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Oviposition preference of *Ceratitis capitata* (Diptera: Tephritidae) at different times after pruning 'Italia' table grapes grown in Brazil

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Abstract

Studies investigating oviposition preference of *Ceratitis capitata* (Wiedemann, 1824) in table grapes (*Vitis vinifera* L.) cultivated in the São Francisco River Valley can provide important information to guide control measures, therefore minimizing damage caused by this species in the region. The aim of this study was to evaluate the oviposition preference of *C. capitata* females for berries cv. 'Italia' collected at five different times (60, 70, 80, 90, and 100 d after production pruning [DAPP]), representing five grapevine growth stages. We also assessed the performance of immature stages of *C. capitata* regarding the physiological development of the berry. The total soluble solid content was significantly higher in berries at more advanced physiological developmental stages (90 and 100 DAPP). Conversely, these berries showed the lowest values of firmness and titratable acidity. With the onset of physiological development, the average number of punctures per berry increased and reached 5.2 per berry in 100 DAPP berries. The infestation level and pupal weight showed a positive correlation with the growth stage. The highest recovery of pupae was observed in 100 DAPP berries (1.54). Pupal viability values ranged from 50.9 to 64.7% independent of berry maturity stage. The physiological developmental stage of the berry did not affect offspring sex ratio. Results obtained suggest that regardless of the female preference for laying eggs on berries in a more advanced physiological developmental stage, females can initiate the attack to bunches of this cultivar at 60 DAPP, even if the berries have unfavorable physicochemical parameters for oviposition and development of larvae.

Key words: Mediterranean fruit fly, development, *Vitis vinifera*, ripening

The Mediterranean fruit fly, *Ceratitis capitata* (Wiedemann, 1824), is among the most destructive agricultural pests worldwide due to high polyphagy, multivoltinism, severe direct damage caused by feeding larvae, indirect damage caused by quarantine restrictions, and its biological success in invading and adapting to diverse habitats (Liquido et al. 1991, Yuval and Hendrichs 1999, Gasperi et al. 2002, Malacrida et al. 2007, De Meyer et al. 2008). Several morphological, physiological, and behavioral traits at different life cycle stages have promoted the invasive and adaptive success of *C. capitata* (Yuval and Hendrichs 1999, Malacrida et al. 2007). As a result of its ability to occupy diverse ecological niches throughout tropical and subtropical regions, *C. capitata* infests a wide variety of hosts around the world depending on their availability (Bateman 1976, Fletcher

1989, Gasperi et al. 1991, Malacrida et al. 1992, Papanicolaou et al. 2016). *Ceratitis capitata* is endemic to sub-Saharan Africa, but a global invasion process has taken place over the past 200 yr, which has led to its colonization of tropical, subtropical, and warm temperate areas (Gasparich et al. 1997, Meixner et al. 2002, Silva et al. 2003, Malacrida et al. 2007). There are established populations of *C. capitata* throughout Africa, the Middle East, the Mediterranean region and other adjacent European countries, the Hawaiian Islands, Australia, and Central and South America (White and Elson-Harris 1992, De Meyer 1998, 1999; Silva et al. 2003; Malacrida et al. 2007; Diamantidis et al. 2009; Carey 2011).

In Brazil, *C. capitata* was reported for the first time in the early 1900s (Ihering 1901). This species was limited initially to

the southern and southeastern regions of the country, with the Recôncavo Baiano region in the state of Bahia, as its northernmost limit until the 1980s (Malavasi et al. 1980, Nascimento and Zucchi 1981). In the early 1990s, *C. capitata* was reported further north in the northeastern region (Morgante 1991) and in the late 1990s in the Amazon (Ronchi-Teles and Da Silva 1996, Silva et al. 1998). At present, this species occurs in 22 of 27 states in Brazil ranging from the state of Rio Grande do Sul in the southern region to states in the North and Northeast regions. In Brazil, *C. capitata* infests 93 hosts in 27 plant families (Zucchi and Moraes 2012). *Ceratitis capitata* is a major quarantine pest in Brazil infesting native and introduced hosts, such as fine table grapes.

