# Chapter 10
# Fruit Fly Nutrition, Rearing and Quality Control

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**Abstract** Tephritid fruit flies are recognized worldwide as an important threat to the horticultural industry. Most of the species belonging to this group are highly polyphagous attacking several important fruits and vegetables. They cause direct damage through larval feeding and indirect losses are associated with quarantine restrictions. The increasing awareness of the damage caused by these fruit flies to the horticultural industry has created a demand for the development of control measures based on integrated pest management (IPM) strategies and the sterile insect technique (SIT). However, success of the majority of these control methods largely depends on the ability to establish cost effective rearing methods of the fruit flies as a pre-requisite to understanding their biology, response to attractants and susceptibility to various biological control agents. In the past decades, considerable advances have been made with regard to formulations of diet for rearing fruit flies and nutritional analyses for both adults and larvae. In general, insects require a diet containing a source of energy, a protein source, vitamins and certain mineral salts. Deficiency in some of these nutrients can influence the quality control parameters of the flies such as body size, survival, pupal weight, adult emergence, longevity, flight ability, fecundity, fertility and mating ability. In this chapter, the role played by nutrition in relation to different quality control parameters is discussed.

**Keywords** Tephritid fruit flies • IPM • SIT • Mass rearing • Quality control parameters • Nutrition

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## 1 Introduction

Adults of the frugivorous tephritid fruit fly species need to feed on a diet rich in amino acids, carbohydrates, vitamins and minerals as well as water for growth, development, survival and reproduction. Being anautogenous, females require protein for egg maturation, while males require protein for production of pheromone and accessory gland secretions as well as for renewal of sperm supplies (Drew and Yuval 2000 and reference therein; Yuval et al. 2007). In nature these species obtain their dietary requirements by feeding on bird droppings, honeydew, plant exudates, extra-floral nectaries, pollen, fruit juice, ripe fruits and microorganisms on both host and non-host trees (Christenson and Foote 1960; Steiner and Mitchell 1966; Bateman 1972). Several species of economic importance belong to this group and necessitating the need to understand their biology, behaviour, host range and other attributes, in order to develop sound management strategies for their suppression, which in turn necessitates maintaining laboratory cultures of these insects on artificial diets. Large-scale mass rearing of insects on artificial diet is also a fundamental requirement for producing good quality flies on a large scale for the sterile insect technique (SIT) and for mass production of parasitoids, which are both essential components of area-wide management of these fruit flies.

Since the beginning of the last century considerable advances have been made with regard to the formulation of diet for rearing fruit flies and nutritional analyses for both adults and larvae (e.g. Tanaka et al. 1965; Tsitsipis 1977; Hooper 1978, 1989; Walker et al. 1997; Vargas et al. 1993; Chang et al. 2001, 2004, 2007; Chang 2009a).

The first meridic adult diet was developed by Hagen and Finney (1950) for the Mediterranean fruit fly (medfly), *Ceratitis capitata* (Wiedemann), the oriental fruit fly, *Bactrocera dorsalis* (Hendel) and the melon fruit fly, *Zeugodacus cucurbitae* (Coquillett) (all Diptera: Tephritidae). This was followed later by the development of a meridic diet for other African species including the olive fruit fly, *Bactrocera oleae* (Gmelin) and the Natal fruit fly, *Ceratitis rosa* Karsch (both Diptera: Tephritidae) (Tsiropoulos 1992 and reference therein). The first chemically defined diet was developed by Hagen (1953) for *B. dorsalis*, *Z. cucurbitae* and *C. capitata*. Tsiropoulos (1981) argued that both the nitrogen in the diet and also the ratio of nitrogen to carbohydrate were important parameters for optimization of a chemically-defined diet for *B. oleae*. He established that a ratio of 1.6:40 of N:C was the best for *B. oleae* reproduction, while a higher nitrogen content in the diet reduced egg production and shortened the life span of the flies.

Like that of the adult diet, development of the larval diet has also been an active area of research in terms of the diet components as well as their effects on fitness parameters of the reared flies. Steiner and Mitchell (1966) provide a detailed account on early studies highlighting the history of the development of the larval media, their modifications to suit the rearing of different fruit flies species, as well as the laboratory techniques for their efficient use. The basic essential ingredients in larval diets are: yeast-based products, sugar, antimicrobial agents, agents for adjusting pH,

water and bulking agents. Conventionally, bulking agents used in larval diet are wheat bran, carrot powder, wheat mill feed, wheat shorts, grain corncob, cane and beet bagasse (Vargas et al. 1983), soybean protein and tissue paper (Kakinohana and Yamagishi 1991). However, there are several limitations associated with the use of these bulking agents. These include, but are not limited to, the need for large storage space, waste management, variability in quality, microbial and pesticidal contamination (Hooper 1987) as well as issues related to availability and cost. This necessitated the search for an alternative to bulking agents in larval diets. The first liquid larval diet without a biological bulking agent was developed by Schroeder et al. (1971) for small-scale rearing of *Z. cucurbitae*.

In further efforts to replace the bulking agents with an inert, reusable sponge and to help overcome the limitations associated with solid-based diets, liquid diets that can be used for large-scale rearing have been developed for *C. capitata* (Chang et al. 2007; Chang 2009b), *B. dorsalis* (Chang et al. 2006; Chang and Vargas 2007; Chang 2009b; Khan et al. 2011) and *Z. cucurbitae* (Chang et al. 2004). The liquid diet for *B. dorsalis* developed by Chang et al. (2006) yielded high quality flies, as the adults reared on this diet were identical to those reared on the conventional mill feed diet in terms of fitness parameters as well as overall performance, paving the way for rearing of this species on liquid diet on a large scale. Following this breakthrough, the liquid diet technology developed has been transferred to several countries across the world for assessment for mass rearing of various fruit fly species (Chang 2009a). Amongst the 14 countries that participated in the liquid diet evaluation, three were from Africa. These were, Kenya (for the African populations of *B. dorsalis* and the mango fruit fly, *Ceratitis cosyra* [Walker]), Mauritius (for the peach fruit fly, *Bactrocera zonata* (Saunders) and *Z. cucurbitae*), and South Africa (for *C. capitata*). Both the Stellenbosch mass-rearing facility and the International Centre of Insect Physiology and Ecology (*icipe*) have adopted the technology for their respective fruit flies on which the liquid diet was evaluated.

In Africa, like other parts of the world, diet and its related nutritional components for laboratory reared fruit flies have improved in several phases. For example, at *icipe* colonies of six fruit flies species (*B. dorsalis*, *C. capitata*, *C. cosyra*, *Ceratitis anonae* Graham, *C. rosa* and *Ceratitis fasciventris* [Bezzi]) are currently in culture. They were initiated on their respective host fruits for 3–7 generations depending on the species. Thereafter, the colonies were maintained on solid carrot-based diet, which is a modification of the diet developed by Hooper (1978) (for more details see Ekesi and Mohamed 2011). The first three species were later adapted to rearing on liquid diet the ingredients of which are similar in composition to that described by Chang et al. (2006) for *B. dorsalis*; efforts are underway to adapt the remaining species on the same media.

