

# Flower differentiation and fruiting dynamics in olive trees (*Olea europaea*): Eco-physiological analysis in the Mediterranean basin

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All relevant data are within the paper and its Supporting Information files.

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**Abstract:** The formation of flowers in sufficient number and quality is a prerequisite for a successful subsequent fruit set. Despite the abundant flowering, olive trees (*Olea europaea*) are characterized by a very low fruit set, and a very severe yield alteration leading to market fluctuation over time. The goal of this paper is to explore and analyze eco-physiological driving factors behind the poor fruit set in Mediterranean olive groves. The key mechanisms causing floral differentiation and extreme yield alternate are functional of plant genetic variability, nutrient competition, and some ecological aspects as a response to climate change. Additionally, olive inflorescence architecture appears to be complex and can vary between cultivars; the olive flower differentiation results in a variable proportion of hermaphrodite, pistillate and staminate flowers among olive cultivars as well as across canopy positions and branches, enhancing nutrient competition between flowers. Self-pollination could be one of the limiting factors for increasing early fruit abscission and extreme alternate fruit-bearing. Hormonal treatments to reduce alternate production in olive trees should be explored. The current review analysis shall help to improve olive grove management, but also for breeding new cultivars more suitable for Mediterranean agro-ecological constraints. Ovule viability and fertilisation, and embryo sac development abnormalities should all be further investigated.

## 1. Introduction

Olive (*Olea europaea*) farming began thousands of years ago in the Middle East and has since spread to the eastern Mediterranean; Spain and Italy produce more than 60% of the world's olive oil (Terral *et al.*, 2004; Herrera-Caceres *et al.*, 2017). Some olive groves have been converted to alternative land uses, such as grazing, due to significant yearly production fluctuation and significant competition for nutrient supplies, such as water (Loumou and Giourga, 2003). For the Mediterranean region's delicate environment, olive grove protection is becoming a priority. *Olea* species are divided into four genetic groupings. According to traditional classification, three of them had close phylogenetic ties and genotypes

that were similar to wild olive genotypes (Angiolillo *et al.*, 1999; Contento *et al.*, 2002). *Olea* is a genus in the *Oleaceae* family with approximately twenty species that thrive in tropical and subtropical climates throughout five continents. Based on the taxonomic position of the genus *Olea* and of its components, four subgenera (subg.) can be distinguished: subg. *Olea* section *Olea*, subg. *Olea* section *Ligustroides*, subg. *Paniculate* and subg. *Tetrapilus* (Besnard *et al.*, 2002; Green *et al.*, 2004). Based on morphology and geographical distribution, *O. europea* should be divided into six subspecies based on morphology and geographic distribution, including: (1) Subspecies *europea*, which includes the two botanical varieties, which are *europea* (cultivated olive) and *Sylvestris* (wild olive), and is widely distributed throughout the Mediterranean region; (2) *Cuspidate* subspecies, which is found in Southeast Asia, southern China; and the Arabian Peninsula in the east and south (Contento *et al.*, 2002; Rugini, 2016). The *O. europea* L. is a frost-sensitive subtropical evergreen indigenous to the Mediterranean region. It has adapted to a semi-arid temperate climate with well-drained soils, a moderate to low pH (below 8.5), and little salinity in the soil (Terral *et al.*, 2004; Doveri and Baldoni, 2007). The olive tree is notable for its abundant bloom, which is followed by a low fruit set and a low yield. Apart from inflorescence structure, cultivars differ substantially in the proportion of a hermaphrodite (bisexual) to staminate flowers on inflorescences (Guevas and Polito, 2004). About approximately 10% to 15% of a mature tree's flowers set fruit, with only 2% to 5% of them developing mature fruits, depending on the location and type (Reale *et al.*, 2006). Low fruit set and the shift from non-functional hermaphrodite flowers to fully functional staminate flowers seems to be the most important and limiting factors for olive tree productivity. The formation of functional staminate rather than entirely functional hermaphrodite flowers throughout development is one of the primary factors determining the fruit setting level of olive flowers (Reale *et al.*, 2009). Although various studies have been done on the differentiation process of olive flowers, there have been very few specialised investigations to document and compare biological flower development and fruit set research among cultivars in this area. Olive farming has been an important part of Mediterranean nutrition, therapeutic body care, economics, and religious rites for millennia (Angiolillo *et al.*, 1999; Rugini, 2016; FAO, 2020). The olive fruit is eaten and pressed

