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Influence of weather conditions and rootstock genotypes on flower bud biology and xylem vessel differentiation in apricot

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Abstract

The aim of this research was to study the involvement of weather conditions and the influence of two *Prunus* rootstocks ('Myrabolan 29/C' and 'Apricot Seedling') on flower bud biology of 'Pisana' (*Prunus armeniaca* L.), one of the most appreciated Italian apricot cultivar, grown in a Mediterranean agro-climatic environment. Anatomical investigations on xylem differentiation within flower buds and biological observations on flowering as well as fruiting were carried out over two consecutive growth seasons. These years were characterized by different weather conditions due to temperatures and rainfall events which influenced the chilling accumulation, blooming time and xylogenesis process. The onset of xylogenesis within flower buds was conditioned by summer temperatures and water availability. The two rootstocks commonly used in apricot, 'Myrabolan 29/C' and 'Apricot Seedling', did not affect the flowering and fruit-set rate of the grafted cultivar. Nevertheless, differences in progressive differentiation of the secondary thickness of procambial cells in xylem vessels were observed.

Key words: *Prunus armeniaca* L., dormancy, xylogenesis, flowering, fruiting

Introduction

Apricot (*Prunus armeniaca* L.) is a deciduous stone fruit species of the temperate climatic zone which is characterized by a long morphogenetic process leading to fruit set. The cycle of flower bud development often lasts from 9 to 10 months, comprising key processes from the floral induction and differentiation to anthesis with, between them, the presence of a dormancy phase (Koutinas *et al*., 2010). Dormancy is a crucial phase determining the inhibition of bud growth over the autumn-winter season, and bud swelling only occurs by the dormancy release (Lang *et al.,* 1987). During dormancy, flower buds evolve continuously without any visible growth, although within buds the vascular tissue progressively differentiate (Bartolini and Giorgelli, 1994). It consists of the transition from vascular tissue (elongated cells, contains densely stained cytoplasm and lacks lignified secondary wall thickenings) to xylem cells, dead cells with lignified walls producing an empty conduit through which water flows (Esau, 1965). Xylem vessels develop from the base of the bud axis up to the floral primordium, reaching the rudimentary sepals and petals, then the anther filaments, and finally the pistil (Ashworth and Rowse, 1982). An irregular xylem differentiation, not assuring the acropetal transport of fundamental elements (*i.e.,* potassium, boron, carbohydrates) could play a significant role in determining the 'quality' of buds produced and their ability to bloom and set fruitlets (Bartolini and Giorgelli, 1995; Bonhomme *et al.,* 2010).

Xylogenesis process, whose onset starts during the summer season, is particularly sensitive to environmental conditions which might interact with inductive signal such as metabolic substances and phytohormones that play a regulatory role in the control of primary vascular differentiation (Fukuda, 1966; Schultz and Matthews, 1993). Previous studies have indicated that a gradual xylem development, and the achievement of specific developmental stages, can be under the influence of temperatures during the winter dormancy (Bartolini *et al.,* 2006a).

Apricot genotypes can differently react to environmental conditions also interacting with the adopted rootstock. The rootstock, responsible for water and nutrient uptake, is selected for specific edaphic conditions, tolerance to pests or diseases, control of scion vigour and/or inducing early production, fruit size and quality (Webster, 1995; Bartolini *et al.,* 2014). However, there is an elusive part regarding the rootstock influence on floral biology and bud development. In particular, we know to date of no studies that directly investigate the interaction between rootstock and xylogenesis.

The present research was carried out to study the involvement of weather conditions and rootstock genotypes on flower bud biology and xylogenesis process in 'Pisana', one of the most appreciated Italian apricot cultivar, well considered in non-EU regions too, and grown in a Mediterranean agro-climatic environment.

