Adv. Hort. Sci., 2013 27(1-2): 5-17

Apricot flower bud dormancy: main morphological, anatomical and physiological features related to winter climate influence

R. Viti*, S. Bartolini, L. Andreini***

* *Dipartimento di Scienze Agrarie, Alimentari e Agro-ambientali, Università di Pisa, Via del Borghetto, 80, 56124 Pisa, Italy.*

** *Istituto di Scienze delle Vita, Scuola Superiore Sant'Anna, Piazza Martiri della Liberta, 33, 56127 Pisa, Italy.*

Key words: budbreak, climate, endodormancy process, *Prunus armeniaca* L.

Abstract: This review examines recent advances regarding flower bud dormancy in apricot, focusing on biological, anatomical, and physiological processes which occur during the induction and depth of dormancy. In a scenario of global climate change, the relationship between endodormancy and winter climate influence is discussed. Dormancy regulation is a complex process necessary for plant survival and development. In fruit species, the knowledge of mechanisms controlling dormancy and establishing its release appears crucial for successful yields. Specific studies have suggested that, when the flower buds are apparently inactive, slow and gradual changes occur in the whorls: organogenesis, such as microsporogenesis processes and vascular connections take place during the entire dormancy period. It has been indicated that an asynchronism 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 an inconstant rate of blooming. Temperature is the main factor involved in dormancy triggering and releasing. In the perspective of global warming, mild winter temperatures could greatly impact apricot ecological cropping systems. Phenological process-based models are considered to be the best tool to study the climatic changes and subsequent expected phenology variation (dormancy and flowering). A new model, calibrated and validated on apricot cultivars, is proposed to predict the dormancy release date in a future scenario.

1. Introduction

In stone fruit trees, the cycle of shoot growth is marked by the development of two bud types: the vegetative and reproductive buds. Vegetative buds comprise bud scales, leaf primordia, and the shoot apical meristem. Reproductive buds have a more complex structure made up of bud scales and flower primordia represented by pistil and stamens. The flower buds of temperate-zone fruit trees are initiated during the previous growing season and several critical steps during bud morphogenesis were identified, from floral induction up to complete bud differentiation (Ryugo, 1990).

During the autumn-winter season, the plant elaborates mechanisms for survival under unfavorable growing conditions by adopting a dormancy strategy to cold temperature acclimation. Meristem activity becomes insensitive to growth-promoting signals (Rohde and Bhalerao, 2007) preserving the buds in a quiescent state under potentially damaging environmental conditions (Ćechová *et al.*, 2012). Bud dormancy starts with the perception by the plant of rest-signals under the influence of short and cool days; this process finishes after an accumulation of chilling temperatures.

The conventional terminology identifies dormancy evolution as: *paradormancy*, when growth is inhibited by endogenous factors outside the dormant structure; *endodormancy*, when growth is regulated by physiological factors within the dormant structure; and *ecodormancy*, when the inability to grow is imposed by environmental factors (Lang *et al.*, 1987). In trees, winter dormancy means endodormancy: during this phase the chilling temperatures are accumulated, and flower buds are unable to respond to warm temperatures required for dormancy breaking (Fig. 1). When the chilling requirement (CR) is fulfilled, buds are in ecodormancy and can react to warm temperatures, but remain in an apparent quiescent state due to persistent low temperatures (Horvath *et al.*, 2003). The release of dormancy is genetically controlled and regulated by complex phenomena affected by various integrated elements whose interaction(s) determine the point in time when release of bud dormancy occurs (Faust *et al.,* 1997). En-

The authors equally contributed to the manuscript.

Received for publication 21 December 2012
Accepted for publication 2 April 2013

vironmental factors (temperature, light, relative humidity, etc.) are directly related to biochemical changes involved in bud dormancy release. In fruit species, understanding the mechanisms controlling dormancy and establishing its release appear crucial for successful yields.

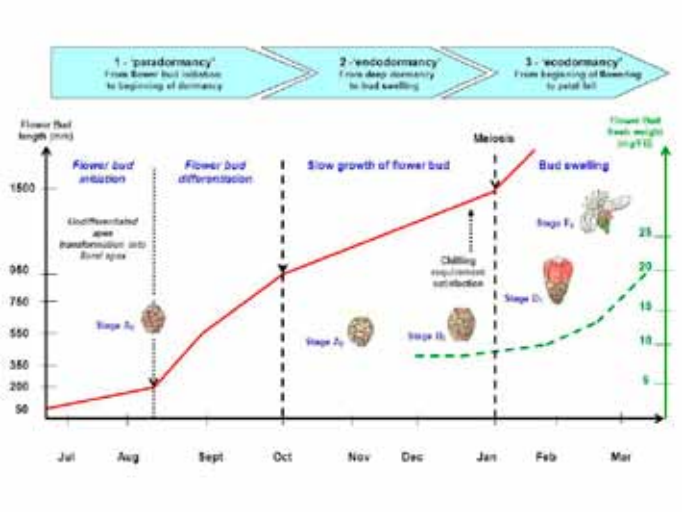

Fig. 1 - Schematic representation of apricot flower bud growth during the annual cycle**.** 1) Paradormancy: from flower bud initiation to beginning of dormancy; 2) Endodormancy: from deep dormancy to bud swelling; 3) Ecodormancy: from beginning of flowering to petal fall. Solid and dotted lines represent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

