Introduction

Olive, *Olea europaea* L., is an economically, socially and culturally important crop in the region lying between 30° north and 45° south in Mediterranean-like climate latitudes (Civantos, 2008). Spain is the first global producer and exporter of olive oil and olives with the highest number of olive trees (more than 300 million; IOOC, 2017). Most of the olive orchards, in Spain, are still cultivated under rainfed conditions. However, the increases in production obtained with irrigation have considerably raised irrigated olive groves area (up to 21%; MAGRAMA, 2017). The olive fruit fly, *Bactrocera oleae* (Rossi; Diptera; Tephritidae), is the major olive pest worldwide, damaging...
5%–15% of the total olive production each year (Haniotakis, 2005). The species is native to the Mediterranean basin and has been recently introduced into California and Mexico, leading to many problems in quarantine protection and international trade (Nardi, Carapelli, Dallai, Roderick, & Frati, 2005; Neokosmidis et al., 2005; Tzanakakis, 2006). This tephritid lays its eggs in olive fruits. After hatching, the larvae feed and grow in the mesocarp, causing it to drop prematurely before maturation, making it unsuitable for eating (table olives) and reducing the quality of the oil produced (Kakani et al., 2010; Santiago-Álvarez & Quesada-Moraga, 2007). The olive fly has become unmanageable worldwide because it has developed resistance to chemical insecticides, which have been overused in bait sprays for *B. oleae* adult control since the early 1960s (Kakani et al., 2008, 2010; Stasinakis, Katsares, & Mavragani-Tsipidou, 2001). Moreover, severe effects of pesticides on nontarget arthropod fauna in olive orchards have been found (Pascual, Cobos, Seris, & González-Núñez, 2010; Ruano et al., 2001). Other strategies against *B. oleae* like cultural and sanitary methods, mass trapping and preventative spraying with kaolin (physical barrier) and copper have a very limited application (Daane & Johnson, 2010; Haniotakis, 2005), although they can be combined with other components of an Integrated Pest Management (IPM) programme (Vargas, Piñero, & Leblanc, 2015). Consequently, there is an urgent need to develop alternatives to synthetic chemicals for olive fly IPM, with emphasis on both biological control and the development of new olive varieties which are resistant to *B. oleae* (Fernández Escobar et al., 2013; Quesada-Moraga, Campos-Aranda, & Santiago-Álvarez, 2010). The genetic resistance of olive germplasm is a key tool for controlling *B. oleae* because olive varieties with olive fruit fly resistance could be used to obtain quality products in both organic and conventional systems and they could also contribute to the reduction in insecticide applications (Rizzo, Virgilio, & Alberto, 2012).

The first step in any varietal development breeding programme is to elucidate the susceptibility of the native varieties to olive fly attack because of the uniqueness of the relationship between this pest and wild and cultivated olives (Tzanakakis, 2006). During the process of olive domestication, selection, and diffusion, a great diversity of varieties was created (Barranco, 2001). Currently, there are more than 1,250 varieties of domestic olives cultivated worldwide that are distinguishable by a large number of both physical and chemical characteristics (Batrolini, 2008). Nonetheless, objectives of olive breeding programmes worldwide are disease resistance, with an emphasis on *Verticillium* wilt and Anthracnose (*Colletotrichum* spp.; Moral et al., 2017; Trapero et al., 2013). The susceptibility of olive varieties to olive fly attack has been mainly linked to both physical (fruit size, colour, skin hardness and olive surface waxes; Gümusay, Ozilbey, Ertem, & Oktar, 1990; Kombargi, Michelakis, & Petrakis, 1998; Neuenschwander, Michelakis, Holloway, & Berchtol, 2009; Rizzo et al., 2012) and chemical properties of olives (emission of volatiles from both olive leaves and fruits and fruit mineral element content; Bononi & Tateo, 2017; Garantonakis et al., 2016; Malheiro, Casal, Cunha, Baptista, & Pereira, 2015, 2016). However, there is little scientific information available on the susceptibility of the Spanish olive varieties to *B. oleae* attack. Thus, it is imperative to acquire information regarding the variety-specific response to this tephritid pest to improve olive fly IPM and breeding programs (Lavee, Avidan, & Ben-Ari, 2014). The goal of present work was to evaluate the susceptibility of 20 widely distributed mill olive and table olive varieties (10 of each) to *B. oleae* over 3 years, as well as to evaluate the effects of irrigation, fruit diameter and oil content on *B. oleae* oviposition preferences.

## 2 | MATERIALS AND METHODS

### 2.1 | Experimental site and study design

The experiments were conducted at the experimental farm “Alameda del Obispo” that belongs to the Institute of Agricultural and Fisheries Research and Training (Córdoba, Spain; 37° 51′ 10.8″N, 4° 48′ 15.3″W) over a 3-year period: 2008–2009, 2010–2011, and 2011–2012 for the mill varieties and 2009–2010, 2010–2011 and 2011–2012 for the table varieties. There were 20 widely distributed olive varieties tested, namely, “Arbequina,” “Cornicabra,” “Empeltre,” “Frantoio,” “Hojiblanca,” “Lechín de Sevilla,” “Nevadillo Blanco de Jaén,” “Pico Limón,” “Picual,” and “Picudo” (mill olive varieties) and “Ascolana Tenera,” “Barnea,” “Callosina,” “Dulzar de Carmona,” “Gordal Sevillana,” “Kalamon,” “Manzanilla de Sevilla,” “Mollar de Cieza,” “Ocal” and “Uovo de Piccione” (table olive varieties).