Material and methods

Plant material and study site: During two consecutive growing seasons (2010-11, 2011-12) experimental trials were carried out on full bearing apricot trees (*Prunus armeniaca* L.) of 'Pisana', cultivar characterized by late blooming and ripening time, and strong fruit attractiveness for the fresh market (Guerriero and Monteleone, 1992). Trees were grafted onto two *Prunus* rootstock genotypes which are commonly utilized in apricot orchard: 'Myrabolan 29C' and 'Apricot Seedling'. The seedling rootstock used for heavy and calcareous soils (Massai and Loreti, 2009), tends to be replaced by clonal rootstocks, such as 'Myrabolan' (*P. cerasifera*) due to several desirable traits including tree uniformity (Moreno, 2009). The clonal selection '29/C' shows

good soil adaptability, high tree vigour, early entry to production, good yield efficiency and fruit traits (Cinelli and Viti, 1995; Egea *et al.,* 2004).

Trials were conducted at the research station of the Department of Agriculture, Food and Environment of Pisa University located in a coastal area of Tuscany (Italy, altitude 6 m a.s.l., lat. 43.02 N, long. 10.36 E). The site is characterized by mild-winters and average annual rainfall of about 600 mm; the soil in orchard was loam, moderately deep, medium texture, slightly alkaline, non-calcareous. Trees were trained to a free palmette system (4 m x 4.5 m) with rows facing east-west. The orchard was not irrigated and managed following the routine conventional horticultural cares (pruning, thinning, fertilization, pest and disease protection).

The experiment was established in a randomized complete block design with five single-tree replication for each scion-stock combination.

Weather conditions: In both years, meteorological data (rainfall, minimum and maximum daily temperatures) were recorded, from summer to spring time. Hourly temperatures were registered by an automatic data-logger (Tynitag Plus ®, West Sussex, UK, 2003) inside the orchard and rainfall data were provided from the local metereological station of the Regional Agro-meteorological Service of Florence (SIR).

Data was presented in relation to the following phenological phases: floral differentiation (June-September); early dormancy (October-November); deep dormancy (December-January); end dormancy (from February onwards).

The amount of winter cold received by the plants was quantified in terms of Chill Units (CU) calculated according to the Utah model (Richardson *et al.,* 1974), starting from the end of vegetative season, at 50% of leaf drop. The Utah model assigns variable weights to differing temperature ranges, resulting in CU : temperatures with a positive effect ranged between 1.5 and 12.4 °C, while temperature with a negative effect are higher than 16 °C. The start of CU accumulation was fixed when the largest negative value of CU was attained in autumn. The threshold of 1000 CU was considered a determinant amount for the fulfilment of chilling requirement in most apricot cultivars (including 'Pisana') under Mediterranean conditions. At the experimental site, an annual average of 800 CU has been recorded over time (Viti *et al.,* 2006; Guerriero *et al.,* 2010).

Flowering and fruit-set entity: Trees were monitored to record flower bud evolution during the two autumn-spring seasons. On labelled one-year old fruiting shoots (n = 15 per trees), the following parameters were recorded: a) initial flower and vegetative bud number; b) monthly count of the persisting flower buds for the evaluation of bud drop; c) blooming time expressed as Julian Day (JD 1= January 1st); d) rate of bloom, determined as F50 when 50% of flowers were open; e) rate of fruiting.

Xylem vessel differentiation: From October to February, in correspondence of the three dormancy phases (early, deep, end), flower buds (n = 25 per scion-stock combination) were periodically collected from the median-apical portion of one-year-old fruiting shoots, randomly cut from the west and top sector of the canopy (Viti *et al.,* 2003). Flower buds were excised with a small portion of twig and fixed in the FAA solution (45% ethyl alcohol, 5% glacial acetic acid, 10% formaldehyde; 8:1:1 v/v). After dehydration through an ethanol alcohol series, the material was embedded in Histoplast and longitudinally sectioned (10 µm) using a Shandom microtone. The slices were de-waxed, re-hydrated and stained with an acridine orange solution (stock acridine orange 0.1% in 1⁄9 Walpole's buffer pH 4.2) and mounted in Synthetic Mountant (Shandon). Observations were performed under a Nikon epifluorescent microscope equipped with a 100 W mercury lamp plus an excitation filter (B, type IF 420–490 nm). Representative microphotographs of selected sections were taken with a digital camera (Olympus C-2000 z) connected to the microscope. The acropetal progression of primary xylem differentiation along the flower bud axis was defined by the following stages (Fig. 1A): *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 (Bartolini and Giorgelli, 1994).

