and the frequent appearance of floral anomalies, such as double and triple pistils, were observed in peach, cultivars 'Crimson Gold' (Garcia-Pallas *et al.* 2001) and 'Pen-Too' (Reinoso *et al.* 2002). Recently, on nectarine cv. 'Lavinia' more than 30% of malformed pistils (double and triple) were observed when treated with 80 ppm of GA₃ (Andreini and Bartolini, in press).

The pattern of apricot floral organogenesis after initiation is typical of other Prunoideae. The first floral organs to appear are sepals and petals followed by the pistil and stamen (Legave 1975); the most internal whorls of the pistil derive from the gradual evolution of the receptacle (Monet and Bastard 1968; Legave 1975). This process requires around two months and is normally completed before leaf fall but not all buds reach the stage of the appearance of the pistil (Legave 1975). Under Mediterranean climatic conditions, flower buds develop more slowly during the coldest period of late autumn, with growth of the pistil, formation and development of the ovule, increasing size of anthers, and differentiation of sporogenous tissues (Legave 1975; Viti and Scalabrelli 1988).

Under different environmental conditions, an earliest appearance of floral anomalies and necrosis has been frequently observed in apricot, in correspondence of the final stage of flower bud differentiation. This problem is not

limited to coastal areas but it has also been reported in Hungary, where the anomalies were evident as early as September-October (Buban *et al.* 1982). In apricot cultivars with serious problems of productivity, such as cv. 'Stark Early Orange', the presence of an early abscission region has been detected and localized at the pulvinar zone, from the end of flower bud differentiation onwards (Bartolini and Viti 1999b). This zone is characterized by intercellular spaces filled with calcium-oxalate crystals (Fig. 4). This condition could be the main cause of the high rate of anomalous flower buds which drop just before blooming, with a consequence decrease in yield.

From deep dormancy to flower bud swelling

The second flower bud growth period is characterized by the dormancy phase, a complex phenomenon due to an interaction between genotype and environment. Actually, the most adopted dormancy terminology was proposed by Lang *et al.* (1987) which identified dormancy phases (Fig. 2) as: *paradormancy* (when growth is regulated by endogenous plant factors outside the bud); *endodormancy* (when growth is regulated by physiological factors inside the bud) and *ecodormancy* (when growth is regulated by external environmental factors). Bud dormancy starts with the perception by the plant of rest-signals under the influence of short and cool days; this natural process allows the tree to survive unfavourable winter conditions and finishes after an accumulation of chilling temperatures. To overcome bud dormancy, each apricot cultivar needs a number of hours ranging from 1 to 8°C and the resumption of bud growth occurs after a specific chilling accumulation defined as chilling requirement (CR). Actually, the most used model to calculate the chilling accumulation is the 'Chill Unit' (CU) according to Richardson *et al.* (1974). When the chilling requirement is satisfied, flower buds become sensitive to warm temperatures ($\geq 12^{\circ}\text{C}$) with the resumption of their active growth. This model has been applied on several apricot cultivars of Italian and foreign germplasm to determine their CR, under the environmental conditions of central Italy (lat. 43°02' N, long. 10°36'E). Results have been able to classify the cultivars into 3 types in relation to their chilling requirement (Guerriero *et al.* 2006a; Viti *et al.* 2006): - type A = low CR, <950 CU (i.e. 'Alessandrino', 'Baracca', 'D'Alessandria', 'Goldrich', 'Ninfa', 'San Castrese', 'Sarriztu I°'); - type B = medium CR, 950 - 1200 CU (i.e. 'Aurora', 'Amabile Vecchioni', 'Bebeco', 'Boccuccia Spinosa', 'Canino', 'Ceccona', 'Fracasso', 'Monaco Bello', 'Moniqui', 'Pelese di Giovanniello', 'Portici 6', 'Precoce d'Imola', 'Nonno', 'San Nicola Grosso', 'Sungold', 'Vitulo'); type C = high CR, > 1200 CU (i.e. 'Bergeron', 'Boccuccia Liscia', 'Polonais', 'Rapareddu', 'Sant'Ambrogio', 'San Francesco', 'Orange Red'). A satisfied CR determines the success of production in apricot and information about the yield behaviour of a given cultivar to be accurately predicted. To find the chilling and heat requirements of cultivars, several experimental approaches (biological, biochemical and histological) were used. In the last few years, several procedures have been proposed to define an appropriate protocol to determine the chilling requirement of a specific genotype. Considering the biological methods, the most simple method is to record the increase in fresh weight of flower buds during the dormant season, after forcing of branches in a growth room at constant temperature of 23°C for 7 days (Bailey *et al.* 1978; Garcia *et al.* 1997; Andres and Duran 1999; Guerriero *et al.* 2000). The chilling requirement is assumed to be fulfilled when an increase of 30% of flower bud fresh weight is recorded (Viti *et al.* 2003). More recently, other methods have been proposed to early detect physiological changes within a flower bud, just before morphological signs of growth reactivation. Investigations have been carried out on the role of free radicals and on their removal (Wang *et al.* 1991; Siller-Cepeda *et al.* 1992). The activity of oxygen-scavenging enzymes (cata-

