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Advancements in Integrated Pest Management strategies for *Bactrocera dorsalis* in Asia: current status, insights, and future prospects

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With 3 figures

Abstract: Oriental fruit fly, *Bactrocera dorsalis* (Diptera: Tephritidae), is an infamous invasive pest species with a broad host range. The pest has spread to most territories worldwide in the last decades, posing an increasing threat to global fruit and vegetable production. Here, we reviewed the current knowledge, control methods and prospects of Integrated Pest

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Management (IPM) strategies against *B. dorsalis* based on a survey on the pest status, damages and current practices conducted in the Asia region. The outcome of the survey pointed to *B. dorsalis* as a major concern as it causes heavy damage in most of the participating countries. Current IPM strategies involve multiple control tactics, but often with over reliance on chemical pesticides. Behaviour-based monitoring and control measures are commonly employed in this region because of ease-of-use and cost-effectiveness, which serve as the key component of the IPM strategies. The sterile insect technique application, though environmental-friendly, sustainable and compatible with IPM, is limited because of high operational cost, ineffective government policy and low social acceptance. Public knowledge and technology transfer, training and hands-on guidance, relevant stakeholder community participation, acceptance and cooperation, are the key levers for sustainable and successful IPM against *B. dorsalis*. More initiatives and research efforts for developing non-chemical control tactics and biopesticides will optimize the existing IPM strategies. Lastly, effective quarantine and phytosanitary measures towards better border biosecurity should be taken to intercept and curtail the risk of *B. dorsalis* expanding its current geographical boundary in the face of global climate change.

Keywords: Tephritidae; oriental fruit fly; male annihilation technique (MAT); sterile insect technique (SIT); IPM; control tactics

1 Introduction

The oriental fruit fly, *Bactrocera dorsalis* (Hendel) (Diptera: Tephritidae), is one of the most destructive and polyphagous agricultural pests, posing significant threats to international trade and agriculture industry worldwide (Clarke et al. 2005; Zhao et al. 2024). The species belongs to a large species complex, the *B. dorsalis* complex, which currently contains close to 90 sibling species. The *B. dorsalis* complex, first described by Drew and Hancock in 1994 with just 52 species, separated the *B. dorsalis sensu stricto* from *B. papayae* Drew and Hancock and *B. philippinensis* Drew and Hancock (both of which are regarded as endemic species to Malaysia and the Philippines, respectively) as different biological units based on the differences of allozymes, geographical distribution and slight morphological variations. Later, *B. invadens*, a new species detected in Kenya in 2003, was also added to the *B. dorsalis* complex (Drew et al. 2005). It was not until a concerted effort using integrative taxonomy approaches by close to 50 researchers from at least 20 countries under the FAO/IAEA's coordinated research project that a significant breakthrough was made in synonymizing the four putative species, *B. dorsalis, B. invadens, B. papayae* and *B. philippinensis*, as one single biological species, *B. dorsalis* (Schutze et al. 2015a, 2015b).

Bactrocera dorsalis attacks more than 250 fruit species belonging to 57 plant families, some of which are commercially important crops, such as mango, carambola, papaya, pineapple, guava, orange, dragon fruit, stone fruit, banana, passion fruit, grape, etc. (Orankanok et al. 2007; Affandi et al. 2023). It causes serious economic damage to horticultural fruit and vegetable production and consequently, a major biosecurity concern to many countries (Li et al. 2023; EPPO 2024).

Tropical regions in South and Southeast Asia are the leading production area of tropical fresh fruits and vegetables in the world, where the horticultural production has been expanded in the past years (Statista database www.statista.com). With high host availability and climatic suitability in this region, *B. dorsalis* could breed continuously, synchronizing with fruiting seasons, and thus precipitate quarantines and trade embargoes.