There were two plots (1 ha each) in the experimental site. One Plot, under drip irrigation, contained 10 mill and 10 table olive varieties, with a total of 160–200 trees. Between eight and ten, randomly distributed 11-year-old olive trees per variety were planted with 7 × 7 m tree spacing. The second plot, under rainfed conditions, contained only the 10 mill varieties and also consisted of 8–10 randomly distributed 11-year-old olive trees per variety (total of 80–100 trees) and 7 × 7 m tree spacing. Thus, the mill varieties were evaluated under both irrigated and rainfed conditions, whereas the table varieties were evaluated only under irrigated conditions. This random distribution of many varieties in the same olive orchard, the experimental unit being the tree and not the plot, helps improving the evaluation of susceptibility of olive varieties to *B. oleae* attack by offering different olive varieties to females under agronomic and climatic uniformity (Supporting Information Figure S1). Drip irrigation was conducted once a week with the same volume from May 1 to September 30 reaching 2,000 m³/ha/year. No phytosanitary treatments were performed during the field trials.

### 2.2 | Monitoring of the *Bactrocera oleae* population

*Bactrocera oleae* flight activity was monitored during all study years using two trapping systems recommended by the Spanish IPM regulations: olfactory plastic McPhail traps (Bioibérica, BCN, ES) baited with diammonium phosphate 4% (Sigma-Aldrich, MO, USA), placed inside the tree canopies facing south, and yellow chromotopic sticky traps placed along the outer side of the trees, also facing south (MAGRAMA, 2014). A total of 16 traps were used to monitor
the B. oleae population; eight were distributed in the rainfed plot and eight in the irrigated plot (four McPhail traps and four chromotropic sticky traps in each plot). The traps were randomly distributed and placed 15 m apart to avoid interference. The trap catches were counted weekly for 10 months, from May of 1 year to March of the following year. The data presented represent the total number of captured insects in both types of traps. Annual rainfall quantities during the study years (2008, 2009, 2010 and 2011) were: 601.7, 724.8, 1,167 and 504.8 mm, respectively.

2.3 | Susceptibility of table and mill olive varieties to Bactrocera oleae under rainfed and irrigated conditions

All trees of each variety (8–10) were sampled eight times at 10-day intervals from September to December to estimate the percentage of B. oleae punctures. For each tree and sampling date, 10 olives were randomly harvested at a height of 1.5 m, circling around the tree to include fruits at all orientations (MAGRAMA, 2014); thus, approximately 80–100 olives of each variety were sampled throughout the sampling period (approximately 24,000 fruits per year of all varieties). The sampled olives were transported in plastic bags to the laboratory and the possible presence of oviposition punctures was determined using a stereoscopic microscope (Nikon Instruments INC., Melville, USA).

2.4 | Relationship between olive fruit traits and oviposition preferences of Bactrocera oleae

To evaluate the influence of fruit traits on olive fly oviposition preferences, the relationships among oil content, fruit diameter and B. oleae infestation in each variety were studied. After examining the fruits for possible oviposition punctures as described above, the transversal fruit radius was measured with a caliper rule, resulting in 10 diameter values for each tree for each sampling date.

FIGURE 1  Flight curves of Bactrocera oleae (as number of adults/trap/date) and precipitation at Alameda del Obispo (Córdoba) in 2008–2009 (a), 2009–2010 (b), 2010–2011 (c) and 2011–2012 (d) based on data from McPhail and yellow chromotropic sticky traps. In 2009–2010, flight curves were only obtained under the irrigated condition because the table olive varieties were not evaluated under the rainfed condition.
To determine the oil content, two fruit samples of 70 g each were taken from each variety and each sampling date (16 samples per each variety). These samples were placed in Petri dishes and dried in an oven at 105°C for 42 hr. Then, the dry weight of each fruit was determined and the percentage of oil was measured by nuclear magnetic resonance following the methods described in Cimato and Attilio (2008).

### 2.5 Statistical analyses

To compare the susceptibility of the different mill and table olive varieties to the olive fruit fly, the areas under B. oleae infestation curves (AUBIC) were calculated using the trapezoidal integration method of SAS (Campbell & Madden, 1990). The area under the pest progress curve is a very useful quantitative summary of pest’s intensity over time, and it is used normally for comparison across years, locations, or management tactics, and for describing quantitative resistance of pests as confirmed by American Phytopathological Society (Jeger & Viljanen-Rollinson, 2001; Litsinger, 1991; Lyman, Bryan, Jeffrey, & Jesse, 1989; Ruesink & Kogan, 1994; Worner, 2014). All data collected over time (eight sampling dates) for each tree were used to calculate the AUBIC. The 8–10 values of AUBIC per variety were subjected to Kruskal–Wallis one-way nonparametric analysis of variance using Statistix 9.0 software (Analytical Software 2008). Spearman’s rank correlations were performed to detect the relationship between the infestation level and oil content and fruit diameter.

