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Full Length Research Paper

Flowering in the wild olive (*Olea europaea* L.) tree (oleaster): Phenology, flower abnormalities and fruit set traits for breeding the olive

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Although, the olive trees produce hermaphrodite flowers, abnormal flowers (flowers with absence or reduced stamens and flowers with absence of pistil) are frequently observed and may reduce fruit set. This study investigates the phenology evolution and the male and female abortion of the oleaster tree (or the wild olive tree) flowers (*Olea europaea* L. *subsp. europaea* var. *sylvestris*) from natural ecosystems represented in two Tunisian Parks. The female abortion was evaluated by the percentage of flowers lacking pistil, and male abortion by differential staining for the cytoplasm of pollen grain. Flower abortion was examined and compared for eight oleaster trees in two different natural sites. At the beginning of flowering (the last two weeks of April), the flower numbers ranged from 15 to 26 flowers per inflorescence. However, one month after blossoming, the fruit set ranged from 1 to 3 drupes per inflorescence. Thus, a significant decrease of flowers per inflorescence was observed on all trees. The percentage of flowers without stamens and flowers without pistil per inflorescence ranged from 5.7 to 38.8% and from 4.9 to 88.1%, respectively depending on the oleaster tree. Moreover, abnormal flowers had effect on fruits number per inflorescence. Indeed, the r^2 linear regression values were 0.89 and 0.83, respectively. Therefore, due to the similar flower abnormalities occurring for the olive trees, the transfer of a low rate of abnormal flowers to cultivated olive may improve the crop.

Key words: *Olea europaea*, oleaster, wild olive trees, stamen abortion, flower without pistil, pollen grain, natural site, drupe abscission.

INTRODUCTION

The olive tree is one of the oldest cultivated tree crop providing two products, oil and table olives. In the Mediterranean region, the olive is the most important crop producing oil. The latter has traditionally been used for pharmaceutical, industrial and consumption purposes. Olive tree (*Olea europaea* L.) includes the cultivated (var. *europaea*) and the wild olive trees or oleaster (var. *sylvestris*) (Green and Wickens, 1989). In Tunisia, the olive trees occupy the third of arable area (DGPA/ONH, 1996). Several reports have pointed out that the oleaster trees were native to Tunisia (Camps-Fabrer, 1997). The molecular diversity revealed that a few cultivars have been issued from the Tunisian oleaster trees based on assignation and admixture analyses (Breton et al., 2006). Using nuclear and chloroplast simple sequence repeat (SSR) markers, it has been reported that the oleaster trees were genuine in Tunisia (Hannachi et al., 2010). The oleaster trees are important in natural flora due to their natural ability to provide shelter for diverse birds and wild plants in harsh environment. Some olive cultivars have been grafted on wild olive trees to support harsh environmental conditions.

Genetic improvement of olive cultivars is based on genetic resources from oleaster and the olive (Hannachi et al., 2008, 2010). Therefore, oleaster trees constitute interesting genetic resources to be taken into consideration and explored. Furthermore, their genetic analysis is a key for understanding some phenomena. The genetic improvement of the olive tree is promoted by crossing cultivars to create new combination of traits.

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Several crosses were made in Tunisia since 1995 to improve oil composition (low content of saturated fatty acids and high oleic acid content), oil yield, disease resistance and organoleptic traits of the final products (Msallem, 2002; Bellini et al., 2008). The knowledge of the extent and the type of genetic variability available and exploitable is essential to a correct layout of breeding programs. The oleaster trees thrive in Tunisia in natural- and agro-ecosystems (Hannachi et al., 2008, 2010). These trees survive well in hard environment conditions without any cultural practices. An adaptation to harsh climates combined with an ability to develop and produce fruits has allowed the exploitation of a wide variety of ecological niches in oleaster trees. Selections from wild populations have been also used to explore the genetic variability of this species (Sedgley, 2004). The oleaster tree is an important genetic resource deserving to be known through, on the one hand, its genetic characte-rization and on the other hand, its technological potentialities. In this regard, the flowering phenomenon constitutes a first step of study.

