Flowering and fruit set in olive: a review

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Abstract

Olive is one of the most ancient fruit trees and has been cultivated for its oil for thousands of years. A mature olive tree produces about 500,000 flowers. They are borne on inflorescences termed panicles. The number of flowers and their distribution on the inflorescence are specific for each cultivar but can change from year to year. The flower position on the inflorescence affects its gender and opening day. The flowers are either perfect (hermaphrodite) or staminate (male). Olive flowers are wind-pollinated; however, they are visited by insects. Critical conditions such as strong and dry winds, rain, and high temperature affect pollination and may reduce fruit set. Most olive cultivars are self-incompatible or partially self-compatible and need to be fertilized by compatible pollenisers to ensure acceptable production. Furthermore, some cultivars are cross-incompatible and cannot fertilize each other. The degree of SIin olive is widely influenced by climatic conditions and therefore varies from environment to environment and from year to year. In a year with normal flowering, 1 to 2% of fruit set is enough for a commercial yield. The fruit follows a double sigmoid growth pattern like other drupes and contains quality oil.

Introduction

Olive is a member of the Oleaceae family, genus *Olea*. Commercial olive trees belong to *Olea europaea* L., the only species which produces edible fruits.The olive tree is originated in the eastern Mediterranean area and has been cultivated for its oil and fruit for millennia (Bertrand, 2002). Today, the demand for olive oil and table olives is increasing in traditional producing areas and elsewhere in the world. Both products have high levels of monounsaturated fatty acids and antioxidant agents and high dietetic value (de la Lastra et al., 2001). The world production of olive fruits in 2011 was about 19.8 million tons (FAOSTAT-website, accessed 21May 2013).

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Table 1
Effects of shoot orientation and inflorescence location on inflorescence characteristics in Frantoio, Kalamata, and Koroneiki

Cultivar	n	Frantoio			Kalamata			Koroneiki		
		Length (cm)	No of flowers	% perfect flowers	Length (cm)	No of flowers	% perfect flowers	Length (cm)	No of flowers	% perfect flowers
Direction		$P =$	$P =$	$P =$	$P =$	$P =$	$P =$	$P =$	$P =$	$P =$
		0.874	0.660	0.607	0.321	0.392	0.188	0.389	0.284	0.617
North	27	3.9	17.3	93.9	3.2	24.6	11.7	3.2	18.6	44.6
South	27	4.1	20.0	84.2	3.2	21.6	20.5	2.7	16.1	29.6
East	27	4.4	21.3	96.6	3.6	23.6	39.0	3.0	16.3	44.0
West	27	4.0	17.2	93.56	3.0	19.3	21.5	2.7	16.7	27.2
Location		$P < 0.001$	$P = 0.003$	$P = 0.449$	$P < 0.001$	$P = 0.004$	$P = 0.085$	$P = 0.034$	$P = 0.030$	$P = 0.451$
Tip	36	4.4 a	20.8 a	91.6	3.4 a	23.4 a	21.2	3.2 a	17.8 ab	35.9
Middle	36	4.3 a	19.5 a	95.2	3.5 a	24.3 a	27.4	3.0 ab	18.5 a	31.3
Base	36	3.5 b	16.5 b	89.4	2.7 b	19.1 b	20.9	2.5 b	14.4 b	41.8

Different letters within each column represent significant differences at $P = 0.05$, Tukey's test (Seifi, 2008).

Olive is a long-lived subtropical, evergreen tree. Some olive trees have been reported to live for more than 1000 years. The olive root system is generally shallow, whether propagated by seed or cutting, penetrating only 90-120 cm in soils. But the lateral spread is remarkable and reaches to 15 m in mature trees. The shoot system is dense and the shoots grow pendulous in some cultivars but upright in others. Olive leaves are opposite, thick and leathery. They reach their final size within 2 weeks and live for 2-3 years (Martin and Sibbett, 2005).

Commercially grown olive cultivars can be self-compatible, partially self-compatible, or self-incompatible. Manzanillo, for example, has been shown to be self-incompatible, requiring cross-pollination from a foreign pollen source for optimal fruit set (Martin et al., 2005). The fruitsare oblong drupes with a smooth, waxy surface. They are green when immature, turning yellow-green, and then red, purple or black at full maturity.This review presents and discusses flowering, pollination, self-incompatibility, and fruit set in olive.