### 3 RESULTS

#### 3.1 Olive fly dynamics

The flight curves indicated that B. oleae was bivoltine in the sampled area (Figure 1). The flight activity by the overwintering generation usually began in the period from early May to early June and ended in late September to mid-October (Figure 1). Flight activity by the overwintering generation ceased sometime between July 10

![FIGURE 2](image-url)  
**FIGURE 2** Susceptibility of different mill olive varieties (AUBIC median ± SE) to Bactrocera oleae under both rainfed and irrigated conditions in this 3-year study. AUBIC, area under B. oleae infestation curves. Lower case letters denote the rainfed condition and capital letters denote the irrigated condition. For each year, columns with the same letter are not significantly different. For each variety, AUBIC with an asterisk (*) indicates a significant difference between the rainfed and irrigated conditions. In 2011–2012 there was no fruit production in the “Picual” trees under irrigated conditions.
and August 30 (Figure 1). The B. oleae population size differed between years, with high population densities in 2008–2009 (captures reached 350 adults/trap/week; Figure 1a), and medium to low densities in the other years (Figure 1b–d). The period of maximum catches occurred between mid- and late October but varied among years (Figure 1). Flight activity by the autumn generation usually began in early November, but the duration of this fly activity varied considerably among years (Figure 1). In 2008 and 2009, the flight activity of this autumn generation ended by early December (Figure 1a,b), whereas in 2011 and 2012, it ended in late January and mid-March, respectively (Figure 1c,d). Olive fly catches were higher in the irrigated plot than in the rainfed plot in all years ($H_{1,127} = 9.65, p < 0.01$; Figure 1).

3.2 | Susceptibility of table and mill olive varieties to Bactrocera oleae under rainfed and irrigated conditions

There were significant differences in B. oleae incidence among mill olive varieties in both rainfed and irrigated conditions in all years of the study (Figure 2). In 2008–2009, B. oleae populations were very high, and there were significant differences among mill olive varieties in susceptibility to B. oleae in both rainfed ($H_{9,88} = 4.45, p < 0.001$) and irrigated ($H_{9,88} = 5.96, p < 0.001$) conditions. The AUBIC ranged from 3.3 to 47.8 and from 15.0 to 65.6 in the rainfed and irrigated conditions, respectively (Figure 2). Again, the “Arbequina” variety was the least susceptible, with average infestation levels of 0.62% and 2.36% in the rainfed and irrigated conditions, respectively (Figure 3b), while the “Nevadillo Blanco de Jaén” variety was the most susceptible, with average infestation levels ranging from 6.7% to 10.3% in the rainfed and irrigated conditions, respectively (Figure 3h).

In 2011–2012, the varieties also differed significantly in their susceptibility to B. oleae in both the rainfed ($H_{9,79} = 10.57, p < 0.001$) and irrigated ($H_{8,71} = 5.9, p < 0.001$) conditions, with AUBIC values ranging from 35.0 to 241.6 and from 75 to 358.3 under rainfed and irrigation, respectively (Figure 2). The varieties exhibited the same susceptibility ranking; “Arbequina” was the least susceptible variety, with average infestation levels ranging from 5.8% to 10.8% in the rainfed and irrigated conditions, respectively (Figure 3c), and “Nevadillo Blanco de Jaén” was the most susceptible variety, with average infestation levels ranging from 36.0% to 48.8% in the rainfed and irrigated conditions, respectively (Figure 3i). The maximum infestation levels for all mill olive varieties under both rainfed and irrigated conditions occurred between late October and late November each year (Supporting Information Table S1).
Table olive varieties also differed significantly in their susceptibility to *B. oleae* during all the years of the study (Figure 4). In 2009–2010, the differences among table olive varieties in their susceptibility to *B. oleae* were significant ($H_{9,80} = 21.64, p < 0.001$). “Callosina” and “Kalamon” were the least susceptible varieties (85.4 AUBIC, averaged across them), while “Gordal Sevillana,” “Ascolana Tenera,” “Barnea” and “Ocal” were the most susceptible varieties (average 316 AUBIC; Figure 4). Significant differences also occurred among table olive varieties in 2010–2011 ($H_{9,82} = 10.95, p < 0.001$). Again, “Gordal Sevillana,” “Ascolana Tenera” and “Manzanilla de Sevilla” were the most susceptible ones, with an average AUBIC value of 128.6, and “Kalamon” was the least susceptible variety, with 23.3 AUBIC (Figure 4). Average infestation levels ranged between 7.1% for “Kalamon” and 30% for “Gordal Sevillana.”

There were also significant differences among table olive varieties in 2011–2012 ($H_{9,64} = 8.26, p < 0.001$). Values of AUBIC varied between 58.1 (averaged for “Callosina” and “Uovo de Piccione”) and 258 for “Ocal” (Figure 4). “Callosina” variety again had one of the lowest infestation levels and “Ocal” had the highest infestation level: averages 10.5% and 41.0%, respectively (Figure 5). The maximum infestation levels for all table olive varieties occurred between early and late November (Supporting Information Table S2).

### 3.3 | Relationship between olive fruit traits and oviposition preference of *Bactrocera oleae*

The correlation coefficients (Spearman) between *B. oleae* infestations of olive fruit and fruit diameter and oil content for all varieties are shown in Table 1.

The correlation coefficients between *B. oleae* infestation of olive fruits and fruit oil content varied greatly from year to year for the same variety and under the same irrigation conditions and were mostly significant (Table 1). In 2008–2009, all the correlation coefficients were significant except those of “Arbequina,” “Cornicabra,” “Hojiblanca,” “Lechin de Sevilla” and “Picual” in irrigated conditions.

In 2010–2011, the correlation coefficient for the Arbequina and Frantoio varieties in the rainfed condition was not significant nor was the correlation coefficient for the Cornicabra variety in the irrigated condition. However, in 2011–2012, all the correlation coefficients between the infestation rate and the oil content were significant except for the Cornicabra variety in the rainfed condition (Table 1).