The Stellenbosch fruit fly rearing facilities in South Africa are the largest in the continent; *C. capitata* is produced on a large scale of 13 million flies/week for the SIT program on grapes in the Hex river valley (Barnes et al. 2007). The colony has been maintained on solid-based larval diet using wheat bran as the bulking agent. However, the inconsistency of the quality of this bulking agent, which is also often contaminated with pesticides, resulted in the colony crashing (Chang 2009a) which

prompted the management to evaluate use of the liquid diet developed by Chang et al. (2004) with the aim of future implementation (Chang 2009a).

## 2 Effect of Fruit Fly Diet on the Fitness Parameters of Different Developmental Stages

### *2.1 Adult Diet*

#### 2.1.1 Effect on Fecundity and Egg Hatchability

Adult diet quality has profound effects on the fecundity of fruit flies. For example, Hagen (1953) demonstrated that amino acids, carbohydrate, vitamins and certain minerals are essential for ovary development in *B. dorsalis*, *Z. cucurbitae* and *C. capitata.* Tsiropoulos (1977) demonstrated that vitamins were crucial for enhancing fertility of *B. oleae* and their absence in the diet led to oviposition of malformed eggs. In a separate study the same author reported that *B. oleae* fed on a vitamin-deficient diet had reduced fecundity and fertility (Tsiropoulos 1980). Interestingly, an excess of either biotin, pyridoxine, inositol or vitamin C also resulted in reduced fecundity in *B. oleae* (Tsiropoulos 1982). Also working with *B. oleae*, Zografou et al. (1998) reported that amino acid analogues affected fecundity and fertility of *B. oleae*. Similarly, addition of 0.25 % Vanderzant's vitamin mixture and 0.05 % cholesterol to the sucrose and yeast hydrolysate diet of the female *B. oleae* diet are thought to increase fecundity and inhibit the production of mottled eggs (George and Ruhm 1977).

Ferro and Zucoloto (1990) and Cangussu and Zucoloto (1997) reported that, although *C. capitata* females produced eggs when fed only sucrose, egg production was significantly enhanced when protein was also consumed. Also Harwood et al. (2013) demonstrated that the egg laying abilities of laboratory-reared *C. capitata* and *Z. cucurbitae* was delayed or suppressed by limiting access to dietary protein. The authors also demonstrated that access to protein at eclosion led to higher reproductive ability in both species.

In a study by Davies et al. (2005) where they varied the content of both yeast and sucrose in the adult diet of *C. capitata*, females laid significantly more eggs when maintained on the highest yeast diet (7.7 %) than when maintained on diets containing lower levels of yeast. Similarly, Manrakhan and Lux (2006) evaluated the effects of three natural food sources, varying in protein and sugar content on, amongst other traits, the reproductive behaviour and fecundity of three African fruit flies: *C. fasciventris*, *C. capitata* and *C. cosyra*. The authors found that females of the first two species had a higher frequency of oviposition when fed on a protein-rich diet, than those fed on a protein-poor diet. Net reproductive rate for these two species also varied with the diet type. In a recent study by Chang (2009b), who tested the effect of various yeasts on production and hatchability of eggs of *C. capitata*, *B. dorsalis* and *Z. curcurbitae*, found that egg production was influenced by yeast type,

but that egg hatchability was not different from that of the control (conventional mill feed diet).

Working with *Z. cucurbitae*, Kaur and Srivastava (1994) demonstrated that the absence of essential amino acids negatively affected flies' sexual maturity and fecundity. Similar findings were reported for *C. capitata* by Chang et al. (2001) who found that flies fed on diets containing ten essential amino acids, eight non-essential amino acids or a combination of cholesterol, inositol and choline, produced significantly fewer eggs than flies fed on the control diet. The most prolific age for egg production by adults was 10-d-old when the greatest number of mature eggs were recorded in the ovaries. Also fecundity of *C. capitata* was significantly reduced by omission of 10 essential amino acids or all eight non-essential amino acids from the adult diet (Chang et al. 2004). Removal of arginine, histidine, isoleucine, leucine, lysine, threonine, tryptophan, methionine, or valine also significantly decreased *C. capitata* fecundity. In contrast, increasing the sugar content in the diet had no effect on egg production or hatchability (Chang et al. 2001).

### 2.1.2 Effect on Male Mating Success

Quality and quantity of food consumed by male fruit flies has a profound effect on male mating success (e.g. Blay and Yuval 1997; Yuval et al. 1998; Field and Yuval 1999; Kaspi et al. 2000; Shelly et al. 2005; Orankanok et al. 2013; Quilici et al. 2013; Haq et al. 2014). The effect of adult food on sexual signaling, an important indicator of mating success, has been extensively documented for both wild and mass-reared male *C. capitata* (Papadopoulos et al. 1998; Kaspi and Yuval 2000; Shelly et al. 2002; Shelly and Kennelly 2002; Shelly and McInnis 2003). Also Manrakhan and Lux (2006) reported that males of *C. fasciventris* and *C. capitata* fed on a protein-rich diet had a higher frequency of calling and mating than those fed on a protein-poor diet; however, diet quality did not influence the mating behaviour of *C. cosyra*. Diamantidis et al. (2008) reported that yeast hydrolysate significantly increased sexual signaling in four populations of *C. capitata*. In a laboratory study using males of a related fruit fly species, *C. rosa* Quilici et al. (2013) demonstrated that the addition of proteins to the adult diet increased mating competitiveness of males for both wild and laboratory reared flies compared to their counterparts fed on sugar only. The authors reported that males fed with a 'full' diet (sugar and hydrolysed yeast) accounted for 85 % of all matings compared with 15 % for those fed with a sugar-only diet. Similarly, *C. capitata* males fed on a high-protein diet achieved a greater number of copulations compared with males fed on a no-protein diet (Joachim-Bravo et al. 2009). More recently, Teal et al. (2013) found that an adult diet enriched with protein hydrolysate and an application of methoprene to adult males or pupae significantly advanced the age at which males of *Z. cucurbitae* become sexually mature and improved the overall reproductive success of the males of this species.

In *B. dorsalis*, immature males deprived of protein (1–12 days old) had very few matings (<5 % total matings), compared with immature males provided with protein

(Shelly et al. 2005). The authors further illustrated that males provided with protein as immature adults, but deprived of protein as mature adults (>12 days old), were competitively inferior to protein-fed males. Orankanok et al. (2013) reported that sterile *B. dorsalis* males fed on sugar–yeast hydrolysate combinations for 2 days post eclosion achieved significantly more matings than males fed only water.

