Influence of different tropical fruits on biological and behavioral aspects of the Mediterranean fruit fly *Ceratitis capitata* (Wiedemann) (Diptera, Tephritidae)

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ABSTRACT. Influence of different tropical fruits on biological and behavioral aspects of the Mediterranean fruit fly *Ceratitis capitata* (Wiedemann) (Diptera, Tephritidae). Studies on *Ceratitis capitata*, a world fruit pest, can aid the implementation of control programs by determining the plants with higher vulnerability to attacks and plants able to sustain their population in areas of fly distribution. The objective of the present study was to evaluate the influence of eight tropical fruits on the following biological and behavioral parameters of *C. capitata*: emergence percentage, life cycle duration, adult size, egg production, longevity, fecundity, egg viability, and oviposition acceptance. The fruits tested were: acerola (*Malpighia glabra* L.), cashew (*Anacardium occidentale* L.), star fruit (*Averrhoa carambola* L.), guava (*Psidium guajava* L.), soursop (*Annona muricata* L.), yellow mombin (*Spondias mombin* L.), Malay apple (*Syzygium malaccense* L.), and umbu (*Spondias tuberosa* L.). The biological parameters were obtained by rearing the recently hatched larvae on each of the fruit kinds. Acceptance of fruits for oviposition experiment was assessed using no-choice tests, as couples were exposed to two pieces of the same fruit. The best performances were obtained with guava, soursop, and star fruit. Larvae reared on cashew and acerola fruits had regular performances. No adults emerged from yellow mombin, Malay apple, or umbu. Fruit species did not affect adult longevity, female fecundity, or egg viability. Guava, soursop, and acerola were preferred for oviposition, followed by star fruit, Malay apple, cashew, and yellow mombin. Oviposition did not occur on umbu. In general, fruits with better larval development were also more accepted for oviposition.

KEYWORDS. Demography; insects; medfly; nutritional ecology; oviposition.

RESUMO. Influência de diferentes frutos tropicais em aspectos biológicos e comportamentais da mosca-das-frutas *Ceratitis capitata* (Wiedemann) (Diptera, Tephritidae). Estudos em *Ceratitis capitata*, uma praga agrícola, pode auxiliar na implementação do programa de controle determinando as plantas com maior vulnerabilidade de serem atacadas e plantas capazes de sustentar sua população em áreas de distribuição da mosca. O objetivo deste trabalho foi avaliar a influência de oito frutos tropicais em alguns parâmetros biológicos e comportamentais de *C. capitata*: porcentagem de emergência, duração do ciclo de vida, tamanho do adulto, produção de óvulos, longevidade, fecundidade, viabilidade dos ovos e aceitação de frutos para oviposição. Os frutos testados foram: acerola (*Malpighia glabra* L.), caju (*Anacardium occidentale* L.), carambola (*Averrhoa carambola* L.), goiaba (*Psidium guajava* L.), graviola (*Annona muricata* L.), cajá (*Spondias mombin* L.), jambo (*Syzygium malaccense* L.), and umbu (*Spondias tuberosa* L.). Os parâmetros biológicos foram obtidos colocando larvas recém eclodidas em cada fruto testado. Nos experimentos de aceitação para a oviposição, as moscas foram expostas a dois pedaços das mesmas frutas. A melhor performance foi obtida com goiaba, graviola e carambola. Larvas criadas no caju e na acerola tiveram performance regular. Nenhum adulto emergiu do cajá, jambo ou umbu. As frutas não influenciaram a longevidade dos adultos, fecundidade das fêmeas, ou viabilidade. Goiaba, graviola e acerola foram preferidos para oviposição, seguidos por carambola, jambo, caju e cajá. Oviposição não ocorreu em umbu. Em geral, frutos nos quais houve um melhor desenvolvimento larval, também foram mais aceitos para oviposição.

PARAVRAS-CHAVE. Demografia; ecologia nutricional; insetos; mosca do Mediterrâneo; oviposição.