for its seed oil, which has been shown to have health-promoting properties when consumed regularly and can be stored and consumed for up to three years if stored properly (Besnard and Bervillé, 2000). The oil is used to make soaps, hair conditioners, massage oils, and other therapeutic products. In terms of nutritional value, as well as economic importance to national economies, they are a necessary food. Olive fruits have been demonstrated to aid in the prevention of coronary heart disease and various cancers due to their high level of monosaturated fatty acids and phenolic compounds (Terral *et al.*, 2004). Despite the fact that olives have been cultivated for many years and various cultivars have been domesticated for their fruit quality, morphological and physiological properties, the Mediterranean region's cultivar selection has not fully responded adequately to alternate fruiting and poor terminal fruit sets (Connor *et al.*, 2014).

## 2. Physiological factors driving olive fruit setting

### *Pistil abortion during olive flowering*

The production of functional staminate flowers rather than completely functional hermaphrodites, which are unable to yield fruit, is one of the primary reasons limiting fruit set in olive (*Olea europaea* L.) (Reale *et al.*, 2009; Newton *et al.*, 2014). Despite their extensive history, many key questions surrounding olives remain unanswered. While there are up to 2,600 different olive cultivars (Rugini and Lavee, 1992), many studies on diversity within *O. europea* have focused on morphology and agronomic behavior, with little research on variety within the *Olea* germplasm to yet. Low fruit set is frequent and varies between olive cultivars (Newton *et al.*, 2014). Pollen flow (Guitian, 2006), resource availability (Terral *et al.*, 2004), predation, environmental stress, or genetic stress are all possible causes (Newton *et al.*, 2014). The olive tree has a low ultimate fruit set due to a high rate of undeveloped pistils later leading to its abscission (Chiappetta *et al.*, 2015). The physiological differentiation processes are driven by competition for resources between growing vegetative and reproductive organs (Dixon, 2012; Erel, 2016). According to cytohistological observations of staminate and hermaphrodite flowers, after the megaspore mother cell develops, the pistil development in staminate flowers is halted (Guitian, 2006; Chiappetta *et al.*, 2015). Biochemical studies demon-

trated that starch granules were only discovered in the ovary, pistil, and stigma of hermaphrodite flowers at this time. The pistils of staminate flowers did not contain any substantial amounts of starch (Wiens *et al.*, 1987; Seifi, 2015). The findings reveal a substantial connection between starch content and pistil formation (Chiappetta *et al.*, 2015). The low chlorophyll content of the gynoecium, the absence of Rubisco activity in the pistils of these two flower types, and the ultrastructure of the plastids discovered by transmission electron microscopy research all point to a secondary source of starch within the flower (Reale *et al.*, 2009; Erel, 2016). In olive varieties, the percentage of hermaphrodite to staminate flowers is also significant and varies (Cuevas and Polito, 2004). Fruit success appears to affect the gender of flowers in distal positions along the inflorescence, as seen by the gender pattern of flower buds in inflorescences with varying fruit placements. Other aspects of andromonoecy in *Caesalpinia* species, such as floral sex ability and fruit set impacts, are examined (Terral *et al.*, 2004; Seifi, 2015). Previous research used potency spectral analysis to look for all possible periodic patterns in yield data; and concluded that even with a fairly regular biennial succession, two or more “on” or “off” years can be observed. Staminate flowers are produced by andromonoecious species to boost reproductive success by increasing male function or redirecting resources away from useless pistils and onto fruits (Huang, 2003).