Adult male diet is also an important determining factor in the length of the female sexual refractory period, an aspect that has significant implication in fruit flies management using SIT. For example, Blay and Yuval (1997) found that *C. capitata* females mated with protein-fed males are more likely to refrain from re-mating compared to females mated with protein-deprived males. Also working with *C. capitata*, Gavriel et al. (2009) reported that females mated with males fed on a protein-deficient diet had higher re-mating receptivity than females mated with protein-fed males. Also in a study on the effect of post-teneral nutrition on reproductive success of male *C. capitata* Yuval et al. (2002) found that females whose first mate was protein-deprived, remated sooner than females whose first mate was protein-fed. Similarly, Haq et al. (2014) working on *Z. cucurbitae* found that females mated with protein-deprived males showed higher re-mating receptivity than females first mated with protein-fed males. Contrary to the findings by the previous authors, Shelly and Kennelly (2002) reported that the inclusion of protein in the male diet of *C. capitata* had no apparent effect on female remating tendency.

Other aspects associated with male mating success, such as copula duration, sperm transfer, male participation in leks and male calling, were also found to be affected by male diet in *C. capitata* and other fruit fly species (Yuval et al. 1998; Field and Yuval 1999; Taylor et al. 2000). For instance, protein-fed C. *capitata* males were more likely to emit pheromone in the lek and consequently copulate more than protein-deprived males (Kaspi et al. 2000). Also Kaspi and Yuval (2000), working in field cages, found that protein-fed sterile males of *C. capitata* were significantly more likely to join leks and emit calling pheromone than sterile males fed only sugar.

### 2.1.3 Effect on Adult Longevity

Results on the effects of adult diet on adult survival are quite variable for different fruit fly species, and even for same species as reported by different authors. For example, in a study to assess the effect of adult diet on longevity of sterile males of *C. capitata*, Barry et al. (2007) found that males fed on diet containing hydrolyzed yeast and sucrose lived longer than those fed on diets containing either sucrose or only water. Also Davies et al. (2005) demonstrated that longevity of *C. capitata* varied with the concentration of the yeast in the adult diet. Similarly, Faria et al. (2008) found that incorporation of protein had a positive impact on laboratory survival of *C. capitata* males. In a study on longevity of *Z. cucurbitae* males fed on hydrolysed yeast and methoprene treatments, it was demonstrated that adult diet quality had a significant effect on survivorship, whereby males fed on the sugar-protein diet throughout showed highest survival compared with those fed on sugar

only (Haq and Hendrichs 2013). In a different study, access to protein increased life expectancies of both *C. capitata* and *B. cucurbitae* (Harwood et al. 2013). The authors also emphasized the positive effect of access to protein immediately after eclosion on the longevity of both species. Also sugar concentration in the diet has been reported by Chang et al. (2001) to have a significant effect on *C. capitata* survival.

Kaspi and Yuval (2000) showed that post-teneral protein feeding by mass-reared sterile male *C. capitata*, improved sexual competitiveness but led to a shorter life span. In contrast, Shelly and Kennelly (2002) and Shelly and McInnis (2003) reported no significant difference in longevity of protein-fed and protein-deprived male *C. capitata*. In a separate study, Shelly et al. (2005) demonstrated similar effects for *B. dorsalis* males whereby, males fed on sugar only or sugar and protein and then only sugar had a comparable survival rate. Also Davies et al. (2005) reported no difference in longevity of *C. capitata* males fed on a sugar–protein diet compared with those fed on sugar only. Furthermore, protein intake had a differential effect on adult longevity in different populations of the same species. For instance, Placido-Silva et al. (2006) who studied the effects of different protein concentrations on longevity of two populations of *C. capitata* found that protein intake increased adult longevity of one population but not that of the other. For *B. oleae* survival of both sexes was significantly reduced by overdosing on biotin and pyridoxine with females being more affected (Tsiropoulos 1982).

## *2.2 Larval Diet*

The larval stage is a very important stage of fruit fly growth and development as it dictates many fitness parameters of the adult flies. Therefore, high quality larval diet is crucial for production of healthy adult fruit flies. Many traits of fruit flies, such as adult reproductive success, larval mortality, larval development time, pupal recovery, pupal weight, adult size, egg hatchability and flight ability of the eclosing adults, are functions of various factors that act individually or in tandem. Although fruit flies are anautogenous, nutritional reserves obtained during the larval stage are one of the four factors known to influence various fitness parameters of the adult flies (e.g. Chang 2004; Chang et al. 2000; Nash and Chapman 2014 and reference therein).

### 2.2.1 Effect on Development of Immature Stages

Chang (2004) assessed the effect of inclusion or removal of amino acids from the larval diet on development of larvae and adults of *C. capitata*. Larval feeding on a diet deficient in ten exogenous essential amino acids (arginine, isoleucine, leucine, lysine, histidine, methionine, phenylalanine, threonine, tryptophan and valine) resulted in larval death. In the same study, larvae reared on diets that lacked all eight

of the non-essential exogenous amino acids (alanine, aspartic acid, cystine, glutamic acid, glycine, proline, serine and tyrosine), or either glycine or serine survived. However, they had significantly delayed larval development. Similarly, Nestel et al. (2004) working with *C. capitata*, noted that removal of non-essential amino acids from larval meridic diets delayed larval and pupal development and also resulted in reduced pupal recovery. In a very recent work evaluating the effect of dietary components on the larval life history of *C. capitata*, Nash and Chapman (2014) found that reducing the protein content of larval diet by 40 % resulted in a significant increase in overall egg to adult mortality by up to 66 % in comparison with the standard baseline diet. They also demonstrated that addition of a novel protein source, casein (i.e. milk protein), to the larval diet increased larval mortality by up to 63 % and also lengthened the larval developmental time by 1.93 days in comparison with those larvae reared on the standard diet (mill feed). Significantly higher proportions of larvae reared on protein-rich diets survived to pupation than those reared on low-protein diets or diets amended with casein. Also the proportion of pupae surviving to adult eclosion was significantly lower when larvae were fed casein compared with larvae fed starch. Variation in carbohydrates had no significant effect on larval survival while it did have a significant effect on pupal survival. Larval and pupal development time was significantly longer when larvae were reared on casein. Carbohydrate diets also had no significant effect on the mean duration of larval development. In contrast, pupal developmental time varied amongst the different carbohydrate diets.

Chang (2009b) evaluated the effect on development of *B. dorsalis* of incorporating different yeasts and wheat germ oil in the larval diet. The three hydrolyzed brewer's yeasts evaluated were FNILS65, FNI200 and FNI210, one glutamine-enriched yeast powder (GSH), one vitamin-enriched yeast powder (RDA500), Korean yeast powder, whole cell yeasts, and various combinations of these treatments. In this study the author established that the type of yeast used had a significant effect on pupal recovery of *B. dorsalis*, which was significantly higher when larvae were fed FNI200 and FNIL65 compared with FNI210. In a similar study, Chang et al. (2007) evaluated several yeast-based products as ingredients in the liquid larval diet of *C. capitata*. They assessed the effect on larval duration, pupal recovery, pupal weight and other traits such as adult emergence, mating success, percentage of fliers, egg production of the subsequent generation and egg hatch rates. Larvae reared in a liquid diet with LBI2240:FNILS65 ratios of either 1:1 or 3:1 performed similarly to those reared on conventional mill feed-based control diets in term of pupal recovery. Recently, Ekesi et al. (2014) demonstrated that African populations of *B. dorsalis* had a higher pupal recovery and pupal weight when the larvae were reared on diet containing an imported Lallemand yeast than when the larvae were reared on a diet containing the local waste brewers' yeast. For *Bactrocera latifrons* (Hendel) it was found that incorporation of varying amounts of bell pepper in the larval diet, as a source of ascorbic acid, significantly increasing pupal recovery by up to 21 % (Chang and Kurashima 1999). Despite this the same authors reported that an addition of ascorbic acid phosphate (>15 mg/g of diet) to

the larval diet had a negative effect on *B. latifrons* development and resulted in reduced pupal recovery and reduced pupal weight.

