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The Role of Male Flowers and Bearing Status on Pollen Germination in Olive (*Olea europaea* L.)

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ABSTRACT

Olive is an andromonoecious plant producing both male and perfect flowers. This study was performed to determine the pollen germination percentage and growth rate of male and perfect flowers of Zard and Roghani cultivars in 2015 at the Tarom olive research station. Three trees from each cultivar (On and Off bearing) were selected. Pollen was collected from male and perfect flowers on the flowering shoots at flower opening stage. These anthers insert the capped glasses. Pollens were incubated in a modified medium that contained 0.8% agar, 10% sucrose, and 100-ppm boric acid. Pollens were spread using a modified medium, separately collected pollens of male and perfect flowers were spread on Petri dishes containing the medium, and then transferred into the incubator for germination at 25°C. After six hours of incubation, the number of germinated pollen grains was enumerated and recorded. The Zard olive cultivar had a higher pollen germination percentage (39.95%) than the Roghani olive cultivar (29.8%). In both cultivars, the male flowers exhibited a pollen germination rate of 48.01%, whereas the perfect flowers demonstrated a lower germination rate of 21.73%. Moreover, the germination rate of perfect flowers was significantly greater in the Zard cultivar (35.2%), in contrast to the Roghani cultivar (20.7%). In both cultivars, the pollen germination rate was 39.48% in the Off-season trees, surpassing the germination rate of 36.38% observed in the On-season trees. Moreover, the Zard cultivar exhibited a significantly higher germination rate of 41.13%, compared to a germination rate of 38.27% found in pollen from the Off-season of the Roghani cultivar. The overall results showed that male flowers of olive trees play an important role in the fertility and fruit set of perfect flowers.

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1. Introduction

Olive (*Olea europaea* L., 2n=2x=46) belongs to the family *Oleaceae*, and is one of the most important fruit crops. Olives are cultivated in many world regions with Mediterranean zone climates (Palomo-Ríos *et al.*, 2021). Olive cultivated area in Iran is around 74 thousand hectares and production is 236 thousand tons. Many native olive cultivars in Iran are cultivated in the olive-growing areas of the country. The most important of these cultivars are Zard and Roghani (Noormohammadi *et al.*, 2007). The Zard cultivar is the most of them, which is cultivated in different regions of the country. This cultivar is dual-purpose and has a higher oil quality. The Roghani is an oil cultivar and is cultivated as a pollinizer alongside Zard (Zeinanloo *et al.*, 2015). Olive cultivars can have andromonoecious inflorescences, which contain both perfect flowers and male flowers. The male flowers may result in aborted pistils, all occurring on the same tree. In the olive trees, the perfect flower includes a small, greenish calyx, four white petals, two stamens with large anthers and one single pistil with a bilobate stigma, a short style and a biloculate ovary with four ovules (Dölek Gencer *et al.*, 2023a).

Each adult olive tree produces around 500 thousand flowers, and in a year where flowering occurs

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normally, a commercial yield can be achieved with 1-2% of fruit set (Rosati *et al*., 2010). In olive trees, self-pollination can be seen in a limited number of cultivars. Cross-pollination improves fruit set and yield compared with self-pollination not only in olives but also in many horticultural crops (Herbert *et al*., 2019). Olive trees usually prioritize the formation of perfect flowers. When there are enough nutritional resources, flowers are the perfect choice. Male flowers appear more frequently in conditions of environmental stress, limited nutritional resources, or after the differentiation of perfect flowers (Dai and Galloway, 2012; Paterno *et al*., 2020; Gao *et al*., 2021).

