Characteristics of Chili (*Capsicum annuum* L.) That Are Resistant and Susceptible to Oriental Fruit Fly (*Bactrocera dorsalis* Hendel) Infestation

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Abstract: The response of chili (*Capsicum annuum* L.) to oriental fruit fly infestation (*Bactrocera dorsalis*) is highly variable among varieties. The differences in the resistance level of chili to oriental fruit fly infestation are presumed to be determined by the characteristics of chili fruit. This study aims to evaluate the morphochemical characteristics of different resistance levels of chili fruits to oriental fruit fly infestation in field conditions. The field test was carried out at the research station of the Indonesian Vegetable Research Institute (IVEGRI), West Java, Indonesia. Six essential derivatives of *C. annuum* from IVEGRI, consisting of three resistant and three susceptible varieties, were established in a prior investigation. The test population included 132 plants, with 22 plants planted for each variety. The resistance parameters observed were oviposition incidence, yield loss, fitness index, and chili fruit characteristics (morphology, nutrition, volatile compounds). The results showed that there were morphological and chemical differences between the varieties resistant and susceptible to oriental fruit fly infestation. The morphological characteristics of the fruit (width, weight, and thickness of fruit flesh) and fruit shape at pedicel attachment had an impact on the resistance level of fruit flies. Meanwhile, volatile compounds, water content, carbohydrates, and fiber content were among the chemical features that influenced oriental fruit fly infestation.

Keywords: antixenosis; *Bactrocera dorsalis*; morphology; nutrition; volatile compounds

1. Introduction

The oriental fruit fly (*Bactrocera dorsalis*) is a major insect pest in chili cultivation in Indonesia that has an economic impact. The damage begins when the female fruit flies lay eggs on chili fruit. After two days, the eggs hatch into larvae and consume the fruit flesh, making the fruit rotten and unable to be sold, causing farmers to lose their crops. Several studies have reported that the rate of loss of chili fruits by fruit flies varies between 40 and 60% and could reach up to 100% loss if there is no fruit fly control [1,2].

The resistance of chili fruits to fruit fly infestation varies across cultivars, as shown by the deterrent index for antixenosis and the fitness index for antibiosis [3]. Experiments by Syamsudin et al. [3] on fifty chili varieties of fruit fly infestation in the laboratory showed that the prevention of oviposition by the chosen method was in the range from 46.01% to 100%; however, the no-choice method was in the range from 11.11% to 99.07%, while the fitness index of oriental fruit fly feeding on chili fruits was in the range from 0.03 to 6.74. These results indicate that the resistance of chili to oriental fruit fly infestation is determined by variety. The difference in the resistance level of chili varieties to fruit flies might be determined by the characteristics of chili fruits. Bosland and Votava [4] reported that chili fruits exhibit a wide range of morphological and chemical features. Morphologically, chili fruits have a high degree of variability in their characteristics (shape, color, and size).
Meanwhile, based on their chemical composition, chili fruits vary in terms of water content, carbohydrates, fats, amino acids, proteins, fragrances, anthocyanins, antioxidants, vitamins, carotenoids, and capsaicinoids. Several studies have shown that the chemical composition of chili changes according to the variety [5,6]. As a result, the diversity of chili fruit traits may have an influence on the resistance level of varieties to fruit flies.

Chili fruits can be protected from oriental fruit fly infestation if they are able to prevent female fruit flies from laying eggs and inhibit larval growth and development. A previous study has identified resistant and susceptible varieties of oriental fruit fly infestation and established a correlation between fruit morphological characteristics and the resistance level of fifty chili varieties to fruit flies. Large-fruited chili varieties from the species of *C. annuum* (large chili) are more sensitive than small-fruited chili varieties from *C. annuum* (curly chili) and *C. frutescens* (cayenne pepper) species [3]. The resistance level of large chili and curly chili varieties to fruit fly infestation can be determined by the differences in the characteristics of each variety. This study aims to evaluate the morphochemical characteristics of different resistance levels of chili fruits to oriental fruit fly infestation in field conditions. This in-depth study is expected to help in the understanding of the mechanism behind chili resistance to oriental fruit fly infestation and hopefully serve as the basis for the initiation of plant breeding programs for chili resistance to fruit flies.