For mill olive varieties, the correlation coefficients between olive fly infestation and fruit diameter also varied greatly from 1 year to another, even for the same variety and under the same irrigation condition, and generally tended to be significant (Table 1). In 2008–2009, all the correlation coefficients were significant except for “Cornicabra,” “Empeltre,” “Lechin de Sevilla” and “Nevadillo Blanco de Jaén” in irrigated conditions (Table 1). In 2010–2011, the correlation coefficients...
were also significant except for those of “Arbequina,” “Nevadillo Blanco de Jaén,” “Pico Limón” and “Picual” in the rainfed condition and the Frantoio variety in the irrigated condition. In 2011–2012, the correlation coefficients were not significant for “Cornicabra,” irrespective of irrigation regime nor for “Frantoio,” “Lechín de Sevilla” and “Picual” in the irrigated condition and the Hojiblanca and Pico Limón varieties in the irrigated condition (Table 1).

A similar trend was discernible for the table olive varieties, which showed significant correlation coefficients between infestation level and fruit oil content in 2008–2009 for all varieties except “Uovo di Piccione” (Table 2). In addition, in 2010–2011, all the correlation coefficients between infestation level and fruit oil content were significant except for “Uovo di Piccione” and “Mollar de Cieza”. Concerning correlation coefficients between infestation

### Table 1: Correlation coefficients (Spearman) between *Bactrocera oleae* infestation level, fruit diameter, and oil content of the mill olive varieties under both rainfed and irrigated conditions for the three study years

| Olive mill varieties | Irrigated condition | 2008–2009 | 2010–2011 | 2011–2012 |
|----------------------|---------------------|-----------|-----------|-----------|
|                      | Oil yield | Diameter | Oil yield | Diameter | Oil yield | Diameter |
| "Arbequina"          | Rainfed   | 0.76*     | 0.85**    | 0.59***   | 0.52***   | 0.78*     | 0.69*     |
|                      | Irrigated | 0.59**    | 0.73*     | 0.92**    | 0.95***   | 0.8*      | 0.92**    |
| "Cornicabra"         | Rainfed   | 0.71*     | 0.95***   | 0.94**    | 0.88**    | 0.66**    | 0.64**    |
|                      | Irrigated | 0.5**     | 0.43**    | 0.57***   | 0.73*     | 0.74*     | 0.56**    |
| "Empeltre"           | Rainfed   | 0.97***   | 0.78*     | 0.77*     | 0.74*     | 0.88**    | 0.89**    |
|                      | Irrigated | 0.81*     | 0.43**    | 0.85*     | 0.75*     | 0.88**    | 0.85**    |
| "Frantoio"           | Rainfed   | 0.95***   | 0.92**    | 0.64**    | 0.79*     | 0.92**    | 0.16**    |
|                      | Irrigated | 0.95***   | 0.73*     | 0.88**    | 0.61**    | 0.88**    | 0.85**    |
| "Hojiblanca"         | Rainfed   | 0.85**    | 0.85**    | 0.87**    | 0.85**    | 0.92**    | 0.85**    |
|                      | Irrigated | 0.42**    | 0.8*      | 0.88**    | 0.89**    | 0.88**    | 0.61**    |
| "Lechín de Sevilla" | Rainfed   | 0.91**    | 0.91**    | 0.89**    | 0.85**    | 0.83*     | 0.64**    |
|                      | Irrigated | 0.45**    | 0.66**    | 0.92**    | 0.84**    | 0.9**     | 0.85**    |
| "Nevadillo Blanco de Jaén" | Rainfed | 0.95***    | 0.92**    | 0.76*     | 0.67**    | 0.87**    | 0.92**    |
|                      | Irrigated | 0.71*     | 0.45**    | 0.89**    | 0.87**    | 0.88**    | 0.71*     |
| "Pico Limón"         | Rainfed   | 0.8*      | 0.85**    | 0.91*     | 0.55*     | 0.75*     | 0.97***   |
|                      | Irrigated | 0.86**    | 0.94**    | 0.95***   | 0.98***   | 0.88*     | 0.48**    |
| "Picual"             | Rainfed   | 0.81*     | 0.71*     | 0.72*     | 0.61**    | 0.97***   | 0.67**    |
|                      | Irrigated | 0.66**    | 0.73*     | 0.94*     | 0.94**    | –         | –         |
| "Picudo"             | Rainfed   | 0.78*     | 0.69*     | 0.89**    | 0.92**    | 0.92**    | 0.93**    |
|                      | Irrigated | 0.9**     | 0.9**     | 0.95***   | 0.93*     | 0.85*     | 0.88**    |

*No correlation has been obtained for the variety Picual due to the total absence of fruits in the trees of the latest.

*p<0.05; **p<0.01; ***p<0.001; ns: not significant.