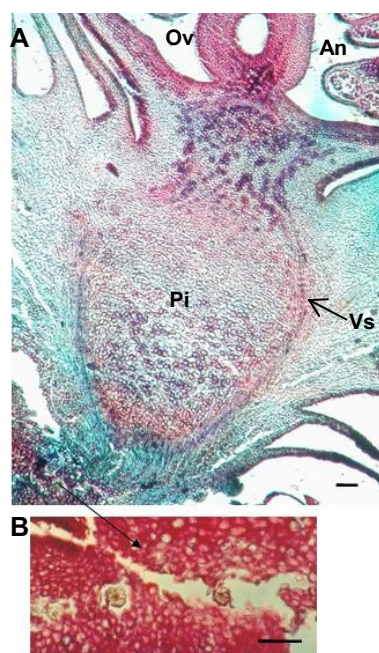


Fig. 4 (A) Median longitudinal section (x 100; scale bar: 200 μm) of a flower bud showing at the pulvinar zone (arrow) the presence of an abscission layer (B) with calcium-oxalate crystals (x 400; scale bar 50 μm). Ov = ovary; An = anthers; Pi = pith; Vs = vascular strands.

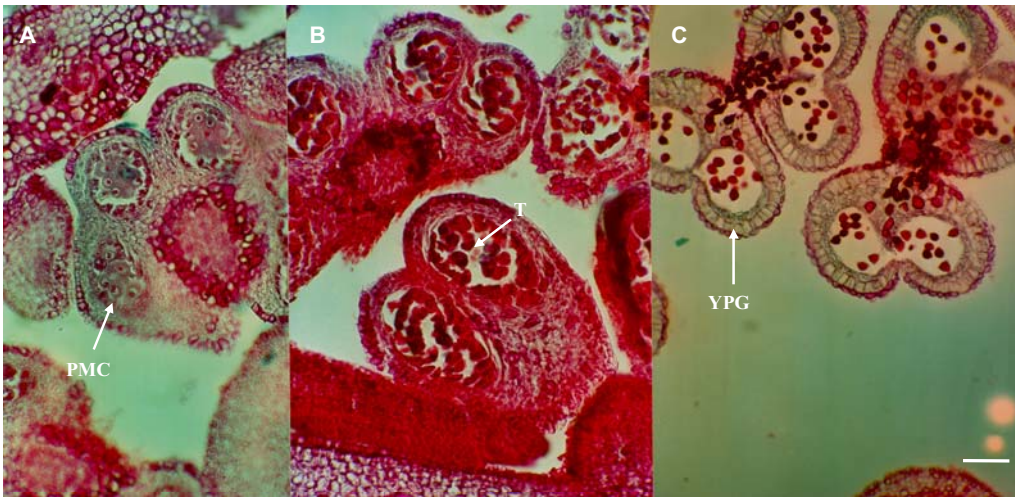


Fig. 5 Main microsporogenesis phases (x 400; scale bar 50 μ m). (A) Pollen mother cells (PMC), (B) tetrads (T), (C) young pollen grains (YPG).

lase, ascorbate peroxidase, and guaiacol peroxidase) and oxidised and reduced glutathione content have been studied in relation to the different chilling requirement of apricot cultivars (Zanol *et al.* 2004; Bartolini *et al.* 2006). The most significant relationship with the break of dormancy was found in the increase of reduced glutathione from deep to the end of endo-dormancy (Bartolini *et al.* 2004).