#### Biennial fruit-bearing in olive trees

Alternate fruiting and determining factors are critical in olive trees. Olive crop productivity has changed greatly over the years, due to the problem of alternating fruit-bearing that has been affecting the trade and consumption in the olive producing countries. Many fruit trees, such as olive trees, may not yield the same crop year after year, with mild to significant annual variations (Rallo *et al.*, 1993; Seifi, 2015). In recent decades, the issue of alternating bearing in fruit trees has received a lot of attention, because of the huge swings in production, the alternating bearing is a common phenomenon in many fruit tree species, causing tremendous labor, marketing, and economic instability (Fig. 1). The concept of “alternate” or “biannual” bearing is defined as the production of heavy fruit “in” one year, followed by light or no fruit the next year (Monselise and Goldschmid, 1982). The development of trust worthy metrics to quantify biannual alternation, its severity

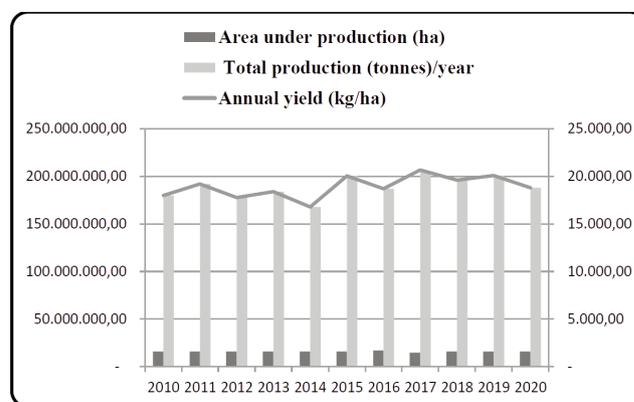


Fig. 1 - Variability of olive world production over 10 years. Adapted from FAOSTAT (FAO, 2020).

(maximum and average deviation from multi-year norms), synchrony at different sites, and other characteristics are clearly of importance. Monselise and Goldschmid (1982) presented two parameters for evaluating fruit production yearly alternation). The first parameter “B” denotes the proportion of biennial, while the second one “I” denotes the amplitude of volatility. Three aspects of olive reproductive biology were investigated by Rallon *et al.* (1993): the biannual cycle, the effect of cultivation on successive reproductive and vegetative processes, and the effect of temperature on bud dormancy are all discussed. Even though appropriate horticultural techniques such as sufficient pruning, thinning, irrigation, etc. are implemented, olive trees will gradually alternate their annual yield. Under good climate circumstances in the whole year, the alternate bearing will be very reduced at a given extent depending on cultivars (Lavee, 2007). A quantitative study relating cultivation to various indices of successive reproductive and vegetative processes revealed that while inhibition of floral induction by developing plentiful fruits is the main factor for biennial bearing, the successive reproductive processes are also important, especially fertilisation stage (Lavee and Avidan, 1993). Rosati *et al.* (2011) also investigated the effect of nutritional conditions on olive biennial fruiting. The researcher concluded that Flowers induction particularly hermaphrodite flowers formation are negatively affected by flowering load (Erel *et al.*, 2016). Furthermore, biochemical studies have been conducted in an attempt to explain the alternate bearing in olive production. The protein content and their composition of “on” and “off” olive trees, especially the protein content in the leaves and bark of one-year-old shoots, have a critical effect on the olive annual produc-

tion (Lavee and Avidan, 1993; Eris *et al.*, 2007), in Koronaiki, Uovo de Piccione, Manzanillo, and Barnea olive cultivars. The overall amount of useable protein in the “off” trees’ leaves was substantially lower than in the “on” plants’ leaves, while the bark revealed an antithetical relationship. The Koronaiki cultivar was the least alternative, presenting the smallest variance in its leaves. In contrast, other cultivars had a comparable percentage of proteins content in their bark. Additionally, Cuevas and Polito (2011) observed that the “off” trees of all cultivars had more crude protein in their bark than the “on” trees of the same cultivars. A 66 crude protein was more expressed in the bark of the “off” trees, rather than “on” years. However, Rosati *et al.* (2011), found that differences in some proteins were smaller in the leaves of “on” and “off” trees (Rosati *et al.*, 2011).