Statistical analysis: Prior to analyses, percentage data were converted into angle values by Arcsin transformation. Analysis of variance (ANOVA) and Student's t-test procedure were performed using the package GraphPad Prism 5 (GraphPad Software, Inc.).

Results and discussion

Weather conditions: The growing seasons of 2010/11 and 2011/12 were characterized by different weather conditions, in terms of temperatures and rainfall events (Fig. 2, Table 1). In 2011/12, maximum temperatures were higher than the previous year, particularly during the summer-autumn season, corresponding with floral differentiation and early dormancy of flower buds. This condition determined strong differences between day and night temperatures, about 3-4 °C more than in 2010/11**.** On the contrary, in the last dormancy phase (end of dormancy), differences between years were not remarkable.

The warm autumn-winter temperatures of 2011/12 caused a markedly late chilling accumulation (Fig. 3): the attainment of 1000 CU threshold occurred at mid February, about 20 days later than 2010/11. In this year, 1000 CU were cumulated corresponding with the third decade of January, as usually recorded in this environmental area (Guerriero *et al.*, 2010; Viti *et al.,* 2010a). Even though 1000 CU accumulation was reached at different times, 'Pisana', cultivar at medium chilling requirement (Guerriero *et al.*, 2000), overcame the flower bud endodormancy in both years (data not shown).

The frost events occurred late, from deep to end of dormancy (December-March), through a total of 16-19 days (Table 1, Fig. 2), with a different distribution and intensity between years, but in agreement with previous reports related to the same environmental area (Guerriero *et al.*, 2010).

Concerning the rainfall data (Table 1), 2011/12 was very dry and the rainfall amount, from floral differentiation phase to the end of dormancy, was about 174 mm against 412 mm of 2010/11. In particular, notable differences (about 200 mm) were detected during the summer-autumn period, from floral differentiation to early phase of bud dormancy.

Flowering and fruit-set: Flowering time was affected by the climatic conditions, independently to the graft combination