### Table 2: Correlation coefficients (Spearman) between *Bactrocera oleae* infestation level, fruit diameter and oil content of the table olive varieties under irrigated conditions for the three study years

| Olive table varieties | 2009–2010 | 2010–2011 | 2011–2012 |
|-----------------------|-----------|-----------|-----------|
|                       | Oil yield | Diameter  | Oil yield | Diameter  | Oil yield | Diameter  |
| "Ascolana Tenera"     | 0.89***   | 0.72*     | 0.69*     | 0.61**    | 0.76*     | 0.53**    |
| "Barnea"              | 0.92***   | 0.95***   | 0.96***   | 0.96***   | 0.57**    | 0.61**    |
| "Callosina"           | 0.85**    | 0.84**    | 0.82**    | 0.78*     | 0.54**    | 0.69**    |
| "Dulzal de Carmona"   | 0.85**    | 0.68*     | 0.86**    | 0.81**    | 0.92**    | 0.57**    |
| "Gordal sevillana"    | 0.9***    | 0.93***   | 0.94***   | 0.83**    | 0.77*     | 0.54**    |
| "Kalamon"             | 0.93***   | 0.91***   | 0.76*     | 0.73*     | 0.82*     | 0.82*     |
| "Manzanilla de Sevilla" | 0.91***  | 0.85**    | 0.91***   | 0.81**    | 0.88**    | 0.78*     |
| "Mollar de Cieza"     | 0.93***   | 0.74*     | 0.52**    | 0.68**    | 0.83**    | 0.52**    |
| "Ocal"                | 0.9***    | 0.95***   | 0.93***   | 0.83**    | 0.82**    | 0.85**    |
| "Uovo di Piccione"    | 0.59**    | 0.16**    | 0.61**    | 0.03**    | 0.73*     | 0.51**    |
level and fruit diameter in this same season, not significant values were obtained for “Ascolana Tenera,” “Mollar de Cieza” and “Uovo di Piccione” (Table 2). In 2011–12, all the infestation-oil content correlation coefficients were significant except those for the Callosina and Barnea varieties, but the correlation coefficients between level of infestation by B. oleae and fruit diameter were not significant for any variety except for “Kalamon,” “Ocal” and “Manzanilla de Sevilla” (Table 2).

4 | DISCUSSION

The olive fly, B. oleae, is a multivoltine species that completes between second and five generations per year depending on the regional and local conditions—primarily temperature and relative humidity (Santiago-Álvarez & Quesada-Moraga, 2007). Bactrocera oleae was bivoltine in the present study area, and adults were caught throughout all four growing seasons. The bulk of the olive fly population overwinters as pupae several cm deep in soil. This was previously revealed by progressive increases of adult fly catches coming from the overwintering pupae formed in the soil at the end of the previous year (Alfaro-Morenzo, 2005; Santiago-Álvarez & Quesada-Moraga, 2007). Bactrocera oleae flight activity ceased from mid-July until the end of August, a period with high temperatures and low relative humidities, in which the olive fly seeks refuge or migrates to more favourable areas (Tzanakakis, 2006). Indeed, at temperatures below 30°C, this tephritid reaches sexual maturation and reproduces normally, whereas temperatures above 30°C and low relative humidity lead to egg resorption and reproductive diapause (Santiago-Álvarez & Quesada-Moraga, 2007). Hence, the increased presence of B. oleae adults in the irrigated olive plot during this adverse period could be attributable to these ecological traits (low temperature and high relative humidity; Gutierrez & Cossu, 2009; Pappas, Broufas, Koufali, Pieri, & Koveos, 2010).

None of the 20 selected widely distributed mill and table olive varieties was resistant to B. oleae, confirming previous observations, which indicated that even wild olive trees are susceptible to this pest (Alvarado, Civantos, & Durán, 2008). It seems that the search and acceptance of olive fruit by B. oleae are determined by visual and chemical signals which remain poorly known (Burrack & Zalom, 2008).

Our results indicated that some fruit variables such as diameter and oil yield can partially explain the susceptibility of mill and table olive varieties to B. oleae; the percentages of fruit infestation increased as the olive fruit increased in diameter and oil yield. Hence, among the mill varieties, the smallest variety, Arbequina, was the least susceptible one during all years of the study in both irrigated and rainfed conditions. Likewise, “Arbequina” was also the least susceptible to B. oleae among several commercially important olive varieties in California during three consecutive years (Burrack & Zalom, 2008). Nonetheless, other unknown variables may also influence fruit selection by adult fly females as revealed by the fact that several small-diameter varieties (i.e., “Nevadillo blanco de Jaén” and “Lechín de Sevilla”) were more susceptible to B. oleae than were higher diameter ones (i.e., “Picudo” and “Pico Limón”).

The relationship between olive fruit size and B. oleae oviposition preferences is a controversial issue. Research exists that indicates that these measures both correlate (Gümusay et al., 1990; Neuenschwander et al., 2009; Rizzo et al., 2012) and do not correlate (Iannotta, Perri, Tocci, & Zaffina, 1999). It has even been proposed that olive fruit size is the most important parameter during the early stages of fruit ripening but, subsequently, it becomes less important due to both the increase in the population density and the presence of particular substances in the olives that induce females to select the smaller drupes for ovipositing (Dominici, Pucci, & Montanan, 1986). In further study, Rizzo et al. (2012) found that quantitative factors such as olive fruit size, shape and colour are significant only if the variety factor is eliminated. It has even been hypothesized that B. oleae females are able to select fruits that are better adapted for the development of their progeny (e.g., larval developmental time, pupal emergence time and pupal weight; Burrack & Zalom, 2008).