2. Materials and Methods

2.1. Study Site

The research was conducted at the research station of the Indonesian Vegetable Research Institute (IVEGRI) (6°47′57″ S, 107°39′01″ E), at 1250 m above sea level (West Java, Indonesia).

2.2. Plant Materials

Six essential derivatives of IVEGRI chili varieties from the species *C. annuum* were used for these experiments, consisting of three resistant varieties (RK-1, RK-2, and RK-3) and three susceptible varieties (RK-4, RK-5, and RK-6) identified from previous research [3]. Each variety was planted in a plot measuring 1 m × 6 m. Each plot was planted with 22 individual plants, resulting in a total plant population of 132 plants. The chili cultivation technique followed the recommendation of IVEGRI [7]. Chili seeds were sown in a nursery tray using a mix of sterile soil medium and organic fertilizer (1:1). Subsequently, one-month-old seedlings were transplanted into planting plots in the field. Plants were maintained by regular weeding, watering, fertilizer application, pest control against thrips, aphids, and mites using a commercial pesticide containing profenofos (1 mL/L), imidacloprid (0.25 mL/L), and mancozeb (2 g/L).

2.3. Resistance of Chili to Infestation of Fruit Flies

In the field, the resistance of chili fruit to oriental fruit fly infestation was determined by counting oviposition incidence, yield loss, and fitness index. Fruit fly oviposition incidence was determined by the number of infested plants divided by the total number of plants. Yield loss was calculated at the harvest period based on the number of infested fruits divided by the total number of harvested fruits. Infested fruits were identified by the presence of ovipositor punctures and/or larvae inside the fruits. The fitness index was calculated using the number and respective weight of pupae, the duration of egg to pupa, and the duration of egg to imago, as described by Syamsudin et al. [3].

2.4. Morphological Characteristics of Chili Fruit

Analysis of chili morphological characteristics focused on 22 fruit traits according to the International Plant Genetic Resources Institute [8]. Observation of morphological characteristics was conducted based on 22 characteristics of chili fruits. The fruit characteristics were number of days until fruiting (D), anthocyanin spots or stripes (A), fruit color before at intermediate stage (FC), fruit set (FS), fruit-bearing period (FB), fruit color at maturity stage (FCM), fruit shape (FSH), fruit length (FL), fruit width (FW), fruit
weight (FWG), fruit pedicel length (FP), fruit wall thickness (FWT), fruit shape at pedicel attachment (FSHP), neck at base of fruit (N), fruit shape at blossom end (FSHB), fruit blossom end appendage (FBA), fruit cross-sectional corrugation (FCS), number of locules (N), fruit surface (FSU), ripe fruit persistence (RFP), placenta length (PL), and varietal mixture condition (VM).

2.5. Analysis of Volatile Compounds

Volatile compounds were analyzed using gas chromatography–mass spectrometry (GC–MS) following the method described by Junior et al. [9] and Kirana et al. [10] with several adjustments. Fruit samples were extracted using the solid-phase microextraction (SPME) method. Four grams of chili fruits was injected into a 40 mL SPME vial containing polytetrafluoroethylene (PTFE)/silicone septa and incubated at 30 °C for 30 min. Samples were taken using SPME fiber 50/30 mm divinylbenzene/carboxen/polydimethylsiloxane-DVB/CAR/PDMS (Supelco Co., Bellefonte, PA, USA) and injected in splitless mode at 45 °C, held for 2 min, and increased to 250 °C in increments of 5 °C/min for 5 min. Column separation used DB-5 MS (Agilent, Santa Carla, CA, USA), and the carrier gas was helium at a rate of 1 mL/min.

Volatile compounds were identified based on the retention time on the GC (Agilent 7890 A) and mass spectrophotometer (Agilent 5975 C) apparatus. The relative volatile compound content data were determined using the NIST08 library. Then, they were tabulated and calculated for the presence index of volatile compounds as the ratio of the presence of volatile compounds to the total detected volatile compounds. The detected volatile compounds were selected based on the area and degree of similarity to the library [11,12].