The submedium region of the São Francisco River Valley (SFRV), at latitude 8–9°S and longitude 40°W, has more than 360,000 ha of irrigable land, a tropical semiarid climate, and encompasses the states of Bahia and Pernambuco in the Northeast region of Brazil (Lima et al. 2014, Cassundé et al. 2017). This region is the largest producer of fine table grapes (*Vitis vinifera* L.) for export in Brazil, and grapes are the most economically important crop in this region with approximately 13,000 ha planted (Brasil 2016). The first *V. vinifera* cultivar introduced in the region was cv. 'Italia', which is the most widely cultivated variety in the region due to its agronomic characteristics, such as vigor, high average production of 30 t ha^{-1} yr^{-1}, reaching up to 50 t ha^{-1} yr^{-1} with proper management (De Souza Leão 2004).

In the last decade, *C. capitata* was reported infesting fine table grapes in vineyards in the SFRV. At that time, the infestation level was low 0.05 pupae per berry (Botton et al. 2005). Recent monitoring data indicated an increase in *C. capitata* populations in vineyards in the region with an average number of flies per trap per day of 2.7 from January to December 2015 (BMB 2016).

One of the challenges faced by Mediterranean fruit fly females is finding adequate oviposition sites. The reproductive success of holometabolous phytophagous insects, such as Mediterranean fruit fly, especially those whose larvae have low mobility, are largely dependent on the resources selected by females via oviposition. Thus, parental traits and decisions, such as the choice of an adequate oviposition site, are critical to offspring survival and success (Yuval et al. 2002, Segura et al. 2007, Dias et al. 2017). Several studies on the host preference and acceptance of *C. capitata* have been carried out to better understand how females select the proper host for oviposition (Joachim-Bravo and Silva-Neto 2004, Diamantidis et al. 2008, Papachristos and Papadopoulos 2009). It has been found that a complex balance of plant physical and chemical factors can affect both the final selection of hosts and tephritid larval development (Joachim-Bravo et al. 2001, Aluja and Mangan 2008, Papachristos et al. 2008, Dias et al. 2017). Studies regarding the effect of different larval host on the offspring have been carried out on *C. capitata* and other polyphagous tephritids. These studies reported that larval development time and survival rates are parameters strongly influenced by hosts (Carey 1984, Krainacker et al. 1987, Liedo and Carey 1996, Vargas et al. 2000, Papachristos et al. 2008). Little or no effect was observed on egg and pupal developmental stage and survival rates (Carey 1984, Krainacker et al. 1987, Celedonio-Hurtado et al. 1988, Liedo and Carey 1996).

Host quality (e.g., size, color, penetrability, fruit maturity) is among the most important extrinsic factor that influences fruit fly oviposition behavior (Aluja and Mangan 2008). Because changes occur in the physicochemical properties of fruit throughout development, it is paramount to identify the developmental stage of the grape berry in which the onset of infestation by *C. capitata* takes place to

most effectively prevent attacks in vineyards. Therefore, this study aimed to determine the preference of *C. capitata* females for table grape berries of cv. Italia at five different grapevine growth stages based on the number of days after production pruning (DAPP). As well, we tested whether the grape cv. Italia is an appropriate host for the development of the immature stages.

Materials and Methods

Study Site
The study was performed at the Biofábrica Moscamed Brasil (BMB) located in Juazeiro, Bahia, Brazil.

Insects
The insects used in the experiments were recovered as pupae from guava fruits (*Psidium guajava* L.) collected in an orchard located in the irrigated perimeter of Maria Teresa, Petrolina (9° 8′ 46.36″ S, 40° 33′ 28.33″ W), in the state of Pernambuco. The collected fruit were placed in plastic trays (38 × 27 × 10 cm) with a layer of vermiculite, covered with voile cloth until larval emergence and pupation and kept in acclimatized rooms under controlled conditions (25 ± 2°C, 60 ± 10% RH, and a photoperiod of 14:10 [L:D] h). After 7 and 14 d, the vermiculite was sieved, and all puparia obtained were placed in acrylic cages (28 × 12 × 12 cm) with a side opening for maintenance. Upon fly emergence, males and females were separated using an aspirator and placed in new cages. This procedure ensured that insects were virgin for the experiments. The adults were fed with a solid diet of sugar and hydrolyzed yeast (Biones Quatá, São Paulo, Brazil) at ratio 3:1 (Silva-Neto et al. 2012) and filtered water ad libitum.