Furthermore, studies on intracellular pH (ipH) have been made to understand the relationships between the bud and its underlying tissues. The ipH is assumed to reflect the 'sink strength' gradients that may determine the nutrient fluxes, the metabolic activity in the bud-underlying tissues complex, and consequently the dormant state of buds (Petel *et al.* 1992; Bonhomme *et al.* 1999). In apricot, when flower buds were still in deep dormancy it was recorded an increase of ipH in tissues of flower primordium just before the first biological sign of growth reactivation (Zanol and Bartolini 2003).

As regards histological approaches, the xylem differentiation process (transition from procambium to xylem cells) within flower bud has been studied in several apricot cultivars. Even when no morphological evolution (bud growth) was noticed, a gradual xylem vessel development occurred during winter and other variant climatic conditions seem involved in this process (Bartolini and Giorgelli 1994). A recent study on the relationship between dormancy overcoming, xylogenesis and microsporogenesis, showed that while in cultivar with a low chilling requirement all these

events matched, in cultivars with a medium and high chilling requirement an asynchrony was observed (Bartolini *et al.* 2006), leading to an inconstant fruit production.

All these studies demonstrated that, dormant flower buds continuously grow but without any visible development; indeed, during the apparent rest period of deep dormancy, processes of micro- and macrosporogenesis take place. As regards microsporogenesis, the following phases have been identified (Fig. 5) in relation to flower bud development (Nyujto and Banai 1975; Viti and Scalabrelli 1988; Viti and Monteleone 1991): a) *Sporigen Cells Differentiation* (sticked cells), during the paradormancy period; b) *Pollen Mother Cells* (diploid microsporocytes differentiated from sporogenous cells that become spherical and separated) and c) *Tetrads appearance* (four haploid microspores produced by meiosis of the pollen mother cells and surrounded by a callose wall), during the endodormancy period; d) *Young Pollen Grains* (isolated microspores produced when the callose wall disappears) at the overcoming of endodormancy e) *Mature Pollen Grains* (full development of the wall constituted of two layers, exine and intine) after the resumption of growth. The tetrad stage has been considered as a signal marking the end of endodormancy (Bordeianu *et al.* 1962; Szabò *et al.* 2002). Nevertheless, other studies have shown that tetrads occur at a later stage of morphological bud growth and are not closely linked to chilling accumulation, since the process of meiosis also takes place in buds exposed to high temperature (Martinez *et al.* 1982;