To improve the olive trees, it is necessary to understand the flowering function in both cultivated and oleaster trees. The ‘perfect’ olive flower is hermaphrodite. The self-pollination may occur, but olive cultivars are mainly self-incompatible. Three modes of abortion were identified in cultivated olive trees: Male sterility (absence of stamens or no functional stamens), female abortion (absence of pistil) and self-incompatibility. Plants can show both male and female abortion as many other processes that failed during microsporogenesis as pollen abortion (Besnard et al., 2000) and megasporogenesis and are under genetic control (Chaudhury, 1993). However, the flowering phenomenon and fertilization are still barely known in oleaster trees.

The objectives of this work were: i) to follow the evolution of flowers number per inflorescence in oleaster trees in two different geographical sites from Tunisia; ii) to determine the proportion of flowers with stamen and pistil abortion per inflorescence and iii) to evaluate the correlation between flower abortion and fruits production per inflorescence.

MATERIALS AND METHODS

Oleaster trees growing in a natural ecosystem represented by two Tunisian Parks: ‘Ichkeul’ and ‘Belvédère’ in the west (altitude 130 m, latitude 37°17′ and longitude 9°67′) and in the east (altitude 66 m, latitude 40°87′ and longitude 8°71′), respectively were used for this study. The oleaster trees were in natural association with *Pistacia lentiscus* L. and isolated from all cultural practices. Four trees were chosen for the reason that they blossom in each locality when most oleaster trees do not blossom in natural conditions.

Flowers number per inflorescence

The phenology study begins with regular observations from January (vegetative development) until May (fruit formation) (Breton et al., 2009). The flowers number per inflorescence was counted every ten days; first sampling began when floral buds had a green colour (March: Initial time Ti) to fruit formation stages (May, Final time Tf) (Table 1). Four terminal twigs were examined for each tree. To count the flower numbers per inflorescence (when floral buds had a green colour) in each tree, one hundred inflorescences were used from each four twig (400 inflorescences per tree).

Stamen and pistil abortion

One hundred inflorescences were collected from each four twig (400 inflorescences per tree) just before anthesis. They were fixed in FPA 50 (90% ethanol at 50%, 5% propionic acid and 5% formaldehyde). The aborted flowers (flower without pistil) per inflorescence were determined by observation under magnifying glass (X 16).

Pollen grains were released from stamens of 30 inflorescences per twig (120 inflorescences per tree) and were immediately immersed in a solution of Alexander (1969): 10 ml ethanol, 1 ml malachite green (1% in ethanol 95°C), 50 ml distilled water, 25 ml glycerol, 5 ml fuchsin acid (1% in the water), 0.5 ml orange G (1% in the water), 2 ml glacial acetic acid, 5 g phenol, 5 g hydrated chloral. Pollen grains were punt between lame and lamella surrounded by small strip for microscopy observation (X 60). Three preparations were observed for each twig. One hundred pollen grains per observation were counted to determine the viable and aborted pollen grain numbers (1200 pollen grains per tree). The viable pollen grains were red-purple whereas the dead ones were green. For each tree, we evaluated the following parameters:

1) Initial number of flowers per inflorescence (INF), when floral buds had a green colour (March: Initial Time Ti)
2) Mean number of flowers (MNF) per inflorescence throughout studied period, from March to May
3) Percentage of flowers lacking pistil (FLP) = (Flowers lacking pistil / Total number of flowers) × 100
4) Percentage of male abortion (PMA) = (Dead pollen / 1200) × 100
5) Final fruits number (FFN) per inflorescence at Tf (Tf: fruit set determined at end of May)
6) Fruit formation parentage per inflorescence (FFP) = (INF / FFN) × 100

Statistical analysis

All results were presented as means ± standard deviation (SD). Each parameter was compared to the mean of all samples by computing the confidence interval. Analysis of variance (ANOVA) was used on all parameters, followed by the Duncan’s multiple range tests using the software Statistica (StaSoft Inc. Johannesburg, ZA). Linear regression was made between male or female abortion and fruits set to look for the effect of sterilities on the fruit production based on the r^2 values.