Flower bud differentiation

Fabbri and Benelli (2000) reviewed the studies conducted on olive flowering and reported that the results confirm the two-step theory of flower bud induction and differentiation in olive, previously suggested by Lavee (1996). In the first step during spring-summer, likely flower buds are simulated to prevent their differentiation into leaf buds. In the second step during autumn-winter and under further favorable conditions, the candidate buds are simulated again to form the flower structures. The final number of flower buds depends on environmental conditions, nutrition, hormonal balance, photosynthesis capacity and other factors in both steps (Lavee, 1996; Salmani, et al., 2014).

Like some other species (Farzami Sepehr and Ghorbanli, 2010; Chaparzadeh and Yavari, 2013), olive flower buds need chilling in winter to open properly, but the chilling influence on flower bud induction and differentiation is still in question (Lavee, 1996; Fabbri and Benelli, 2000). Most olive cultivars follow alternate bearing and normally produce small numbers of flowers and fruits after a heavy yield (Lavee, 1985).

Inflorescence morphology

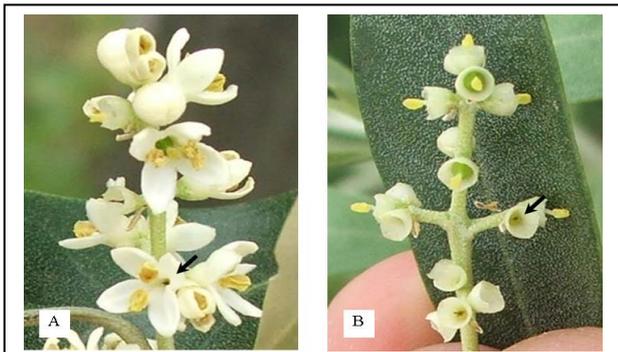An adult olive tree produces about 500,000 flowers a year (Martin et al., 2005). Olive

Fig. I. An olive inflorescence (panicle) including perfect and staminate (arrows) flowers before (A) and after petal abscission (B).

flowers are grouped in inflorescences, called panicles (Fig. I). The inflorescences are usually borne at the axil of leaves on shoots developed in the previous season. In some conditions, especially in warmer climates and after a relatively cold winter, inflorescences are also seen at the shoot apex (Lavee, 1996). They may rarely develop on 2- or 3-year-old shoots (Lavee, 1996). Apical inflorescences had significantly more flowers ($P < 0.001$) but the same length and percentage of perfect flowers (Seifi, 2011).

The inflorescence length depends on the cultivar and varies from 3 to 8 cm (Lavee, 1985). The number of flowers per inflorescence also depends on the cultivar and normally is between 15 and 30 (Martin and Sibbett, 2005) but may vary from year to year, from tree to tree, from shoot to shoot, and from inflorescence to inflorescence (Brooks, 1948; Lavee and Datt, 1978; Lavee, 1985; Cuevas et al., 1994; Lavee, 1996; Lavee et al., 2002; Reale et al., 2006). Previous studies (Seifi, 2011) showed that shoot orientation had no significant effect on any characteristic in Frantoio, Kalamata, and Koroneiki, while location had significant effects on the length of the inflorescence and number of flowers in all cultivars but not on the percentage of perfect flowers (Table 1). It seems that the base inflorescences were shorter and had fewer flowers in all cultivars. In Koroneiki, the differences were not significant between the base and middle inflorescences in length and between the base and tip inflorescences in the number of flowers. Inflorescences may also be different in structure. Table 2 shows the main

structures observed in Manzanillo, Mission, and Frantoio in 2005. The most common structures were 2 in Manzanillo and 3 in Mission and Frantoio (Seifi, 2008).