In andromonoecious plants, there have been several hypotheses proposed about the evolution and maintenance of male flowers in a hermaphroditic system. The hypothesis of resource reallocation is the first one. The consumption of male flowers is lower than perfect flowers, and the resources saved by producing male flowers can be redirected towards producing more perfect flowers (Gao *et al*., 2021; Shwe *et al*., 2020). A higher leaf/flower ratio and nitrogen fertilizer, as demonstrated by other researchers (Lyu *et al*., 2023) promotes perfect flower production. The differentiation of male flowers in olive has been demonstrated to be influenced by the growing conditions, including moisture availability, nutrients, and low assimilation status (Reale *et al*., 2009). An increase in pistil abortion and the formation of male flowers can be caused by nutritional deficiencies, which may affect pollen production or quality (Rosati *et al*., 2011; Jianhua *et al*., 2024). In this case, the formation of male flowers could be the result of the nutritional deficit. If male flowers have been able to take advantage of the nutrition resources stored in the plant after the female abortion, it is anticipated that there will be more pollen grains or a higher yield of pollen grains compared to perfect flowers (Cuevas, 2024; Dai and Galloway, 2012). This hypothesis is true for several taxa, in which male flowers are smaller or lighter than perfect flowers (Dai and Galloway, 2012; Niu *et al*., 2017; Zhang and Tan, 2009). The pollinizer attraction hypothesis is the second one. Male flowers can increase fruit set in perfect flowers blooming at the same time as male flowers, which could increase pollinator visits without removing pollen from pollinators (Calviño *et al*., 2014). Aksoy and Dalkılıç (2019) believed perfect flowers formed fruit, and staminate flowers acted as pollen sources for requisite pollination. The objective of this study was to determine the possession of male flower pollen germination against perfect flowers for Zard and Roghani cultivars.

2. Materials and methods

2.1. Plant material

This experiment was carried out at Tarom Olive Research Station, Zanjan, Iran in 2015. The station's latitude and longitude were 49° 05′ east and 36° 47′ north, respectively, and the altitude of the station was 350 m above sea level. This evaluation was carried out in 2015 to determine of pollen tube growth rate and pollen quality of Zard and Roghani cultivars in male and perfect flowers on the On and Off trees. Moreover, the number of flowers per inflorescence and the percentage of perfect flowers of these cultivars were recorded. Three trees of uniform size and age were selected for each cultivar, three in the On-year and three in the Off-year. The olive trees were planted in 8×8 m spacing and irrigated with a drip irrigation system while being subjected to the same horticultural practices.

The central inflorescences of the Zard and Roghani cultivars were harvested when the flowers opened. The number of flowers per inflorescence in each cultivar was recorded, and then the percentage of perfect flowers for each cultivar was calculated. To estimate pollen germination in each cultivar, covered jars were used to collect the anthers. For this purpose, anthers of male and perfect flowers of each cultivar were separately collected and kept in a refrigerator at 4°C until the pollen was cultured. After the pollen collection was complete, the modified germination culture medium (Pinney and Polito, 1990) was prepared, which included 0.8% agar, 10% sucrose, and 100 ppm boric acid. A soft brush was used to gently place the pollens onto the Petri dishes that contained the culture medium. The Petri dishes were moved to an incubator at 25°C for germination (Azimi *et al*., 2008). Data recording and enumeration were carried out after six hours of incubation.

2.2. Statistical analysis

To analyze the number of flowers per inflorescence and percent perfect flower of Zard and Roghani cultivars a complete randomized block design (RBCD) was used with three replications. The estimate of pollen germination was analyzed by a factorial experiment based on a completely randomized design (CRD) with three replications. Factors included cultivars (Zard and Roghani), bearing status (On and Off trees) and flower type (male or perfect flowers). Data was analyzed using SAS 9 (Copyright 2002 by SAS Institute Inc.) software.

3. Results and discussion

The number of flowers in the inflorescence and the percent of perfect flowers had a significant difference at (P<0.001) between the Roghani and Zard olive cultivars. The number of flowers in inflorescence of the Roghani and Zard cultivars was 21.8 and 15.2 (Fig. 1), respectively. Furthermore, the percentage of perfect flowers was higher in the Zard cultivar (35.2%) compared to the Roghani cultivar (20.7%).