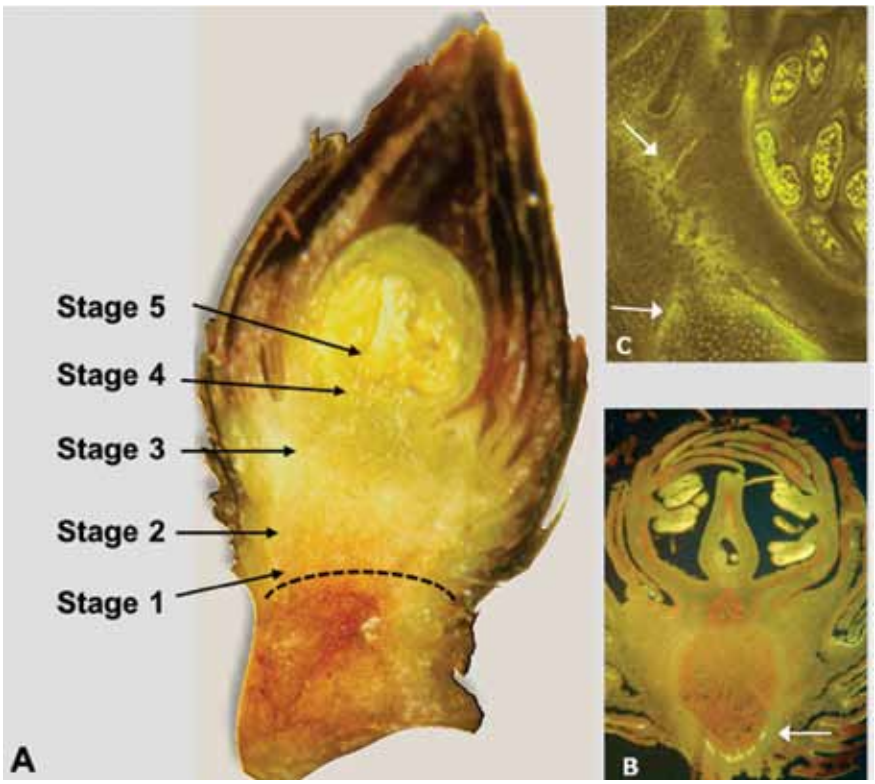

Fig. 1. (A): Representation of xylem vessel differentiation along the flower bud axis (from Bartolini *et al.*, 2006b). Fresh hand section of a flower bud observed under stereomicroscope (x 15): *Stage 1* (at the base of the axis); *Stage 2* (at 1/2 of the axis); *Stage 3* (at 3/4 of the axis); *Stage 4* (at the base of the ovary); *Stage 5* (inside the pistil). Dotted line indicates the pulvinar juncture. (B-C): Median longitudinal sections of flower buds stained by acridine orange reaction under epifluorescent microscope; arrows show the xylem vessels at *Stage 1* (B, 40x), and *Stage 3-4* (C, 100x).

Table 2. Two-way ANOVA results. Variables: xylem stages at early, deep and end of dormancy phases

Main effects	Early	Deep	End
	P	P	P
Year	< 0.0131*	0.8244 ^{NS}	0.5003^{NS}
Rootstock	0.1259 ^{NS}	0.1860 ^{NS}	0.2641 ^{NS}
Interaction			
Year x Rootstock	0.1259 ^{NS}	0.0170*	0.8217^{NS}

NS: Not significant; *: Significant at $P \leq 0.05$

(Fig. 4). In 2011-12, characterized by warm temperatures which determined late winter chilling, the flowering time took place during the second decade of March, about 6 days earlier than the previous year. This early flowering could have been also affected by warm temperatures after dormancy breaking which led to a fast fulfillment of heat requirements (data not shown). Moreover, the drought conditions occurred in the summer-autumn period of 2011-12 could have a role in the phenological evolution of flower buds. The mechanism by which the summer drought advance the bud opening in the next season may be mediated by a hormonal imbalance under drought which arrests plant growth and induces earlier bud formation (Rinne *et al.,* 1994; Arora *et al.,* 2003; Horvath *et al.*, 2003). In contrast, well-watered plants keep their growth for longer, so that bud formation starts later (Sanz-Perez and Castro-Diéz, 2010).

Flowering and fruiting entity was not influenced by the rootstock (Fig. 5), in agreement with previous studies (Hirst and Ferree, 1995; Bartolini *et al.,* 2014). It is possible that, under our pedological conditions, the type of soil did not let to express the peculiarity of the two tested rootstocks. In both years, flowering percentage reached good levels (≥40%), in accordance to usual values recorded for apricot (Viti *et al.,* 2006). However, strong differences in fruiting percentage were recorded between years, ranging from 7% (2011) to 38% (2012). The lowest fruit entity of 2011 could be attributed to late frosts occurred from the second decade of February onwards (Fig. 2). It has been established that frost events close to bud break are related to shoot loss and lower yield (Mullins *et al.*, 1992). Apricot varieties with early flowering time are particularly sensitive to freezing temperatures at the fulfilment of flower bud endodormancy (Rodrigo, 2000; Viti *et al.*, 2010b). The reproductive organs are affected by spring frosts as a consequence of the morphological and physiological status of swelling buds, characterized by a fast dehardening against sub-zero temperatures (Sazalay *et al.,* 2006).

Xylem vessel differentiation: The anatomical observations confirmed that, within flower buds, a progressive differentiation of the secondary thickness of procambial cells in the xylem vessels took place during the autumn-winter season, when no growth changes were visible. During the three phases of bud dormancy (early, deep, end), the sequence of different xylem stages was identified (Fig. 6), from stage 1 (xylem vessels at the base of the flower bud axis) to stage 4 (xylem vessels up to the ovary). In our study, the xylem continuity between the floral

Table 1. Mean minimum and maximum temperatures (°C), differences between mean day and night temperatures (Dif., °C), number of frost days (temperatures below 0 °C) and rainfall (mm) recorded over a 2-year period (2010-2012), during the floral differentiation and the following dormancy phases: early dormancy (October-November), deep dormancy (December-January), end dormancy (February onwards)