2.6. Oriental Fruit Fly Response to Selected Volatile Compounds

Determination of selected volatile compounds was tested on oriental fruit fly response using the preference choice method [13,14] with several adjustments. The volatile compounds of interest were dissolved in 100 ppm methanol. A 200 µL volume of the solution was dripped on a black cloth attached to the artificial egg-laying place, while 200 µL of methanol was used as a control. Twenty-five pairs of fruit flies (28 days old) were placed in cages (20 cm × 20 cm × 20 cm). The number of ovipositions and the number of eggs oviposited were recorded. The test was repeated 16 times. Observation was conducted from 11.00 to 15.00 h West Indonesian Time.

2.7. Analysis of Nutritional Content

Chili fruits (without seeds and placenta) were grounded into powder and subjected to nutritional content analysis to determine water, carbohydrate, and fiber content [15].

2.7.1. Water Content

Two grams of the sample was dried in an oven at 105 °C until a constant weight was reached. Water content (%) was determined by dividing the weight of the dried sample by the weight of the sample before drying.

2.7.2. Carbohydrate Content

Five grams of the sample was placed into an Erlenmeyer flask, followed by the addition of 200 mL of 30%HCl solution, and then heated. After cooling, the solution was neutralized with 10% NaOH. The solution was then transferred to a volumetric flask with distilled water added up to 500 mL and filtered. A total of 10 mL of the solution was pipetted and added to a 250 mL Erlenmeyer flask with Luff Schooli solution (that was filtered and supplemented with a few boiling stones), followed by the addition of 15 mL of distilled water. Erlenmeyer flasks containing samples and blanks (without samples) were installed on a standing cooler before being heated. The heater was regulated so that the contents of the Erlenmeyer flasks could boil within ±3 min and were maintained for 10 min. It was then cooled rapidly under flowing water. Subsequently, 15 mL of 20% I2KI solution and
25 mL of 25% H$_2$SO$_4$ were unhurriedly added. After the reaction was complete, titration was carried out with thiosulfate (Na$_2$S$_2$O$_3$) 0.1 N solution and starch solution indicator. Carbohydrate content was calculated using the formula \((A_t \times F_p/g) \times 0.90 \times 100\), where \(A_t\) is the number in the Luff Schoorl table, \(F_p\) is the dilution factor, and \(g\) is the sample weight (mg).

2.7.3. Fiber Content

Two grams of the sample was weighed on a preweighed glass. The glazed glass was attached to the extraction heater, and 50 mL of 1.25% H$_2$SO$_4$ was added and boiled for 30 min. Then, it was rinsed with hot water before adding 50 mL of 3.25% NaOH and boiling for 30 min. Subsequently, it was rinsed with 96% ethanol and heated in an oven at 105°C for 1 h. The sample was removed from the oven and cooled in a desiccator for 30 min. Drying and cooling were repeated until a constant sample weight was reached. Fiber content (%) was obtained by calculating the weight of the sample after drying divided by the weight of the sample before drying.

2.8. Data Analysis

Differences in observational parameters between varieties were tested using the Kruskal–Wallis statistical test. Multivariate analysis among parameters used principal component analysis. Data analysis used the PAST program version 3.14 [16] and MetaboAnalyst 5.0 [17].

3. Results

3.1. Resistance Characteristics

Resistant varieties RK-1, RK-2, and RK-3 showed lower incidence, yield loss, and fitness index values than susceptible RK-4, RK-5, and RK-6 varieties (Figure 1). The average oviposition incidence of fruit flies was higher in susceptible varieties (25.9–41.6%) than in resistant varieties (12.8–17.2%) (Figure 1a). Susceptible varieties also had higher yield loss (17.1–36.5%) than resistant varieties (2.4–7.5%) (Figure 1b). Furthermore, the average fitness index was higher in susceptible varieties (1.9–8.2) than in resistant varieties (0.3–0.9) (Figure 1c). RK-5 was the most susceptible variety, with an average fitness index of 8.2.