RESULTS

Number of flowers per inflorescence

The flowers’ number per inflorescence was determined on each oleaster tree at Ti (1st March, when floral buds had a green colour) and Tf (May, fruit formation). At Ti, the mean flowers number per inflorescence ranged from 16.73 (OI1) to 26.37 (OI4) in the oleaster trees from the Ichkeul Park. It ranged from 12.58 (OB4) to 16.78 (OB1)

Table 1. Different flowering stages with their corresponding sampling dates.

Date	Flowering stage
March 1st at Ti	Bud had green colour
March 10 - March 20	Bud had green colour
March 30 - April 10	Bud had white colour
April 10 - April 20	Beginning of flowering
April 30	Flowering
May 10 at Tf	Fruit formation

Table 2. Number of flowers (INF) and of drupes initiated (FFN) per inflorescence at Ti and Tf, respectively, pollen and flower abortion rate (%) from oleaster trees,

Parameter	Initial number of flowers Ti (INF)	Final fruits number per inflorescence at Tf (FFN)	Percentage of male abortion (PMA)	Percentage of flower lacking pistil (FLP)
OI1	16.73 ± 1.23^{b}	3.11 ± 0.95^{b}	35.90 ± 3.90^{f}	4.91 ± 1.09^{b}
OI2	16.77 ± 0.53^{b}	1.80 ± 0.6^{ab}	18.10 ± 2.90^{c}	14.35 ± 1.65^{c}
OI3	24.11 ± 1.22^{c}	1.70 ± 0.66^{ab}	28.87 ± 2.13^{e}	30.75 ± 1.25^{d}
OI4	26.37 ± 0.55^{c}	3.00 ± 1.00^{ab}	5.66 ± 1.34^{a}	1.49 ± 0.51^{a}
OB1	16.78 ± 1.78^{b}	2.70 ± 0.60^{ab}	15.23 ± 1.23^{c}	30.43 ± 2.43^{d}
OB2	14.90 ± 1.90^{ab}	1.41 ± 0.29^{a}	38.83 ± 1.83^{f}	88.12 ± 1.12^{f}
OB3	13.61 ± 1.61^{ab}	1.46 ± 0.26^{a}	10.22 ± 2.22^{b}	36.38 ± 1.38^{e}
OB4	12.58 ± 1.45^{a}	1.15 ± 0.17^{a}	23.69 ± 1.69^{d}	12.56 ± 1.56^{c}
Mean OI	20.98 ± 0.88^{A}	2.40 ± 0.66^{A}	22.13 ± 2.57^{A}	12.87 ± 1.12^{A}
Mean OB	14.47 ± 1.68^{B}	1.68 ± 0.33^{B}	21.99 ± 1.74^{B}	41.87 ± 1.62^{B}

OI: Oleaster trees from Ichkeul Park; OB: Oleaster trees from Belvédère Park; Ti: 1st March when bud had green colour; Tf: Time of drupe formation, May. Each value presents mean ± standard deviation (SD). Superscript small letters with different letters in the same column indicate significant difference between all Oleaster trees ($P < 0.05$). Superscript capital letters with different letters in the same column indicate significant difference between oleaster trees from both stations ($P < 0.05$) analyzed by Duncan's multiple range test.

in oleaster trees from the Belvédère Park. The average numbers were 20.98 and 14.47 in Ichkeul and Belvédère Parks, respectively (Table 2). ANOVA1 applied within oleasters from Ichkeul Park showed significant differences ($p < 0.05$) only of two parameters: The INF (Initial Number of Flowers at Ti) and FFN (Final Number of Fruits). ANOVA2 applied within oleaster trees from Belvédère Park showed a significant difference ($P < 0.05$) of only the Final Number of Fruit (FFN). ANOVA3 applied on all oleasters from both Parks showed significant differences of all studied parameters (Table 3). Besides, two flower types were observed: i) The perfect flower is evidenced by its large pistil which is light green when immature and deep green when opened at full bloom :ii) The staminate flower is characterized by tiny pistils or aborted, barely rising above the floral tube base (corolla base); and small brown, greenish-white or white style.