Regarding the possible chemical signals that may influence B. oleae oviposition preferences, it has been revealed that the degree of susceptibility of olive fruits to fly infestation and damage depends on the release of bioactive molecules from the β-glucosidase/oleuropein reaction in the damaged tissues (Spadafora et al., 2008). Accordingly, varieties with high activation of this enzyme after fly punctures exhibit high resistance to B. oleae (Delkash-Roudsari, Zibaee, & Abbci-Mozddehi, 2015). Indeed, previous research on olive surface waxes indicated that their components could both stimulate and deter oviposition and that these components varied with olive variety and with fruit maturity (Kombargi et al., 1998). More recently, it has been demonstrated that olive volatiles such as toluene and α-copaene could be B. oleae oviposition promoters and fruit mineral element content (Bononi & Tateo, 2017; De Alfonso, Vacas, & Primo, 2014; Garantonakis et al., 2016; Malheiro et al., 2015). In the present work, the B. oleae infestation level of each variety tended to be both earlier and slightly higher under the irrigated condition than under the rainfed condition. This result supports the previous report by Bjelis, Masten, and Imala (2008) and may be due to the earlier ripening and greater firmness of irrigated fruits (Rizzo et al., 2012).

The present study, which includes the 20 most widely distributed mill and table olive Spanish varieties, is an extensive survey of olive variety responses to B. oleae and it also provides key information for wide-area olive fly pest management decisions, because the most susceptible varieties can contribute to B. oleae population increases in olive variety mosaic landscape patterns, thereby improving the timing, sequence and intensity of monitoring efforts and spraying of insecticides determined by GPS-based forecasting models. Our results also reveal that fruit size and oil content at least partially explain the oviposition preferences of B. oleae, although yet-unknown factors may also operate. Likewise, irrigation tended to promote both B. oleae incidence and infestation and should also be considered in pest management decisions. Based on these results, the
susceptibility of olive tree varieties to B. oleae must be considered in IPM programs because varieties play a very important role in making the populations of this key pest manageable.

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AUTHOR CONTRIBUTION

EQM, CSÁ and MY conceived and designed research. EQM, CSÁ, SCG, GCM and AAF conducted the experiments. MY analysed the data. MY and EQM wrote the manuscript. All authors approved the manuscript.