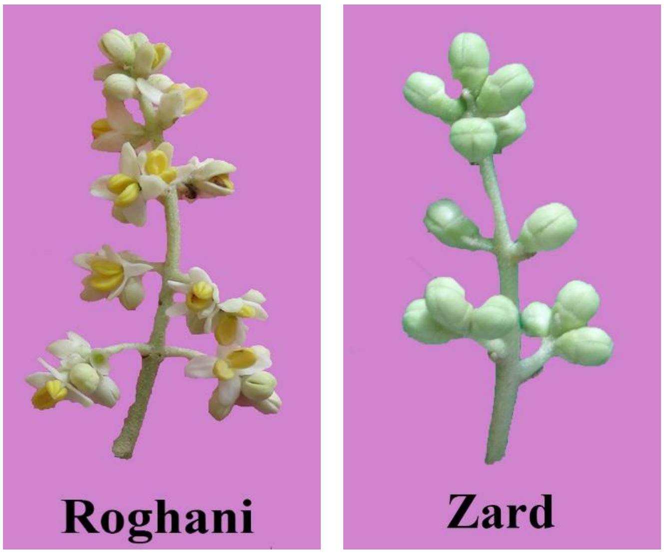

Figure 1. Inflorescence of Roghani and Zard olive cultivars.

Analysis of variance revealed significant differences (p<0.001) among cultivars, bearing status, flower type, and the interactions between cultivar-flower type and bearing status-flower type. The interaction between cultivar-bearing statuses showed a significant difference (p<0.05) between the Roghani and Zard olive cultivars (Table 1). The pollens of the Zard cultivar, which exhibited a germination rate of 39.95%, were superior to those of the Roghani cultivar, which achieved a germination rate of 29.8% (Fig. 2).The off-tress pollens had a germination rate of 39.48 percent, which was superior to the on-tree cultivar, which had a germination rate of 36.38 percent (Fig. 3).

Table 1. Variance analysis of pollen germination percentage of Zard and Roghani cultivars.

Source of variation	df	MS Pollen germination percent
Replication	2	1.552
Cultivar (a)	1	141.62***
Bearing status (b)	1	117.48***
a × b	1	14.57*
Flower type (c)	1	4617.60***
a × c	1	119.26***
b × c	1	75.26***
a × b × c	1	0.12ns
Error	1	1.167
CV (%)		2.84

ns, *, ** and ***: non-significant and significant at 5, 1 and 0.01 percent, respectively.

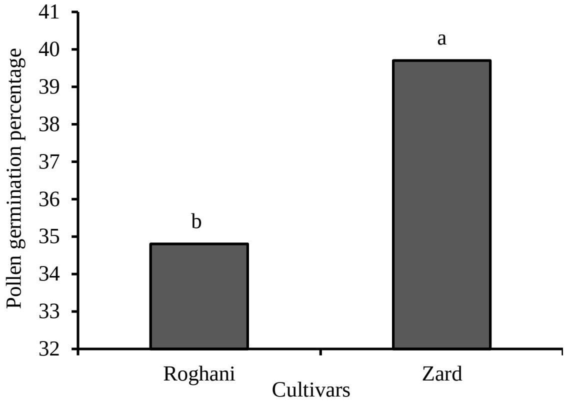

Figure 2. Pollen germination percentage of Zard and Roghani cultivars.

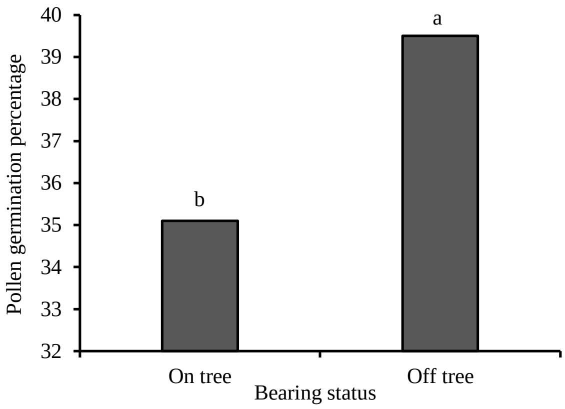

Figure 3. Pollen germination percentage of On and Off trees of both cultivars.