Other nutritional components of the larval diet that are essential for fruit fly development are vitamins. For example, Chang et al. (2001) found that the addition of vitamins improved larval development, pupal recovery and pupal weight in *C. capitata*. In a separate study Chang and Li (2004) demonstrated the positive effect of the addition of niacin and other B vitamins to diet on larval development of *C. capitata*.

Pupal weight is an important fitness parameter that determines adult size, which has a significant bearing on fly fertility, fecundity, longevity, flight ability and male mating success. In turn, pupal weight is affected by several factors; the most important is the quality of the larval diet. For instance, Kaspi et al. (2000) reported that protein-fed C. *capitata* males were heavier and emerged with more protein and lipid than protein-deprived males.

### 2.2.2 Effect on Adult Fitness Traits

Female fecundity and egg hatchability are important quality control parameters that are influenced by the quality and quantity of the larval diet. For example, Kaspi et al. (2002) investigated the effect of larval diets containing varying amounts of protein and sugar on the size, developmental time, nutritional status and reproductive maturation of *C. capitata*. The authors found that protein- and sugar-fed flies were larger in size, developed faster, and had more nutritional reserves than the protein-deprived flies. Furthermore, the protein-fed males became sexually active earlier than the protein-deprived males, while protein-fed females were more fertile than protein-deprived females. Chang (2009b), who tested the effect of various yeasts on production and hatchability of eggs of *C. capitata*, *B. dorsalis* and *Z. curcurbitae*, found that egg production was significantly influenced by the yeast type. Also Ekesi et al. (2014) found that adult emergence, fecundity and egg hatchability of African populations of *B. dorsalis*, were higher for flies from the larvae reared on diets containing an imported Lallemand yeast compared with those from diet containing the local waste brewers' yeast. However, flight ability was not affected by the yeast type. In a recent study, Nash and Chapman (2014) found that a 40 % reduction in the quantity of protein resulted in a significant increase (26.5 %) in the overall egg to adult mortality of *C. capitata* compared with the standard baseline diet. In contrast, Chang and Kurashima (1999) demonstrated a considerable increase in adult emergence of *B. latifrons* after incorporation of bell pepper in the larval diet.

Another important fitness parameter is flight ability, which is of vital significance in flies to be used in SIT programmes (Collins and Taylor 2010). One of the factors that determines the flight ability of fruit flies is the quality of the larval diet. For instance, in a study comparing different yeasts as ingredients of larval diet of *B. dorsalis*, Chang (2009b), found that flies from larvae reared on diet containing FNI200 and FNIL65 had significantly better flight ability and mating success than those reared on Korean yeast. Also the flight ability of *B. dorsalis* increased with the

amount of wheat germ oil in the larval diet (Chang and Vargas 2007). The authors postulated that fatty acids and vitamin E in wheat germ oil are responsible for enhancing the flight ability. Similar effects of enhancement of flight ability as a result of inclusion of wheat germ oil in the larval diet has also been reported for the Mexican fruit fly, *Anastrepha ludens* (Loew) (Pascacio-Villafa et al. 2015). Likewise, *C. capitata* reared without fatty acids had compromised flight ability (Cho et al. 2013). Cho et al. (2013) evaluated two larval diets: a conventional mill feed diet and a fatty acid-deficient liquid diet, on the flight ability of *C. capitata*. The authors found that only 20.7 % of flies from larvae reared on the fatty acid-deficient diet displayed full flight ability. However, 97 % of those from larvae reared on mill feed diet displayed full flight ability. The authors speculated that the nutritional deficiency might have induced over-expression of the flightless-I protein (or fli-I gene) resulting in reduced numbers of flies with normal flight ability. In general, Chang and Coudron (2007) demonstrated that wheat germ oil influenced the stage-specific quality of several fruit fly proteins such as stress proteins, detoxification proteins and glutathione-related proteins. Additional reports by Chang et al. (2010) further substantiated the findings that one mechanism of wheat germ oil actions in insect nutrition is the modulation of gene expression. In addition to fatty acids, vitamins were also reported to enhance *C. capitata* adult emergence and flight ability (Chang et al. 2001; Chang and Li 2004).

Larval diet quality also had significant effects on immature development of *B. oleae*. Hanife (2008) reported that 77 % of *B. oleae* larvae reared on an agar-based diet completed development and achieved significantly higher pupal weight compared with those reared on the control cellulose diet.

## 3 Endosymbionts and Fruit Fly Nutrition

Many insect taxa harbour microbial organisms in their bodies that affect their biology, physiology, nutrition and reproduction. Endosymbiotic gut-associated microbial communities have long been believed to have mutualistic associations with different species of fruit flies (e.g. Petri 1910; Hagen et al. 1963; Buchner 1965; Hagen 1966; Drew et al. 1983; Manousis and Ellar 1988; Tsiropoulos 1989; Behar et al. 2009). These mutualistic associations could enhance the host immune system, or be nutritional, especially for insects that rely on an inadequate food source such as fruit flies. The first symbiotic association in Diptera was described for *B. oleae* (Petri 1904, 1905, 1906, 1907, cited in Tsiropoulos 1992). Later, Hagen et al. (1963) and Hagen (1966) proved that endosymbiotic bacteria have a significant role in fruit fly development. The authors found that *B. oleae* fed on a complete diet produced normal progeny, but addition of antibiotic to the diet resulted in larval mortality. Also using antibiotic in *B. oleae* diet and radiolabeled food Tsiropoulos (1989) was able to establish that four amino acids (alanine, hydroxyproline, proline and tyrosine), which are crucial for *B. oleae* development, were produced by the biosynthetic activities of their gut microflora. Also working with *B. oleae*, Ben Yosef et al.

(2010) tested the hypothesis that symbiotic bacteria contributed to the adult fly's fitness in a diet-dependent manner. When females were fed a diet containing non-essential amino acids as the sole source of amino nitrogen, egg production was significantly enhanced in the presence of bacteria. However, the presence of bacteria did not affect fecundity of adults fed the sucrose-poor diet, or the protein-rich diet. In the light of their results, the authors concluded that bacteria were able to compensate for the skewed amino acid composition of the diet. In a recent study on *B. oleae* Ben Yosef et al. (2014) proved that the predominant gut bacterium, *Candidatus Erwinia dacicola*, was an essential element in the nutritional ecology of this fruit fly species. They demonstrated that the presence of the bacteria significantly enhanced *B. oleae* egg production by contributing essential amino acids and metabolizing urea into an available nitrogen source. The authors also established that bacteria were beneficial to females relying on bird droppings as a food source, but not to those feeding on honeydew. They also highlighted the fact that the evolution of this symbiosis has allowed adult flies to utilize nutritionally unbalanced food in nature.