Apricot *(Prunus armeniaca* L.) is characterized by a restricted spread in the Mediterranean basin and its adaptability to specific environments is strongly influenced by the ability of certain cultivars to overcome flower bud dormancy (Viti *et al.,* 2010). Climatic-environmental factors may heavily influence flower bud dormancy breaking, affecting the entity of appearance of floral anomalies and determining irregular and/or insufficient fruit bearing (Clanet and Salles, 1972; Legave *et al.,* 1984; Viti and Monteleone, 1995). Cold winter temperatures influence the time of bud dormancy release and, consequently, the CR of a genotype (Garcia *et al*., 1999). Most of the known apricot cultivars are characterized by a high CR (Table 1); more than 1000 Chill Units (CU) are required to overcome bud dormancy (Guerriero *et al*., 2006). In Mediterranean apricot growing areas, characterized by a mild-winter climate, many cultivars have an inadequate satisfaction of CR. During a short or mild rest season (Garcia *et al.,* 1999), the unsatisfactory CR can determine an incomplete release of flower bud dormancy, a late bud break with scanty blooming and a high flower bud drop (Viti and Monteleone, 1991; Erez, 2000). Thus, CR is a key factor for breaking dormancy and knowledge about it has practical significance and economic impact on the control, maintenance and production of woody plants (Fennell, 1999). This statement appears crucial for the crop management of apricot cultivars in most cultivation areas.

Table 1 - Chilling Units (CU) required to induce break of endo-dormancy in flower buds of several apricot cultivars. Starting date and amount (%) of flowering are reported

Cultivars	CU	Flowering	
		Starting date	%
San Castrese	870	1 Mar	57
Goldrich	950	7 Mar	18
Sarritzu I°	950	7 Mar	51
Alessandrino	1000	7 Mar	10
Baracca	1000	14 Mar	21
D'Alessandria	1000	10 Mar	5
Bebeco	1030	7 Mar	15
Canino	1030	2 Mar	34
Moniqui	1125	5 Mar	2
Aurora	1140	29 Feb	2
Amabile Vecchioni	1140	2 Mar	30
S.Nicola Grosso	1140	9 Mar	25
Bergeron	1225	17 Mar	1
Rapareddu	1250	7 Mar	23
Polonais	1300	9 Mar	5
Orange Red	1450	14 Mar	1
Stark Early Orange	not defined	not defined	0
Mean	1100		
SD	151		

The present paper examines the dormancy process of apricot flower buds, focusing on biological, anatomical, and physiological changes that occur during the endodormancy phase in relation to winter temperature influence within the context of global climate change.

2. Morphological and anatomical features

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 stamen and pistil; the most internal whorls of the pistil derive from the gradual evolution of the receptacle (Monet and Bastard, 1968; Bartolini *et al.,* 2013). This process requires about two months and is normally completed before leaf fall but not all buds reach the stage of pistil appearance (Legave, 1975).

Apricot flower bud evolution was described for the first time by Baggiolini (1952). The classification has been revised to describe accurately the progress of flower bud phenological development by the addition of sub-phases within each phenological stage (Bartolini *et al.,* 2004). Figure 2 depicts the evolution of flower bud phenological stages from deep dormancy (stage A) until petal fall (stage H). The stages related to the dormancy process are referred to as: 1) stage A_0-A_2 during endodormancy; 2) stage B_1- E_2 from ecodormancy to bud swelling; and 3) stage F_1-H from beginning of flowering to petal fall. Dormant buds (stages A_0, A_1, A_2) are characterised by a conical shape, rounded at the base, with the brown bud scales tightly closed (A_0) or

Fig. 2 - 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). From Bartolini *et al.* (2004).

more enlarged (A_1 and A_2); at the beginning of bud swelling (stages B_1 and B_2) the pink sepal tips appear; at stages C_1 and C_2 sepals are clearly visible; at stages D_1 and D_2 full bud swelling takes place with the appearance of the white petal tips; at stages E_1 and E_2 petals are clearly visible; at stages F_1 and F_2 full flowering occurs; at stages G and H petal fall begins with the end of flowering.

During endodormancy, the accumulation of chilling temperatures occurs and it is usually believed that flower bud development is arrested because no clear signs of growth are evident. However, specific studies have shown that bud growth is hardly perceptible, although constant (Alonso *et al.,* 2005). The buds are metabolically active and continue their development during the entire winter, leading to bud break. In peach flower buds continuous anatomical development during the late autumn and winter dormancy period were observed, without macroscopic changes (Reinoso *et al.,* 2002). Apricot flower buds also have a gradual and prolonged development during morphogenesis since their organogenesis is not generally completed until just before anthesis (Erez and Couvillon, 1987). During the first stage (A) a minimal variation in bud size and weight was detected. Indeed, during December and January, when buds are apparently still dormant, it was possible to detect a continuous growth in weight and size. The parameters of weight increase and height/width ratio have revealed a statistically appreciable slow and progressive buds growth from the middle of December (Guerriero *et al.,* 1986; Scalabrelli *et al.,* 1991).