#### *Endo-genetic factors*

The olive crop (*Olea europaea*) is a genetically diverse fruit in horticulture (Kour *et al.*, 2018). Cytosine methylation is an essential epigenetic regulator of transposon silencing, heterochromatin organization, genomic imprinting, and gene expression, according to an investigation of endogenous factors (Zhang *et al.*, 2006). Thus, all flowers in andromonoecious plants are claimed to be bisexually started, despite the presence of spatial patterns within inflorescences and plants (Hamanishi and Campbell, 2011). In addition to the biochemical difference, Cuevas and Polito (2004) confirmed that the dry weight of hermaphrodite flowers was 19% larger than the dry weight of staminate blooms begun at similar places on the panicle. Because there were no significant differences in stamen weight, the author hypothesized that this discrepancy was mostly attributable to pistil and petal weight. Delph (1997), on the other hand, found no significant differences between staminate and hermaphrodite flowers in pollen amount per anther or pollen quality, as evaluated by viability, germination, and ability to fertilize other flowers. Furthermore, no link between gender and anthesis timing was discovered. On the other hand, Sedgley and Griffin (2013), found that the flower’s position inside the panicle was linked to anthesis timing and gender. The Blooms on the tip and major pedicels were hermaphrodite and opened first, whilst flowers on subsidiary pedicels were mostly staminate and achieved anthesis last. In summary, the majority of the findings support the notion that pistil abscission is linked to resource competition among ovaries,

and that genetic differences in pistil abscission between olive cultivars can be explained by changes in pistil mass and sink strength (Zilberman *et al.*, 2007; Song *et al.*, 2014). Additionally, flower bud induction is a long-term process in the olive tree that is controlled by a variety of internal and external stimuli. Marone and Fiorino (2010) conducted experiments to identify the meristems that give birth to various types of shoots, as well as the fundamental mechanisms influencing the evolution of the apical meristem and its lateral buds. Observations led to the discovery of a vertical succession of two types of buds in the same bud complex: the “main” bud and, in the upper position, the “accessory” bud, the former having a reproductive function and the latter specialized in environmental exploitation (vegetative role). They concluded that the generation of new bearing vegetation is confined to the central leader in “mature” shoots, and all branches arising from accessory buds are committed to burst new vegetation. The findings by Fabbri and Benelli (2000) also backed the theory of the two-step induction leading to flower bud differentiation, which appears to begin around the end of fall. On the other hand, the impact of seasonal variations in the phenolic content of olive cultivar’s leaves (*Olea europaea* L) on the cultivar’s alternating bearing have been suggested to be associated to the alternatate bearing too. In 2008 (off year), Mert *et al.* (2013) reported a substantial variations in the amount and distribution of these phenolics in the leaves (on year). Chlorogenic and p-coumaric acids were abundant in the “on” year, but other phenolic compounds were scarce. The chlorogenic and p-coumaric acid levels were low during the “off” year, while the levels of the other phenolic acids were high. In the “on” and “off” years, the Same Authors discovered a negative connection between chlorogenic acid and caffeic acid concentrations: caffeic acid levels were high, while chlorogenic acid levels were low. Comparing the “on” and “off” years, they concluded that the contents of chlorogenic acid, caffeic acid, 3-hydroxycinnamic acid, and p-coumaric acid were considerably different.

#### *Ovary abortion and incomplete embryo development*

The findings back up the theory that pistil abortion is linked to ovaries competing for resources, and they imply that genetic variations in pistil abortion between olive cultivars might be explained by changes in pistil mass and sink strength (Ji *et al.*, 2010; Rosati *et al.*, 2011). In andromonoecious species, pis-

til abortion is thought to be an evolutionary adaptation to save resources by balancing the quantity of pistils with the resources available. As a result, pistil abortion is likely to be higher in large-fruited varieties. Rosati *et al.* (2011) working with olive cultivars with varying ovary/fruit mass discovered that pistil abortion, represented as a percentage of staminate flowers, was positively associated with the average ovary mass at bloom. Furthermore, both ovary mass and pistil abortion were inversely linked with the number of perfect flowers per inflorescence, whereas both factors increased the number of staminate flowers per inflorescence (Famiani *et al.*, 2019) (Fig. 2). Thus, the above researchers, among others, suggested that the leaf-bud ratio, as well as the amount of leaves present for each inflorescence bud, are two factors that influence pistil abortion in olives (Fig. 2). The olive flowers will develop poorly if the number of leaves decreases; and the number of aborted pistils will rise as the number of leaves decreases.