Studies on the biology and behavior of economically important species such as *Ceratitis capitata* (Wiedemann) (Diptera, Tephritidae) – a major pest of fruit trees worldwide (Christenson & Foote 1960; Bateman 1972; Zucchi 2001) – have contributed for the management and control of agricultural pests. The studies have provided insight for the theoretical approaches to the life history and dynamic distribution of species in different host plants, in addition to baseline information on emergence percentage and mortality for the development of prediction models of population growth and control (Carey 1993).

Several factors can affect the biological and demographic parameters of populations, such as: mass-rearing, body size, adult feeding, and larvae host (Carey 1989). Studies on larvae hosts have shown the influence of several host plants on the demographic parameters of *C. capitata* larvae (Carey 1984; Krainacker *et al.* 1987; Zucoloto 1993).

In addition to species biology and demography, oviposition behavior has an important role in the distribution of insect populations among host plants, especially among the holometabolous phytophagous species (Thompson & Pellmyr 1991), where survival of immature flies depends on the nutritional resources selected by adult females (Renwick 1989). Several studies show the controversial and numerous factors influencing oviposition behavior in insects (Jaenike 1990; Barron 2001; Leather 2002; Scheirs 2002), but the main hypothesis for behavior evolution is that females choose hosts that are able to maximize offspring survival and development, in a positive correlation between oviposition preference and larvae performance (Thompson 1988; Thompson & Pellmyr 1991). In this context, a host plant must be able to allow the specimen to complete its normal development in nature (Hanson 1983). A plant becomes a host when two factors occur: the selection by the females at the moment of oviposition and the offspring survival. Oviposition behavior and offspring performance are apparently controlled by different gene sets and therefore, the relationship between preference and performance does not always occur (Futuyma & Peterson 1985; Jaenike 1990). Thus, the introduction of a new host plant in the "menu" of an insect is determined both by female oviposition behavior and immature survival and development (Barron 2001).

Literature data show that although females of holometabolous insects can oviposit in several different hosts, they present a hierarchical behavior by choosing some hosts more often than others (Thompson 1988). In the absence of a favorite host, females can oviposit in less preferred hosts (Wiklund 1981) and a polyphagous species such as *C. capitata* can also oviposit in usually no-host plants (Aluja & Mangan 2008). The choice of a potential host is determined also by the presence of competitors or natural enemies and by female physiology (Thompson 1988; Jaenike 1990), among other factors. Host plant condition has been recognized as a key factor in controlling agricultural pests. However, assessing such a condition is not a simple task (Aluja & Mangan 2008).

From an evolutionary point of view, the range magnitude of insect hosts has both increased and decreased (Bernays 1998). Aluja & Mangan (2008) reviewed the literature on the issue and suggest that most species of Tephritidae as the most phytophagous insects tend to specialization. They also report that the host status of highly polyphagous species such as the fruit flies must be analyzed at three levels: species, population, and individual levels due to the high variability in patterns of host plant use.

In Brazil, the species *C. capitata* was introduced in the early 20th century. According to the data compiled by Zucchi (2001), the fly is currently widespread in 16 states and attacks 58 host species, 20 of which are native species. In the Brazilian Northeast, specifically at the San Francisco Valley (Juazeiro, BA – Petrolina, PE) – the greatest fruit tree export region in the country, *C. capitata* appears as one of the most destructive pests, receiving high levels of investments for technical control, including the SIT (Sterile Insect Technique) (Enkerlin 2005).

Data on the biology and the oviposition behavior of this species can help identify its preferred hosts, those hosts able to support the fly population, and other potential hosts. According to Aluja & Mangan (2008), potential hosts are those not yet infested in the field, but already infested in controlled conditions and considered able to sustain the larval cycle due to the high adaptability of flies.

The aim of the present work was to evaluate the influence of eight traditionally grown and sold tropical fruits in the Northeast of Brazil, on the biological parameters and oviposition behavior of the fruit fly *C. capitata*. The different fruits were compared only by the nutritional point of view, i.e. chemical and physical aspects of the interior of the fruit that affect the development and survival of offspring. Other variables that can also affect oviposition behavior, such as fruit color, shape, and density, in addition to presence of competitors or natural enemies were not studied.