Number of fruits per inflorescence

At Tf (fruit formation), the mean fruits number per inflorescence ranged from 1.70 (OI3) to 3.11 (OI1) and from 1.15 (OB4) to 2.70 (OB1) according to the oleaster trees from Ichkeul and Belvédère parks, respectively (Table 2). Significant difference was observed between oleaster trees from both stations (Table 3). Furthermore, the evolution of flowers number per inflorescence is illustrated on Figure 1a and b. Three main phases can be distinguished for both parks:

Phase 1: From 1st to 25 March, the number of flowers decreased moderately.
Phase 2: From 25th March to 5th April, the number of flowers decreased remarkably
Phase 3: After 5th of April, the number of flowers decreased moderately till it became constant after two months.

This evolution was probably correlated with climate conditions (Figure 1c and d). At the beginning of observation at Ti (1st March, when floral buds had a green colour), the daily temperatures maxima and minima were 19.32 and 7.83°C (Ichkeul), 20.60 and 9.99°C (Belvédère). The wind speeds were 20.70 and 22.96 km/h in both Parks, respectively. Theses climatic conditions could influence the initial number of flowers at Ti. The decrease in number of flowers may be related with increase of daily

Table 3. Analyse of variance within oleaster trees from Ichkeul Park (ANOVA1), within oleaster trees from Belvédère Park (ANOVA2) and within all oleaster trees (ANOVA3).

Parameter	Source of variation				F-Statistic	*P* value
	Model SS	Model MS	Error SS	Error MS		
ANOVA1 within oleaster trees from Ichkeul Park						
INF	118.25	39.42	14.67	1.83	21.50**	0.00035
FFN	23463.00	7821.00	8.00	1.00	7821.00**	3.32^{E}-14
PMA	74.92	24.97	18193.33	2274.17	0.01*	1.00
FLP	210.67	70.22	22208.00	2776.00	0.03*	0.99
ANOVA2 within oleaster trees from Belvédère Park						
INF	2690.92	896.97	16280.00	2035.00	0.44*	0.73
FFN	135.00	45.00	8.00	1.00	45.00**	2.36^{E}-05
PMA	177.58	59.19	19265.33	2408.17	0.02*	0.99
FLP	962.25	320.75	13306.67	1663.33	0.19*	0.90
ANOVA3 within all oleaster trees from both two Park						
INF	34804.96	4972.14	504.00	31.50	157.84**	0.0080
FFN	30394.29	4342.04	48.67	3.04	1427.52**	3.77^{E}-21
PMA	40374.00	576.71	224.00	14.00	41.19**	1.00^{E}-17
FLP	42362.96	6051.85	426.67	26.66	227.01**	0.00099

***: F-Statistic (> F theory at 5% = 3.7257): significant difference at $p < 0.05$; *: no significant difference. SS: Sum of squares; MS: Mean square.

maxima and minima temperatures and wind speed and with decrease of daily precipitation.

Male and female abortion

The percentage of pollen abortion (PMA) ranged from 5.66 (OI4) to 35.90% (OI1) with an average of 22.13% for the oleasters from Ichkeul Park, and from 10.22 (OB3) to 38.83% (OB2) with an average of 21.99% for the oleasters from Belvédère Park (Table 2). Moreover, the female abortion varied from 1.49 (OI4) to 30.75% (OI3) and from 12.56 to 88.12% (OB2) for the trees from Ichkeul and Belvédère Parks, respectively (Table 2).

The linear regression between male or female abortion, and the fruits set of oleaster trees are shown in Figure 2a and b, respectively. Both male and female abortion had an effect on fruit set. The regression coefficient r^2 values were 0.892 (male abortion and fruits set) and 0.826 (female abortion and fruits set).