During this apparent rest period, anatomical observations revealed that processes of microsporogenesis, macrosporogenesis and xylogenesis take place. As regards microsporogenesis, the following phases have been identified (Fig. 3) in relation to flower bud development (Nyújtó 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; 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 made up of two layers, exine and intine) after the resumption of growth. The tetrad stage has been considered 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 late stage of morphological bud growth and they are not closely linked to chilling accumulation, because the meiosis process took place also in buds exposed to high temperature (Martìnez-Tellez *et al.,* 1982; Felker *et al.,* 1983; Viti and Scalabrelli, 1988). Contradictory studies have shown that winter dormancy sets a boundary between the development of the sporogenous tissue and further microspore development (Julian *et al.,* 2011). These authors observed that, in autumn, stamens develop until the differentiation of sporogenous tissue, remaining in this anatomically quiescent stage during the three months of winter; microspore development took place only after dormancy.

Fig. 3 - Main microsporogenesis phases (x 400). **a**) Pollen Mother Cells (PMC); **b), b$_1$**) Tetrads (T) and **c**) Young Pollen Grains (YPG).

Concerning gyneceum development and the related macrosporogenesis, a later evolution than stamen and microsporogenesis process was observed. Morphologically, the pistil has a lengthwise growth that can be divided into different phases: intensive growth during paradormancy; slow growth during endodormancy; and increased growth during ecodormancy, at first very slowly then followed by a significant rapid rise a few weeks before flowering (Szalay and Nemeth, 2010).

Anatomical observations showed that the first signs of the ovary can be detected in October. Several studies have found a well-developed embryo sac at anthesis; Egea and Burgos (1995) found a frequent presence at anthesis of ovules without the sac being formed. In apricot, two to three ovules/ovary are usually noted, but at anthesis they are frequently malformed and quickly degenerate. Ovule

number seems to be related to agronomic and climatic conditions, rather than genetics (Egea and Burgos, 1995; Burgos and Egea, 1993; Albunquerque *et al.,* 2002).

At the end of the endodormancy process (end of winter-beginning of spring), a rapid weight increase and the complete development of floral verticils at the transition from phenological stage B (visual beginning of bud swelling) up to stage D (appearance of the white petal tip) have been observed. In this period, elongation of pistil and stamen filaments occurs while mature pollen grains and complete gynaecium development take place only few days before blossoming (Luna *et al*., 1990). In concomitance with the effective warm temperatures, female and male gametophytes become functional.

During the temporary delay of visible bud growth, the process of xylem development within the flower bud axis occurs. The bud, during early growth, is connected to the stem through a parenchymatous zone, traversed by a procambial strand. In several *Prunus* species, it was observed that, during winter, vascular tissues are not completely differentiated and the connection between the flower primordium and the bud axis is formed only by the procambium (Ashworth and Rowse, 1982). This tissue, which constitutes the vascular strands, is made up of elongated cells and contains densely stained cytoplasm and lacks lignified secondary wall thickenings (Esau, 1965). The differentiation process consists of the transition from this meristematic tissue to xylem cells, i.e. dead cells with lignified walls producing an empty conduit through which water flows. In apricot, gradual xylem development was observed during winter, when no bud growth changes were visible. The acropetal progression of primary xylem differentiation along the flower bud axis was defined by five stages according to Bartolini and Giorgelli (1994): *stage 1* = at the base of the axis; *stage 2* = at ½ of the axis; *stage 3* = at ¾ of the axis; *stage 4* = at the base of the ovary; *stage 5* = inside the pistil (Fig. 4). Stage 3 appears to be the most significant with regard to breaking dormancy because it is in concomitance with the first morphological sign of bud growth resumption. A good relationship between an advanced xylem differentiation ('stage 3') and endodormancy release was observed in cultivars with a low chilling requirement (i.e. 'San Castrese'). The availability of nutritional elements throughout xylem supply in correspondence with bud growth reactivation could be a factor determining flowering regularity. A correlation between an increase of certain elements (i.e. potassium and boron) by the xylem acropetal transport and bud swelling has been observed (Hanson and Breen, 1985; Essiamah and Eschrich, 1986; Bartolini and Giorgelli, 1995). On the other hand, in cultivars with a high chilling requirement (i.e. 'Orange Red'), xylem 'stage 3' occurs when flower buds are still in endodormancy. This early anatomical trait of flower buds does not coincide with the reactivation of bud growth; it could be hypothesized that the newly formed vessels might preserve the ability to function in water transport. This feature was confirmed by a recent research where a good syncronism between overcoming