Phases	Min. Temp. (°C)		Max. Temp. (°C)		Dif. (°C)		Frost days(< O°C)		Rainfall (mm)	
	2010-11	2011-12	2010-11	2011-12	2010-11	2011-12	2010-11	2011-12	2010-11	2011-12
Differentiation	15.5 ±2.1*	16.5 ±2.5	26.9 ±2.5	30.8 ±2.7	11.4 ±2.5	14.3 ±3.0	0	0	169.0	63.0
Early dormancy	9.6 ±2.0	9.4 ±2.9	16.9 ±4.2	20.5 ±2.9	7.3 ±2.4	11.1 ±3.2	0	0	197.4	100.4
Deep dormancy	4.7 ±1.7	4.6 ±4.1	11.2 ±3.5	14.1 ±2.5	6.9 ±2.6	9.7 ±2.7	15	10	30.8	11.4
End dormancy	4.1 ±2.9	2.2 ±2.5	14.3 ±2.4	11.9 ±6.7	10.2 ±2.9	10.2 ±5.1	1	9	25.0	0
Total							16	19	412.2	173.8

*Mean values ± Standard Deviation

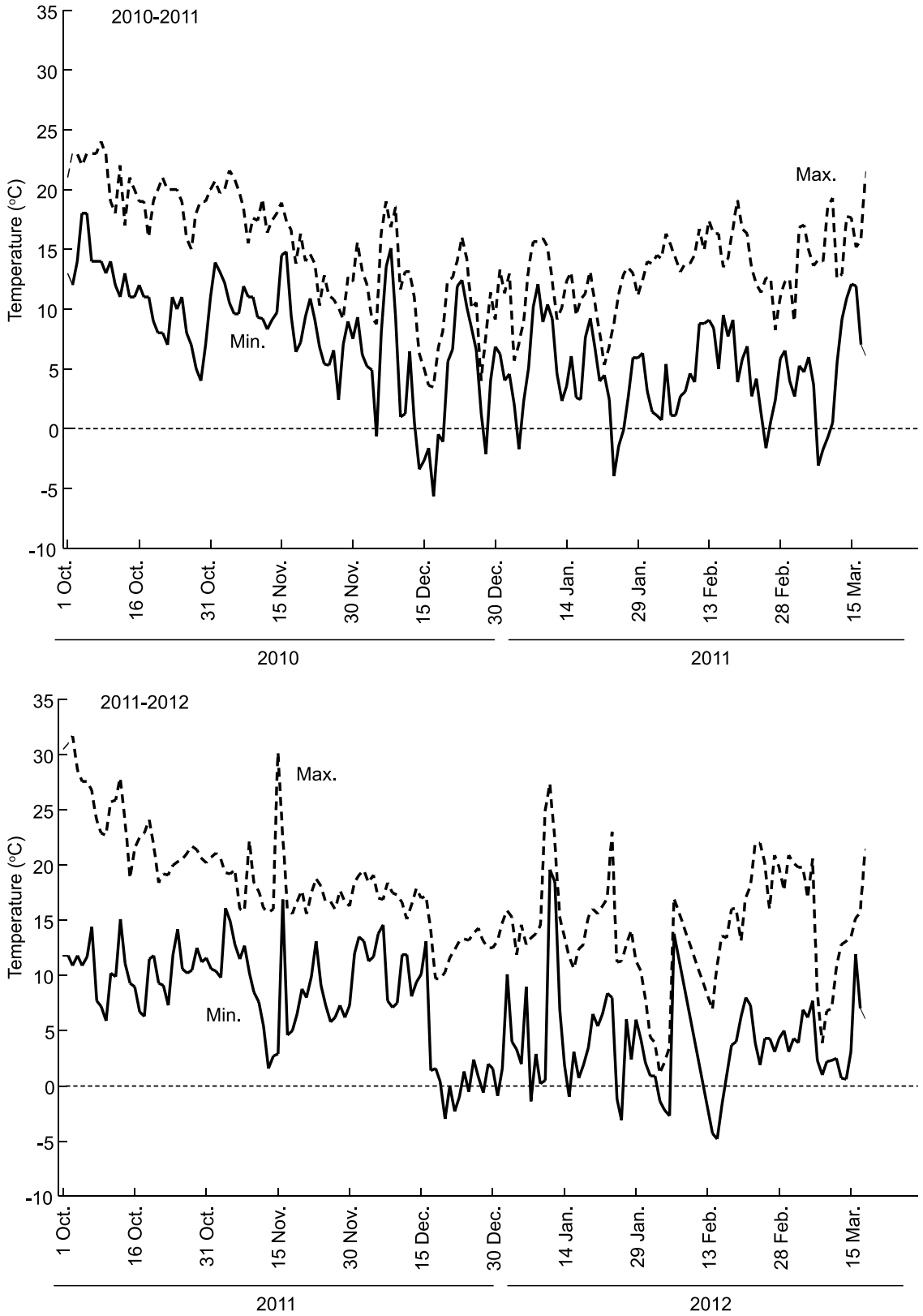

Fig. 2. Daily minimum and maximum temperatures recorded from October to March over a 2-year period (2010-2012).

primordium and the bud axis (stage 5), was not detected according to previous researches in which this stage has been established only at the pre-flowering phase (Bartolini *et al.,* 2006b).