Pollen germination rates differed between flower types within both cultivars. Male flowers had a higher pollen germination percentage than perfect flowers. Specifically, male flowers in both cultivars had a pollen germination rate of 48.01%, while perfect flowers had a rate of 21.73% (Fig. 4). Pollen collected from the off-trees of the Zard cultivar exhibited a notably higher germination rate of 41.13% in contrast to the 38.27% germination rate in the Off-trees pollen of the Roghani cultivar. Importantly, no significant difference was detected in the pollen germination percentages between the Roghani off trees and the Zard on trees. However, germination of On-trees Roghani pollen was lower than Zard cultivar (Fig. 5).

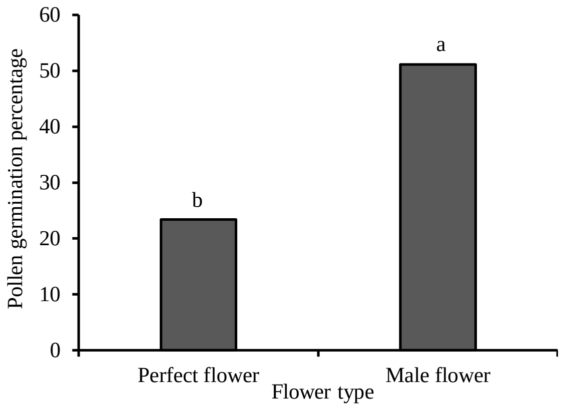

Figure 4. Pollen germination percentage of male and perfect flowers of both cultivars.

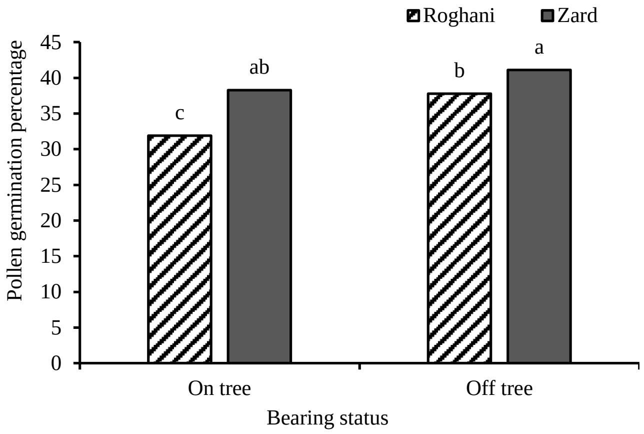

Figure 5. Interaction effects of cultivar and bearing status on pollen germination percentage.

It was observed that pollen from Zard male flowers exhibited a significantly higher germination rate of 56%. In contrast, the male flowers of the Roghani cultivar demonstrated a lower germination percentage of 41%. Although no significant differences were noted in the germination rates of pollen from perfect flowers across the two cultivars, the pollen germination from Zard perfect flowers was found to be higher than that of the Roghani cultivar (Fig. 6). The interaction between tree-bearing status (On or Off) and flower type (male or perfect) revealed that pollen from the male flowers of trees with no fruit (Off) had significantly higher germination rates. However, there was no significant difference in pollen germination rates between perfect flowers of trees with or without fruit (Fig. 7).

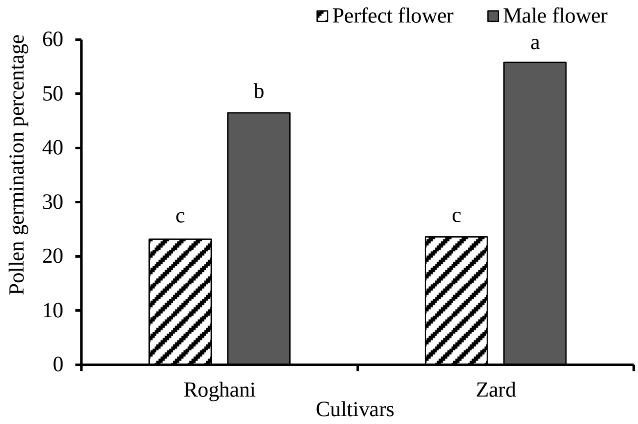

Figure 6. Interaction effects of cultivar and flower type on pollen germination percentage.