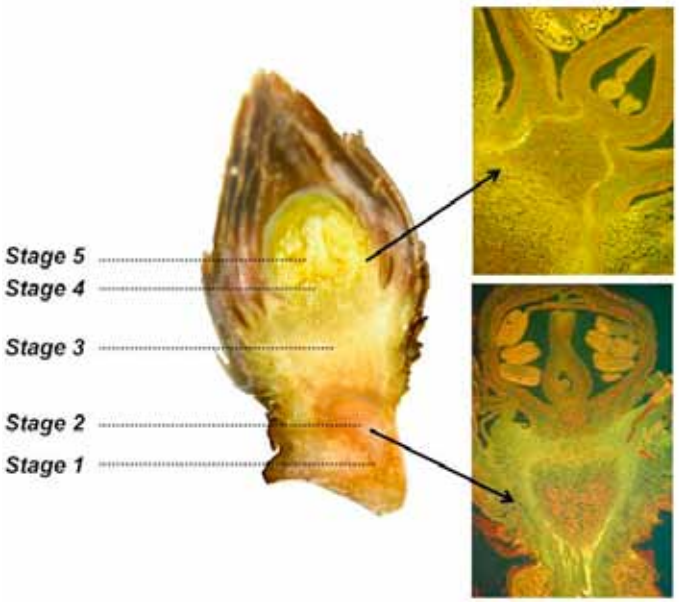

Fig. 4 - Representation of xylem vessel differentiation along the flower bud axis, from Bartolini *et al*., 2006: *stage 1* (at the base of the axis); *stage 2* (at ½ of the axis); *stage 3* (at ¾ of the axis); *stage 4* (at the base of the ovary); *stage 5* (inside the pistil).

dormancy, xylogenesis and microsporogenesis, was found in cultivars with a low CR, while in cultivars with a medium or high CR an asynchrony between such processes was observed (Bartolini *et al.*, 2006 a), leading to inconstant blooming and fruit yield.

3. Physiological features

Control of plant dormancy is the result of multifactorial regulatory networks in which nutrients, phytohormones, genes, proteins and climatic factors (namely temperature and photoperiod) are involved at some point in time (Chao and Anderson, 2010). Light and temperature climate parameters are important determinants in several aspects of dormancy. In northern temperate regions, the stimulus for induction of growth cessation and dormancy has been considered to be primarily controlled by short photoperiod (Allona *et al.,* 2008). Increasingly, several authors have shown that temperature may replace or strongly mediate this short photoperiod dormancy response in woody species (Kalcsits *et al*., 2009; Tanino *et al.,* 2010).

The onset and release of dormancy state might begin with the perception of a signal by the plant upon exposure to chilling temperatures (Or *et al.*, 2002). Then, it would be followed by transduction of this signal via a cascade of biochemical events to the stage where it imposes or releases repression of bud meristematic activity (Faust *et al.*, 1997). Many cellular activities leading to morphological, physiological and biochemical changes take place inside the bud during the transition period from endodormancy to active bud growth, including respiratory rate, reserve carbohydrate mobilisation, water content increase, energy transport, and gene expression.

'Sink strength' and carbohydrates

Considering that the bud of a woody plant is morphologically complex and constituted by organs differing in structure and physiology, the bud anabolic potential is partially regulated by the "sink strength" of dormant and non-dormant tissues influencing the subsequent capacity to accumulate metabolites (Crabbé and Barnola, 1996). During early bud growth, the parenchymatous zone, which represents the connection between bud and stem, is fed through the symplasm of this region (Pétel and Gendraud, 1996). Thus, plant dormancy and dormancy breaking appear to depend on peculiar short distance relationships between the bud and its underlying tissues (Champagnat, 1973; Gendraud and Pétel, 1990). In peach, during the dormant period, the parenchyma shows a strong ATPase activity driving a powerful proton extrusion, with a consequent pH cytoplasmatic alkalisation linked to enzyme activity (Pétel *et al.,* 1992; Petél and Gendraud, 1996). A relationship between changes in intracellular pH (pHi) and bud dormancy release has been observed, first, in Jerusalem artichoke and peach vegetative buds (Marquat *et al*., 1996; Aue *et al.*, 2000), and subsequently in apricot buds (Zanol and Bartolini, 2003), suggesting the involvement of pHi changes as signalled by growing evidence (Zimmermann *et al.*, 1999). In particular, when apricot flower buds were still in deep dormancy, an increase of pHi in the flower primordia tissues was found, just before the first sign of growth reactivation, usually denoted by a significant bud weight increase (Fig. 5). The changes in pHi values might be useful to detect in advance bud growth capacity, showing the potential competitive sink for nutrients between the different bud tissues from dormancy to growth resumption (Zanol and Bartolini, 2003). The pHi measurement is a good parameter to estimate 'sink strength' determining the nutrient fluxes (Gendraud and Pétel, 1990; Bonhomme *et al*., 1999; Robert *et al*., 1999).