The growth-rate of the developmental stages of xylem vessels produced a different temporal pattern. In both years and graft combinations, at early dormancy (October-November), stage 1 was the most representative status of xylem differentiation (Fig. 6, Fig. 1B). While in 2010-11 only this stage was recorded, in 2011-12 stage 2 was also found. Between years, the differences in xylem onset could be due to dissimilar climatic conditions of the summer seasons (temperature and rainfall), during the flower bud differentiation phase. In Table 2, ANOVA test showed the effect of the year on the xylem differentiation, and a significant

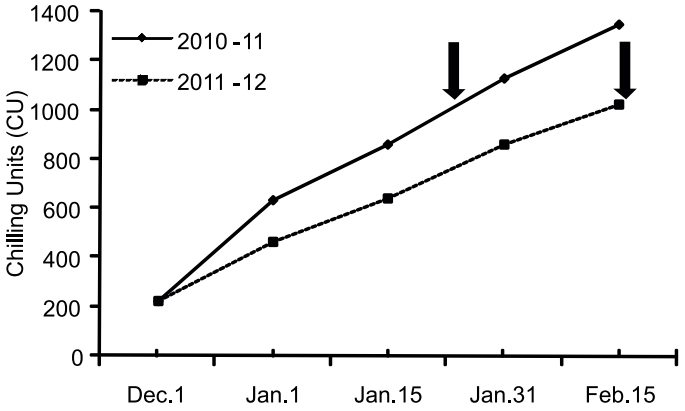

Fig. 3. Chilling Unit (CU) accumulated over a 2-year period (2010-2012), from December 1st to February 15th. Arrows indicate the accumulation of 1000 CU.

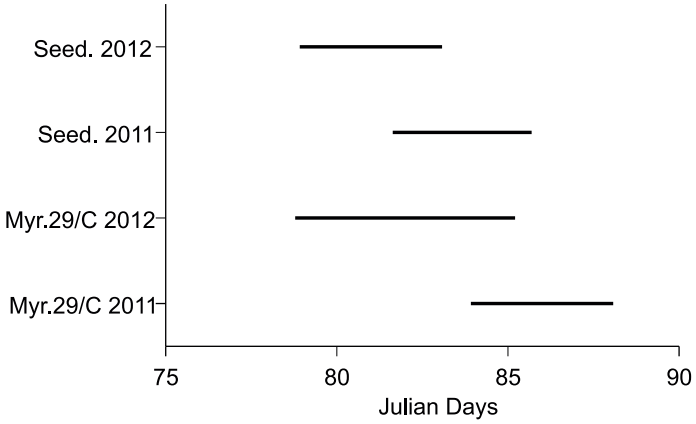

Fig. 4. Flowering time (Julian Days) recorded over a 2-year period (2011 and 2012) in 'Pisana' cultivar grafted onto 'Myrabolan 29/C' and 'Apricot Seedling'.