Table 2
Percent of the inflorescences' main structures in olive (Seifi, 2008)

Structures	n	1	2	3
Manzanillo	45	22.2	42.2	11.1
Mission	45	17.8	11.1	48.9
Frantoio	45	28.9	24.4	31.1
Mean percent		23.0	25.9	30.4

Flowering

Olive flowers are small and consist of four fused green sepals, four white-yellowish petals, two stamens, and two carpels (Fabbri et al., 2004). The petals are fused at their base and drop as a unit, often with the stamens attached (Martin et al., 2005). The style is short and thick with a relatively large stigma. There are two types of flowers: perfect flowers, which have functional pistils, and staminate flowers, whose pistils have degenerated (Fig. I). The pistil degeneration can occur at any stage of development (Lavee, 1985; Fabbri et al., 2004), and water and nutrient stresses during flower development can lead to abortion (Martin and Sibbett, 2005). The number of staminate flowers is controlled genetically and environmentally; therefore, it may vary from year to year, from tree to tree, from shoot to shoot, and from inflorescence to inflorescence (Badr and Hartmann, 1971; Lavee et al., 2002; Fabbri et al., 2004; Martin and Sibbett, 2005).

The flower position on the inflorescence also affects its gender (Bouranis et al., 1999; Dimassi et al., 1999; Ateyyeh et al., 2000; Cuevas and Polito, 2004; Martin et al., 2005). In comparison with staminate flowers, perfect flowers are more often located at tips. (Brooks, 1948; Griggs et al., 1975; Bouranis et al., 1999; Ateyyeh et al., 2000; Martin et al., 2005) and middle (Dimassi et al., 1999). Seifi et al., (2008)

showed that in a cultivar with a high percentage of staminate flowers (Manzanillo and Mission), the perfect flowers were mainly in the terminal positions and the staminate flowers on the laterals. Removing the distal half of the inflorescences in which the flowers tend to be perfect 30 days before full bloom, decreased pistil abortion in the remaining flowers. This suggests competition between the flowers for nutrients, which may cause higher pistil abortion in lateral positions. The percentage of staminate flowers has no significant effect on yield (Lavee et al., 1996), except for some clones of Ascolana in some years with less than 5% of perfect flowers (Lavee et al., 1996; Lavee et al., 2002). Abnormal flowers are also common in some cultivars. Flowers with three or four stamens and five, six, or eight petals have been reported (Lavee, 1985).

Blooming

Inflorescence development is slow and usually takes 4 to 6 weeks from inflorescence bud opening to anthesis (Lavee, 1985). When the inflorescences reach a length of about 2 cm, they start to elongate rapidly, and when they are about 2/3 of their final length, the flower buds begin to expand (Lavee, 1996). Anthesis normally takes 2-3 days in an individual inflorescence, 5-6 days in an individual tree, but 10-15 days in cooler seasons and environments (Fabbri et al., 2004). When the temperature is unstable, anthesis may occur in more than one flush, but the first flush usually sets the fruits that reach maturity (Lavee, 1985). The flower position on the inflorescence also affects its opening. In Mission, for example, the first flowers to open were always located on the primary branches, and the last to open on the secondary branches in 79% of cases (Cuevas and Polito, 2004).In Manzanillo, Mission, and Frantoio the percentage of perfect flowers was higher at the beginning of the opening period and reduced towards the end of anthesis. Within an individual inflorescence, the position of the flower influenced the opening day. The first flowers to open were those located in terminal positions followed by those located on the laterals (Seifi et al., 2008). As soon as a flower opens, it is considered mature and ready to be fertilized, but not before (Suarez et al., 2012).
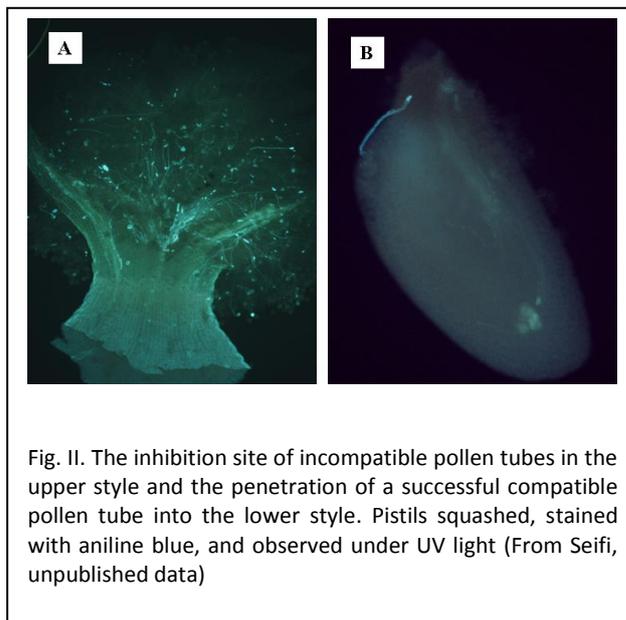