To better understand the current control situation of *B. dorsalis* in Asia countries, a survey was conducted on local farming practices from 48 local researchers, extension workers and farmers belonging to 16 countries in Asia. The questionnaires enquired the farmers about the pest status of *B. dorsalis* and the estimated vegetable and fruit damage in their farms (survey form is available online in the supplementary file). The survey also acquired information on the biotic and abiotic factors that caused heavy damage and rapid spread of *B. dorsalis* in their respective countries. The farmers were required to (a) scale the relative relevance of the five components of an IPM package (Chemical control, Biological control, Behaviour-based control, Agronomic control and Monitoring and early pest detection) practiced on their farms from 0 to 10, with the total sum of score at 10, and (b) provide the products or methods most used in each of the IPM components. Similarly, the farmers were also asked to rate the challenges (Knowledge on biology and its presence, Cost of insecticide applications, Control failure by insecticides, Cost associated with non-chemical control) faced in managing the pest species. Lastly, we collected the information on farmers' expectation on the types of assistance received from researchers, extension specialists and the government to provide useful inputs in managing *B. dorsalis*.

Based on the summary of the survey on the pest status, damages and current practices conducted in the regions, we then provide a timely and updated review of the knowledge, control methods and prospects of IPM on the invasive *B. dorsalis* in different scenarios in Asia. We also addressed potential challenges and gaps, and identified new and novel concepts and approaches for a better pest control solution, with the hope to empower regional cooperation on integrated and sustainable control strategies in the future.

2 Origin, expansion and current geographical distribution

The origin and global spread routes of *B. dorsalis* were a highly debated topic and a few routes have been proposed. It was first proposed based on the record of its presence in 1912 that *B. dorsalis* originated from Taiwan (Hardy 1973) and subsequently spread through Southeast Asia and South Asia during the 20th century (Aketarawong et al. 2007; Qin et al. 2018; Zhang et al. 2023). However, based on the taxonomic history, Clarke et al. (2019) has clarified that the pest was already present in East India since late 18th century under the synonym name of *Musca ferruginea* by Fabricius in 1794.

Recent large-scale SNP dataset analysis of 487 *B. dorsalis* genomes by Zhang et al. (2023) corroborated with the claim by Clarke et al. (2019). It was shown that *B. dorsalis* originates from the southern India and independently spread through three invasion routes worldwide (Zhang et al. 2023). Owing to human-assisted carriage and high dispersal capability, *B. dorsalis* has now spread to most territories worldwide (at least 75 countries), including tropical and subtropical regions of Asia, Pacific, Africa, Europe, America and Oceania (Hardy & Adachi 1956; Hendel 1912; Drew & Hancock 1994; Chailleux et al. 2021; Sookar et al. 2021; Grechi et al. 2022; Deschepper et al. 2023).

The invasive potential of *B. dorsalis* to a new habitat is greatly facilitated by the increasing international trade and climatic changes, together with several biotic advantages, e.g., high reproductive potential, short life cycle, high dispersal ability and broad host range (Gutierrez et al. 2021; Wang et al. 2023; Zhang et al. 2023; Zhao et al. 2023). *B. dorsalis* has exhibited a rapid range expansion in recent decades, particularly in the face of global climate change, and it is disastrous if this pest continues extending to high latitude areas and acquire high cold hardiness from cold-hardening or acclimation. Although the magnitude of this plasticity appears low (Pieterse et al. 2017), recently, this species has extended its Asian range northward into regions previously thought unsuitable, e.g., central areas of China (Jaffar et al. 2023). The risk areas of *B. dorsalis* in the northern and southern hemisphere have expanded along with global climate change and the distribution range is predicted to extend poleward (Cai et al. 2023a). Few cases showed that the early detection of incipient populations and the adoption of strict interception programmes could result in successful eradication, but once established, it seemed very hard to prevent its rapid spread.

In the case of Africa, the delayed incursion response to eradicate the invasive *B. dorsalis* from the African continent due to initial inaccurate identification as a new species, *B. invadens*, has caused the species' expansion across most tropical parts of Africa within less than 10 years (Lux et al. 2003; Ekesi et al. 2006). Among tephritid fruit flies, species displacement or exclusion often occurs when an invader encroaches in the territory occupied by a different species, either native or pre-established in a previous invasion (Moquet et al. 2021). Most examples of interspecific competition have demonstrated that invasive *B. dorsalis* was highly competitive and outcompete the other native species where they invaded (see a summarized list in Duyck et al. 2004; Moquet et al. 2021).