Grape Samples
All grapes used in the experiments were of the cv. Italia and were from a commercial vineyard located in the irrigated perimeter of Nilo Coelho (9° 18′ 16.64″ S, 40° 25′ 57.11″ W) in the state of Pernambuco. The selection criteria were no previous use of insecticides and absence of the pest in the vineyard according to the monitoring reports from the previous week. The grape bunches were collected at 60, 70, 80, 90, and 100 DAPP, thus representing the following grapevine growth stages: 32, 33, 34, 35, and 36, respectively, according to the system proposed by Coombe (1995). These grapevine growth stages were described as follows: 32 (beginning of bunch closure, berries touching—if bunches are tight), 33 (berries still hard and green), 34 (berries begin to soften, and soluble solid contents start increasing), 35 (berries begin to color and enlarge), and 36 (berries with intermediate soluble solid values). The bunches were bagged in paper bags properly identified according to the developmental stage and taken to the Laboratory of Entomology at the BMB. We started the study with 'Italia' grapes at 60 DAPP, based on preliminary observations by BMB technicians, who had detected the presence of *C. capitata* in Jackson traps on vineyards and signs of infestation in bunches at 80 DAPP.

The grape bunches were examined under a stereoscopic microscope (Leica, model EZ4D, at 40× magnification) to check for the presence of oviposition scars by *C. capitata*, and any infested grapes were discarded. After this, the bunches were selected for the number of berries (on average 21 berries per bunch), rinsed with water, and placed in plastic trays (38 × 27 × 10 cm) with a layer of paper towel at the bottom and covered with voile cloth. Subsequently, the trays were kept at 5°C in a refrigerator until the beginning of the experiment (24 h later).

Berry Physicochemical Parameters

Physicochemical parameters were determined at the Postharvest Physiology Laboratory of Embrapa Semiárido. For each grapevine growth stage evaluated, a sample of 2 kg of grapes was used. We determined titratable acidity (TA), total soluble solid content (SS), and firmness (resistance of the berry under pressure). The firmness was determined using an electronic fruit texture analyzer (Stable Micro System, model TAXT. Plus; 2-mm-diameter tip). We used five replicates of 20 berries for each grapevine growth stage and one measurement per berry. The SS content was determined by direct reading of the pulp berry extract with a digital refractometer (ATAGO, model PAL-1), and the results were expressed in ºBrix (AOAC 2002). TA was estimated using titration with 0.1 molar solution of sodium hydroxide (NaOH) and expressed as grams of tartaric acid/100 ml of juice (AOAC 2002). For the SS and TA evaluations, five replicates of juice obtained from 20 grape berries were used for each grapevine growth stage.

Oviposition Preference of *C. capitata* Females: Choice Test

The experiment was carried out in field cages ($2.80 \times 2.90 \times 2.0$ m) containing two potted *Ficus* sp. plants to provide shade and mating surfaces for insects and support for the grape bunches. In total, 100 couples, sexually mature (10–12 d old), virgin, and without previous oviposition experience, were released in each cage. One day later, five grape bunches, one of each growth stage, were offered simultaneously as oviposition substrate to females. After 24 h, the fruits were removed from the cages and taken to the laboratory to determine the presence of oviposition scars by *C. capitata* and the percentage of infested berries per bunch. During the experiment, adults were provided food (filter paper strips with sugar) and water ad libitum in 10-ml glass vials. This study was carried out in a randomized block design with five treatments (grapevine growth stages-DAPP), three cages concomitantly (blocks), and was repeated four times. In total, 12 repetitions (bunches) were used for each stage.