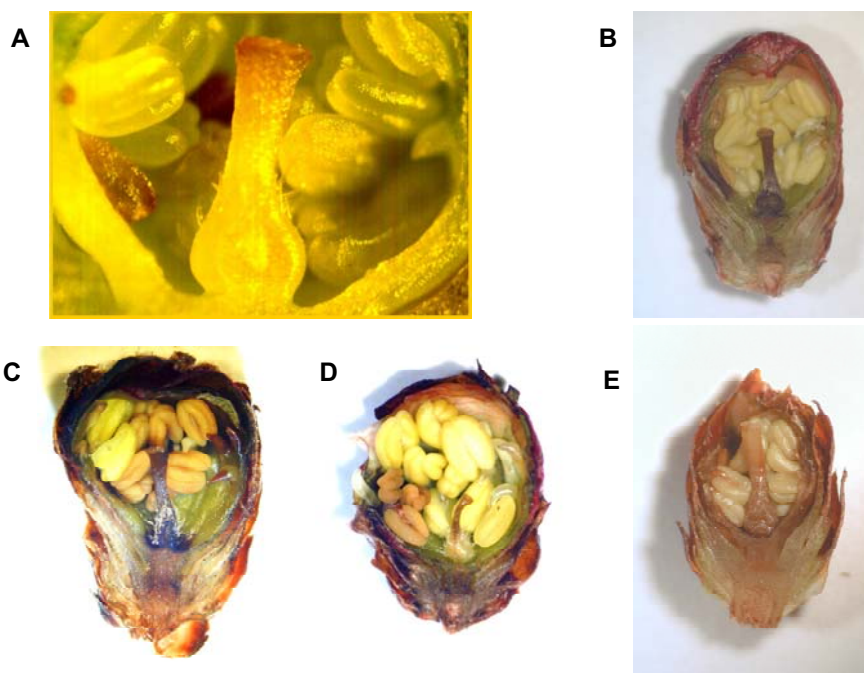


Fig. 6 Different types of flower bud anomalies observed under stereomicroscope. (A) browning of stigma; (B) browning of pistil; (C) necrotic pistil; (D) underdeveloped and necrotic pistil and browning anthers; (E) browning tissues due to a spring frost.

Felker *et al.* 1983; Viti and Scalabrelli 1988).

During the winter period, an unsatisfactory chilling requirement, as a consequence of a short or warm rest season (Garcia 1997), can determine an incomplete resumption of flower bud dormancy with scantily blooming resulting in a high flower bud drop (Viti and Monteleone 1995; Erez 2000). In Mediterranean growing areas, from endodormancy to bloom, apricot is characterized by high flower bud drop. These buds show, as a first step, the browning of primordia followed by tissue necrosis of pistils and stamens (Legave 1978, 1984). All floral anomalies (Fig. 6), e.g. pistil abortion and/or necrosis of flower buds, that may occur during bud and flower development, are currently and too easily attributed to unfulfilled chilling requirement. Therefore, floral anomalies or necrosis would be unrelated to the fulfilment of chilling requirement and can be mainly attributed to a post-dormancy effect (Viti and Monteleone 1993; Legave 2002).

A specific climatic determinism of floral necrosis has been proposed, involving mainly temperature and photoperiod; in particular, high minimum temperatures (>10°C for several consecutive days) during dormancy affect the appearance of pistil necrosis alone or associated with stamens necrosis (Legave *et al.* 2004), although a correlation between the flower anomalies and the satisfaction of chilling requirement has not been clearly demonstrated (Guerriero and Bartolini 1991; Viti and Monteleone 1991; Legave 2002, 2006b). Moreover, studies on floral anomalies, recently carried out under French and Italian climatic conditions using a standard methodology, demonstrated that floral necrosis and flowering time are two independent characters (Legave *et al.* 2006a).

When flower buds overcome dormancy (end of winter-beginning of spring) a rapid increase in weight and the complete development of floral verticils is observed with the transition from phenological stage B (visual beginning of bud swelling) to stage D (appearance of the white petal tip) (Figs. 1, 2). In this period elongation of the pistil and stamen filaments occurs, pollen grains mature and the complete development of the gynoecium occurs only a few days before blossoming (Luna *et al.* 1990). At the same time, a large number of flower bud anomalies appeared and it is possible to observe browning or necrosis of the whole pistil or localized on the ovary, style, and stigma (Fig. 6A-D). This damage is irreversible and the buds drop just before or after blooming. These anomalies can be a consequence of adverse climatic factors like late frosts. Several authors have pointed out how the frost resistance in deciduous tree buds is higher during winter and decreases considerably than in early spring. At this time tissues of floral primordium can be affected by intracellular ice crystals causing severe damages to flower buds (Lasheen *et al.* 1970; Burke *et al.* 1976; Quamme 1978; Proebsting and Andrews 1982). Apricot flower buds are particularly sensitive to early spring frost injuries because of their greater cell hydration that occurs at the breaking of dormancy (Szalay *et al.* 1999). At this time, the xylem vessel continuity between bud axis and ovary is established and ice can propagate into flower tissues (Bartolini and Giorgelli 1994; Bartolini *et al.* 2006). After spring frosts, cellular damage is usually due to extra-cellular ice crystals that destroy the cell wall integrity; the killed apricot flower buds show specific internal symptoms (Fig. 6E) such as browning and necrosis of tissues affecting ovary, pistil, stamens or the whole bud (Viti and Monteleone 1993; Rodrigo 2000).