Fig. II. The inhibition site of incompatible pollen tubes in the upper style and the penetration of a successful compatible pollen tube into the lower style. Pistils squashed, stained with aniline blue, and observed under UV light (From Seifi, unpublished data)

Pollination

Olive flowers produce a large number of pollen grains (Griggs et al., 1975; Lavee, 1986), which are triangular in shape with a netted surface (Lavee, 1985). Although olive flowers are wind-pollinated, they are visited by insects including honeybees, which may assist pollination (Lavee, 1985; Free, 1993). Olive flowers do not produce nectar, and insects collect only pollen grains (Lavee, 1985). Critical conditions such as strong and dry winds, rain, and high temperature affect pollination and may reduce fruit set (Lavee, 1986; Conner and Fereres, 2005). Although olive pollen can be carried by wind as far as 12 km (Fabbri et al., 2004), the effective pollination distance (EPD) has been reported to be 30 m in normal conditions (Ayerza and Coates, 2004; Fabbri et al., 2004; Sibbett and Osgood, 2005). Ten percent of pollenisers within the EPD of the main cultivar is enough to ensure a good yield (Lavee, 1996). Due to the excessive amount of pollen and its high distribution, there is no correlation between the viability of pollen and fruit set (Lavee, 1986). The viability of olive pollen is usually high (Lavee et al., 2002).

Pollen grains land on the stigma and germinate to produce pollen tubes, which grow through the style to fertilize the eggs to form

embryos. Pollen tubes need appropriate air temperature to grow properly. In cooler temperatures, pollen tubes grow slowly and may fail to reach the ovules or reach them after their degeneration. High temperatures also inhibit pollen germination and slow down or stop the pollen tube (Bartoloni and Guerriero, 1995). On the other hand, hot and dry conditions may shorten the receptivity period of the stigma (Martin et al., 2005). Effective pollination period (EPP) is defined as the period during which pollination can produces fruit set. EPP in olive has been reported to vary between 4 and 12 days depending on the cultivar and season (Cuevas et al., 2009). Most pollen tubes are inhibited in the stigma before entering the transmitting tissue in the style, and normally one or two pollen tubes grow towards the ovary, one reaches the carpels, and one penetrates one of the four ovules (Ateyyeh et al., 2000; Seifi, et al., 2011) (Fig. II).

Self-incompatiblty (SI)

Successful sexual reproduction in angiosperms depends on a series of events, in which a pollen grain attaches to a receptive stigma, adheres and hydrates, germinates, and produces a tube that grows through the style and towards the ovary to fertilize the eggs and form an embryo. Outbreeding (cross-fertilization) increases genetic variability and consequently imparts strong evolutionary potential. Different mechanisms have evolved in flowering plants to promote outbreeding such as SI, monoecy, dioecy, dichogamy, and male sterility. SI is the most widespread mechanism (Franklin-Tong and Franklin, 2003; Hiscock and McInnis, 2003) and is estimated to be present in more than half of the species of angiosperms (de Nettancourt, 1977; McClure and Franklin-Tong, 2006).

SI is defined as "the inability of a fertile hermaphrodite seed-plant to produce zygotes after self-pollination" (de Nettancourt, 1977; de Nettancourt, 2001). SI prevents inbreeding (self-fertilization) by recognition and rejection of self or self-related pollen (Hiscock and McInnis, 2003). It seems that SI arose later than the separation of families because some closely-related families have different systems of SI. Solanaceae and Convolvulaceae, for example, are two closely-related families with gametophytic and sporophytic systems, respectively (Kowyama et al., 2000). Steinbachs and Holsinger (2002) argued that SI has evolved at least 21 times during the evolution of flowering plants.