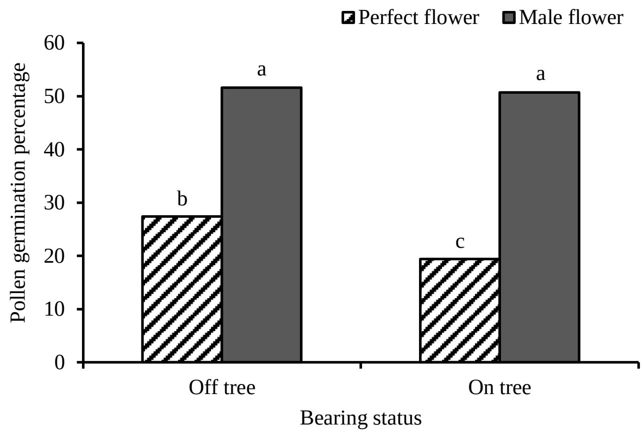

Figure 7. Interaction effects of bearing status and flower type on pollen germination percentage.

An analysis of the tripartite interaction effects among cultivars, bearing status, and flower types revealed that the pollen germination percentage of male flowers from off trees of the Zard cultivar was significantly higher than that observed in other treatments. Furthermore, the pollen germination of male flowers from on trees of the Zard cultivar exhibited a similar rate to that of male flowers from off trees of the Roghani cultivar. Conversely, the lowest pollen germination rates were documented in the perfect flowers of both on and off-trees for both cultivars (Table 2).

Table 2. Interaction effects of cultivar, bearing, and flower type on pollen germination percentage.

Character	Roghani	Zard
Off tree- Perfect flower	18.4^{d}	20.5^{d}
Off tree- Male flower	45.3^{b}	56.1^{a}
On tree- Perfect flower	28.0^{c}	26.70^{c}
On tree- Male flower	47.6^{b}	55.5^{a}

Means with the same letter are not significantly different at (p<0.01).

The findings of this study indicated that the Zard olive cultivar exhibited a higher percentage of pollen germination compared to the Roghani cultivar (Fig. 2). Numerous studies have demonstrated considerable variability in pollen germination percentages among different olive cultivars (Azimi *et al.*, 2018; Vuletin Selak *et al.*, 2013). Moreover, Hechmi et al. (2015) demonstrated that pollen germination for four olive cultivars ranged from 24.8% to 59.3%. Koubouris et al. (2012) reported that the pollen germination percentages for three olive cultivars—Koroneiki, Kalamata, and Mastoidis—ranged from 52.2% to 63.4%. Additionally, the viability of the pollen for these cultivars was observed to be between 74.9% and 80.7%.

Quality, source, and amount of pollen play an important role in increasing the yield of olive orchards (Mazzeo *et al.*, 2014; Vuletin Selak *et al.*, 2013). Pollen quality, germination, viability, and flowering and fruiting periods have been linked by various studies (Riella *et al.*, 2022; Mazzeo *et al.*, 2014). Significant differences were observed in the pollen germination ability of different olive cultivars (Azimi *et al.*, 2018; Şenbaş *et al.*, 2022; Dölek Gencer *et al.*, 2023b). The pollen germination of male flowers in off-trees was higher than that of perfect flowers (Fig. 3). The quality of olive flowers (male and perfect) in trees of Off-year was higher than that of On-year trees (Cuevas, 2024; Mazzeo *et al.*, 2014). Pollen germination percentage, growth rate and pollen tube length of male flowers in Barbados nut (*Jatropha curcas*) were higher than perfect flowers (Abdelgadir *et al.*, 2012). In andromonocious plants, due to the presence of a sexual system with two different forms (male and perfect flowers), the reproduction of perfect flowers is increased with the pollen of male flowers (Calviño *et al.*, 2014).