3.2. Morphological Characteristics of Chili Fruit

Observation of 22 characteristics of fruits revealed that 10 characteristics differed across varieties, while the other 12 characteristics showed no variation among the six varieties tested. Eight of the ten characteristics showed a significant difference among varieties, while the other two did not (Supplementary Table S1). The fruit morphological characteristics that are capable of discriminating resistant and susceptible varieties include width, weight, fruit set, fruit wall thickness, fruit shape at pedicel attachment, and fruit surface (Figures 2 and 3). In comparison to susceptible varieties, resistant varieties had a significantly narrower fruit width (Figure 2a), significantly lighter fruit weight (Figure 2b), significantly higher fruit set (Figure 2c), significantly smaller fruit wall thickness (Figure 2d), significantly smaller fruit shape at the pedicel attachment (Figure 2e), and significantly rougher fruit surface (Figure 2f).
Figure 1. Resistance of six chili varieties to oriental fruit fly infestation in the field, as shown by (a) oviposition incidence, (b) yield loss, and (c) fitness index. RK-1, RK-2, and RK-3 are resistance varieties; RK-4, RK-5, and RK-6 are susceptible varieties. Different letters above each column indicate significant differences between the mean values.

Figure 2. Cont.
Figure 2. Characteristics of chili fruits against oriental fruit fly infestation, as shown by (a) fruit width, (b) fruit weight, (c) fruit set, (d) fruit wall thickness, (e) fruit shape at pedicel attachment, and (f) fruit surface. Different letters above each column indicate significant differences between the mean values.

Figure 3. Morphological performance of chili fruits used in this. RK-1, RK-2, and RK-3 are resistant varieties; RK-4, RK-5, and RK-6 are susceptible varieties.

The fruit morphological characteristics (width, weight, wall thickness, and base shape of fruits) were positively correlated (value: >0.6) with the incidence, yield loss, and fitness index (Figure 4). Based on the position of the variety in the quadrant, the most susceptible variety to oriental fruit fly infestation was RK-5 since it was in the quadrant with the resistance parameter, while the most resistant variety was RK-3, as it was in the quadrant opposite the resistance parameter (Figure 5).
Figure 4. Correlation of morphological and resistance characteristics of chili fruits: days to fruiting (D), fruit set (FS), fruit-bearing period (FBP), fruit color at maturity stage, fruit shape, fruit length (FL), fruit width (FW), fruit weight (FWG), fruit pedicel length (FPL), fruit wall thickness (FWT), fruit shape at pedicel attachment (FSHP), fruit surface (FSU), ripe fruit persistence, placenta length, and varietal mixture condition. Oviposition incidence (OI), yield loss (YL), and fitness index (FI).

Figure 5. Morphological and resistance characteristics of chili fruits based on PCA: days to fruiting (D), fruit set (FS), fruit-bearing period (FB), fruit length (FL), fruit width (FW), fruit weight (FWG), fruit pedicel length (FP), fruit wall thickness (FWT), fruit shape at pedicel attachment (FSHP). Oviposition incidence (OI), yield loss (YL), and fitness index (FI).
3.3. Characteristics of Volatile Compounds

Fifty-eight types of volatile compounds were detected through GC–MS analysis. Chromatogram profiles between resistant and susceptible varieties of chili showed a difference except for RK-1. The presence of volatile compounds was more varied in susceptible chili varieties than in resistant varieties (Figure 6). Seventeen of the fifty-eight volatile compounds detected by GC–MS had an area greater than 2% (Table 1). Further analysis of the 17 dominant volatile compounds showed that 8 volatile compounds (furan, 2-methyl-; formic acid, 2-methylbuthyl ester; furan, 3-butylytetrahydro-2-methyl-, trans-; 1,9-decadiyne; trans-3-decene; 4-octene, 2,6-dimethyl-, [S-(E)]; cis-2,6-dimethyl-2,6-octadiene; β-cis-ocimene) were correlated with oviposition incidence (Figure 7), and two compounds had a quality value above 90%. Interestingly, β-cis-ocimene was only detected in susceptible variety RK-5 in a significant amount (Table 1).