DISCUSSION

The initial number of flowers cannot evolve to fruits after pollination and fertilization, a decrease of fruits number was observed at Tf (fruit formation). The drastic decrease in flowers number and the reduced final set reveals an important abscission phenomenon which may have several causes such as flower, nutrition and competition between fruits. The decrease of the flower number would be correlated with climatic conditions such as the temperature, the wind and precipitation (Bardely and Griggs, 1963; Cuevas et al., 1994). Olive trees bear their fruits on the subsequent shoot growth and bloom seasons. Flowers bloom in inflorescence containing hermaphrodite (perfect) and male (staminate) flowers. The extent of pistil abortion depends on genotype (Brooks, 1948) and largely on nutritional conditions (Uriu, 1959). Some authors suggested that the flowers types (staminate and perfect) were related to a genetic effect (Lavee, 1985; Cuevas et al., 2001). The fruit set results from the interaction between the olive tree physiology and the environment. The major factor in reducing fruit set may not be due to pistil abortion only, but also to the intense competition among the remaining perfect flowers on an inflorescence.

The abscission of flowers is also responsible for the small percentage of fruit retained at maturity in cultivated olive trees (Fernandez-Escober, 1993). Abscission of flowers in which the pistils are unable to reach a certain size, suggests that competition for nutriment supplied among developing fruits and other active growing organs, is the cause (Fernandez-Escober, 1993; Cuevas et al., 1994). It has been reported that in a year with normal flowering, 1 to 2% final fruit set will result in a high commercial olive yield (Lavee, 1985). Similarly, we noted that in the absence of cultural practices, the oleaster trees were able to produce drupes (1.15 to 3.11 fruits per inflorescence). Therefore, these trees would be valuable genetic resources. It has been suggested that flowers