MATERIAL AND METHODS

The *C. capitata* strain used in this research has been kept at the Laboratory of Insect Nutritional Ecology (IBio/UFBA) for approximately 12 years; occasionally, wild flies have been introduced. Maintenance of the strain follows the methodology described by Zucoloto (1987).

The fruits tested were: acerola (*Malpighia glabra* L.), yellow mombin (*Spondias mombin* L.), cashew (*Anacardium occidentalis* L.), star fruit (*Averrhoa carambola* L.), guava (*Psidium guajava* L.), soursop (*Annona muricata* L.), Malay apple (*Syzygium malaccensis* L.), and umbu (*Spondias tuberosa* L.). These fruits have considerable socioeconomic importance, especially in the Northeast of Brazil, and all of them have had records of infestation by *C. capitata* (Zucchi 2001; Araujo *et al.* 2005). The fruits were purchased in supermarkets to reduce the possibility of obtaining infested fruits. Before use, the fruits were washed to remove agricultural residues and then stored in refrigerator or freezer to maintain their qualities.

To evaluate the development and immature survival, twenty-five newly hatched larvae of *C. capitata* were placed on small pieces (±5.0 g) of fruit, on Petri dish lined with filter paper. New pieces of fruit were added daily, until the end of larval development. Six replicates of each fruit were tested, and the following parameters were analyzed: emergence percentage, life cycle duration (hatching to emergence), egg production during the first five days of female life, before the oviposition period (pre-oviposition period), and adult size (estimated by measuring a wing vein, R_{4+5} to cu-m). Fifteen females in each fruit had their wings measured and the eggs counted.

Acceptance of fruits for oviposition (oviposition preference) was assessed using no-choice tests. Five couples of newly emerged flies were placed in plastic cages (9.0 x 7.5 cm) containing water and a yeast-based diet. At the oviposition peak (approximately 15 days after emergence), the tested fruits were offered for female oviposition in two small pieces (5.0g) placed at equidistant locations. Twenty-four hours later the old pieces were replaced by fresh ones, and the test was concluded 48 hours later. All fruit pieces were identified and frozen for later counting of the eggs. Ten replicates were performed for each fruit. The cages had fluorescent lamps (12 hours of light) to stimulate oviposition. Results of these tests were compared with immature performance tests for each fruit.

Adult longevity and fecundity, and egg viability (F_2) were used to evaluate fruit influence on adult performance. The tests were performed only with cashew, guava, soursop, and star fruit, the only fruits with sufficient numbers of emerged adults.

Adult longevity was measured in 50 couples in each fruit. The specimens were separated by sex, placed individually in transparent cages (9.0 x 7.5 cm), and fed with saturated sugar solution and water *ad libitum*. The adults were observed daily, until death.

Female fecundity was assessed by placing five sexually mature couples in a transparent cage (15 x 13 cm) and feeding them with sucrose solution, water, and a yeast based diet to increase egg production. Adult protein intake increases egg production (Cangussu & Zucoloto 1997). Eggs were counted daily until the female death. Ten replicates were conducted for each fruit.

Egg viability was studied in 100 eggs of flies reared in each fruit. The eggs were collected, transferred to a Petri dish (50 x 10 mm) containing moistened filter paper, and observed every 12 hours for larvae eclosion. All experiments were conducted at 25ºC and 75% relative humidity, in the dark (larvae experiments), or 12 hours of light per day (adult experiments).

The biological parameters and oviposition preferences were compared using one-way ANOVA and the Tukey-Kramer's test for multiple comparisons. The Kruskal-Wallis test (with Dunn's test for multiple comparisons) was used to analyze the longevity data. All tests were performed using GraphPad Instat Software (1997 version, San Diego), at a critical value for an error probability of 5%.