SI systems are classified on the basis of floral morphology, genetic control of the pollen phenotype, and the inhibition site. There are two kinds of SI based on floral morphology: heteromorphic SI, in which the flowers of the interbreeding plants have different structures, and homomorphic SI, in which the flowers of the interbreeding plants have the same visible morphology. On the basis of genetic control of the pollen phenotype, homomorphic SI is divided into two groups: sporophytic and gametophytic systems. There is also another kind of SI called late-acting or ovarian, in which inhibition does not happen in the stigma or in the style but later in the ovary (Sedgley, 1994).

Most olive cultivars are self-incompatible or partially self-compatible and need to be fertilized by compatible pollenisers to ensure a commercial yield (Lavee, 1986; Lavee, 1990; Besnard et al., 1999; Dimassi et al., 1999; Moutier, 2002; Fabbri et al., 2004; Conner and Fereres, 2005). They may set some fruits in monocultivar culture but benefit greatly from cross-pollination. Many studies have been conducted on the SI of olive cultivars and according to their results olive cultivars have been classified into three groups: self-incompatible, partially self-compatible, and self-compatible. From 547 olive cultivars classified by FAO (FAO-website, accessed 20 Nov 2012), according to the degree of SI, 348 cultivars (63.62%) have been recorded as self-incompatible, 94 cultivars (17.18%) as partially self-compatible, and 105 cultivars (19.20%) as self-compatible.

Until recently, the olive SI system and its molecular mechanism were unclear. Some authors suggested a GSI system (Ateyyeh et al., 2000; Orlandi et al., 2005). The olive has been reported to have bi-nucleate pollen grains (Wu et al., 2002; Rodriguez-Garcia et al.,2003b) and wet stigmas (Ateyyeh et al., 2000; Wu et al., 2002) although dry stigmas have also been reported (Rodriguez-Garcia et al., 2003a). Incompatible pollen tubes are inhibited after germination and

inside the stigma tissue rather than on the surface of the stigma (Cuevas and Polito, 1997; Ateyyeh et al., 2000; Orlandi et al., 2005; Seifi et al., 2011) (Fig. II). The characteristics of bi-nucleate pollen grains, wet stigma and pollen tube inhibition after germination are mostly found in plants with GSI (Heslop-Harrison and Shivanna, 1977; de Nettancourt, 1997). However, the defining characteristic determining the system of SI to be gametophytic or sporophytic is the genetic behavior of the pollen. The SI phenotype of germinating pollen in the gametophytic system is determined by the haploid genotype of the pollen (gametophyte) (Newbigin et al., 1993; McCubbin and Kao, 2000; de Graaf et al., 2006) and in the sporophytic system by the diploid genotype of the pollen donor (sporophyte) (Newbigin et al., 1993; McCubbin and Kao, 2000).

Previous studies reported Koroneiki as a self-compatible cultivar (Lavee, 1986; Lavee et al., 2002) and Picholine, Leccino, Kalamata, Manzanillo, Picual, and Arbequina as self-incompatible or partially self-compatible cultivars (Griggs et al., 1975; Lavee, 1986; Androulakis and Loupassaki, 1990; Dimassi et al., 1999; Ghrisi et al., 1999; Wu et al., 2002; Mookerjee et al., 2005; Diaz et al., 2006; Seifi et al., 2012). Furthermore, some cultivars are cross-incompatible and cannot fertilize each other (Griggs et al., 1975; Cuevas and Polito, 1997; Martin et al., 2005; Mookerjee et al., 2005). Ascolana and Mission were shown to be cross-incompatible with Manzanillo (as a host) and Barouni with Sevillano (as a host) (Martin et al., 2005). Kalamata was incompatible with Arbequina, Azapa, and Picual (Seifi et al., 2012).

Cross-incompatibility has been reported to be reciprocal or bidirectional in some pairs of cultivars such as Manzanillo and Mission (Griggs et al., 1975; Cuevas and Polito, 1997; Martin et al., 2005), while some other authors showed that it is not always reciprocal (Moutier et al., 2001; Lavee et al., 2002). Moutier (2002) reported that Picholine is incompatible with Manzanillo (as a host) but not in the opposite direction. Lavee et al. (2002) could not find reciprocal consistency after their long-term (12 years) and large-scale (36 cultivars) experiment.