![Figure 6](image_url)

Figure 6. Presence of volatile compounds released resistant and susceptible varieties of chili fruit. Different letters above each column indicate significant differences between the mean values.

Table 1. Dominant volatile compounds from six chili varieties detected by GC–MS.

| No. | RT (min.) | Volatile Compounds | Q (%) | Relative Area (%) |
|-----|-----------|--------------------|-------|-------------------|
|     |           |                    |       | RK-1  | RK-2  | RK-3  | RK-4  | RK-5  | RK-6  |
| 1   | 4.36      | Furan, 2-methyl-   | 91    | 0     | 0     | 10.52 | 12.43 | 0     |        |
| 2   | 4.6       | 1-Hexyne, 5-methyl-| 38    | 11.7  | 0     | 0     | 0     | 0     |        |
| 3   | 5.87      | Silanediol, dimethyl| 2     | 5.21  | 0     | 0     | 17.26 | 0     |        |
| 4   | 6.03      | Acetamide, 2-fluoro | 3     | 10.26 | 3.91  | 0     | 0     | 0     |        |
| 5   | 6.19      | Formic acid, 2-methyl butyl ester | 35 | 0     | 0     | 0     | 0     | 28.4  |        |
| 6   | 9.52      | Furan, 3-butylytetrahydro-2-methyl-, trans- | 9    | 0     | 0     | 0     | 0     | 5.36  |        |
| 7   | 11.41     | 1,9-Decadiyne      | 27    | 0     | 0     | 3.33  | 0     | 0     | 0     |
| 8   | 11.84     | trans-3-Decene     | 37    | 0     | 0     | 0     | 0     | 0     | 3.2   |
| 9   | 12.19     | 4-Octene, 2,6-dimethyl-, [S-(E)]- | 64   | 0     | 0     | 0     | 0     | 0     | 2.75  |
| 10  | 13.14     | cis-2,6-Dimethyl-2,6-octadiene | 80   | 0     | 0     | 0     | 0     | 5.19  | 0     |
| 11  | 14.5      | β-cis-Ocimene      | 91    | 0     | 0     | 0     | 0     | 0     | 17.81 |
| 12  | 21.74     | 1,4-Benzenedi-methanethiol, 2TBDMS derivates | 36   | 0     | 2.36  | 0     | 0     | 0     | 0     |
| 13  | 42.25     | 2-Tetradecanol     | 35    | 0     | 0     | 0     | 2.78  | 0     | 0     |
| 14  | 43.1      | 1-Octadecane       | 35    | 7.23  | 0     | 0     | 0     | 0     | 0     |
| 15  | 43.61     | Butyl dodecyl ether | 35   | 7.51  | 0     | 0     | 4.07  | 0     | 0     |
| 16  | 44.26     | Isobutyl nonyl carbonate | 50 | 0     | 0     | 0     | 2.25  | 0     | 0     |
| 17  | 46.38     | 1-Decanol, 2-hexyl  | 22    | 12.67 | 0     | 0     | 0     | 0     | 0     |

1 RT = retention time; 2 Q = quality.
Figure 7. Correlation of seventeen volatile compounds to oviposition incidence (OI) of oriental fruit fly in chili fruit. The number at the horizontal axis represents the volatile compounds described in Table 1.

Principal component analysis also mapped the position of resistant varieties and susceptible varieties in each quadrant. The volatile compounds released by RK-5 were similar to those emitted during oviposition incidence, and RK-5 was identified as the variety with the highest oviposition incidence (Figure 8).

Figure 8. Relationship of volatile compounds released by six chili varieties (RK1-RK6) with the oviposition incidence (OI) of oriental fruit fly.

A further test to confirm that insects were attracted to β-cis-octimene showed that female fruit flies responded to the volatile compounds (octimene) by increasing the number of ovipositions (Figure 9a) and eggs laid (Figure 9b) compared to the control treatment.
Nutritional characteristics of six chili varieties (RK1–RK6) on (a) water content, (b) carbohydrate content, and (c) fiber content. Different letters above each column indicate significant differences between the mean values.