Development of *C. capitata* in Grape Berries

We evaluated the influence of grapevine growth stage on immature development and survival rates. For this, we used 12 bunches of each growth stage, previously exposed as oviposition substrate to females of *C. capitata* during the choice test (see experiment above). Each bunch was weighed, placed into a plastic container (500 ml) with vermiculite as pupation substrate, covered with voile cloth, and kept in a room under controlled environmental conditions (25 ± 2°C, $65 \pm 10\%$ RH, and a photoperiod of 14:10 [L:D] h). Pupae were collected at 14, 21, and 28 d after grapes infestation. Pupae collection times were selected according to results of preliminary experiments with *C. capitata* larvae on grapes under laboratory conditions, which showed that larval development was slower on this host. Pupae were placed into plastic cups (100 ml) until adult emergence. To evaluate the influence of the host on puparium weight, 1 d after pupation, 50 pupae of each grapevine growth stage were weighed individually on an analytical balance (*OHAUS Adventurer*, model AR3130, precision of 0.0001 g). After emergence, the adults were sexed. The following parameters were evaluated: number of pupae per bunch, infestation level (pupae per berry), pupal viability, pupal weight, and offspring sex ratio. The experiment was carried out in completely a random design with five treatments (grapevine growth stages–DAPP) and 12 repetitions (bunches) for each biological parameter mentioned above. For pupal weight, we used 50 pupae for each grapevine growth stage.

Statistical Analysis

Prior to statistical analysis, the Kolmogorov–Smirnov test for normality and Bartlett test for homogeneity of variances were applied to all data. When these assumptions were not met, the mathematical transformations $\sqrt{x} + 1$ and arcsine $x/100$ were used, the latter for the data to be expressed as percentage. Physicochemical differences among the berries from the five grapevine growth stages tested were determined by one-way analysis of variance (ANOVA) followed by Tukey's test to compare means. To determine the effect of grapevine growth stage on female oviposition preference, data from number of ovipositions per berry and percentage of infested berries per bunch were submitted to one-way ANOVA followed by Tukey's test (HSD). Data regarding number of pupae recovered per bunch, infestation level (pupae per berry), viability of the pupal stage, and pupal weight were also subjected to one-way ANOVA, followed by Tukey's test. For each growth stage of the berries, differences between the number of pupae recovered at 14, 21, and 28 d were determined with one-way ANOVA, and means were separated by Tukey's test. The number of male and female progeny recovered was evaluated with the Student's *t*-test. The relationship between the number of punctures per bunch and recovered pupae was determined by the Pearson correlation. All data were analyzed with the STATISTICA program v.10.0 (StatSoft Inc. 2001, Tulsa, OK).

Results

Berry Physicochemical Characteristics

The results of the berry physicochemical analysis are shown in Table 1. Firmness and TA were significantly lower in berries at more advanced physiological developmental stages (at 100 and 90 DAPP; firmness: $F_{(4, 25)} = 165.48$; $P < 0.05$; acidity: $F_{(4, 25)} = 216.17$; $P < 0.05$). These two parameters were similar in berries at 60, 70, and 80 DAPP. Conversely, the opposite was observed for the total soluble solid content (SS). This chemical parameter was lower in berries at 60, 70, and 80 DAPP than in berries at 90 and 100 DAPP, showing a monotonic increase in the level of SS content with physiological development of the berry ($F_{(4, 25)} = 277.69$; $P < 0.05$; Table 1).

Oviposition Preference of *C. capitata* Females: Choice Test

Oviposition was detected in berries of all five growth stages of the 'Italia' grapes evaluated (Table 2). The number of ovipositions per berry ($F_{(4, 55)} = 18.13$; $P < 0.05$) and ovipositions per bunch ($F_{(4, 55)} = 15.23$; $P < 0.05$) were highest in berries at 100 DAPP, reaching averages values of 5.24 ± 0.52 and 105.25 ± 9.81, respectively. The maximum number of ovipositions per berry was detected in berries at 100 DAPP (18 ovipositions per berry). The berries at 60, 70, and 80 DAPP were less preferred by the females as oviposition substrate. The percentage of infested berries was, on average, higher than 85% for the bunches at the five grapevine growth stages (DAPP), and no significant statistical differences were detected among the five treatments evaluated ($F_{(4, 55)} = 0.34$; $P = 0.8504$; Table 2).