RESULTS

The best performances of the biological parameters (Table I) occurred in guava, soursop, and star fruit, with emergence averages equal or above 60%, life-cycle 14–18 days and 12–21 eggs/female. Larvae reared on cashew and acerola fruits had regular performances: 30–45% emergence, 19–20 days of life-cycle, and 06–11 eggs/female during the pre-oviposition period. No adults emerged from larvae reared on yellow mombin, Malay apple, or umbu. Adults reared on the different fruits had similar sizes at emergence ($p > 0.05$).

Oviposition preference was ranked from higher to lower: guava, soursop, and acerola were first, followed by star fruit, Malay apple, cashew, and yellow mombin (Fig. 1). Flies did not oviposit on umbu. In general, fruits providing better larvae development were also well accepted for oviposition.

Fecundity, adult longevity, and egg viability were not statistically different among flies fed on cashew, star fruit, soursop or guava during the immature stage ($p > 0,05$) (Table II).

Table I. Performance of the biological parameters of *Ceratitis capitata*. The data represent the means and standard deviations of six replicates for each fruit tested with 25 larvae each. Means followed by same letters in column do not differ statistically. One-way ANOVA with Tukey-Kramer for multiple comparisons with 5% significance level.

Fruits	Emergence (%)	Life cycle duration (days)	Egg production/female	Adult size (mm)
Acerola	28.7 ± 4.7a	20	11.1 ± 9.8ab	3.1 ± 1.2a
Yellow mombin	0	0	0	0
Cashew	45.3 ± 6.5b	19	6.1 ± 9.7a	2.7 ± 0.08a
Star fruit	60.7 ± 7.8c	14	21.9 ± 16.8b	2.7 ± 0.05a
Guava	76.6 ± 12.7c	18	18.7 ± 9.7b	2.6 ± 0.09a
Soursop	87.3 ± 5.9d	16	12.3 ± 3.2ab	2.7 ± 0.04a
Malay apple	0	0	0	0
Umbu	0	0	0	0

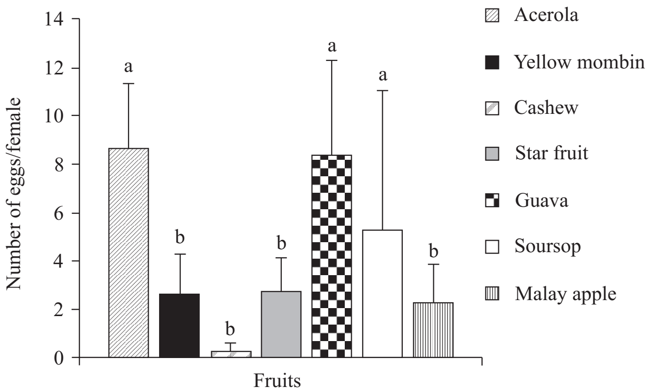

Fig. 1. Oviposition preference of *C. capitata* females. The data represent the means and standard deviations of 10 repetitions for each fruit tested. Means followed by different letters show statistical differences. One-way ANOVA with Tukey-Kramer for multiple comparisons with 5% significance level.

Table II. Influence of larval feeding on longevity, fecundity and eggs viability (F1) of *Ceratitis capitata* adults. The data represent the means and standard deviations. There was no statistical difference in any of the parameters used. Test analysis of variance (One-way ANOVA) with Tukey-Kramer for multiple comparisons at 5% significance for fertility and eggs viability experiments and the non-parametric Mann-Whitney test for longevity experiments.

Fruits	Longevity (days)		Fecundity (Number of eggs/female/day)	Eggs viability (%)
	Male	Female		
Guava	27.3 ± 3.6	27,4 ± 3.1	20.6 ± 2.1	72 ± 9.2
Cashew	26.1 ± 1.9	26,8 ± 3.5	17.9 ± 2.3	64 ± 13.5
Star fruit	26.3 ± 3.1	27,8 ± 3.3	19.2 ± 2.9	63 ± 13.4
Soursop	27.9 ± 3.6	25,8 ± 3.4	17.9 ± 3.1	61 ± 11.9

DISCUSSION

Food consumption highly determines the growth, development, and reproduction of species. Therefore, the quantity and quality of food consumed by immature insects determine their early development and adult lives, and affect the demographic parameters of populations (Slansky & Scriber 1985).