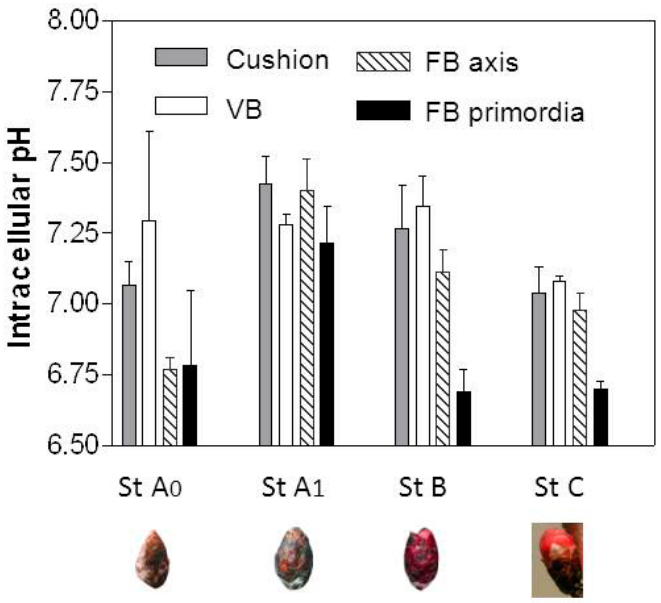

Fig. 5 - Intracellular pH at different phenological stages (from St A_0 to St C). Changes in different tissues: Cushion, Vegetative Bud (VB), Flower Bud (FB) axis, Flower Bud (FB) primordial.

The energy source for budbreak comes mainly from the mobilization of products stored in the perennial parts of the tree. Carbohydrates are the main source of energy for the metabolic changes that occur during the dormant period and for spring sprouting and blooming (Flore and Layne, 1996; Sherson *et al.,* 2003). Changes in the content of carbohydrates in different tissues from vegetative and reproductive structures were found during dormancy, associated with chilling temperatures (Wang and Faust, 1987; Valentini *et al.,* 2006).

There was a significant decrease in starch concentration in the bark tissue of *Prunus* sp. due to exposure to chilling temperatures (González-Rossia *et al.,* 2008). The effect of low temperatures on starch and sugar concentration during the rest period can be explained: amylase activity is induced by cold temperature, increasing starch hydrolysis and, consequently, sugar concentration (Elle and Sauter, 2000; Bonhomme *et al.,* 2005).

Soluble sugars, important signalling molecules involved in many processes in the life-cycle of plants, are also related to the dormancy period and involved in increased frost resistance (Tabuenca, 1975; Sheen *et al.,* 1999; Smeekens, 2000). In particular, starch levels were negatively correlated with hardiness but most soluble sugars were positively correlated (Jones *et al.,* 1999).

Glucose, fructose, and sorbitol were the main sugars in the bark tissues of peach, nectarine, plum and apricot; sorbitol concentrations varied significantly with chilling accumulation (Bonhome *et al*., 2005; González-Rossia *et al.,* 2008). In other sorbitol-synthesizing plants, such as sweet cherry (*Prunus avium* L.), sucrose is the most predominant soluble carbohydrate during dormancy (Keller and Loescher, 1989). In peach primordia, especially the floral ones, very high concentrations of transport forms of carbohydrates (sucrose and sorbitol), imported during growth capacity recovery, were found (Bonhomme *et al.,* 2005). From autumn to mid-winter, a significant relationship between total sugars and starch concentrations, with a marked increase in amounts of sorbitol, fructose, glucose and sucrose, was found in the bark tissue of stone and pome fruits, coinciding with a decrease in starch content (Wang and Faust, 1987; González-Rossia *et al.,* 2008).

Free radicals and antioxidant mechanisms

Studies have shown that free radicals, activated oxygen species (AOS), implicated in a number of biological phenomena, are produced in dormant buds of some fruit species, where their removal seems to be associated with bud break as a result of changes in antioxidant systems (Wang *et al*., 1991). The generation of AOS, particularly H_2O_2, during stress has been proposed as part of the signalling cascade leading to plant response (Anderson *et al.*, 1998). The plant's antioxidant defence system, via enzymatic and non-enzymatic mechanisms (i.e. amino acids, glutathione, acid ascorbic, carotenoids, α-tocopherol), provides protection against high levels of free radicals responsible for the

peroxidation of membrane lipids and the destruction of proteins (De Kok and Stulen, 1993).

Antioxidative enzymes, individually or cooperatively, have been viewed as a defensive team that protect cells from active oxygen damage performing a detoxifying function (Kranner and Grill, 1996). Superoxide dismutase (SOD), catalase (CAT), ascorbate peroxidase (APX), guaiacol peroxidase (GPX) and glutathione reductase (GR) are the main antioxidative enzymes involved in the reduction of H_2O_2 to H_2O (Schmidt and Kunert, 1986; Noctor and Foyer, 1998; Rojas-Beltran *et al*., 2000). Maximum H_2O_2 accumulation could act as a signaling molecule to trigger the sequence of reactions to break endodormancy (Kuroda *et al.*, 2002). During the dormancy process, biochemical analysis conducted on apricot flower buds revealed CAT and GPX as the most involved enzymes, with significant increases of activity at the release of endodormancy, particularly in cultivars with a low or medium CR (Viti *et al.,* 2013). Other metabolites such as glutathione and antioxidant proteins were associated with increased capacity for free radical scavenging (Siller-Cepeda *et al*., 1991). Glutathione (γ-glutamyl-cysteinyl-glycine) is generally considered to be a ubiquitous sulfhydryl-containing tripeptide in living cells (Fahey *et al*., 1975), being the main reserve and long-distance transport form of reduced sulfhydryls which are indispensable for protein synthesis (Rennemberg, 1982). It is an important metabolite in stabilizing the cell redox state during the cold hardening process (De Kok and Stulen, 1993). In particular, in stressed plants, reduced glutathione (GSH) protects protein thiol groups from auto-oxidation (Kranner and Grill, 1996). GSH is oxidized to glutathione disulfide (GSSG) and, under normal conditions, is reduced efficiently back to GSH by the action of glutathione reductase (Foyer *et al.,* 2001). The major portion of the glutathione in the cell is maintained in the reduced state, and a high reduced/oxidized ratio (GSH/GSSG) is necessary for numerous physiological functions. Glutathione was suggested as one of the strong factors in controlling bud dormancy, first, in grape (Tohbe *et al.,* 1998); later, in apricot flower buds a significant relationship between the end of endodormancy and the increase of GSH/GSSG ratio was found (Bartolini *et al.*, 2004). In cultivars with low-medium CR the reduced and oxidized glutathione ratio (GSH/GSSG) increased in accordance with the end of endodormancy, while in cultivars with high CR the GSH/GSSG ratio was kept low during the rest period. This could suggest that a minimum threshold in antioxidant activities could be crucial for scavenging free radicals during the rest season.