Several studies on the SI of olive cultivars have resulted in variable and conflicting results. Frantoio, for example, was concluded to be self-compatible in some reports (Sharma et al., 1976; Fontanazza and Baldoni, 1990; Fabbri et al., 2004) but self-incompatible in others (Wu et al., 2002; Mookerjee et al., 2005). Koroneiki also has been reported to be self-compatible by Lavee (1986) and Lavee et al. (2002) but self-incompatible by Mookerjee et al. (2005). The variation of results might be due to confusion in cultivar identity and the use of homonyms and synonyms (Bartolini et al., 1994; Lanza et al., 1996; Mekuria et al., 1999), contamination that may happen during pollen collection, flowering shoot isolation, and hand pollination in controlled crossing, annual changes in the total number of flowers in trees (Lavee et al., 2002), and climatic conditions (Lanza et al., 1996; Mekuria et al., 1999).

Pollen-incompatibility in olives is widely influenced by climatic conditions; thus, it may vary from area to area and from year to year (Griggs et al., 1975; Lavee, 1986; Androulakis and Loupassaki, 1990; Lavee et al., 2002). It has been shown that pollen tubes grow more vigorously following cross-pollination (Ghrisi et al., 1999; Cuevas et al., 2001). High temperatures inhibit self pollen tube growth in the style (Griggs et al., 1975; Fernandez-Escobar et al., 1983), while cross-compatible pollen tubes are less affected (Lavee et al., 2002). Therefore, in high temperatures cross-fertilization is more likely to happen than self-fertilization.

Fruit set

In a year with normal flowering, 1 to 2% of fruit set is enough for a commercial yield (Lavee, 1986; Lavee, 1996; Fabbri et al., 2004; Martin et al., 2005). In 'off' years, when the flowering is weak, fruit set may increase to 10% (Martin et al., 2005). Normally one fruit per inflorescence develops, except for some cultivars with small fruits such as Koroneiki and Arbequina (Lavee, 1986; Conner and Fereres, 2005), or when a high number of the inflorescences are removed (Lavee et al., 1996). After pollination, the first flowers to drop are staminate flowers. Then, unfertilized perfect flowers and fertilized young fruits are dropped as a result of competition. Fruits are the

main site of carbohydrate consumption (Bernard, et al., 2012). In Manzanillo, the two drops overlap, but their peaks are 8 and 13-15 days after full bloom, respectively. Twenty-five days after full bloom, the number of fruits stabilizes, and only a few may subsequently drop as a result of competition (Rapoport and Rallo, 1991), although the competition among olive fruits starts at bloom and the fruit set is inversely proportional to flower/fruit size (Rosati et al., 2010).

The olive fruit is a drupe with a mesocarp containing oil (22%), water (50%), proteins (1.6%), carbohydrates (19.1%), cellulose (5.8%), and minerals (1.5%) (Doveri and Baldoni, 2007). Fruit growth follows a double sigmoid curve like other drupes. It usually consists of three separate stages: growth as a result of cell division, hardening of the endocarp when mesocarp growth stops, and the second growth phase due to cell enlargement (Lavee, 1986; Fabbri et al., 2004). In normal conditions, only fertilized ovaries remain on the inflorescences, but under some conditions, especially on inflorescences with no normal fruits, some parthenocarpic fruits (shot berries) may develop (Lavee, 1996). Cross-pollination is reported to decrease the number of shot berries (Griggs et al., 1975; Fernandez-Escobar and Gomez-Valledor, 1985). They are small and round (regardless of the normal fruit shape of the cultivar) and reach maturity earlier than other fruits (Lavee, 1986; Lavee, 1996).

Conclusion

The presence of SI in olive cultivars obliges growers to plant more than one cultivar in their orchard. Fabbri et al. (2004) recommended three or four cultivars in a commercial orchard to guarantee good fruit set even if the main cultivar is considered self-compatible. Because olive cultivars might be cross-incompatible, it is important to know which cultivars are best to grow together. The selected cultivars, also, must have overlapping anthesis. Better understanding of floral morphology and phenology is necessary for growers to optimize cross-pollination and fruit set. Some other advantages of planting more cultivars in the orchard are diversification of oil quality,

spreading harvest requirements, minimizing risk from environmental variability and changing market preferences, and ensuring annual commercial yields despite the alternate bearing habit of olive trees (Archer, 1996; Conner and Fereres, 2005).

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