Another African fruit fly species associated with symbiotic bacteria is *C. capitata* (e.g. Marchini et al. 2002; Yuval et al. 2010 and reference therein; Hamden et al. 2013; Augustinos et al. 2015; Gavriel et al. 2011). Behar et al. (2008) studied the gut bacterial communities in *C. capitata* and their impact on the flies' longevity. The authors found that inoculations with different species in the Enterobacteriaceae increased *C. capitata* longevity. In contrast, longevity was reduced by inoculations with high levels of the pathogenic bacteria, *Pseudomonas aeruginosa* (Schröter) Migula. Based on their results, the authors suggested that the community of Enterobacteriaceae within the gut of *C. capitata* may, in addition to their positive impact on nitrogen and carbon metabolism, development and copulatory success, also have an indirect effect to host fitness by preventing the establishment or proliferation of pathogenic bacteria. Ben-Yosef et al. (2008) compared the mortality rates between antibiotic-treated *C. capitata* and non-treated *C. capitata* when they were either maintained on sugar, or on full diet. They reported that eliminating the gut bacterial population prolonged longevity, but only for the flies fed on sugar, indicating that the effect of bacteria on lifespan was diet dependent.

Ben Ami et al. (2010) demonstrated that the addition of the bacterium *Klebsiella oxytoca* (Flügge) Lautrop (the dominant species of gut bacterium of several tephritid species [Behar et al. 2008, and reference therein]) to the diets of male *C. capitata* being mass-reared for SIT, significantly improved their copulatory performance. They also found that the addition of the bacteria to the post-irradiation diet not only enhanced the level of beneficial bacterial communities within the flies gut, but also resulted in decreased levels of the potentially pathogenic genus *Pseudomonas*.

Gavriel et al. (2011) also tested the effect of diets enriched with *K. oxytoca*, on sexual performance of sterile *C. capitata* males. They established that enriching the sterile male diet with this bacterium considerably improved mating competitiveness in the laboratory as well as in field cages. They also reported that sterile males fed on bacteria-enriched diet had longer life spans and were able to inhibit female remating receptivity more efficiently. Enhancement of sexual performance in male

*C. capitata* (the Vienna-8 strain) at emergence, as well as increases in male size when mass-reared on a larval diet enriched with *Klebsiella pneumonia* (Schröter) Trevisan, *Enterobacter* spp., or *Citrobacter freundii* (Braak) Werkman and Gillen have also been reported by Hamden et al. (2013).

In a very recent study Augustinos et al. (2015) reported that incorporation of *Enterobacter* sp. as a supplement to the larval diet of *C. capitata* resulted in reduced rearing duration as well as an improvement of both pupal and adult productivity without affecting other fitness traits such as pupal weight, sex ratio, male mating competitiveness, flight ability and longevity under starvation. Yuval et al. (2010) provides a review of recent studies on the effects of endosymbiotic bacteria on fitness of *C. capitata*.

Similar mutualistic associations of bacteria have been reported for non-African-tephritids. For example, as early as 1983 Drew et al. (1983) found that diets of bacteria, sugar and water resulted in increased fecundity of the Queensland fruit fly, *Bactrocera tryoni* (Froggatt), compared with those fed on the conventional diet of autolyzed waste brewer's yeast, sugar and water. The author concluded that the type and abundance of bacteria on leaves and fruit surfaces have an important role in the life history of tropical fruit flies. In a recent study to determine the gut bacterial community in *Bactrocera tau* (Walker) and their effect on fecundity of this species, Khan et al. (2014) identified eight genera and nine species of bacteria in the family Enterobacteriaceae. They further established that *B. tau* females fed on a protein diet supplemented with either *Proteus rettgeri* (Rustigian and Stuart) or *K. oxytoca* had a considerably higher mean number of ovarioles per ovary compared with those fed on a protein diet only.

Ben-Yosef et al. (2015) presented a different aspect of the mutualistic association between bacteria and fruit flies. The authors demonstrated that the bacterium *C. Erwinia dacicola* enabled *B. oleae* larvae to overcome host-plant defences when developing in unripe olive fruits. They suggested that the bacterium counteracted the effect of oleuropein found in unripe olives that confer immunity against fruit fly infestation.

## 4 Quality Control Parameters and Recording

The concept of quality control is relevant to all kinds of production programmes, regardless of the facilities used. In general, it is defined as 'The sum of all attributes deemed necessary or desirable to achieve a stated objective or expected function' (Boller and Chambers 1977).

Quality control provides a means of optimizing insect mass rearing by identifying and gradually correcting deficient production processes, thereby preserving the genetic variability of the strain (Leppla and Ashley 1989). Therefore, quality control procedures involve development, colonization, maintenance and various other processes that affect the production and use of insects for pest management purposes. Leppla and Ashley (1989) categorized quality control of mass-reared insects

into three main interrelated elements: (1) Production quality control which manages the consistency, reliability and timeliness of the production output; (2) Process quality control assures the performance of the production process so that unacceptable deviations do not occur in product quality; and (3) Product quality control regulates the conformity of the product to acceptable standards of quality and predicts the effectiveness of the product in performing its intended function. Aspects of mass-rearing environments that directly affect the quality of fruit flies include artificial larval and adult diets as well as rearing conditions (light intensity, photoperiod, insect density, temperature, humidity etc.), which influence quality control parameters such as body size, survival, pupal recovery, pupal weight, percent adult emergence, percent survival, longevity, flight ability, fecundity, fertility, percent egg hatch and mating ability of the reared insects (Calkins 1989; Vargas 1989; Walker et al. 1997; FAO/IAEA/USDA 2003). Apart from *C. capitata* and *B. dorsalis*, which have been reared for decades in different parts of the world (Vargas 1989) with great levels of success, the mass rearing procedures for the majority of economically important African fruit fly species, such as *C. cosyra*, *C. fasciventris* and *C. rosa*, are little known and documented.

In this regard, biological parameters are evaluated to identify possible deficiencies and to predict insect quality. Production can immediately be improved through testing of key and sensitive parameters and feedback mechanisms. Tests should be practical, uncomplicated, efficient and reproducible. A minimum number of parameters using the smallest sample size are recommended. In fruit fly mass rearing, important parameters include pupal recovery, pupal weight, percent adult emergence, percent survival, flight ability, percent fecundity and percent egg hatch (Calkins 1989; Walker et al. 1997; FAO/IAEA/USDA 2003). Walker et al. (1997) noted that there are variations between individual fruit fly species in any country and within the same species from different countries, but that there is a range that indicates that a colony is healthy. At the *icipe* facility, quality assurance is based on the following parameters: (1) pupal recovery from the number of eggs seeded should be >60 %; (2) pupal weight, using measurements of 100 pupae of the same age, should be consistent; (3) adult emergence should be >70 %; (4) percent fliers should be >80 % and (5) percent egg hatch, using records from 100 eggs, should be >70 %. The production and quality assurance in the Stellenbosch *C. capitata* SIT rearing facility in South Africa largely follow the guidelines developed by FAO/IAEA/USDA (2003) which was updated in 2014 (FAO/IAEA/USDA 2014).