In apricot, several studies have been carried out in order to screen for specific frost hardiness and the results showed a different degree of frost tolerance in relation to genotype and phenological stage of flower buds (Bartolini and Viti 1999a; Bartolini *et al.* 2006). After the break of endodormancy, some genotypes, such as cultivars 'Haggith', 'San Castrese', 'Boccuccia Spinosa' and several new Italian selections showed a high tolerance to freeze damage at the critical temperature of -8°C tested under artificial conditions (Guerriero *et al.* 2006b). Some early blooming culti-

vars, although heavily damaged by spring frost in full bloom, recorded higher yield because high flower buds set (Bassi *et al.* 1995). Thus, finding high bloom setting genotypes could be seen as a possible way to select for frost avoidance and tolerance.

From beginning of flowering to petal fall

During this period, the complete development of female and male gametophytes takes place and all organs became functional within a few days in relationship to the occurrence of effective warm temperatures. The flower buds (Fig. 1) showed the transition from phenological stage E (petal appearance) to stage H (petal fall). At this time, the appearance of anomalies causes significant problems due to morphological abnormalities of pistil and stamen so as a reduction of male and female fertility.

During fruit set, process that follows fertilization, most apricot cultivars require specific edaphoclimatic conditions (Williams 1970; Burgos *et al.* 1991). In particular, cold and warm temperatures can influence pollen viability, stigma receptivity, pollen tube elongation, embryo sac growth, and ovule longevity with a reduction of fruit set (Eaton and Jamont 1964; Lichou *et al.* 1995; Albuquerque *et al.* 2004a). During the pre-flowering phase, at phenological stages D and E, warm temperatures (>25°C for several days) can determine deleterious effects inducing an early flowering and the appearance of imperfect flowers (Guerriero *et al.* 1985; Egea and Burgos 1998). Double pistils with a short style (Fig. 7) have been observed and described as a variable trait in different apricot cultivars (Viti and Monteleone 1991; Guerriero and Bartolini 1995; Rodrigo and Herrero 2002). The stigmatic surface can be also affected by warm temperatures injuring the integrity of papillae with a fast collapse and the loss of turgidity (Fig. 8). This occurrence determines a strong reduction of pollen adhesion on the stigmatic surface (Viti *et al.* 1999). Burgos *et al.* (1991), on several apricot cultivars ('Moniqui Fino', 'Pepito del Cura', 'Velazquez Fino') under Spanish conditions, observed a decrease of the stigmatic receptivity when temperatures were higher than 25°C. High temperatures can also negatively affect pollen germination, pollen tube growth along the style and the vitality of ovule (Viti and Monteleone 1991; Egea and Burgos 1992; Fig. 9). In apricot, it has been found that, to reach high percentages of pollen germination and pollen tube growth along the style, the optimal temperature ranges from 10 to 20°C (Vachun 1981; Egea *et al.* 1992). At blooming time, a lack of synchronism between ovule receptivity and pollen tube elongation has been frequently observed in some Spanish apricot cultivars (Albuquerque *et al.* 2000). This event heavily reduced the effective pollination period hindering the subsequent fertilization (Burgos and Egea 1993; Egea and Burgos 1998; Albuquerque *et al.* 2000).



Fig. 7 Morphological flower anomaly. Double pistils with short style (x 10; scale bar 500 µm).