Heavy damage, economic losses and environmental issues from pesticide misuse practices have been witnessed in some regions. Due to its efficient dispersion and establishment of adventive populations in various tropical and subtropical regions, the threat of rapid spread underscores the urgent need for more in-depth studies on effective IPM solutions and establishing a regional collaborative network among agricultural and research agencies. Its persistent dispersal, expansion and damage pose immense challenges for researchers and farmers seeking to mitigate its impacts to agricultural products and international trade.

3 Biology, ecology and behaviour

3.1 Biology

Bactrocera dorsalis, a holometabolus insect, undergoes four life stages from eggs, larvae, pupae and adult for a complete life cycle. All dacine fruit flies, including *B. dorsalis* are diurnal insects and spend most of the daytime in food foraging, feeding and oviposition (Clarke 2019). The flies feed on various carbohydrate sources such as floral nectar, fruit juice and honey dew for energy provision. Like other frugivorous *Bactrocera* spp., gravid female *B. dorsalis* lay eggs beneath the skin of ripened or ripening fruits where the subsequent larvae emerge and feed before leaving the fruit to pupate in the soil (Han et al. 2011; Li et al. 2024). Upon adult emergence, protein foraging and feeding is essential for male and female flies to realize their reproductive potential. Females are autogenous and need protein for ovarian development (Drew & Yuval 2000), while males require protein for sperm maturation, sex pheromone biosynthesis and other mating related traits, e.g., sexual behaviours and copulatory success (Gui et al. 2023). In nature, protein resources come from leaf-surface leachates (which contain amino acids, organic acids and sugars) and bird feces (Clarke 2019). Post-emerging flies perform extensive flights for food and protein prior to mating, while the mature fruit flies often search for mating sites and host fruits for oviposition (Fletcher 1989). Localised movement and non-dispersive behaviour are often observed when hosts are plentiful (Fletcher 1987). However, when food resources are declining, the flies may move out in search for resources.

3.2 Seasonal population dynamics

The species is multivoltine and generally completes four to ten generations per year with considerable overlaps across

generations depending on the temperature around its native range and host availability (Han et al. 2011; Wei et al. 2017; Li et al. 2019; Clarke 2019; Clarke et al. 2022; Cai et al. 2023b). The population dynamics of fruit flies are greatly influenced by temperature, rainfall and host availability (Clarke 2019). An appropriate amount of monthly rainfall (100–200 mm) is necessary to provide suitable soil and atmospheric moisture content to facilitate pupation, mating and oviposition activities (Liu et al. 2019). The optimum development temperature of *B. dorsalis* ranges between 25 °C to 30 °C (Li et al. 2013). Hence, the temperatures and moisture range within the South and Southeast Asian regions offered an ideal climatic condition for fruit fly population growth. Under these optimum conditions, the abundance of *Bactrocera* spp., including *B. dorsalis* is strongly correlated with host plant availability, abundance and phenology (Clarke 2019). The presence of primary and secondary crops in an agroecosystem, as well as non-crop plants, contribute to sustain the population dynamics of polyphagous *B. dorsalis* (Clarke 2019).

3.3 Mating behaviour

The dacine flies are dusk-mating insects. *B. dorsalis* males initiate courtship behaviour during sunset when light intensity decreases to below 1000 lx (Wee & Tan 2000). Males perform active wing fanning (for sex pheromone dispersal) to attract conspecific females. When the attracted females arrive in vicinity, males mount on the back of the approaching females by inserting the male aedeagus into female ovipositor. Once successful, the mating pair remained in copulatory posture from dusk to dawn, ca. 9 to 10 hours (Wee & Tan 2000).

Unlike the monophagous species, *B. dorsalis* employ a non-resource-based mating system, i.e. the leks, which is the congregation of males at a communal display area to attract and court potential mates leading to copulation, is common in polyphagous tephritid species (Benelli et al. 2014). At leks, male flies perform male-male competition (intrasexual selection) while the female flies are making active choices of mates (intersexual selection) (Benelli et al. 2014). The males of *B. dorsalis* are polyandrous while multiple mating is also common among the female flies, with 1–3 days of refractory period (Wee & Tan 2000). The knowledge of mating, sexual communication and the traits indicating male fitness and sexual competitiveness involved in sexual selection may contribute to the improvement of sterile insect technique (SIT) and IPM programs (Benelli et al. 2014).