## *4.1 Quality Control of Fruit Flies Reared on Solid Larval Diets*

On solid diets, Khan (2013) demonstrated that the parental egg hatch of the fruit fly, *B. tryoni* was significantly lower when reared on carrot diet (75 %) and lucerne diet (70 %) compared to Hooper's bran diet (82 %) and Vargas' bran diet (80 %). The $F_1$

egg hatch follows the same trend observed above on the different diets, with flies reared on Hooper's bran diet achieving the highest egg hatchability (83 %) followed by the Vargas' bran diet (82 %). The developmental duration of the larval stages was was not significantly different on the four different diets (Khan 2013). The larval duration on these diets ranged between 10 and 11 days. The mean pupal weight was significantly greater for pupae recovered from Hooper's bran diet (10 mg) and the lucerne diet (10 mg) than from Vargas' bran diet (8 mg). The Hooper's bran diet (1260 ± 97.1) showed mean pupal yields of approximately double those found from lucerne (658 ± 16.2) and carrot (674 ± 150.8) diets. Despite the high variability, there were no significant differences between the different diets. However, there were substantial differences amongst the diets in pupal recovery. The percentage pupal recovery was not significantly different on Hooper's bran diet and Vargas' bran diet. Although, the pupal recovery was lowest on lucerne and carrot diets, no statistically significant difference were reported. According to the studies conducted by Khan (2013), a greater proportion of flies emerging from pupae reared on carrot diet were males compared with those from pupae reared on any of the bran diets (Hooper's bran diet and Vargas' bran diet), which all had sex ratios closer to 50:50. The mean sex ratio of adults emerging from the lucerne diet was intermediate but it was not significantly different from the bran diets. This observation is supported by Khan (2013) who indicated that it is not uncommon to find that the proportion of each sex surviving to pupation differs on different diets. Adult emergence was reasonably good when reared on the four solid diets ranging from > 90 % for the lucerne and carrot diets to < 70 % for Vargas' bran diet. Adult emergence was poorest (67 %) on Vargas' bran diet, being significantly lower than any of the other diets. The percentage fliers, which is the number of pupae that either failed to emerge or failed to fly following eclosion, were significantly lower for pupae reared on Hooper's bran diet and Vargas' bran diet than on the lucerne and carrot diets, which had high adult emergence. Rate of fliers, was highest on the lucerne diet (61 %) compared with Hooper's bran diet, Vargas' bran diet and carrot diet. Higher mean egg production per female per day was observed for adult flies from larvae that had been reared on Hooper's bran diet and Vargas' bran diet than for adult flies from larvae that had been reared on lucerne diet or carrot diet. Egg latency (the period between adult emergence and the first egg being laid by a cohort of flies) was significantly shorter for flies reared on the lucerne diet than for those reared on the carrot diet, Hooper's bran diet or Vargas' bran diet. Overall, when compared with other recent studies (Collins et al. 2008; Collins and Taylor 2010) and the recommended standards from the FAO/IAEA/USDA (2003), percentage fliers and rate of fliers in the studies carried out by Khan (2013) on solid diet were low. According to Collins and Taylor (2010) and Collins et al. (2008), this may be due, in part, to the lower light intensity used which may have reduced flight ability.

Ekesi and Mohamed (2011) explored several bulking compounds including wheat, carrot, boiled cassava, sugarcane bagasse for mass-rearing *B. dorsalis, C. fasciventris* and *C. rosa*, and carrot supplemented with mango powder for mass-rearing *C. cosyra*. They found that, for *B. dorsalis*, pupal recovery was generally greatest when they were reared on wheat (65 %) followed by sugarcane bagasse

(55 %) and carrot-based (54 %) diets, with the smallest recoveries in the cassava-based diet (32 %). Pupal weight was not significantly different amongst carrot, wheat and sugarcane bagasse-reared flies and ranged between 13.6 and 14.1 mg. However, pupae reared on the cassava-based diet were significantly lighter (12.5 mg) compared with the other three media. Adult emergence was significantly higher on carrot and wheat-based diets (80–86 %) compared with the sugarcane bagasse-based diet (70–77 %). Fecundity over a 10 days period was also significantly higher on the carrot, wheat and sugarcane bagasse diets (342–366 eggs per female) than on the cassava-based diet (233 eggs per female). For *C. fasciventris* and *C. rosa*, all quality control parameters from carrot and wheat diets outperformed those from sugarcane bagasse and cassava diets. For *C. cosyra*, diets of carrot, carrot supplemented with mango and sugarcane bagasse were used. The study showed that supplementing carrot with mango powder significantly increased pupal weight, egg production and egg hatchability compared with the other diets. The authors recorded a pupal weight of 10.5–11.7 mg when reared on carrot supplemented with mango powder, 9.2 mg on carrot alone and 7.2 mg on sugarcane bagasse. In fruit fly mass rearing, high pupal weight is a desirable characteristic in the production process, as it is a good indicator of the ultimate body size of the eclosing adult. Churchill-Stanland et al. (1986) found that the size of adult *C. capitata* was important for mating success and noted that 8 and 9 mg insects achieved greatest mating success than those that weighed 6 and 4 mg. Fly size is also a determinant of insect fertility and fecundity. Overall, they concluded that quality control parameters from carrot, carrot supplemented with mango and wheat diets were superior for mass rearing of *B. dorsalis*, *C. fasciventris*, *C. rosa* and *C. cosyra* compared with diets based on sugarcane bagasse or boiled cassava.

## *4.2 Quality Control of Fruit Flies Reared on Liquid Larval Diets*

Studies were done by Khan (2013) on *B. tryoni* in three liquid diets: Fay's liquid starter diet (Fay 1989), Chang's 2006 liquid diet (Chang et al. 2006) and Chang's 2007 liquid diet (Chang et al. 2007). Egg hatch was significantly higher for adults reared on Chang's 2006 liquid diet than the other diets and it was similar for adults reared on Fay's starter diet or Chang's 2007 liquid diet. Larval developmental time was significantly (12 days) longer for larvae reared on Chang's 2007 liquid diet than for larvae reared on Chang's 2006 liquid diet or Fay's starter diet. Mean pupal weight and mean pupal yields were similar for all three liquid diets. However, the percentage pupal recovery was significantly higher on Chang's 2006 diet than either Chang's 2007 liquid diet or and Fay's starter diet. From the flies emerging from pupae reared on Fay's starter diet and Chang's 2007 liquid diet, a greater proportion of females were observed in comparison with the number eclosing from pupae reared on Chang's 2006 liquid diet. Also adult emergence was very poor: 50 % for

Fay's starter diet, being significantly lower than Chang's 2007 liquid diet (72 %) and Chang's 2006 liquid diet (83 %). Percentage fliers was significantly lower for individuals reared on Fay's starter diet compared with Chang's 2007 liquid diet and Chang's 2006 liquid diet. The lowest adult emergence, flight ability and eggs/female/day were recorded for individuals reared on Fay's starter diet. The percentage egg hatch of the F1 generation was highest for flies reared on Chang's 2006 liquid diet (87 %), followed by Chang's 2007 liquid diet (84 %). These quality control parameters are inferior to those reported by Collins et al. (2008), Collins and Taylor (2010) and the recommended standards from the FAO/IAEA/USDA (2003). The absence of adequate overhead lighting was found to be the major cause of the low values recorded (Collins et al. 2008; Collins and Taylor 2010).