Hormonal involvement

The endogenous system of hormonal regulation mediates the annual transition from growth to dormancy due to the shortened length of autumn days and reduction of daily mean temperatures (Thimann, 1985). Knowledge of hormonal regulation of dormancy processes has become increasingly more complex, particularly with recent findings of auxin-and ethylene-triggered abscisic acid induction revealing more responses mediated by abscisic acid (ABA) than originally considered (Tanino, 2004). ABA has long been studied as a potential mediator of short-induced cessation of growth and initiation of bud dormancy in trees (Guak and Fuchigami, 2001). An increase in its activity or its accumulation in the fall is an indispensable condition for the onset of apical growth inhibition, and an essential prerequisite for emergence of the dormant state and the ability to adapt to winter frosts in apricot tress (Kuzina and Kalinina, 1993). Kawamata *et al.* (2002) found that free ABA levels in buds increased suddenly at onset of dormancy and decreased afterward. Chen *et al.* (2002) suggested that changes in dormancy status are more closely related to changes in ABA receptivity than to changes in ABA levels. ABA affects dormancy progression through its action on dehydrins or membrane permeability (Jacobsen and Shaw, 1989). Moreover, the regulatory effect of ABA in growth inhibition, dormancy, and thermoregulation in woody plants is realized only with the action of other phytohormones: auxins, gibberellins, and cytokinins (Back and Richmond, 1971). Gibberellin GA_3 was tested in peach buds to promote bud burst under conditions of prolonged dormancy (Erez *et al*., 1971). The comparatively high levels of GA_3 found in mid-winter could be one of the factors that control the process of anther and gynoecium development (Basconsuelo *et al.,* 1995).

Molecular features

Population and quantitative genetics studies indicate that phenological traits such as time to bud set, chilling requirement and time to bud flush show significant genetic variation, and that such traits are often controlled by multiple genes exhibiting small effects (Howe *et al*., 2003; Rohde *et al*., 2011). Dormancy signals, impacting numerous physiological processes, involve changes in the expression patterns of numerous regulatory genes that could play a key role in dormancy transition (Horvath *et al.,* 2008). In contrast to paradormancy, the molecular aspects of endodormancy are poorly understood. The molecular biology of endodormancy has been analysed in several recent studies by global approaches where an initial set of candidate genes involved in cold- or light-induced dormancy in tree species were described (Bielenberg *et al.,* 2008). Gyllenstrand *et al*., (2007) found a significant and close correlation between growth rhythm (both bud set and bud burst) and the expression pattern of an FT (flowering locus T) homologue, suggesting that FT is a key integrator of photoperiodic and thermal signals in the control of growth rhythms in gymnosperms. Additionally, the substitution of a single amino acid can transform an FT protein from an activator into a suppressor of flowering. Thus, the limited but tantalizing linkage between the floral regulatory machinery and seasonal growth cessation and bud set, through regulation of FT and FT-like genes, suggests a general model for endodormancy regulation (Horvath, 2009).

Flowering locus C (FLC)-like genes have been shown to be regulated differentially during the satisfaction of

CR in vegetative buds of poplar (Chen and Coleman, 2006). Furthermore, Bielenberg *et al.* (2008) revealed a cluster of six MADS-box transcription factors (named dormancy-associated MADS-BOX or DAM genes) as candidate genes for the regulation of terminal bud formation in evergrowing peach. The expression of two of these genes, DAM5 and DAM6, is suppressed by chilling temperatures and inversely correlated with bud break rate in peach (Jimenez *et al.,* 2010), whereas DAM4 and DAM6 expression is promoted by short photoperiods (Li *et al.,* 2009). Similar genes were expressed differentially during dormancy induction, maintenance and release also in apricot. In *Prunus mume*, Yamane *et al.* (2008) have generated two SSH/MOS (subtractive hybridization supplemented with mirror orientation selection) libraries containing gene pools that are expressed preferentially in endodormant buds in comparison with paradormant or ecodormant buds to search for the genes that are up-regulated by endodormancy induction or down-regulated by endodormancy release. Differential screening and sequencing indicated that genes involved in gibberellin metabolism, stress resistance, cell wall modification, and signal transduction, such as transcription factors, are up-regulated in endodormant buds. At transition from dormancy to active bud growth, genes related to carbohydrate and energy metabolism have been specifically identified in *Prunus armeniaca* L. Céchová *et al*., (2012) have observed strong expression of xyloglucan endotransglycosylase/hydrolase (XTH) and EXGTA1 (endoxyloglucan transferase) in the week before, and during, the exit of apricot flower buds from endogenous dormancy.