### 3. Ecological factors

#### *Nutrients resources distribution and plant nutrition factors*

A variety of alterations in the activation and inhibition of endogenous metabolic pathways are involved in the manifestation of alternative bearing. Pistillate abortion, known as andromonoecy, which refers to the generation of both perfect (hermaphroditic) and staminate blooms, is thought to be influenced by resource competition (Haberman, 2019).

According to Rallo *et al.* (1993) and Cuevas and Polito (2011), the high variation in the proportion of staminate flowers observed in olive trees, branches, shoots, and even inflorescences within the same shoot, could be part of a general reproductive strategy that adjusts maternal investment in gender expression in response to available resources and environmental conditions. If nutrient shortages cause increased pistillate abundance and staminate flower development, Solomon (1985) and Emms (1993) suggest that the nutrition deficiency could also alter pollen output or pollen quality. If this is the case, staminate flowers would be regarded as a result of nutritional deficiency, and andromonoecy would be regarded as a process of partial flower abortion (Lavee and Avidan, 1993; Cuevas and Polito, 2011). In contrast, if staminate flowers benefit from the resources conserved by pistillate miscarriage, we should expect more pollen grains or higher pollen performance from staminate flowers than from hermaphrodite flowers (Song *et al.*, 2012). Vining *et al.* (2012) and Guevas and Polito (2013) investigated the synthesis and use of carbohydrates linked with regular and alternation fruiting in the olive production cycle. Male flowers are more likely to appear on the less fed secondary pedicels, where fruit set is unlikely to happen; while hermaphrodite flowers are more likely to form on the apex and major pedicel of the inflorescences. However, some studies have found that flower position has no effect; for example, in the 'Mission cultivar', the fate of a certain floral meristem is not mixed, and gender cannot be firmly attributed to a certain inflorescence location (Delph, 1984;

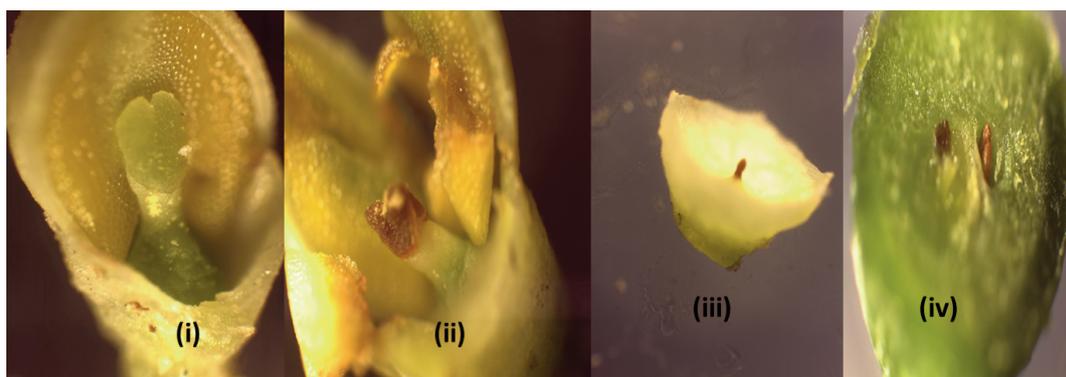


Fig. 2 - Illustration of some olive flowers development biological stage by a Light microscope: A longitudinal view of hermaphrodite flower before anthesis (i), A hermaphrodite flower with a degenerating (ii), an aborted pistil (iii), a transverse view of an ovary expansion with one functional ovule and 3 others degenerating (iv) Electron micrograph of the phytoprotective film of Chi-Pyro-Film, after spraying on a smooth surface at a temperature of 18 to 25°C (a and b). Chitosan strawberry leaf covered with a film formed by Chi-Pyro-Film (c).

Haberman, 2019).