Ekesi and Mohamed (2011) used liquid diet with ingredients that were similar in composition to those described by Chang et al. (2006) for larval rearing of four fruit fly species: *B. dorsalis*, *C. fasciventris*, *C. rosa* and *C. cosyra*. The authors found that *B. dorsalis* reared on this liquid diet had a 60 % percent pupal recovery rate, 14 mg mean pupal weight, 92 % percent adult emergence rate, a mean of 214 eggs laid over a 10-days period (fecundity), a 72 % $F_1$ egg hatch rate (egg fertility) and a flight ability or flier rate of 82 %. For *C. fasciventris* the mean values recorded were 28 % pupal recovery, 6 mg pupal weight, 65.8 eggs (fecundity, 10 days), 70 % adult emergence, 65 % egg fertility and flight ability (78 %), while for *C. rosa* and *C. cosyra* the mean values recorded were inferior for all these parameters in the liquid-based diet (Ekesi and Mohamed 2011). This was unexpected, given that the nutritional content of the liquid diet was quite high and had previously been found suitable for the development of other *Ceratitis* species such as *C. capitata* (Chang et al. 2007). Since fruit fly adaptation to artificial diets varies with species (Souza et al. 1988; Tsitsipis 1983; Kamikado et al. 1987), it is likely that the *Ceratitis* species in the study conducted by Ekesi and Mohamed (2011) would require a prolonged period of adaptation to the liquid diet to achieve the recommended quality control parameters. This is in accordance with other studies demonstrating that insect adaptation to artificial diet varies with the species and that at least ten generations were required for *C. capitata* to adapt to an artificial diet (Souza et al. 1988). About three or four generations were required for *B. oleae* to adapt (Tsitsipis 1983) and *Z. cucurbitae* required 14 generations to reach a permanent plateau (Kamikado et al. 1987).

Khan et al. (2011) also compared three different liquid diets with the aim of identifying easily available and low-cost protein sources as ingredients for mass production of larval *B. dorsalis*. There were no significant differences in quality control parameters such as total number of pupae produced (3350), larval duration (7 days) male: female ratio (51:49) and percentage egg hatch (88.5 %) of *B. dorsalis* reared on the control liquid diet and the modified diets. Furthermore, the pupal density (0.6), pupal weight (12.5 mg), percentage adult emergence (98 %) and percent fliers (79 %) were almost the same amongst the control diet and the modified diets. The authors concluded that liquid diet containing baking yeast, soy bran and soy protein (2:1:1) used as sources of protein was highly promising for mass rearing of *B. dorsalis* under laboratory conditions. According to the authors, the advantage of

this liquid diet is that obviates the need to use a starter diet as described in Fay and Wornoayporn (2002) and a bulking agent, thus saving on labour costs and storage space. Liquid based diets with recyclable substrate systems are cost effective ways to produce high quality mass-produced tephritid fruit flies.

### 4.2.1 Effects of Yeast in Liquid Diets

Ekesi and Mohamed (2011) compared two yeast types in liquid diet and found that pupal recovery (62 %), pupal weight (13 mg), adult emergence (88 %) fecundity (no. eggs/female/10 days = 368 eggs) and egg hatch (70 %) of *B. dorsalis* reared on diet containing Lallemand yeast was significantly higher than on the diet with the local waste brewers' yeast, though the type of yeast did not affect the number of fliers (81 and 80 % for Lallemand and waste brewers' yeast, respectively). According to the authors, the inferior quality control parameters recorded for the waste brewers' yeast could be attributed to the high protein content of the local waste brewers' yeast that might have been detrimental to the development of *B. dorsalis*. The authors recommended that the quantity of local waste brewers' yeast in liquid diet should be reduced and the impact of this reduction be assessed on *B. dorsalis* production.

## *4.3 Quality Control of Fruit Flies Reared on Host Fruit Larval Diets*

Via (1986) reported a positive correlation between preference and offspring performance of fruit flies on different host plants in nature suggesting that these insects have the ability to choose the host plant on which their offspring develop best and fastest. For example, Krainacker et al. (1987) studied the quality control parameters for *C. capitata* reared on 24 different hosts and reported larval development times between 6.9 days for larvae reared on tomato and 11.7 days for those reared on grape (*Vitis vinifera* L.). Carey (1984) and Rivnay (1950) obtained similar results for *C. capitata* reared on many of these same hosts. In contrast, when *C. capitata* was reared on apple (*Malus domestica* Borkh.), which is an unfavourable host, almost all the eggs hatched within a period of 2 days but the larval developmental duration took approximately 18 days and pupal duration took 10 days (Papadopoulos et al. 2002). The developmental time parameters reported by Papadopoulos et al. (2002) were found to be longer than those reported by Krainacker et al. (1987) and Carey (1984) on the fruits of several other hosts, such as blackberry (*Rubus rubrisetus* [Rydb]), cherry (*Prunus avium* [L.]), plum (*Prunus americana* Marsh.), mango (Mangifera indica [L.]), blueberry (Vaccinium corymbosum [L.]) and raspberry (Rubus idaeus [L.]). The high larval mortality as well as the long developmental period on the hosts described above indicates that these hosts were not favourable

hosts for C. capitata, probably because of their nutritional elements, the texture of the flesh, and secondary compounds, that are all factors that determine the suitability of a host for development (Krainacker et al. 1987; Zucoloto 1993; Kaspi et al. 2002).

According to Krainacker et al. (1987) C. capitata larval survivorship ranged from 1 % for those reared on apricot (Prunus armeniaca [L.]) and papaya (Carica papaya L.) to 68 % for those reared on blackberry. These values are generally below those reported by Carey (1984) and Papadopoulos et al. (2002) with immature survival rates of > 80 % for both the eggs and pupae while the larval survival rate was relative low (>40 %). Pupal survivorship reported by Krainacker et al. (1987) was 59 to 96 %, which is in agreement with the figures reported by Carey (1984). Krainacker et al. (1987) also found that the average pupal size of C. capitata when reared on various host fruits ranged from 1.71 mm (e.g. on tomato) to 1.97 mm (e.g. on lychee [Litchi chinensis Sonn.]). Pupae with the largest mean diameters were recovered from flies reared on fruit from from rutaceous hosts.

Arita and Kaneshiro (1988) compared the mating success of male C. capitata raised on two different host fruits. When competing for mates in the same arena they found that, although significantly smaller in size, males emerging from coffee (Coffea arabica [L.]) copulated more frequently than males emerging from cherry. This observation was further supported by Whittier et al. (1994) and Kaspi et al. (2000) who reported that male copulatory success in C. capitata was not due to their body size, as protein-fed males were more likely to start calling earlier, and, consequently more likely to copulate than protein-deprived males.