3.4. Nutritional Characteristics

In this study, the nutritional characteristics of chili were tested, including water, carbohydrates, and fiber content. The results showed that there were significant differences in water content between varieties \( p = 0.0004 \), as susceptible varieties had higher water content compared to resistant chili varieties except for RK-5 (Figure 10a). The carbohydrate content of resistant chili varieties was significantly lower than susceptible chili varieties \( p = 0.0005 \) (Figure 10b). On the other hand, resistant varieties had a considerably higher fiber content than susceptible chili varieties \( p = 0.0004 \) (Figure 10c).

Figure 8. Relationship of volatile compounds released by six chili varieties (RK1–RK6) with the oviposition index (OI) of oriental fruit fly. Note: -cis-ocimene (O) and control (C). Different letters above each column indicate significant differences between the mean values.

Figure 9. Response of oriental fruit fly to \( \beta \)-cis-ocimene, as shown by the number of ovipositions (a) and eggs laid (b). Note: \( \beta \)-cis-ocimene (O) and control (C). Different letters above each column indicate significant differences between the mean values.

Figure 10. Nutritional characteristics of six chili varieties (RK1–RK6) on (a) water content, (b) carbohydrate content, and (c) fiber content. Different letters above each column indicate significant differences between the mean values.
Principal component analysis revealed a correlation between the nutritional characteristics of chili fruits and their resistance level to oriental fruit fly infestation. Water content (WC) and carbohydrates (C) were positively correlated with the fitness index (IF) (correlation coefficients were 0.79 and 0.90, respectively). Meanwhile, the fiber content (F) was negatively correlated with the fitness index (correlation coefficient was $-0.92$) (Figure 11).

![Figure 11](image-url)  
**Figure 11.** Correlation of water content (WC), carbohydrate content (C), and fiber content (F) with the fitness index (FI) of oriental fruit fly in six chili varieties.

Principal component analysis also mapped the position of the varieties tested. Based on the quadrant position, the RK-5 variety was shown to be the most susceptible to oriental fruit fly infestation since it was in the same quadrant as the fitness index (Figure 12).

![Figure 12](image-url)  
**Figure 12.** Relationship of water content (WC), carbohydrate content (C), and fiber content (F) with the fitness index (FI) of oriental fruit fly in six chili varieties.
4. Discussion

In field conditions, there were variations in the resistance and susceptibility of chili varieties to oriental fruit fly infestation. The obtained fitness index values were higher than those reported by Jallow and Zalucki [18] for *H. armigera* in corn (0.2), cotton, and cowpea (0.6), as well as in artificial media (1.2). The fitness index describes the ability of fruit flies to complete one or more phases of their life cycle inside chili fruits. The results of this research indicate that the fitness index of the oriental fruit fly is highly determined by the chili variety. Based on the resistance characteristics, our findings also corroborate previous studies stating that the variety impacts the resistance of chili to fruit fly infestation. In corn, resistant and susceptible varieties have been used as components of a push–pull strategy in pest control [19]. Accordingly, the susceptible chili varieties identified in this study have a pull characteristic capable of attracting fruit flies for oviposition. As a consequence, breeding activities aimed at reducing the pull characteristic in susceptible varieties should be able to minimize oviposition incidence.

In comparison to resistant chili varieties, susceptible chili varieties featured larger, wider, and heavier fruit, thicker flesh, and a wider fruit base. The width and weight of the fruits, as well as the thickness of the fruit flesh, are characteristics that determine the size of bigger or smaller chili fruit. Meanwhile, the fruit shape at pedicel attachment is a qualitative characteristic following the fruit surface area. A chili fruit with a narrow surface area may have a pointed base shape, while a chili fruit with a wider surface area may have a rounded base shape. The fruit size is correlated with the resistance level since female fruit flies mostly attack host plants with large fruits. Large fruit size can ensure the survival of oriental fruit fly larvae. According to Nufio and Papaj [20], oriental fruit fly imago developed from larvae in larger fruit survive longer than larvae developed in small fruits. Similar findings have also been reported, stating that there is a correlation between fruit size and fruit fly attack levels of several commodities, such as in mangos, tomatoes, and oranges [21–23]. The larger the fruits, the greater the likelihood that they will serve as a host for insect pests such as fruit fly species.