3.4 Behaviour attraction to methyl eugenol

Males of certain *Bactrocera* spp., including *B. dorsalis*, are highly attracted to and feed upon methyl eugenol (ME), a plant-derived semiochemical discovered by Howlett in 1912 (see also review by Tan & Nishida 2012). The attraction of *B. dorsalis* males to ME is concomitant with early sexual development (Wong et al. 1989) and effective at low quantity (Wee et al. 2002; Hee et al. 2015). This sex- and age-related attraction to ME was then manipulated to successfully eradicate and suppress *B. dorsalis* in isolated populations (Koyama et al. 1984; Steiner et al. 1970). It was not until more than 80 years later the reason behind the strong interaction between fruit fly and ME was revealed. The ingestion of ME is highly linked with the production of highly competitive sex pheromones that enhance male courtship activities, render them mating advantages and ultimately promote reproductive success (Tan & Nishida 1996). The knowledge of sexual competitiveness enhancement by ME treatment has contributed to SIT by improving sterile males' mating competitiveness and having mating advantage when competing with feral males (Shelly et al. 2010).

A systematic ablation of the chemosensory organs showed, that *B. dorsalis* males rely on their antennae for long range (> 100 m) foraging of ME while the maxillary palps are responsible for locating ME source at short range (< 40 m) prior to feeding (Chieng et al. 2018, Ono et al. 2021). For a long time, the underlying molecular mechanism of olfactory detection of ME by *B. dorsalis* males remain unclear and has been a popular research exploration by many researchers (Chen et al. 2022). The ME odour molecules passed through the pores of chemosensilla and bind to the odorant binding protein (OBP) present in the sensilla lymph. Thyese odorant-ligands then bind to the olfactory receptors (OR) on the surface of olfactory receptor neurons (ORNs), resulting in signal transduction. The ME receptor is an OR as a highly conserved co-receptor (ORCO) is required for ME detection in *B. dorsalis* (Zheng et al. 2012). There are 49 OBPs annotated in *B. dorsalis* (Chen et al. 2019). Amongst these, BdorOBP56f-2 (BdorOBP2) was found to be involved in ME perception in *B. dorsalis*, with significant ME-induced transcriptional expression (Liu et al. 2017). By silencing BdorOBP56f-2 (BdorOBP2) using RNAi, the sensitivity of *B. dorsalis* to ME was reduced significantly. Recent analyses RNA-Seq and qRT-PCR have shown that ME detection involves odorant receptors OR88a and OR94b1 in mature *B. dorsalis* males' antennae (Liu et al. 2018; Zhang et al. 2024). ME elicited consistent responses in the BdorOR88a- and BdorORCO-expressing *Xenopus* oocytes, and RNAi knocking down resulted in a significant reduction (Liu et al. 2018). These studies have shown that reduced expression of OR or ORCO leads to a decrease, but not entirely, in the attraction of male flies to ME.

Apart from ME, *B. dorsalis* males are also attracted to other plant-derived chemicals such as β-caryophyllene and zingerone (Tan & Nishida 2000; Ranaweeera & Hee 2024) but their potential use in control and management of *B. dorsalis* has not been explored.

4 Outcome of survey of current control measures of *B. dorsalis* in Asia

From the survey response of the 16 participating Asian countries (indicated in Fig. 1A), *B. dorsalis* was the major pest of concern where the average estimated fruit damage was between 40% to 60%. It was apparent that heavy damage and rapid spread of *B. dorsalis* is common in all the countries surveyed, which is largely attributed to the following aspects: diverse host availability and alternative hosts, favorable climatic conditions, ineffective quarantine measures, poor sanitation measures, increasing transboundary trade and transportation, lack of technical knowledge and public awareness on pest management with no action plan or only implement control during fruiting season.