Gross fecundity of females reared on the fruits of 24 different hosts by Krainacker et al. (1987), ranged between 490 and 690 eggs/female while net fecundity from half of the hosts was between 350 and 450 eggs/female. The gross fecundity rates are similar to those reported by Shoukry and Hafez (1979) at equivalent temperatures, but are less than those reported by Carey (1984) at 25 °C. This difference may have been due to temperature differences between studies (Rivnay 1950).

Krainacker et al. (1987) reported an average life span of male and female C. capitata of 60 and 50 days, respectively. This is contrary to the figures reported by Papadopoulos et al. (2002), who found that the greatest longevity of male and female C. capitata was 142 and 91 days, respectively. This variation in life expectancy between the two sexes has been attributed to reproductive cost, which is higher in females than in males, hormonal differences, and other behavioural and physiological differences between the two sexes (Vargas and Carey 1989; Carey et al. 1995). This is also in accordance with the report by Bozzini and de Murtas (1975), Rossler (1975) and Shoukry and Hafez (1979).

Laboratory studies of B. zonata on fruits of six host species revealed that guava (Psidium guajava L.) was the most preferred host with pupal recoveries of 434 pupae/fruit, followed by ber (Ziziphus mauritiana Lamk; 177 pupae/fruit), banana (Musa sp.; 120 pupae/fruit), apple (13 pupae/fruit), chikoo (Manikara zapota [L.] Royen; eight pupae/fruit) and citrus (Citrus sp.; five pupae/fruit) (Rauf et al. 2013). Additional studies conducted by Sarwar et al. (2013) on mango, peach (Prunus persica [L.] Baksch) and apple fruits revealed that mango was the most preferred host

followed by peach and apple, based on the mean number of pupae (173.2, 150 and ten, respectively) formed. The pupal weight varied significantly across the different host fruits with pupae recovered from mango weighing 6.40 mg, from peach 6.3 mg and from apple 6.1 mg. The percentage emergence of B. zonata was 84.5 %, 81.1 % and 75.1 % on mango, peach and apple, respectively. The results support the observation that oviposition depends upon the decision to select an appropriate host that can support the development of their offspring (Fontellas-Brandalha and Zucoloto 2004; Joachim-Bravo et al. 2001).

Mir et al. (2014) assessed the quality control parameters of Z. cucurbitae when reared on cucumber as a natural host source. The developmental duration of the eggs was 12–24 h with a mean of 16.8 ± 6.2 h. These results are in agreement with those reported by Waseem et al. (2012) and Khan et al. (1993) who reported an incubation period of 24.4 to 38 h on cucumber. Shivarkar and Dumbre (1985) reported an incubation period of 1.2 days on watermelon (Citrullus lanatus [Thunb.] Matsum and Nakai), while Koul and Bhagat (1994) recorded an incubation period of 1.0–5.1 days when Z. cucurbitae was reared on bottle ground (Lagernaria siceraria [Molina] Standl.). According to Mir et al. (2014) the mean larval developmental period was 4.5 ± 1.1 days. This is slightly lower compared with studies conducted by several other authors who reported larval developmental periods of 5–22 days (Renjhen 1949), 5–11 days (Singh and Teotia 1970), 3–8 days (Doharey 1983) and 15 days (Shivarkar and Dumbre 1985). The pupal duration reported by Mir et al. (2014) varied between 8 and 9 days with a mean of 8.4 ± 0.51 days. This is consistent with earlier reports on the pupal period of Z. cucurbitae by Narayanan and Batra (1960), Agarwal et al. (1987), Dhillon et al. (2005), Shivayya et al. (2007), Waseem et al. (2012) and Langar et al. (2013) who all reported pupal periods of 8–9 days on cucumber. According to Mir et al. (2014), the copulation period of Z. cucurbitae varied between 2 and 4 h, which is in accordance with the reports by Vishva (2005), Shivayya et al. (2007) and Waseem et al. (2012), who found that a mating period of more than 30 min was required for sperm transfer to occur, and that the amount of sperm transferred increased progressively for up to 4 h. The preoviposition period was 12.4 ± 2.4 days and varied from 10 to 15 days, whereas the oviposition period was 18.2 ± 5.61 days and ranged from 12 to 28 days. This is consistent with the findings of Hollingsworth et al. (1997), Khan et al. (1993), Koul and Bhagat (1994) and Langar et al. (2013). Fecundity of sexually mature adult female Z. cucurbitae range between 58 and 92 eggs with a mean of 75.8 ± 12.5 while egg hatchability was found to be 86.1 ± 0.5 % (Mir et al. 2014). These findings are in agreement with those of Atwal (1986) and Langar et al. (2013) who recorded 58–95 and 50–91 eggs per female during her entire life span, respectively.

Additional studies conducted by Sarwar et al. (2013) with Z. cucurbitae on four different vegetable crops: bitter gourd (Momordica charantia L.), aubergine (Solanum melongena L.), muskmelon (Cucumis melo L) and pumpkin (Cucurbita pepo L.) indicated that pupal recovery was generally greatest from bitter gourd (134.1) followed by aubergine (8.3) and least from muskmelon (3.8) and pumpkin (3.8). Pupal weight was also significantly different, ranging between 4.6 mg for individuals reared on pumpkin to 4.19 mg for individuals reared on bitter gourd.

Adult emergence was significantly higher from bitter gourd (82.6 %) compared with from aubergine (73.7 %), muskmelon (67.2 %) and pumpkin (56.4 %). A mean total of 110.8 adults emerged from pupae formed when Z. cucurbitae was reared on bitter gourd which was significantly more than when reared on aubergine, muskmelon and pumpkin (6.1, 2.4 and 2.2, respectively).

Khan et al. (2011) also conducted a similar study aimed at understanding the relative suitability of fruits from different host plants for performance of Z. cucurbitae in terms of pupal number and subsequent adult emergence. More pupae developed when larvae were reared on bitter gourd (202) than cucumber (Cucumis sativus [L.]; 193), sponge gourd (Luffa cylindsica L.; 179), aubergine (Solanum melongena [L.]; 124), sweet gourd (Cucurbita maxima [D.]; 118), bottle gourd (Lagenaria siceraria [Mol.] Standl; 115), pointed gourd (Trichosanthes dioica [Roxb.]; 92) and ash gourd (Benincasa hispida [Thunb.]; 64). The fewest pupae developed when larvae were reared on tomato (Solanum lycopersicum [L.]; 49). The percentage emergence of Z. cucurbitae across the different host species was significantly different and ranged from 9.2 % on sponge gourd to 85.1 % on pointed gourd, 85.4 % on ash gourd and 87.0 % on bottle gourd. Few studies have been done on the suitability of different host plants for rearing of Zeugodacus species. These findings shed light on the necessity for further research to collect extensive data on demographic patterns and niche differentiation of these polyphagous, invasive fruit flies.

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