Development of *C. capitata* in Grape Berries

The average number of pupae recovered per bunch rose with increasing physiological development of the berries, and significant differences were detected among the grapevine growth stages (DAPP; $F_{(4, 55)} = 6.62$; $P < 0.05$). The lowest average number of recovered pupae was observed in bunches from plants at 60 DAPP (Table 3). No correlation was found between the number of recovered pupae and number of ovipositions per bunch at 60 DAPP ($r = -0.1348$;

Table 1. Mean values (± SE) of physicochemical characteristics of grapes of cv. Italia at five grapevine growth stages

Stage[a]	Firmness[b]	TA[c]	SS[d]
60	11.21 ± 0.11b (10.86 –11.48)	1.93 ± 0.02a (2.01–1.86)	3.30 ± 0.08d (4.00–4.40)
70	12.28 ± 0.44ab (10.89–13.36)	1.65 ± 0.03b (1.59 –1.73)	4.10 ± 0.07d (4.00 –4.40)
80	12.45 ± 0.13a (12.14–12.87)	1.33 ± 0.03c (1.26 –1.40)	5.80 ± 0.11c (4.60 –5.20)
90	5.13 ± 0.27c (4.27–5.78)	1.39 ± 0.06c (1.20 –1.53)	10.00 ± 0.18b (7.30 –8.20)
100	5.21 ± 0.37c (4.76 –5.04)	0.49 ± 0.01d (0.45 –0.53)	12.00 ± 0.40a (11.00–13.40)

Values within a column sharing a letter did not differ significantly by Tukey's test ($P < 0.05$). Values in parentheses indicate the range of variation of the biological parameter evaluated.

[a]Days after production pruning (DAPP).

[b]Firmness expressed in Newton.

[c]Titratable acidity expressed as grams of tartaric acid per 100 ml.

[d]Soluble solid content, expressed in °Brix.

Table 2. Mean values (± SE) of number of berries per bunch, punctures per berry, and the infestation index of berries per bunch of *C. capitata* ovipositing on grapes of cv. Italia at five grapevine growth stages

Stage[a]	Berries per bunch (no.)	Punctures per berry (no.)	Ovipositions per bunch (no.)	Infested berries per bunch (%)
60	21.83 ± 0.49 (20–23)	1.82 ± 0.18c (1–6)	39.50 ± 3.80c (23–64)	84.65 ± 3.76a (61–100)
70	22.00 ± 0.55 (20–24)	2.35 ± 0.30bc (1–0)	51.08 ± 6.72bc (25–80)	89.90 ± 3.20a (70–100)
80	21.50 ± 0.60 (20–23)	2.33 ± 0.22bc (1–8)	49.67 ± 4.24bc (24–79)	90.64 ± 3.97a (50–100)
90	20.42 ± 0.48 (18–23)	3.52 ± 0.26b (1–11)	72.25 ± 5.99b (24–102)	93.87 ± 3.41a (61–100)
100	20.20 ± 0.46 (18–21)	5.24 ± 0.52a (1–18)	105.25 ± 9.81a (44–163)	95.74 ± 1.60a (84–100)

Values within a column sharing a letter did not differ significantly by Tukey's test ($P < 0.05$). Values in parentheses indicate the range of variation of the biological parameter evaluated.

[a]Days after the production pruning (DAPP).

$P = 0.6762$), 70 DAPP ($r = -0.3426$; $P = 0.2756$), 80 DAPP ($r = 0.1091$; $P = 0.7358$), and 90 DAPP ($r = -0.3190$, $P = 0.3122$). However, a positive correlation was observed between these two parameters for berries at 100 DAPP ($r = 0.6812$; $P < 0.05$).

The infestation level was also correlated with the development physiological stage of the berry (DAPP; $F_{(4, 55)} = 7.19$; $P < 0.05$), and differences were detected between the berries that correspond to the most advanced grapevine growth stages (90 and 100 DAPP) and the initial growth stages (60, 70, and 80 DAPP). On average, the highest number of pupae per berry was detected in bunches at 90 DAPP (15.75) and 100 DAPP (30.55; Table 3).