The IPM pyramid was constructed based on the proportionate scores given by the interviewee for each of the current control measures they adopted (Fig. 1B). The survey feedback showed that one-third of the farmers used chemical pesticide sprays (32.5%) to manage *B. dorsalis*, followed by behaviour-based control (21.2%) and agronomic practices (21.0%). Fewer farmers used monitoring and early detection techniques (14.8%), and biological control agents was the least adopted method (10.6%). A wide range of insecticide classes and families were used, which included anthranilic diamides (e.g. chlorantraniliprole), organophosphate (e.g. malathion), spinosyn (e.g. spinosad), phenylpyrazole (e.g. fipronil) and neonicotinoids (e.g. thiamethoxam and imidacloprid), which resulted in high levels of insecticide resistance (Jin et al. 2011; Wei et al. 2017; Jaffar et al. 2023).

Behaviour-based control, such as male lure-baited traps, yellow sticky traps and protein bait traps, was commonly used by the farmers in monitoring and controlling tephritid fruit flies. This strategy manipulated the olfactory and visual sensory of *B. dorsalis*, as the species is known to be highly attracted to ME, a powerful male lure that is effective at nanogram level (Wee et al. 2002; Hee et al. 2015), and yellow hue (wavelength of 570–580 nm) of the visible light spectrum (Wang et al. 2022). Other behaviour-based methods used included protein bait spray/traps, targeting the virgin females and males that need protein food for sexual maturation (Cornelius et al. 2000).

Agronomic measures such as orchard sanitation, fruit bagging, destruction of infested fruits have been some of the most effective pre-harvest population control strategies (Hossain et al. 2020), but were acknowledged by the farmers to be time-consuming and labour-intensive with high operation cost.

The use of male lures in monitoring and early detection is effective in managing existing populations, expansion and invasion of *B. dorsalis*. For instance, for countries with large geographical areas and a long north-south extent (latitudes) such as China, early detection and monitoring of *B. dorsalis* expansion following global climate change is an important preventive control against this species (Liu et al. 2019). Conservation and field release of arthropod natural enemies are rarely employed due to the lack of knowledge and mass-rearing facilities which are unaffordable by smallholders. Few farmers employed biological control applications such as entomopathogens and biopesticides such as *Bacillus thuringiensis* (*Bt*) insecticides.

The survey revealed the top three challenges for local farmers in controlling this destructive fruit pest: (1) lack of knowledge on the presence and biology of *B. dorsalis*; (2) high cost associated with alternative non-chemical control measures; and (3) high cost associated with multiple spraying of insecticides and labour costs. The expectation of the local farmers includes more effective and environment-