In holometabolous phytophagous insects, adult females face the challenge of finding appropriate food for the immature insects, during oviposition (Via 1986; Thompson 1988). In general, the female behavior can be shaped by processes of natural selection related to two events: i. the phytochemical coevolution between plants and phytophagous insects, and ii. the selective pressure of natural enemies (Aluja & Mangan 2008). The former has led to the discussion about the discrimination degree among generalist (polyphagous) and specialist (olygophagous and monophagous) host insects (Wilklund 1981).

According to Bernays (2001), polyphagous insects have less ability than monophagous insects in perceiving and discriminating among large quantities of volatile substances (neural limitation hypothesis). Other authors argue that polyphagous insects choose their hosts primarily by the nutritional value of plants, and specialists by secondary substances (Edwards & Wratten 1980).

In our study, although a polyphagous species, *C. capitata* showed discrimination capability and hierarchy in oviposition preference for several fruits tested. This suggests a preference association with the nutritional value of the fruit to feed the larvae; in general, fruits with the largest numbers of eggs were also the best in providing insect development at the immature stage. This can be an advantage in the evolutionary trait because females preferred appropriate resources for their offspring, according to the preference-performance theory. This event may also be related to the hypothesis of evolution of the oviposition behavior, which states females will choose plant species that maximize larvae survival and development (Thompson & Pellmyr 1991; Janz 2002). Studies on this subject are still controversial. According to Joachim-Bravo & Zucoloto (1997), there was no correlation between oviposition preference and larval performance in *C. capitata* if deemed the nutritional value of the artificial diet. Furthermore, Fernandes-da-Silva & Zucoloto (1993) did not observe any oviposition preference of *C. capitata* for the most nutritional fruit parts. However, it is possible to infer that females of *C. capitata* in nature can recognize the most suitable hosts and lay more or less eggs accordingly, with consequences for the relevance of particular plants to sustain the species population.

According to Malavasi & Morgante (1980), host origin is one of the determinants of fruit infestation levels in Brazil, with native fruits being more infested by *Anastrepha* (native of the Americas) and exotic fruits by *C. capitata* (native of the Mediterranean).

In the Anacardiaceae family, especially in genus *Spondias*, several fruit species are hosts of Tephritidae, mainly *Anastrepha* spp. (Malavasi *et al.* 1980; Zucchi 2000). In our study, *C. capitata* larvae did not perform well on umbu (*S. tuberosa*) or yellow mombin (*S. mombin*), resulting in absence of emergence and suggesting that these fruits cannot sustain *C. capitata* populations from a nutritional standpoint. These fruits were rarely accepted for oviposition, indicating the possible occurrence of an association between preference and performance among these flies. Recent field data showed that umbu infestation by *C. capitata* was recorded for the first time in 1999–2000 in Rio Grande do Norte state (Brazil), at a low rate (0.04 pupae/Kg of fruit) (Araujo *et al.* 2005). Yellow mombin was reported as host for *C. capitata* by Malavasi *et al.* (1980), according Zucchi (2001). Recent infestation studies, however, have reported yellow mombin as a host only for *Anastrepha* (Carvalho *et al.* 2004; Souza *et al.* 2007; Leal *et al.* 2009).

No adult emergence was observed in Malay apple. According to Zucchi (2001), only Costa Lima (1926) reported Malay apple as a host for *C. capitata* in Brazil. Our results for oviposition preference showed its unattractiveness to females, indicating a potential inadequacy of Malay apple as host for *C. capitata*.

Of all the fruits belonging to the Anacardiaceae family as tested in our study, cashew was the only one to provide a reasonable development of immature individuals. Cashew was not preferred by females for oviposition, supporting the few infestation records obtained in field. Only Canal D. (1997), in the north of Minas Gerais state (Brazil), recorded cashew as *C. capitata* host. The correlation of results obtained here and the infestation data collected in the field suggest that the low infestation by *C. capitata* was probably caused by the inadequate nutrition provided by cashew.