Olive is an andromonoecious species that produces both male and perfect flowers on the same tree. The rates of pollen germination exhibited variability among different flower types within each cultivar. Notably, male flowers demonstrated a higher percentage of pollen germination compared to perfect flowers (Fig. 4 and 6). The primary function of male flowers in olive is to provide pollen for pollination. A plant can affect pollen supply by affecting the phenology of male flowers or by increasing the total number of pollen grains (Cuevas, 2024). The viability and germination rate of olive pollen grains depends on the genotype of olive cultivars (Azimi *et al.*, 2018; Dölek Gencer *et al.*, 2023b; Vuletin Selak *et al.*, 2012). In most instances, the prevalence of male flowers surpasses that of female flowers in pomegranate plants (Ikram *et al.*, 2023). The quantity and quality of male flowers are crucial for sufficient pollination and fruit set due to these reasons (Aksoy and Dalkılıç, 2019). Koubouris et al. (2012) observed difference in the amount, size, or germination of olive pollens. Moreover, Dai and Galloway (2012) showed that not only the amount of pollen grain production in Maypop (*Passiflora incarnata*) is higher than that of perfect flowers, but also in natural conditions, the seed production by male flowers pollens is two times more than that of perfect flowers. According to Abdelgadir et al. (2012), Pollen derived from the hermaphroditic flowers of *Jatropha curcas* exhibited reduced viability, decreased germination rates, and shorter pollen tubes that also presented abnormal morphological characteristics, in contrast to the pollen sourced from male flowers. Moreover, hermaphrodite flowers have a lower pollen viability.

The presence of male flowers in olive trees demonstrates which flowers were exclusively used for pollen production. Each olive flower, regardless of its type, produces pollen grains. It is estimated that a single olive flower can produce up to 200,000 pollen grains, which are well-suited for wind pollination. Additionally, the most anomalous flowers observed in olive cultivars are associated with the ovary. Moreover, ovarian abortion may occur due to factors such as the absence of the ovary, its underdevelopment, morphological abnormalities, or ovarian instability. Consequently, it has been proposed that the formation of male flowers in olive trees incurs lower energetic costs compared to the development of perfect flowers. Hence, the resources conserved through the production of male flowers may be reallocated to enhance the development of perfect flowers, in accordance with the resource reallocation hypothesis (Kamath *et al.*, 2017). This hypothesis is supported by observations in certain species, where male flowers exhibit smaller and more slender characteristics compared to perfect flowers. Notable examples include Caper (*Capparis spinosa*) as reported by Zhang and Tan (2009), Maypop (*Passiflora incarnata*) studied by Dai and Galloway (2012), and Olives (*Olea europaea*) investigated by Cuevas (2024). The functionality of male flowers in olive trees could be optimized to increase compatibility among varieties (Cuevas, 2024).

4. Conclusion

Significant differences were observed between the Roghani and Zard olive cultivars in terms of the number of flowers per inflorescence and the percentage of perfect flowers. The Roghani cultivar had more flowers per inflorescence than the Zard cultivar, but the Zard cultivar had a higher percentage of perfect flowers. Pollen germination rates were superior in the Zard cultivar compared to the Roghani cultivar. Additionally, male flowers in both cultivars exhibited higher pollen germination rates than perfect flowers. Ultimately, the fertilization of perfect flowers and subsequent fruit set in olive trees are strongly influenced by the presence and function of male flowers.

Conflict of interests

All authors declare no conflict of interest.

Ethics approval and consent to participate

No humans or animals were used in the present research. The authors have adhered to ethical standards, including avoiding plagiarism, data fabrication, and double publication.

Consent for publications

All authors read and approved the final manuscript for publication.

Availability of data and material

All the data are embedded in the manuscript.

Authors' contributions

All authors had an equal role in study design, work, statistical analysis and manuscript writing.

Informed consent

The authors declare not to use any patients in this research.

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