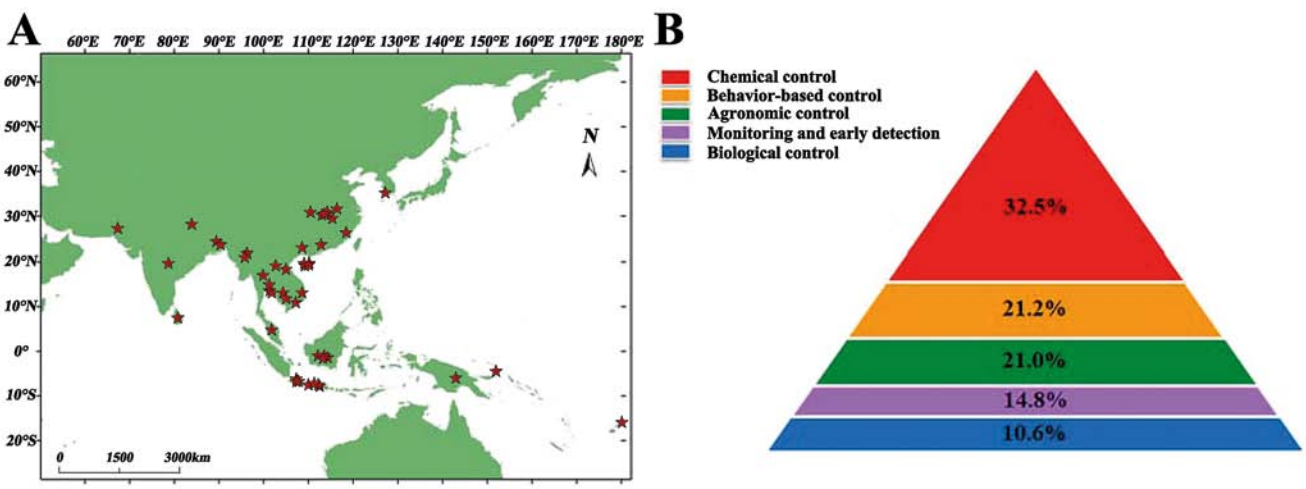

Fig. 1. (A) Survey responses on the current IPM adoption against *Bactrocera dorsalis* from researchers, extension workers and farmers (n = 48, indicated with stars) in Asia region, and (B) an IPM pyramid showing the proportions of different control strategies adopted by the local farmers from the survey.

friendly products (biopesticides, green technology, etc) and knowledge sharing on pest management skills and experiences from researchers and extension specialists. Future initiatives need to improve farmers' education to raise awareness and knowledge of control techniques and the environmentally sustainable management of this pest. With the rise of international trade, global tourism and climate change, regional cooperation and collaboration is necessary to prevent the spread and expansion of the highly mobile and high temperature-tolerant *B. dorsalis*.

5 Current IPM strategies employed against *B. dorsalis*

5.1 Quarantine

Quarantine interception programmes are required during cross-border exchange for countries with suitable climates to curtail the entry of invasive *B. dorsalis* (Fig. 2). Typically, strict quarantine measures or phytosanitary treatments are adopted to treat the agricultural commodities. These include inspection at the entry point and fumigation, hot-water immersion, vapor heat or cold treatment in the exporting countries (Lin et al. 2020; Srimartpirom et al. 2023). Strict quarantine interception and combinations of monitoring for early detection and eradication are the best way to prevent and restrict the spread of *B. dorsalis* in a new area.

5.2 Chemical control and insecticide resistance

Insecticides play an important role in fruit fly control and management (Fig. 2). Application of insecticide includes baiting (bait spray or station) and cover spray (insecticide pulverization) (Navarro-Llopis et al. 2015). Bait spray to plants that used as a shelter is considered as an important tool for the perimeter control of fruit flies. In addition, bait spray laced with insecticide can play a role in luring and killing (Navarro-Llopis et al. 2013). Currently, insecticides such as imidacloprid, chlorpyrifos, thiacloprid, malathion, zeta-