We also found a clear preference-performance relationship in guava and soursop, two native fruits. Compared with other fruits, they received more eggs and provided better immature performance. Although often known as a primary host plant of genus *Anastrepha* (Araujo *et al.* 2005), guava is also reported as *C. capitata* host in Brazil (Zucchi 2001) and in other regions of the world (Woods *et al.* 2005). In Brazil, different studies show that guava infestation by *C. capitata* is lower than by *Anastrepha* (Malavasi *et al.* 1980; Uchoa-Fernandes *et al.* 2002; Araujo & Zucchi 2003; Corsato 2004). However, guava can adequately host and sustain populations of *C. capitata* in terms of nutrition and attractiveness for oviposition. A possible competition with *Anastrepha* might explain the lower rate of *C. capitata* on guava. Studies show the occurrence of interspecific interactions between polyphagous species of Tephritidae introduced in areas already occupied by other polyphagous species of Tephritidae, resulting in niche changes and a decrease in number of individuals belonging to the pre-established species (Duyck *et al.* 2004). In this case, we can expect that *C. capitata* changes or displaces niches of *Anastrepha.* Other studies suggest that *Anastrepha* species compete with *C. capitata* for oviposition on the same fruits. Castilho (1987) noted that adults of *Anastrepha striata* Schiner attack adults of *C. capitata,* and remove them from the guava fruit. In laboratory experiments with mango, Camargo *et al.* (1996) observed that *Anastrepha obliqua* Macquart removed *C. capitata* of fruits in 60.4% of the encounters, indicating that *A. obliqua* is probably a better competitor because it is bigger.

Soursop has been reported as *C. capitata* host in Brazil by Canal D. (1997) and as occasional host in other regions (Thomas *et al.* 2008). Woods *et al.* (2005) refer to soursops as non-primary hosts but report that 103 individuals of *C. capitata* emerged from a single fruit. This soursop infestation index per Kg of fruit (296 individuals/Kg of fruit) was greater than the mango infestation index (228 individuals/Kg of fruit) obtained in the same study. These data support our results related to soursop nutritional quality for the development of immature *C. capitata*.

The results we obtained with acerola and star fruit were not compatible with the preference-performance relationship. Acerola is well-accepted for oviposition, as reported in studies showing its high infestation by *C. capitata* (Albuquerque *et al.* 2002; Araujo *et al.* 2005; Souza *et al.* 2008). However, unexpectedly, acerola emergence percentage was lower than in other fruits preferred for oviposition. It could be happen because, in laboratory, acerola had faster maturity than star fruit.

Star fruit has been registered as host of *C. capitata* (Zucchi 2001; Feitosa *et al.* 2007), with high levels of infestation (Araújo *et al.* 2005). In our study, although the fruit nutritional value was appropriate for immature individuals, it was not well accepted for oviposition when compared with other fruits. However, it is interesting to note that the rates of infestation by *C. capitata* do not always coincide with female oviposition preferences. Kolbe & Eskafi (1989), who studied the infestation pattern by *C. capitata* on different hosts in a region in Guatemala, found that some fruits with moderate infestation were preferred for oviposition. In contrast, other fruits with high numbers of pupae per kilogram were less preferred for oviposition. Further studies should be conducted on the factors leading to such results.

Unlike the development of immature individuals, adult parameters (adult longevity, fecundity, and egg viability in F_2 generation) apparently were not affected by larvae rearing on different fruits. Studies have shown that higher protein ingestion during the immature phase improve adult performance, such as higher fecundity rates (Ferro & Zucoloto 1990; Cangussu & Zucoloto 1997).

When explaining the data obtained in the present study, we must consider that a selection among the immature individuals might have occurred during the larval stage and, consequently, those who reached adulthood emerged with minimum necessary nutritional reserves even when on poor hosts. This hypothesis can be supported by the different emergence percentage results obtained among all the fruits tested. Therefore, we can argue that the fruit nutritional traits are more important for individuals at immature development stages than for the adult biological parameters. These are rather primarily determined by adults´ diet.

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