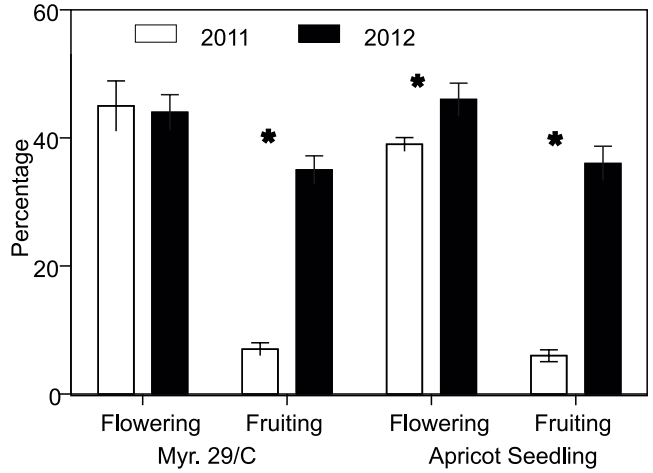

Fig. 5. Percentage of flowering and fruiting recorded over the spring-summer season of 2011 and 2012 in 'Pisana' cultivar grafted onto 'Myrabolan 29/C' and 'Apricot Seedling'. Mean values (± Standard Error).

interaction 'year x rootstock' for the deep dormancy variable was detected. The warmest summer of 2011 determined a fast xylem differentiation observed from the early dormancy onwards. The persisting warm conditions during the autumn season, also determined a higher appearance of stages 3 and 4 at the end of dormancy (Fig. 1C), as a consequence of the decline of winter chill, leading to a delayed CU accumulation (Fig. 3). The role of warm temperatures, as important external factor resulting in significant induction of xylem differentiation, was revealed

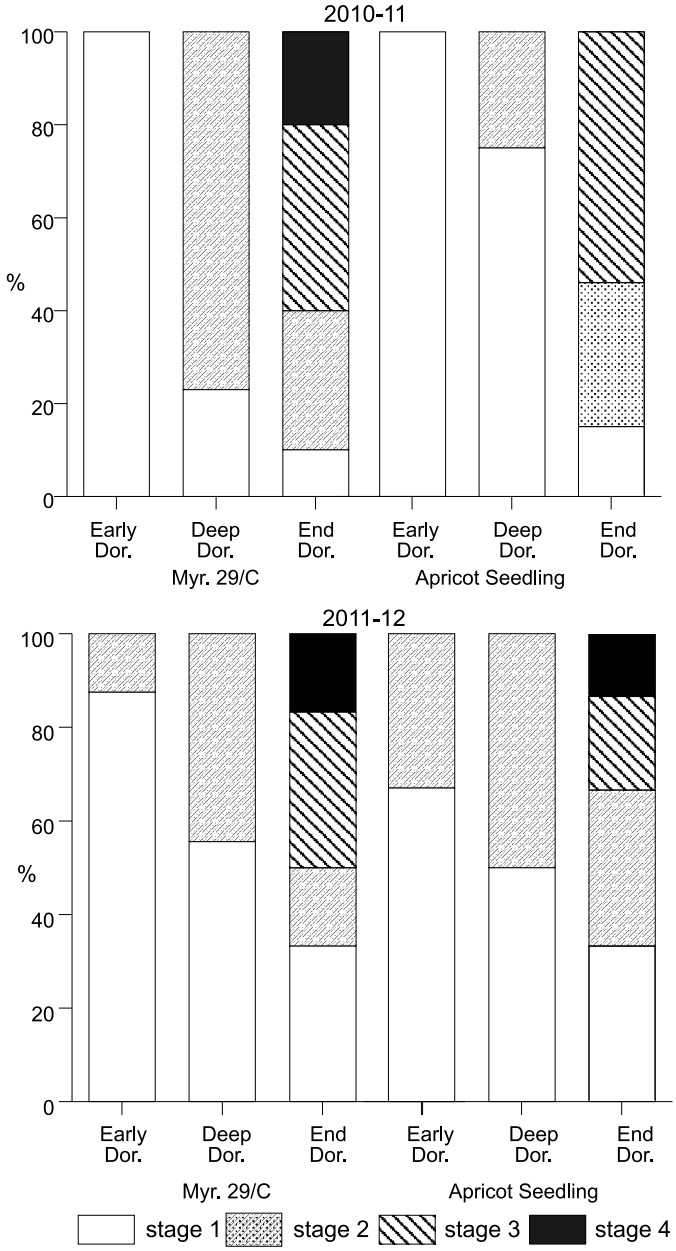

Fig. 6. 'Pisana' apricot cultivar grafted onto 'Myrabolan 29/C' and 'Apricot Seedling': distribution (%) of xylem vessel differentiation stages (from *Stage 1* to *Stage 4*) detected in flower bud axis over a 2-year period (2010-2012), during the following dormancy phases: early dormancy (October-November), deep dormancy (December-January), end dormancy (February onwards).