Several studies have shown an association between the volatile compounds of host plants and insect activity. Female insects employ the volatile compounds emitted by host plants to mark a place for oviposition and to choose male fruit flies [24–26]. The volatile compounds released by host plants can be detected by insects during the period of searching and selecting host plant locations [27,28]. Chili releases various kinds of volatile compounds [5,29,30]. The composition of volatile compounds is assumed to be correlated with the resistance level of chili to herbivore infestation such as fruit flies. The results of this study corroborated earlier findings that the volatile compounds generated by host plants are directly correlated with the process of host searching by oriental fruit flies [10,14,19,25,31–33]. Susceptible chili varieties released volatile compounds, including β-cis-ocimene, which acted as an attractant for oriental fruit flies seeking oviposition, consequently indicating high oviposition incidence. Due to the high level of fruit fly mobility, volatile compounds are detected by their antenna, and they use this information to determine the existence of food sources and locations for ovipositing their eggs [34]. Therefore, lowering the concentration of this dominant compound in susceptible chili varieties will decrease the level of fruit damage caused by oriental fruit fly infestation. Farré-Armengol [35] stated that β-ocimene is one of the most ubiquitous volatile substances in floral scents and plays multiple important roles in plants, which vary depending on the organ and time of emission.

Hafsi et al. [36] reported that the water content, carbohydrate content, and fiber content of the host plant all contribute to the interaction between the host plant and oriental fruit fly species. Similarly, our result showed that resistant chili varieties have lower carbohydrate content and higher fiber content than susceptible chili varieties. The nutrition content of fruit on the host plant could influence larval growth and development as a food source after the eggs hatch. It has also been reported that oriental fruit fly larvae thrive on fruit from the Solanaceae family [34,37]. The larval growth and development of *Bactrocera zonata*,...
Ceratitis catoirii, C. capitata, and C. rosa were positively correlated with carbohydrate content and fiber content but negatively correlated with water content. In contrast, the larval development of Dacus demmerezi and Zeugodacus cucurbitae was positively correlated with water content but negatively correlated with carbohydrate content. Meanwhile, the development of Neoceratitis cyanea larvae was positively correlated with water content and fatty acid content. According to Fontellas and Zucoloto [38], the fruit of the host plant with a higher carbohydrate content was more suited for the larvae of Anastrepha obliqua from the Tephritidae family, as the larvae move toward the carbohydrate-rich portion of the fruit. Fernandes-da-Silva and Zucoloto [39] also showed a correlation between female Ceratitis capitata oviposition site selection and the carbohydrate content of the host fruits. This study supported the results of the above studies in which female flies chose fruit with a high carbohydrate content for oviposition.

Additionally, this study clarified the antixenosis mechanism of chili resistance to the oriental fruit fly. Antixenosis is the capacity of plants to resist insects by reducing or preventing their ability to colonize. Because resistant chili varieties do not release attractive volatile compounds, they are not selected by the female oriental fruit fly for oviposition and, therefore, exhibit a lower yield loss than susceptible chili varieties. Another antixenosis mechanism is that resistant chili varieties have low water and carbohydrate content, which prevents oriental fruit fly larvae from growing and developing in chili. This corresponds to the low value of the fitness index. This study provides a future direction for breeding programs for chili varieties resistant to fruit flies. However, further research is required to strengthen the results of this study, including the use of biotechnology to isolate and characterize the genes involved in the production of ocimene volatile compounds and to identify the chemical content of chili fruit, including primary and secondary metabolites that may affect the growth and development of oriental fruit fly larvae.