Research is still in progress to study changes in the expression in regulatory genes involved in numerous physiological signals related to the dormancy process.

4. Influence of mild temperatures during the dormancy process

The complex process of dormancy is affected by a close interaction between genotype and environment, where photoperiod and temperature are the main factors involved in triggering and releasing. Their individual and combined effects change during the transition from a dormant to a non-dormant state (Caffarra *et al*., 2011).

Apricot culture is greatly restricted by climatic conditions, with a decisive influence on development and productivity (Quamme *et al.,* 1982; Guerriero and Bartolini, 1991). It is well known that some cultivars are closely linked to their geographical origin and, consequently, have a low adaptability to other climatic conditions (Bassi *et al.,* 2006). Autumn-winter temperature trends seem to be the main cause of this low plasticity related to the need for adequate and specific satisfaction of CR for dormancy breaking (Viti *et al.,* 2010). A warm climate may prevent or delay this process. In fact, during winter mild temperatures have a negative impact on endodormancy release due to an unfulfilled CR. In this situation, apricot is frequently affected by the appearance of floral anomalies, e.g. pistil abortion and/or browning and/or necrosis of flower buds, which are usually attributed to unfulfilled CR. However, a correlation between flower anomalies and CR satisfaction was not always achieved (Guerriero and Bartolini, 1991; Viti and Monteleone, 1993; Legave, 2002). At present, knowledge about the mechanisms and nature of anomalies is still scant but, on several genotypes, a genetic determinism has been found through analysis of different apricot progenies (Legave *et al.,* 2006).

From a physiological point of view, climatic conditions affect inductive signals regarding metabolism and phytohormones involved in the control of several events such as primary vascular differentiation micro- and macrosporogenesis (Aloni, 1980; Creber and Chaloner 1984; Fukuda, 1996). In apricot flower buds, xylem differentiation was found to be slow when the winter minimum mean temperatures were predominantly below zero (Bartolini *et al*., 2006 a). Moreover, during the autumn-winter season, after a minimum threshold of chilling amount, the supply of constant warm temperatures stimulated the development of vascular elements, at least in cultivars with a low-medium CR (Bartolini and Giorgelli, 1995). As regards the microsporogenesis process, the post-meiotic phase is crucial because temperature may influence the transition from tetrads to pollen grains (Viti and Scalabrelli, 1988). A lack of synchronism between dormancy release, xylem differentiation and microsporogenesis evolution has recently been demonstrated under warm winter conditions (Bartolini *et al.,* 2006 b; Andreini *et al.,* 2012).

The negative role of certain temperatures is confirmed also during the ecodormancy stage. In particular, temperature fluctuations affect different stages of reproductive development and this stress might lead to developmental asynchrony in pollen–pistil–ovule functioning, leading to reduced fertilization levels (Hedhly, 2011).

Considering such events, determining the effectiveness of temperature regimes on dormancy release has, for a long time, been a focus of many studies. Several models have been proposed to predict the response of buds to chilling, establishing the CR of each specific genotype. The most simple one was introduced by Weinberger (1950) who simply defined the 'chilling hours' as the number of hours at or below 7°C. The method of Bidabé (1965) calculates the effect of given temperatures either for chilling or heat requirements by exponential models. The Utah model weights the efficiency of different temperatures for CR fulfillment (Richardson *et al.,* 1974 and 1975). This model is the best tailored for cool and temperate regions (Seeley, 1996), while under warm conditions (i.e. the subtropical regions) Erez *et al.* (1990) proposed the 'dynamic model' as a better indicator for peach CR estimation. The model assigned negative values to high temperatures (negation of rest) during endodormancy (Allan *et al.,* 1993). Bonhomme *et al.* (2010), indicate a simplified smoothed Utah model as the best for French conditions, introducing a more broad range of effective temperatures to break dormancy.

…and what about dormancy processes with regard to climatic changes?

Global warming of the climate system is unequivocal from observations of increases in average air temperatures in many parts of the world (Legave *et al.,* 2009). Since the end of the 1980s, this temperature change has influenced plant phenology, and in the future further climate changes will probably have an impact on crop yields (Chuine and Cour, 1999; Chmielewski *et al.,* 2004). Mean temperatures will probably rise between 1.8 and 4.0°C by the end of the 21st century, according to IPCC reports.