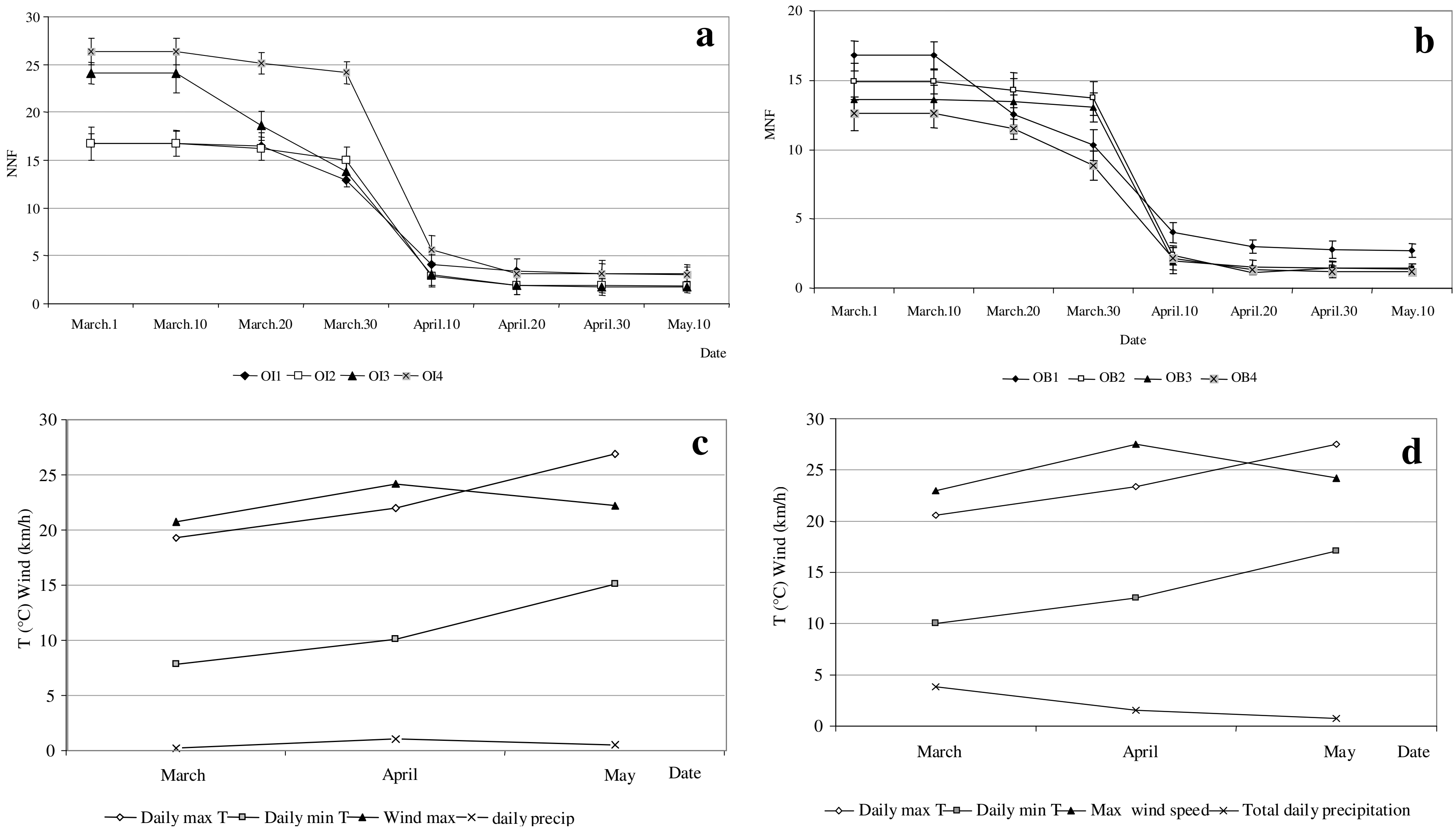

Figure 1. Evolution of number of flowers per inflorescence (NMF) of oleaster trees (a) from Ichkeul and (b) from Belvédère Parks.

lacking stamens may reduce pollen quantity and also reduce fruit set in the olive cultivar ‘Mission’ (Cuevas and Polito, 2004). The partial viability of pollen is common in olive trees. For example, it has been signalled that the dead pollen percentage ranged from 10 to 20% in Picholine marocaine cultivar (Walalli et al., 1984), from 1.8 to 4.6% in Meski (Mehri et al., 1992), and an average of 0.5% in Chétoui Tunisian cultivars (Mehri et al., 1992).

The pistil abortion is a known phenomenon in some crops. It has been noted that in cultivated