Despite the fact that staminate flowers originate in less desirable locations, the findings showed that the conditions that cause pistil abortion have no effect on their function. In fact, Nitrogen tended to improve blooming intensity but not floral quality; nevertheless, it consistently reduced fruit set. The amount of phosphorus in the soil was linked to the creation of beautiful blooms and fruit set. Potassium supplementation had a minor influence on olive yield (Erel *et al.*, 2013). Pollen grains from staminate flowers, on the other hand, do not profit from the transfer of resources saved by pistil abortion, as Emms (1993) discovered. Because sexual reproduction resources are limited, it is sometimes argued, on theoretical grounds, that an increase in resources given to male function comes at the expense of resources dedicated to female function, and vice versa (Delph, 1984). Furthermore, Guevas and Polito (2003) observed that in hermaphroditic flowers, larger resource allocation to pistils occurs, while stamen dry weight does not rise in staminate flowers in response to reduced pistil allocation. The positive association discovered in hermaphroditic flowers between petal, stamen, and pistil dry weight shows that conditions that favor pistil development also favor resource investment in stamens and petals (Lavee and Avidan, 1993). Plants do not shift resources from the pistil to the stamens in staminate flowers, according to patterns of resource allocation to floral organs in other andromonoecious species (Lavee and Avidan, 1993; Emms, 1993). Reale (2009) showed that nutritional deficits can impact pollen production or pollen quality, in addition to increased pistil abortion and generation of staminate flowers. If this is the case, staminate flowers would be regarded as a result of nutritional deficiency, while andromonoecy would be regarded as a simple process of incomplete floral abscission. Even though, staminate flowers gain from the resources saved by pistillate miscarriage (Song *et al.*, 2012), we should expect more pollen grains or greater pollen performance from staminate flowers compared to hermaphrodite flowers. In this situation, the ailment could be viewed as a precursor to monoeciousness (Vining *et al.*, 2012). During the annual and biennial cycles, there are claimed to be dramatic changes in the carbohydrate components of leaves. Sugars and starches are substantially higher at the start of a bearing year than at the start of a non-bearing year, according to Duyvelshoff (2011),

polysaccharides are extensively hydrolyzed throughout winter. Low temperatures and good flower induction seem to be linked to a high carbohydrate content (Rosati *et al.*, 2006). The influence of seeds on floral induction in growing fruits has also been underlined. Seed-produced auxin has been seen moving from the seed to the fruit spur. In a biennial cultivar (Laxton's Superb), the mobility is larger than in a regular bearing cultivar ('Cox's Orange Pippin') (Zhang, 1993). Long ago, it was suggested that seeds may deprive a key metabolite essential for flower initiation (Duyvelshoff, 2011). The function of nutrition in pistillate abortion in olives revealed that high leaf/flower ratios and nitrogen fertilization increase hermaphroditic flower formation, which is consistent with feminization trends in andromonoecious plants developing under favorable climatic conditions (Solomon, 1985; Rosati *et al.*, 2006). As a result, the wide range of staminate flower proportions observed in olive across years, trees, branches, shoots, and even inflorescences within the same shoot could be part of a general reproductive strategy that adjusts maternal investment in sex expression in response to available resources and environmental conditions (Rosati *et al.*, 2006). The latter stated that high amounts of metabolites or photosynthates may be associated with high hormone levels, which is consistent with prior findings by Durand (1990) and Frankel and Galun (2012), who determined that hormone concentration and sex expression in plants had a close relationship. Female flowers grow near younger leaves, which have high auxin levels, according to the same authors. The favorable effect of phosphorous on female reproductive development was independent of total carbohydrate availability, according to Erel (2016) in his study on the influence of phosphorous nutrient levels on reproductive development. As a result, the researcher hypothesized that Phosphorous nutrition had a favorable influence on productivity measures that was unrelated to carbohydrate reserves or carbohydrate transit to the developing inflorescence. In addition, Fernández (2009) and Reale (2009) discovered that phosphorous nutrient levels were connected to the rate of reproductive bud burst, inflorescence weight, rate of hermaphrodite flowers, pistil weight, fruitlet persistence, fruit set, and the overall number of fruits produced. Pollen viability was consistently high in Phosphorus deficient trees, the authors reported, presumably due to higher carbohydrate availability,

in contrast to female reproductive organs.