Over the period 1910-2003, climate warming was already in motion with a minimum temperature increase of 0.25°C per decade, as reported for the Californian San Joaquin Valley (Baldocchi and Wong, 2007). The most striking feature of climate change in eastern Asian countries during the past century may be the remarkable winter-season warming (Kwon *et al.,* 2008). As a consequence, significant impact can be expected on winter dormancy and spring bud-burst for crops and natural vegetation in this region, as has been observed in Europe (Chmielewski *et al.,* 2004). In the Mediterranean area, the winter climate shows a tendency to become progressively milder (Guerriero *et al.,* 2010; Menzel *et al*., 2011). In this context, certain years (i.e. 2006-2007) were characterized by constantly very mild autumn and winter temperatures: the minimum values occasionally went below 0°C, while the maximum values often exceeded 15°C (Luterbacher *et al*., 2007; Viti *et al.*, 2010). Thus, over the past twenty years a progressive reduction of chilling amount was recorded (Fig. 6).

In the global warming scenario, phenological process-based models are considered the best tool to study the climatic changes and subsequent expected phenology alteration (Chuine *et al.,* 2003). BRIN is a recent phenological model, calibrated for grapevine, able to predict, simultaneously, timing of budburst and flowering (García de Cortázar-Atauri *et al.,* 2009). This model computes the dormancy period using Bidabe's Cold Action model (Bidabé, 1965), and the post-dormancy period by the sum of hourly temperatures (growing degree hours-GDH, method of Richardson *et al*., 1974). Recently, the BRIN model has been calibrated and validated also for apricot cultivars under the climatic conditions of southern France allowing an effective prediction of dormancy release date (Andreini *et al.,* 2013). As a consequence, BRIN model could be applied in a "A1B" future scenario taking into account two aspects valuable for all cultivars: a delayed dormancy break and an early flowering. Advances in modeling will be made using the experimental data of dormancy release to calibrate forecast models that can reproduce the physiological behaviour of the three. According to Bonhomme *et al.* (2010) further study will consist in testing a wide panel of data and also assessing the introduction of the optimized endodormancy release model as sub-model into bud break/bloom phenological model. This will likely improve them and could be very interesting for phenological predictions in the global change context.

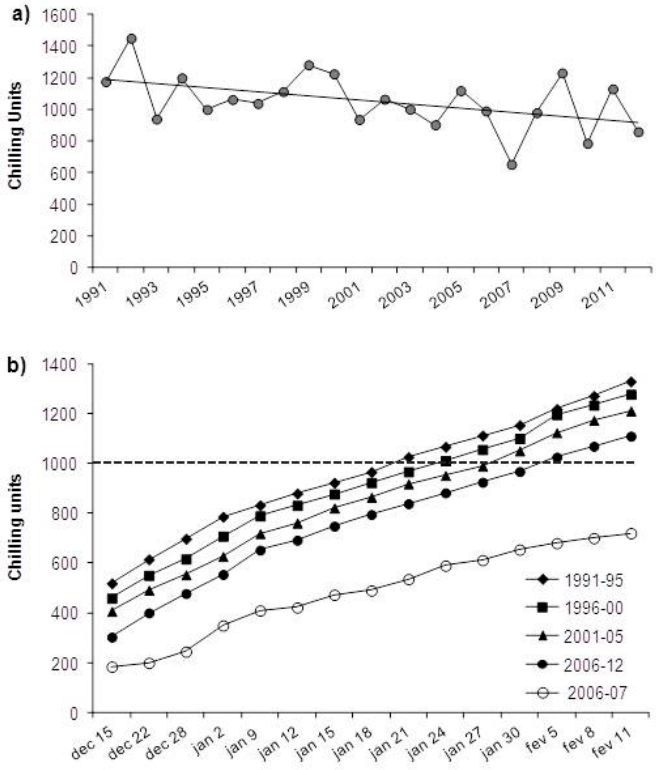

Fig. 6 - Chilling Units accumulation from 1991 to 2012 : a) during winter season, b) on 31 January. Data recorded under the climatic conditions of the Tuscany coastal area.

Concluding remarks and perspectives

Survival and competitive success of woody plants depend on a precise timing of growth, winter dormancy in synchrony with seasonal changes in temperature. In particular, apricot is a species sensitive to satisfying the CR and thus achieving the release of dormancy and bud break. Several cultivars of different geographical origins are heavily affected by the problem of dormancy release, which is one of the main causes of inconstant yields. The effect of temperature on the induction and depth of dormancy may explain some of the observed annual variation in dormancy and CR for its release.

The picture emerging from this work points to a complex relationship between winter temperatures and several biological processes in response to overcoming dormancy in flower buds. In particular, it has been demonstrated that climatic conditions characterized by mild autumn-winter seasons can affect the regular development of flower bud organs, leading to the appearance of anomalies. Moreover, several studies have indicated that an asynchronism among 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 for an inconstant rate of blooming. At this time, knowledge of the mechanisms involved in dormancy is still fragmentary although recent studies of global gene expression in dif-

ferent species have carried us several steps forward, providing an excellent basis for elucidating function of genes and components thought to be involved in temperature and other environmental signaling.

In a context of global warming, mild winter temperatures could greatly impact apricot cropping systems. Forthcoming research on this particular topic will be crucial and of great economic importance. A new model, calibrated and validated on apricot cultivars, is proposed to predict the dormancy release date in a future scenario. Specific breeding programs, focusing on rustic cultivars more appropriate for particular environmental conditions, should provide additional improvements in apricot culture in the Mediterranean basin.

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