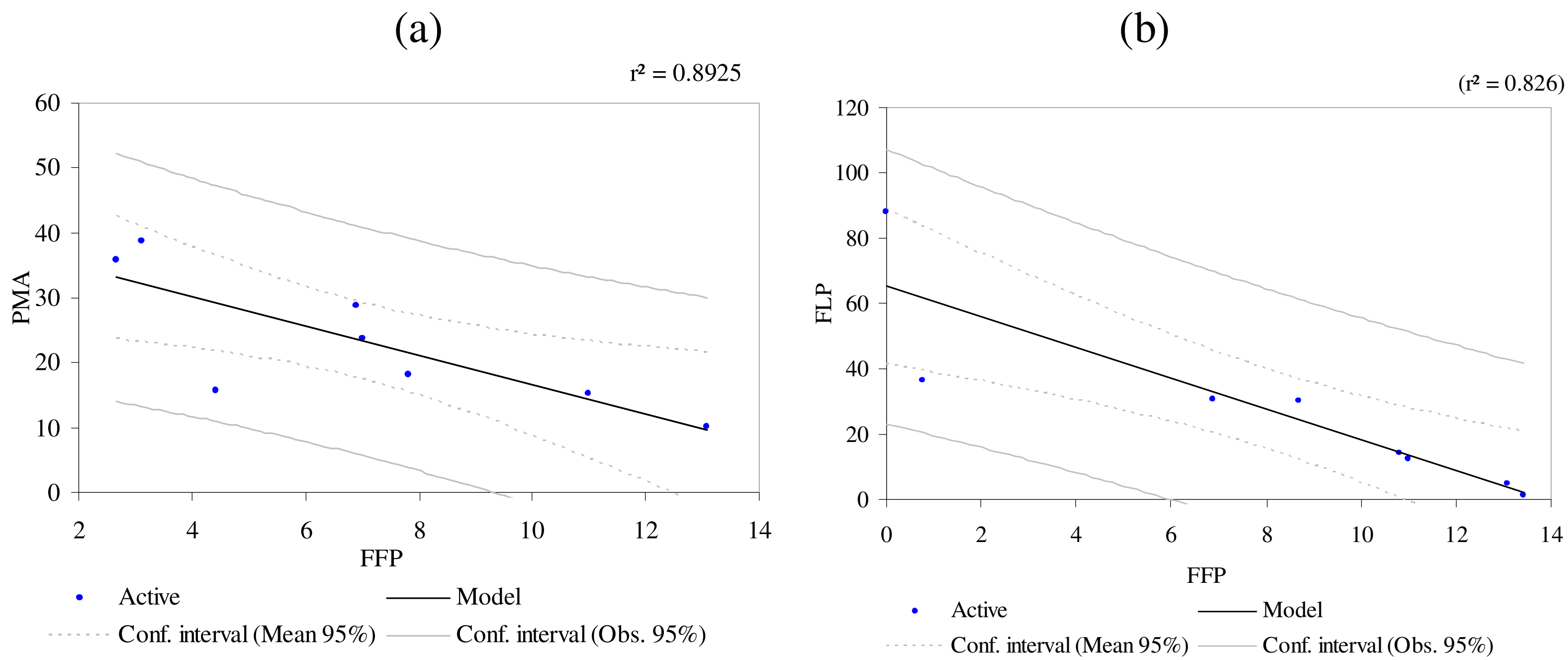

Figure 2. Linear regression between (a) percentages of male abortion (PMA), (b) percentages of flowers lacking pistil (FLP) and fruit formation percentage per inflorescence (FFP) in oleaster trees from two Parks.

olive trees the flowers would be female sterile by pistil abortions (Cuevas and Polito, 2004). In this study, we noted that it is also common in oleaster trees. The pistil abortion percentage ranged from 4.91 to 88.12% depending on oleaster trees. In cultivated olive trees, the pistil abortion percentage has an average of 60.73% in cv Manzanilla and 6.71% in cv Arbequina (Ghirsi et al., 1999). The perfect flower proportion in olive trees was essentially controlled by genetic factor (Fernandez-Escobar, 1992). Moreover, environmental and climatic conditions also influence the perfect flowers development in olive tree (Fernandez-Escobar et al., 1992; Cuevas et al., 1994). Female and male abortion have been reported independently in apricot (Burgos and Egea, 1994), as well as in many other tree crops (Sedgley and Griffin, 1989), but have been attributed to adverse environmental conditions. To the best of our knowledge, the female and male abortions in oleaster trees have not been studied so far. In this work, the male and female abortions, the fruit set, and the number of flower in abscission were remarkably different in both geographical sites. We hypothesized that the climatic conditions have an effect on oleaster trees flowering.

The phenotypic expression of a crop is the reflection of combined effect of genotype and environment. The phenotypic responses to changes in environment are not the same for all genotypes and the consequences of variation in genotypes are dependent on environment. Better understanding of genotype – environment interaction in flowering expression, is a basis for determining crop breeding strategies and provides useful information to identify stable genotypes over a range of environments. Therefore, determination of the nature of genotype and environmental variations present in the plant characters and its magnitude are essential to set up breeding programs. Olive breeding requires using new genotype resources such as the oleaster trees which are characterized by harsh environmental conditions adaptation (Zohary, 1994). Therefore, it is required to know the flowering expression in these trees.

Conclusion

The oleaster trees represent important plant material with valuable traits such as the good adaptation to harsh environmental conditions, disease resistance (Métro and Sauvage, 1955), and valuable oil composition (Hannachi et al., 2008). In natural-ecosystems, some oleaster trees in harsh conditions were able to produce drupes, thus showing environmental adaptation. Our results suggest that the flowering process in these trees may be different from the one in cultivars. Therefore, these trees would be useful to improve the olive.

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