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REFERENCES

Alfaro-Moreno, A. (2005). Entomología agraria: Los parasitos de las plantas cultivadas. Soria, Spain: Excm. Diputación Provincial de Soria.
Alvarado, M., Civantos, M., & Durán, J. M. (2008). Plagas. In D. Barranco, R. Fernandez-Escobar & L. Rallo (Eds.), El cultivo del olivo (pp. 514–523). Madrid, Spain: Mundi-Prensa.
Barazza, D. (2001). Variedades y patrones. In D. Barranco, R. Fernandez-Escobar & L. Rallo (Eds.), El cultivo del olivo (pp. 514–523). Madrid, Spain: Mundi-Prensa.
Batrolini, G. (2008). Olive germplasm (Olea europaea L.) cultivars, synonyms, cultivation area, collections, descriptors. Retrieved from http://www.oleadb.it/olivodb.html.
Bjelis, M., Masten, T., & Imala, M. (2008). Olive fruit infestation by olive fruit fly Bactrocera oleae (Gmel.) in dry and irrigated growing conditions in Dalmacija. Cereal Research Communications, 36, 1731–1734.
Bononi, M., & Tateo, F. (2017). Preliminary data on volatile composition of olive fruits of CV. "SIMONA" and possible relationship to resistance to fly oviposition. Italian Journal of Food Science, 29, 582–590.
Burack, H. J., & Zalom, F. G. (2008). Olive fruit fly (Diptera: Tephritidae) ovipositional preference and larval performance in several commercially important olive varieties in California. Journal of Economic Entomology, 101, 750–758. https://doi.org/10.1603/0022-0493(2008)101[750:OFFDTO]2.0.CO;2
Campbell, C. L., & Madden, L. V. (1990). Introduction to plant disease epidemiology. New York, NY: John Wiley & Sons.
Cimato, A., & Attilio, C. (2008). Conservation, characterization, collection and utilization of the genetic resources in olive. Technical paper (CFC/IOOC/03) p 27.
Civantos, L. (2008). La olivicultura en el mundo y en España. In D. Barranco, R. Fernandez-Escobar & L. Rallo (Eds.), El cultivo del olivo (pp. 17–35). Madrid, Spain: Mundi-Prensa.
Daane, K. M., & Johnson, M. W. (2010). Olive fruit fly: Managing an ancient pest in modern times. Annual Review of Entomology, 55, 155–169.
De Alfonso, I., Vacas, S., & Primo, J. (2014). Role of alpha-Copaene in the susceptibility of olive fruits to Bactrocera oleae (Rossi). Journal of Agriculture and Food Chemistry, 62, 11976–11979. https://doi.org/10.1021/jf504821a
Delkash-Roudsari, S., Ziaee, A., & Abbci-Mozddehi, M. R. (2015). Effects of olive varieties on α- and β-glucosidase activities in the larvae of Bactrocera oleae Gmelin (Diptera: Tephritidae). Trakia Journal of Sciences, 1, 41–50. https://doi.org/10.15547/tjs.2015.01.006
Dominici, M., Pucci, C., & Montanan, G. E. (1986). Dacus oleae (Gmel.) ovipositing in olive drupes (Diptera, Tephrytidae). Journal of Applied Entomology, 101, 111–120. https://doi.org/10.1111/j.1439-0418.1986.tb00838.x
Fernández Escobar, R., De la Rosa, R., León, L., Gomez, J. A., Testi, F., Orgaz, M., ... Trapero, A. (2013). Evolution and sustainability of the olive production systems. In N. Arcas, F. N. Arroyo López, J. Caballero, R. D’Andria, M. Fernández, R. Fernandez Escobar ... R. Zanoli (Eds.), Present and future of the Mediterranean olive sector (pp. 11–42). Zaragoza, Spain: CIHEAM/JOC.
Garantonakis, N., Varikou, K., Markakis, E., Bioruraki, A., Sergentani, C., Psarras, G., & Koubouris, G. C. (2016). Interaction between Bactrocera oleae (Diptera: Tephritidae) infestation and fruit mineral element content in Olea europaea (Lamiaceae: Oleaceae) cultivars of global interest. Applied Entomology and Zoology, 51, 257–265. https://doi.org/10.1007/s13355-016-0397-4
Gümüşay, B., Ozilbey, U., Ertem, G., & Oktar, V. (1990). Studies on the susceptibility of some important table and oil olive cultivars of Aegean Region to olive fly (Dacus oleae Gmel). In Turkey. Acta Horticulturae, 286, 359–361. https://doi.org/10.17660/ActaHortic.1990.286.73
Gutierrez, A. P., & Cossu, Q. A. (2009). Effects of climate warming on olive and olive fly Bactrocera oleae (Gmelin) in California and Italy. Climatic Change, 95, 195–217. https://doi.org/10.1007/s10584-008-9528-4
Haniotakis, G. (2005). Olive pest control: Present status and prospects. IOBC/WPRS Bulletin, 28, 1–9.
Iannotta, N., Perri, L., Tocci, C., & Zaffina, F. (1999). The behavior of different olive cultivars following attacks by Bactrocera oleae (Gmel.). Acta Horticulturae, 474, 545–548. https://doi.org/10.17660/ActaHortic.1999.474.112
[IoOC] International Olive Oil Council (2017). World olive oil figures. Retrieved from http://www.internationaloliveoil.org/statistics/view/131-world-olive-oil-figures.
Jeger, M. J., & Viljanen-Rollinson, S. L. H. (2001). The use of the area under the disease-progress curve (AUDPC) to assess quantitative disease resistance in crop cultivars. Theoretical and Applied Genetics, 102, 32–40. https://doi.org/10.1007/s001220051615
Kakani, E. G., Ioannides, I. M., Margaritopoulos, J. T., Seraphides, N. A., Skouros, P. J., Tsitsipis, J. A., & Mathiopoulos, K. D. (2008). A small deletion in the olive fly acetylcholinesterase gene associated with high levels of organophosphate resistance. Insect Biochemistry and Molecular Biology, 38, 781–787. https://doi.org/10.1016/j.ibmb.2008.05.004
Kakani, E. G., Zygouridis, N. E., Tsoumani, K. T., Seraphides, N., Zalom, F. G., & Mathiopoulos, K. D. (2010). Spinosad resistance development in wild olive fruit fly Bactrocera oleae (Diptera: Tephritidae) populations in California. Pest Management Science, 66, 447–453.
Kombargi, W. S., Michelakis, S. E., & Petrakis, C. A. (1998). Effect of olive surface waxes on oviposition by Bactrocera oleae (Diptera: Tephritidae). Journal of Economic Entomology, 91, 993–998. https://doi.org/10.1093/jee/91.4.993
Lavee, S., Avidan, B., & Ben-Ari, G. (2014). Trends in breeding new olive varieties in Israel for quality and economic management. Agricultural Sciences, 5, 701–709. https://doi.org/10.4236/as.2014.58073
Litsinger, J. A. (1991). Crop loss assessment in rice. In E. A. Heinrichs & T. T. Miller (Eds.), Rice insects: Management strategies (pp. 1–65). New York, NY: Springer.

Lyman, L. M., Bryan, F. J. M., Jeffrey, L., & Jesse, A. L. (1989). Estimation and analysis of insect populations. In L. L. McDonald, B. F. J. Manly, J. Lockwood & J. A. Logan (Eds.), Lecture notes in statistics (pp. 93–107). New York, NY: Springer.

(MAGRAMA) Ministerio de Agricultura, Alimentación, y Medio Ambiente (2014). Guía de gestión integrada de plagas olivar. [Text article]. Retrieved from [http://www.mapama.gob.es/es/agricultura/temas/sanidad-vegetal/GUIAOLIVAR%20(2)_tcM30-57939.pdf](http://www.mapama.gob.es/es/agricultura/temas/sanidad-vegetal/GUIAOLIVAR%20(2)_tcM30-57939.pdf)

Malheiro, R., Casal, S., Cunha, S. C., Baptista, P., & Pereira, J. A. (2015). Olive flies from portuguese cultivars coobraçosa, madural and verdeal transmontana: Role in oviposition preference of Bactrocera oleae (Rossi) (Diptera: Tephritidae). PLoS One, 10, e0125070. [https://doi.org/10.1371/journal.pone.0125070](https://doi.org/10.1371/journal.pone.0125070)

Malheiro, R., Casal, S., Cunha, S. C., Baptista, P., & Pereira, J. A. (2016). Identification of leaf volatiles from olive (Olea europaea) and their possible role in the ovipositional preferences of olive flies, Bactrocera oleae (Rossi) (Diptera: Tephritidae). Phytochemistry, 121, 11-19. [https://doi.org/10.1016/j.phytochem.2015.10.005](https://doi.org/10.1016/j.phytochem.2015.10.005)