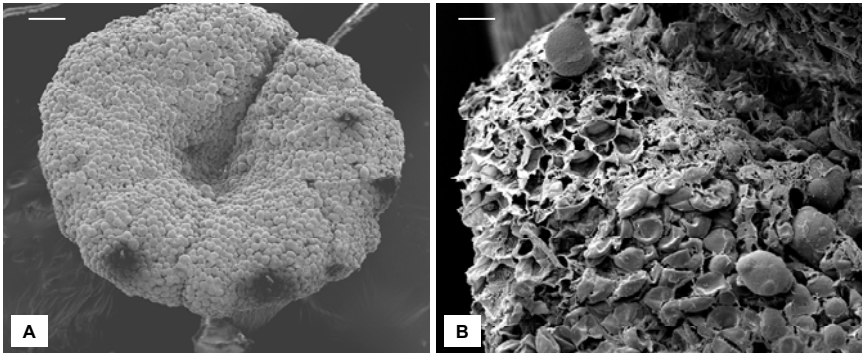


Fig. 8 Stigmatic surface view at LT-SEM. (A) healthy tissues; (B) collapsed papillae (Minnocci, pers. com.) (x 100; scale bar 100 μ m).

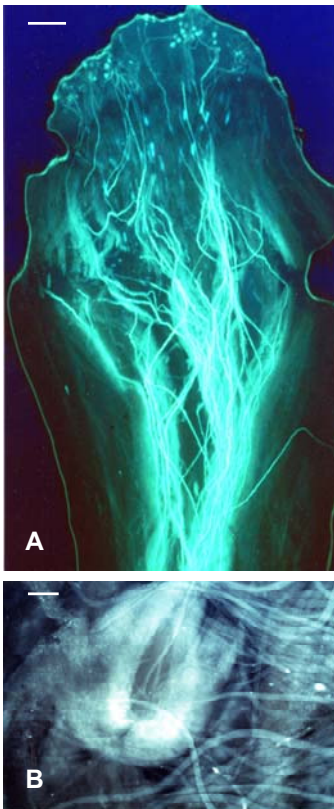


Fig. 9 *In vivo* pollen germination along the style (A) and ovule degeneration (B) under fluorescent light. A: x 200; scale bar 25 μ m; B: x 400; scale bar 50 μ m.

A recent study showed that ovule development, flower production, and flower quality seem to be more influenced by the genotype than year-to-year weather variability (Albuquerque *et al.* 2004b). However, Egea and Burgos (1994) found high variations among the years rather than the cultivars.

PHYSIOLOGICAL AND GENETIC TRAITS AFFECTING THE APPEARANCE OF FLOWER BUD ANOMALIES

During the whole period of flower bud development, the appearance of anomalies can be also related to physiological and genetic factors. Tissue necrosis could be a consequence of strong diversion of sugars by adjacent tissues that would result in the depletion in floral primordia of storage carbohydrates. Carbohydrates concentration and composition in buds change from endodormancy to postdormancy (Moing *et al.* 1994). During dormancy, buds hydrolysed the starch reserves and increased their freezing protection by sucrose synthesis. At dormancy release, buds exhibited important sink strength and were able to accumulate carbon reserves (sorbitol, stachyose+raffinose and starch) which were used for growth metabolism, inducing budburst (Marquat *et al.* 1999). For this process, the availability of carbohydrates in and around the bud meristematic apex could play a determinant role (Bonhomme *et al.* 2005). Selli *et al.* (1985) and Vasudevan

et al. (1998) showed that carbohydrate concentrations were significantly lower in injured floral buds than in healthy floral buds in peach and grape, respectively. In apricot, it has been found that the mobilization of pre-stored starch reserves within the pistil had a positive role during pollination and fertilization processes enhancing the pollen tube growth in the style and the ovule vitality (Rodrigo *et al.* 2000).

Another relevant source of floral anomalies could be related to the habitus of a genotype that affects fruit production. In apricot, the different positions of flower buds on the tree canopy and the type of shoots influence floral abnormalities and flower bud abortion (Viti *et al.* 2003; Legave *et al.* 2006b). Apricot genotypes are characterized by different types of shoots (Guerriero 2003): -fruiting shoots (one-year-old shoots, more than 40 cm long), -brindles (one-year-old fruiting shoots of weak vigour, 10-25 cm long) and -spurs (very short fruiting shoots, 1-3 cm long). A different level of anomalies and bud drop between spurs and fruiting shoots has been observed: flower buds on spurs showed the lowest percentage of anomalies due to a better physiological preparation leading to a lesser degree of competition between buds than long shoots (Guerriero and Bartolini 1991). The position of the flower bud on the shoot heavily influences the appearance of anomalies. It has been observed that buds of the medium-apical portion of fruiting shoots west orientated and at the top of the canopy, were bigger and had a low percentage of anomalies, which were relevant in the medium-basal portion (Viti *et al.* 2003). At the base of the fruiting shoot, the flower buds were small and often presented irregular growth (Guerriero *et al.* 1985). The percentages of flower bud drop from long shoots were higher (60-75%) than in short shoots (about 20%), with many malformed flower buds (Legave *et al.* 1982) and frequent poor quality of the fruits (Albuquerque *et al.* 2003).