5. Conclusions

The characteristics of chili in the field, such as large fruit, ocimene (volatile compounds), high water content, high carbohydrate content, and low fiber content, may affect the resistance level to oriental fruit fly (B. dorsalis) infestation. Chili uses an antixenosis defense mechanism modulated by volatile compounds to prevent oriental fruit fly infestation. Female fruit flies lay eggs in response to ocimene released by susceptible chili varieties. On the other hand, resistant chili varieties do not release this substance and hence prevent female fruit flies from ovipositing their eggs. Thus, ocimene can be used as a chemical marker to identify chili resistance to oriental fruit fly attacks.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/horticulturae8040314/s1, Table S1: Twenty two chili fruit characters based on IPGRI, AVRDC, and CATIE (1995).

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28. Brevault, T.; Quilici, S. Flower and fruit volatiles assist host-plant location in the tomato fruit fly Neoceratitis cyanescens. *Physiol. Entomol.* 2010, 35, 9–18. [CrossRef]

29. Rodríguez-Burruezo, A.N.; Kollmannsberger, H.; González-Mas, M.C.; Nitz, S.; Fernando, N. HS-SPME comparative analysis of genotypic diversity in the volatile fraction and aroma-contributing compounds of Capsicum fruits from the annuum-chinense-frutescens complex. *J. Agric. Food Chem.* 2010, 58, 4388–4400. [CrossRef]

30. Pino, J.; Fuentes, V.; Barrios, O. Volatile constituents of Cachucha peppers (Capsicum chinense Jacq.) grown in Cuba. *Food Chem.* 2011, 125, 860–864. [CrossRef]

31. Cornelius, M.L.; Duan, J.J.; Messing, R.H. Volatile host fruit odors as attractants for the oriental fruit fly (Diptera: Tephritidae). *J. Econ. Entomol.* 2000, 93, 93–100. [CrossRef]

32. Dudareva, N.; Martin, D.; Kish, C.M.; Kolosova, N.; Gorenstein, N.; Fälldt, J.; Miller, B.; Bohlmann, J.R. (E)-β-Ocimene and myrcene synthase genes of floral scent biosynthesis in snapdragon: Function and expression of three terpene synthase genes of a new terpene synthase subfamily. *Plant Cell* 2003, 15, 1227–1241. [CrossRef] [PubMed]

33. Aluja, M.; Mangan, R.L. Fruit fly (Diptera: Tephritidae) host status determination: Critical conceptual, methodological, and regulatory considerations. *Annu. Rev. Entomol.* 2008, 53, 473–502. [CrossRef]

34. Fletcher, B. The biology of dacine fruit flies. *Annu. Rev. Entomol.* 1987, 32, 115–144. [CrossRef]

35. Farré-Armengol, G.; Filella, I.; Llusia, J.; Penuelas, J. β-Ocimene, a key floral and foliar volatile involved in multiple interactions between plants and other organisms. *Molecules* 2017, 22, 1148. [CrossRef] [PubMed]

36. Hafsi, A.; Facon, B.; Ravigne, V.; Chiroleu, F.; Quilici, S.; Chermiti, B.; Duyck, P.-F. Host plant range of a fruit fly community (Diptera: Tephritidae): Does fruit composition influence larval performance? *BMC Ecol.* 2016, 16, 40. [CrossRef]

37. Allwood, A.; Chinajariyawong, A.; Kritsaneepaiboon, S.; Drew, R.; Hamacek, E.; Hancock, D.; Hengsawad, C.; Jipanin, J.; Jirasurat, M.; Krong, C.K. Host plant records for fruit flies (Diptera: Tephritidae) in Southeast Asia. *Raffles Bull. Zool.* 1999, 47, 1–92.

38. Fontellas, T.M.d.L.; Zucoloto, F.S. Nutritive value of diets with different carbohydrates for adult Anastrepha obliqua (Macquart) (Diptera, Tephritidae). *Rev. Bras. Zool.* 1999, 16, 1135–1147. [CrossRef]

39. Fernandes-da-Silva, P.G.; Zucoloto, F.S. The influence of host nutritive value on the performance and food selection in Ceratitis capitata (Diptera, Tephritidae). *J. Insect Physiol.* 1993, 39, 883–887. [CrossRef]