The recovery of pupae at 14, 21, and 28 d after the exposure of bunches to infestation is shown in Fig. 1. For each grapevine growth stage tested, significant differences were detected between the three time intervals evaluated (60 DAPP: $F_{(2, 33)} = 9.90$; 70 DAPP: $F_{(2, 33)} = 9.49$; 80 DAPP: $F_{(2, 33)} = 7.89$; 90 DAPP: $F_{(2, 33)} = 9.53$; 100 DAPP: $F_{(2, 32)} = 4.63$; $P < 0.05$). Pupae recovery was much higher at 21 d after infestation for berries at 60, 80, and 90 DAPP. However, a different behavior was observed for berries at 70 and 100 DAPP, with a similar number of pupae recovered at 14 and 21 d after infestation. For all five grapevine growth stages, pupae of *C. capitata* were recovered at 14, 21, and 28 d after infestation, which shows intrapopulational variation in the rate of larval development.

Pupal weight was influenced by the development physiological stage of the berry ($F_{(4, 245)} = 87.34$; $P < 0.05$; Table 3). The lowest average pupal weight was observed in berries at 60 and 70 DAPP and the highest average pupal weight in berries at 100 DAPP (10.12 ± 0.27 mg). No effect from the developmental stage was observed on pupal viability ($F_{(4, 55)} = 0.68$; $P = 0.6072$). Average values for this parameter were as follows: 51.31 ± 9.41; 50.98 ± 5.82; 53.42 ± 9.36; 64.68 ± 3.86, and 52.82 ± 3.62, for berries at 60, 70, 80, 90, and 100 DAPP, respectively.

No significant differences were detected regarding female and male emergence in the offspring recovered from the bunches of the five grapevine growth stages evaluated (60 DAPP: $t = 0.01$; df = 22; $P = 0.6610$; 70 DAPP: $t = 0.66$; df = 22; $P = 0.1589$; 80 DAPP: $t = 1.78$; df = 22; $P = 0.4992$; 90 DAPP: $t = 0.35$; df = 22; $P = 0.7199$; 100 DAPP: $t = 1.09$; df = 22; $P = 0.4842$). The physiological developmental stage of the berry had no effect on the sex ratio of the progenies obtained in the experiment ($F_{(4, 52)} = 1.08$; $P = 0.3767$), which ranged from 0.53 to 0.70 (Table 3).

Discussion

The location and acceptance of host fruits by tephritid females is a complex process in which both physical and chemical signals from the host plant are involved (Vargas et al. 1991, Aluja and Prokopy 1992, Aluja and Mangan 2008). Among the important visual and tactile stimuli are color, shape, and size of fruit (McInnis 1989; Levinson et al. 2003). In addition, among the important chemical stimuli are semiochemicals produced and released by the host plant, host-marking pheromones, and volatiles released during fruit ripening (Hernandez et al. 1999, Rattanapun et al. 2009). The oviposition preference hierarchy of *C. capitata* females in the present study regarding the physiological developmental stage (DAPP) of the grape berries is likely due to the changes in the physicochemical composition during ripening. Our physicochemical results indicated that berries at 90 and 100 DAPP were less firm, had lower acidity and higher soluble solid content, and showed a higher number of ovipositions per berry. These changes in berry physicochemical composition are consistent with grape ripening. The observed values of SS, acidity, and firmness are expected for the cv. Italia in the physiological developmental stage studied.

Table 3. Mean values (± SE) of biological parameters of *C. capitata* immatures and adults in grapes of cv. Italia at five grapevine growth stages