in several woody species (Bartolini *et al.,* 2006b; Begum *et al.,* 2008). Nevertheless, a late chilling accumulation occurred in 2011-12, the significant threshold of 1000 CU, required by 'Pisana' cultivar to release the flower bud endodormancy, was attained, achieving stages 3 and 4 (Fig. 6). It has been confirmed that the accumulation of about 1000 CU is a trigger level for the appearance of the most advanced xylem stages, stimulating the bud growth under natural conditions (Bartolini *et al.,* 2006a; Andreini *et al.,* 2012).

Xylem differentiation patterns observed in a 2-year period could also be affected by different expositions of trees to water availability during the summer season. The heavy rainfall of 2010 could have had an influence contributing to a slowdown in xylem differentiation. It has been demonstrated that an excess of

water in the soil during the growing season induces the flooding phenomena, which can cause several anomalous responses of plant, such as inhibition of vegetative and reproductive growth and morphological changes (Hook and Scholtens, 1978; Kavase, 1981). Limited rainfall events occurred in the summer of 2011, in concomitance with warmer temperatures, did not affect the onset and progression of xylogenesis process. This feature could be explained taking into account that several physiological and biochemical changes occur in response to drought stress in various plant species. Although controversies are still prevailing on the balance of phytohormones in response to drought stress, endogenous indole-3-acetic acid (IAA) was reported to increase under drought stress (Lopez-Carbonell *et al.,* 1996; Kutlu *et al.,* 2009). This hormone, being involved in xylogenesis process (Aloni, 1980), could elucidate the advance in xylem stages recorded at early dormancy, after drought conditions.

Considering the graft combinations, in both years, differences in xylem vessel development were observed only at the end of dormancy (Fig. 6). Flower buds from 'Pisana' onto 'Myrabolan 29/C' showed a higher percentage of advanced xylem differentiation (stage 3 and 4) than 'Apricot Seedling'. This occurrence was particularly marked in 2010-2011 when a slow vascular development was detected in Seedling, and stage 4 was not identified up to the last flower bud sampling. However, this feature did not influence the resumption of flower bud growth, confirming the relationship between endodormancy release and attainment of stages 3. At this stage, the availability of nutritional elements throughout the xylem supply could be a factor determining the flowering regularity. A correlation between the increase of certain elements (*i.e.* potassium and boron) by the xylem acropetal transport and the bud swelling has been observed (Hanson and Breen, 1985; Bartolini and Giorgelli, 1995; Bonhomme *et al.,* 2010).

Under the environment of Tuscany, the dissimilar weather conditions (temperature and rainfall) of the two studied growth seasons influenced the flower bud biology of apricot assessed on 'Pisana', one of the most appreciated Italian cultivar. The different summer-autumn temperatures determined changed patterns in CU accumulation, blooming time and xylogenesis process. Nevertheless, 'Pisana' cultivar showed a great ability to release from endodormancy leading to satisfactory flowering rates. This occurrence also took place under inadequate weather conditions due to limited rainfall events and warm temperatures which determined a delay of CU accumulation.

This study suggests that the onset of xylogenesis within flower buds is influenced by summer temperatures and water availability. Contrary to what we had expected, warm and drought summer conditions did not negatively influence the xylem development which showed more advanced differentiation stages in comparison to the wettest summer season.

The two commonly adopted rootstocks in apricot, 'Myrabolan 29/C' and 'Apricot Seedling', did not influence the flowering and fruit-set rate of the grafted cultivar. However, differences in progressive differentiation of the secondary thickness of procambial cells in the xylem vessels were observed. Flower buds from 'Pisana' onto 'Apricot Seedling' showed a slower xylem progression which did not impact the regular bud development under our pedological environment.

In conclusion, 'Pisana' cultivar, despite rootstock and climatic conditions, showed a high environmental adaptability confirming the key role played by the genetic feature.

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