Studies about the genetic determinism of apricot floral anomalies are actually very few. Recently, the inheritance of floral anomalies has been studied in several cultivars and in progenies derived from controlled crosses (Legave *et al.* 2004). Particular attention was given to progenies issued from 'Stark Early Orange' (SEO), a cultivar very susceptible to flower bud anomalies and mainly introduced in breeding programs for its resistance to Sharka (*Plum pox virus*, PPV). The distribution of floral anomalies within seedlings showed a similar trend in regions with different climatic conditions. The high susceptibility of SEO was transmitted to a large part of the progeny, although the distribution of the floral abortion changed according to the year from 40 to 80%, showing also a strong climatic effect. These results, obtained by observations on the agronomical behaviour of progenies, could be able to hypothesize that floral anomalies may be a character under genetic control with quantitative inheritance (Legave *et al.* 2006a). The authors suggest a genetic determinism of this trait that might involve several loci; however, this aspect will be still explored by specific genomic studies.

CONCLUDING REMARKS AND PERSPECTIVES

This review examines the recent advances about the source of flower bud anomalies in apricot. Several important cultivars of different geographical origins are heavily affected by flower anomalies which are one of the main causes responsible of inconstant yields. The emerging picture points to a complex set of factors involved in the appearance of anomalous buds that can be revealed at anytime of the bud's ontogenetic cycle, in correspondence of different phases of flower bud growth. Physiological, biological, environmental and agronomical factors affect the survival of a flower bud from the beginning of differentiation to the blooming time.

It is well known the significant role of the environmental conditions that, interacting with signals inner the tree such as metabolic compounds and phytohormones, can act as regulatory factor which determines the appearance of anomalous flower buds. Such factors can lead to browning and necrosis of tissues. Recent studies have provided new insight into key developmental processes occurring in the period between winter and spring. The primary focus and challenge for Mediterranean countries are around the bud dormancy release phase. As consequence, studies have focused on temperature as the main climatic factor. It has been demonstrated that an unsatisfied chilling requirement, under climatic conditions characterized by temperate autumn-winter seasons, can determine cell degenerations inside the flower bud leading to the appearance of anomalies. Moreover, several studies indicate that an asynchronisms between biological (i.e. endodormancy release, microsporogenesis evolution), anatomical (i.e. xylem vessel differentiation) and biochemical (i.e. changes in metabolic compounds and enzymes) events could represent further causes determining inconstant rate of blooming. Cold or hot temperatures occurring during the final phase of the flower bud development (end of dormancy, pre-flowering stage) may have negative effects on the male and female fertility or damage the flower buds with a lack of swelling.

Despite the overall progress obtained, the period after harvest, during the flower bud induction and differentiation, that represents the potential production of the next year, lacks rigorous scientific analysis. In particular, little information is available regarding the relationship between physiological disorders and appearance of earliest anomalies. In addition, the genetic involvement on this adverse event requires further study. This aspect has remained largely unexplored in apricot and the biological evidences achieved have to be corroborated by specific molecular investigation on genes involved in cell degenerative processes of flower bud tissues.

By understanding this intriguingly complex pathway, we can effectively attempt to know the symptoms that could be able to predict the appearance of anomalous buds. This could have great economic importance by improving apricot yield as researchers and growers take into account the current effort to adopt more rustic cultivars. This area holds much promise for future research providing new knowledge of fundamental scientific interest.

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