Stages[a]	Pupae per bunch (no.)	Infestation index[b] (no.)	Pupa wt (mg)	Adults recovered per bunch (no.)		Offspring sex ratio (♀/(♀+♂))
				♀ (no.)	♂ (no.)	
60	9.58 ± 1.53b (1–17)	0.44 ± 0.08b (0.04–0.85)	4.04 ± 0.28d (1–7)	2.45 ± 0.53A (0–6)	2.55 ± 0.64A (0–7)	0.53 ± 0.10a (0–1)
70	14.00 ± 2.57b (2–33)	0.63 ± 0.12b (0.0–1.57)	4.10 ± 0.23d (1–8)	4.75 ± 1.46A (0–15)	3.25 ± 0.78A (0–9)	0.54 ± 0.08a (0–1)
80	10.83 ± 2.22b (1–21)	0.50 ± 0.10b (0.04–1.00)	5.68 ± 0.24c (1–9)	4.42 ± 0.99A (0–11)	2.17 ± 0.68A (0–7)	0.69 ± 0.06a (0–1)
90	15.75 ± 2.83b (7–39)	0.76 ± 0.13b (0.32–1.86)	7.54 ± 0.23b (3–11)	5.67 ± 1.48A (0–19)	5.25 ± 1.27A (0–14)	0.57 ± 0.08a (0–1)
100	30.55 ± 5.38a (8–69)	1.54 ± 0.30a (0.38–3.83)	10.12 ± 0.27a (6–14)	8.67 ± 1.56A (2–17)	6.67 ± 1.66A (0–21)	0.56 ± 0.07a (0.38–1)

Values followed by the same lowercase letter in the column or uppercase letter in the same line did not differ significantly by Tukey's test ($P < 0.05$) and Student's *t*-test ($P < 0.05$), respectively. Values in parentheses indicate the range of variation of the biological parameter evaluated.

[a]Days after the production pruning (DAPP).

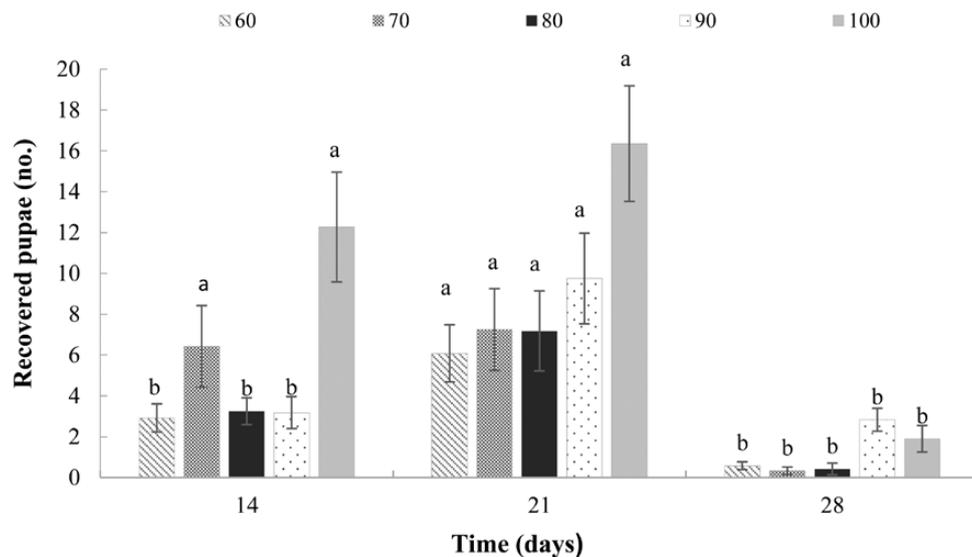[b]Number of pupae per berry.

Fig. 1. Mean values (± SE) of pupae recovered per grape bunch of cv. Italia at 14, 21, and 28 d post-oviposition. Columns of the fill type capped by the same letters do not differ significantly by Tukey's test ($P < 0.05$).

Several studies have reported the preference of tephritid females to oviposit in ripe or ripening fruit, which have a softer pericarp (Oi and Mau 1989, Jang and Light 1991, Hernandez et al. 1996, Rattanapun et al. 2009). Rattanapun et al. (2009) observed a preference of *Bactrocera dorsalis* (Hendel, 1912) (Diptera: Tephritidae) females to oviposit on softer parts of mangoes (*Mangifera indica* L.), which had higher levels of soluble solid content. Regarding *C. capitata*, Joachim-Bravo et al. (2001) registered higher oviposition activity on the ripest parts of papayas (*Carica papaya* L.). Santana (2012) reported a preference gradient of oviposition of *C. capitata* females on Barbados cherry (*Malpighia glabra* L.) in distinct maturation stages and the highest number of ovipositions on ripe fruit. These results corroborate our findings on the oviposition preference of *C. capitata* females for berries in initial maturity stages (90 and 100 DAPP).