#### *Environmental factors*

According to ecophysiology research, the degree of alternance bearing in fruit production is strongly reliant on environmental variables and can vary significantly between growing regions depending on climate (Terral *et al.*, 2004; Fernández, 2015). A research done on the influence of climatic conditions on the ratio of hermaphrodite to male flowers and fruit set, in regular and alternating olive varieties, found out that different inductive circumstances are created by harsh climate conditions. In seasons with a lot of blooms, staminate flowers are plentiful and the number of flowers per inflorescence is fairly low (Erel *et al.*, 2013; Erel *et al.*, 2016). Even among the same cultivar at different locales, the effects of tree age have been studied as debatable and presumably not uniform (Song *et al.*, 2014). The alternation phenomena can be triggered by environmental factors. Because of its self-sustaining features, cyclic activity can last for years after it is started (Emms, 1993). Different tree species, as well as the same tree species cultivated in various climates, may have different relevant conditions. The same tree species can be cultivated in a variety of environments, such as irrigated vs. arid culture, somewhat warm and humid vs. hot and dry summers, overcast vs. bright days, and so on. Conditions that do not trigger in one zone may become triggers in another or for different trees within the same zone (Hamanishi and Campbell, 2011). Monselise and Goldschmid (1982) investigated the impact of plant size and light intensity interactions on sex expression. The percentage of female and hermaphrodite flowers was highest when large plants were exposed to full sunshine. That is, when high light intensity was combined with a big plant size, the percentage of female and hermaphrodite flowers was larger than when each component was used alone (Karapatzak *et al.*, 2012). Furthermore, it was discovered that both high light intensities and plant size increase female flowering. "Plants that are cultivated in full sunlight, with appropriate hydration, and embedded in an appropriate substrate are sturdy and produce female flowers in the majority of cases. Male flowers are produced by less vigorous plants that are frequently planted in the shade or lack enough nutrients (Fernández *et al.*, 2009). When the olive is cultivated in a greenhouse at a minimum temperature of 16°C and a maximum temperature of 27-30°C, flower production is absolutely suppressed, alt-

hough it does occur when cultivated in California during the winter. He also came to the conclusion that morphological alterations in the bud are linked to an increase in blooming, which is regulated by the treatment time (Terral *et al.*, 2004). The classic example of the change in woody plants throughout a large climatic area relates to climatic factors that can trigger the biennial cycle. Spring frosts in deciduous trees, for example, or unusual drought stress during the set in warm locations, are examples of such triggers. Outside of the cycle, however, it is normal for woody plants and trees to swap places with their neighbors. Individual branches could even be out of sync with the rest of the tree (Monselise and Goldschmidt, 1982). To some extent, the effects of temperature on flowering, fruit set, and fruit development have been examined. Due to influences on pollen germination and pollen tube expansion in the fertilization process, high day and night temperatures (300°C/200°C) during the growing season might impair yield potential, resulting in flower death following anthesis (Karapatzak *et al.*, 2012; Haberman, 2019).

#### **4. Conclusions**

Despite the fact that olive farming has been practiced in the Mediterranean agricultural ecosystem since ancient time, the productivity of some olive groves is hampered by the floral divergence leading to the low fruit set. On one hand, the pistil abscission can be viewed as an evolutionary response in the Mediterranean ecology that balances pistil numbers with available resources. On the otherhand, benefit of developing staminate flowers in olive trees can also be seen as adaptative strategy to increase male flowers activity and dispersal efficiency, as well as to boost pollinator attraction. Thus, in olive trees, the transition from hermaphrodite to staminate flowers can be regarded as a strategy to maximize the ability of male flowers by allocating biochemical plant resources to male and female tasks in the most efficient way possible. Pollination fitness and additional resources are provided for the reduced number of pistil growth, if the optimal number of staminate flowers exceeds the number of pistils. However, further research should be done on how to balance the ecological flower adaptability and the olive productivity. Thus, there is a need to adjust the variability of the ratio between hermaphrodite and staminate flowers,

as well as the histological structural study that goes along with it. Hormonal treatments to reduce alternance production in olive trees should be also explored. Ovule viability and fertilisation, as well as embryo sac development during flower differentiation and fruit abscission, should all be further investigated too. Lastly, cross-effect pollination's on fruit value between olive cultivars, as well as the synchronization of flowering and fruit set, in the Mediterranean ecology could be also of great interested to improve olive productivity.

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