Moral, J., Carlos, J. X., José, R. V., Luis, F. R., Juan, C., & Antonio, T. (2017). Variability in susceptibility to Anthracnose in the world collection of olive cultivars of Cordoba (Spain). Frontiers in Plant Science, 8, 1892. [https://doi.org/10.3389/fpls.2017.01892](https://doi.org/10.3389/fpls.2017.01892)

Nardi, F., Carapelli, A., Dalai, R., Roderick, G. K., & Frati, F. (2005). Population structure and colonization history of the olive fly, Bactrocera oleae (Diptera, Tephritidae). Molecular Ecology, 14, 2729–2738. [https://doi.org/10.1111/j.1365-294X.2005.02610.x](https://doi.org/10.1111/j.1365-294X.2005.02610.x)

Neokosmidis, A., Livaniou, E., Zikos, C., Paravatou-Petsotas, M., Ragoussis, V., Ragoussis, N., & Evangelatos, G. (2005). Olive fruit fly (Bactrocera oleae, Gmelin) pheromone determination in biological samples, by an enzyme-linked immunosorbent assay (Elisa). IOBC/WPRS Bulletin, 28, 19–27.

Neuenschwander, P., Michalakis, S., Holloway, P., & Berchtol, W. (2009). Factors affecting the susceptibility of fruits of different olive varieties to attack by Dacus oleae (Gmel.) (Dipt., Tephritidae). Journal of Applied Entomology, 130, 174–188. [https://doi.org/10.1111/j.1439-0418.1985.tb02770.x](https://doi.org/10.1111/j.1439-0418.1985.tb02770.x)

Pappas, M. L., Broufas, G. D., Kouflali, N., Pieri, P., & Koveos, D. S. (2010). Effect of heat stress on survival and reproduction of the olive fruit fly Bactrocera (Dacus) oleae. Journal of Applied Entomology, 135, 359–366.

Pascual, S., Cobos, G., Seris, E., & González-Núñez, M. (2010). Effects of processed kaolin on pests and non target arthropods in a Spanish olive grove. Journal of Pest Science, 83, 121–133. [https://doi.org/10.1007/s10340-009-0278-5](https://doi.org/10.1007/s10340-009-0278-5)

Quesada-Moraga, E., Campos-Aranda, M., & Santiago-Álvez, C. (2010). Control de plagas. In J. A. Gómez (Ed.), Sostenibilidad de la producción de olivar en Andalucía (pp. 277–330). Cordoba, Spain: Instituto de Agricultura Sostenible.

Rizzo, R., Virgilio, C., & Alberto, L. (2012). Relation of fruit color, elongation, hardness, and volume to the infestation of olive cultivars by the olive fruit fly, Bactrocera oleae. Entomologia Experimentalis et Applicata, 145, 15–22. [https://doi.org/10.1111/j.1570-7458.2012.01311.x](https://doi.org/10.1111/j.1570-7458.2012.01311.x)

Ruan, F., Lozano, C., Tinaut, A., Peña, A., Pascual, F., García, P., & Campos, M. (2001). Impact of pesticides on beneficial arthropod fauna in olive orchards. IOBC/WPRS Bulletin, 24, 113–120.

Ruesink, W. G., & Kogan, M. (1994). The quantitative basis of pest management: Sampling and measuring. In L. Robert & W. H. Luckmann (Eds.), Introduction to insect pest management (pp. 309–352). New York, NY: Wiley.

Santiago-Álvez, C., & Quesada-Moraga, E. (2007). The olive fruit fly. Oleae, 26, 60–61.

Spadafora, A., Mazzuca, S., Chiappetta, F. F., Parise, A., Perri, E., & Innocenti, A. M. (2008). Oleuropein-specific-β glucosidase activity marks the early response of olive fruits (Olea europaea) to mimed insect attack. Agricultural Sciences in China, 7, 703–712. [https://doi.org/10.1016/S1671-2927(08)60105-4](https://doi.org/10.1016/S1671-2927(08)60105-4)

Stasinakis, P., Katsares, V., & Mavragani-Tsipidou, P. (2001). Organophosphate resistance and allelic frequencies of esterases in the olive fruit fly Bactrocera oleae (Diptera: Tephritidae). Journal of Agricultural and Urban Entomology, 18, 157–168.

Traper, C., Serrano, N., Arquero, O., Del Río, C., Traper, A., & López-Escudero, F. J. (2013). Field resistance to Verticillium wilt in selected olive cultivars grown in two naturally infested soils. Plant Disease, 97, 668–674. [https://doi.org/10.1094/PDIS-07-12-0654-RE](https://doi.org/10.1094/PDIS-07-12-0654-RE)

Tzanakakis, M. E. (2006). Insects and mites feeding on olive: Distribution, importance, habits, seasonal development and dormancy. Boston, MA: Brill.

Vargas, R. I., Piñero, J. C., & Leblanc, L. (2015). An overview of pest species of Bactrocera fruit flies (Diptera: Tephritidae) and the integration of biopesticides with other biological approaches for their management with a focus on the Pacific region. Insects, 6, 297–318. [https://doi.org/10.3390/insects6020297](https://doi.org/10.3390/insects6020297)

Worner, S. P. (2014). The importance of core biological disciplines in plant biosecurity. In G. Gordon & M. Simon (Eds.), The handbook of plant biosecurity (pp. 73–117). Dordrecht, the Netherlands: Springer. [https://doi.org/10.1007/978-94-007-7365-3](https://doi.org/10.1007/978-94-007-7365-3)

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