However, it is noteworthy that we also detected ovipositions on berries at 60, 70, and 80 DAPP. The presence of eggs in less preferred fruit free choice conditions in the laboratory may be due to the presence of host-marking pheromone deposited by *C. capitata* in highly infested fruit (Prokopy et al. 1978, Silva et al. 2012). Conversely, Krainacker et al. (1987) suggested that this kind of behavior could also be related to the lack of fine host discrimination in *C. capitata*, which could also contribute to its polyphagy.

The number of pupae recovered per bunch was highest at more advanced physiological developmental stages, which *guajava* ted the influence of chemical characteristics of the substrate (SS and acidity) on larval development and survival. During ripening, grape berries undergo several structural changes, such as thinning of the cell wall in the mesocarp cells, expansion of the cellular volume, changes in the exocarp and vascular tissues, among others. These changes make the berries less firm (Keller 2010), which could make larval development and movement easier inside the berries. Acidity and soluble solids content also change with fruit ripening. A decrease in acidity may be due to the dilution of organic acids as a result of the increase in the berry volume (Rizzon et al. 2000). An increase in the level soluble solids content is linked to an increase in the synthesis of fructose and glucose.

In our study, pupae of *C. capitata* were recovered from infested berries in the five developmental stages of 'Italia' grapes tested. Our results contrast with those of Zart et al. (2011) for *Anastrepha fraterculus* (Wiedemann, 1830) (Diptera: Tephritidae) wine grapes. These authors did not find well-developed larvae in berries of the grape cv. 'Moscato Embrapa' when bunches were exposed to infestation by *A. fraterculus* during the phenological subperiod of pea and bunch closure. In the cv. 'Niagara Rosada', these authors found

ovipositions in bunches at the beginning of the ripening process and also at the fully ripened stage. However, larvae did not pupate under laboratory conditions for the latter cultivar.

The berry physiological developmental stage also influenced pupal weight of *C. capitata*. This is an important parameter because it directly interferes with adult survival of *C. capitata* (Krainacker et al. 1989, Liedo and Carey 1996). The success of the metamorphosis from pupa to adult depends mostly on a proper larval development, which depends on the quality of the feeding substrate because this is the trophic stage during which food is ingested and stored for pupation and adult emergence (Cruz et al. 2000, Labandeira 2005). However, our results showed that about 50% of the recovered pupae hatched regardless of the berry developmental stage. Moreover, a decrease in larval development was observed in this host as pupae were recovered at 21 and 28 d after infestation in berries at 60, 70, 80, 90, and 100 DAPP. Our results contrast with those for *C. capitata* on other hosts (Krainacker et al. 1987, Fernandes-da-Silva and Zucoloto 1993, Costa et al. 2011). Our results on 'Italia' grapes suggest that factors other than the physicochemical composition of the grapes influenced the adequacy of this substrate for the larval development of *C. capitata*. Papachristos et al. (2008) did not observe a correlation between SS content, pH, acidity, and larval and pupal survival of *C. capitata* in different *Citrus* species either. According to these authors, the changes in other compounds of the fruit pulp (e.g., fatty acids, aminoacids, monoterpens, and glycosylate flavonoids) could play a determinant role in the development and survival of immature stages of *C. capitata* in citric species.

Our results showed that *C. capitata* females preferred to oviposit on 'Italia' grapes during the initial maturity stages (when berries begin to color, enlarge, and with intermediate soluble solid values), which is associated with choosing a better substrate, sweeter, and less acid for the proper development of the immature stages. However, females can initiate infestation in vineyards of this cultivar at 60 DAPP, when fruits still have physicochemical characteristics that are unfavorable for oviposition and development of immature stages. The fact that females oviposited on a nutritiously unfavorable host may represent an advantage for *C. capitata* when preferred hosts are scarce. Moreover, our results also help to better understand vineyard infestation rates and the susceptibility of different physiological developmental stages of Italia berries to *C. capitata* in the region of the São Francisco River Valley.

Acknowledgments

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