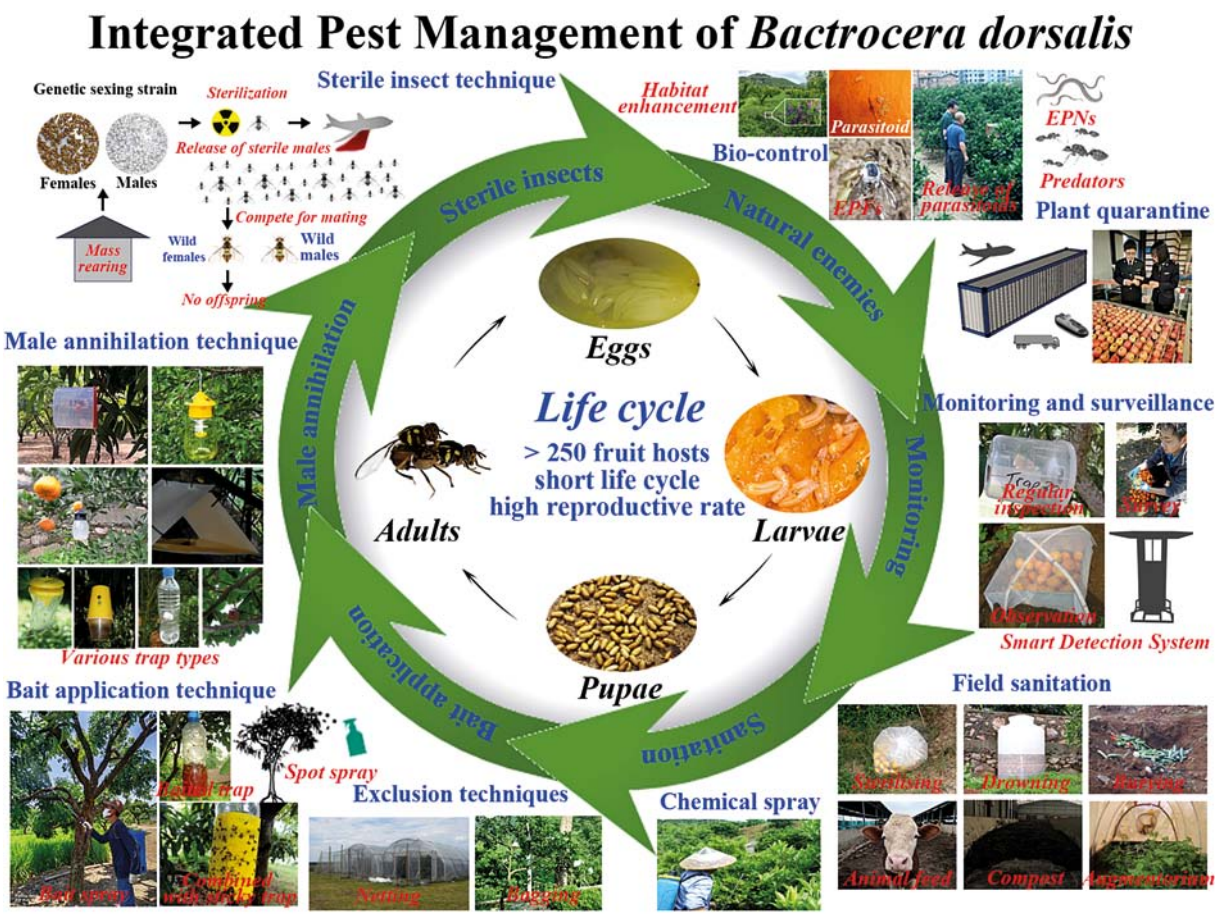

Fig. 2. Illustration of IPM strategies against *Bactrocera dorsalis*. The IPM program consists of six main components including population monitoring, field sanitation, BAT, MAT, SIT and application of natural enemies targeting different life stages of *B. dorsalis*. Plant quarantine is needed for the early detection and prevention in those pest-free areas. The use of exclusion techniques such as bagging and netting is applied in the cultivation of high-value fruits and vegetables. Chemical pesticides can be used in conjunction with other trapping or bag-sterilising measures, but pesticide spraying should be only employed as an emergency treatment.

cypermethrin and fipronil were used against more than 21 fruit fly species, including *B. dorsalis* and *Ceratitis capitata* (Dias et al. 2018). The use of chemical insecticides is a primary method in fruit fly control, however, increasing studies suggested that fruit flies have evolved high levels of insecticide resistance due to the long term and high frequency of insecticide applications (Jiang et al. 2014). The high insecticide resistance in fruit flies may contribute to pest outbreaks. In this case, chemical pesticides are recommended to be used in conjunction with other trapping or bag-sterilising measures, but pesticide spraying should only be employed as an emergency treatment.

5.3 Behaviour-based management and control

5.3.1 Detection, delimitation, survey and monitoring

There are four types of trapping surveys that are used in fruit fly monitoring: (1) Detection surveys determine whether a pest is present in an area; (2) Delimiting surveys are used to establish the boundaries of a pest incursion; (3) Monitoring surveys designed to determine how successfully a program is progressing. This could be for fruit fly suppression in established areas or to determine the efficacy of an eradication campaign and (4) Verification surveys are used to confirm the pest status after an eradication has been implemented (FAO 2018).

ME has been used for monitoring and control of several fruit fly species. *Bactrocera dorsalis* and other ME attracted species are captured in traps containing the lure and a toxicant to kill the male flies. ME is generally dispensed as a liquid or polymeric plug (FAO 2018). Solid dispensers, aged up to 10 weeks were equally as efficacious at trapping flies as fresh liquid lures presented on cotton wicks. The solid lure dispensers are easier to handle and safer to the operator than the liquid lures (Shelly et al. 2022). There are various types of traps available for male fruit fly monitoring including but not limited to Steiner, Lynfield and multilure and variations of these (FAO 2018).

Female and male flies are trapped using a diluted liquid protein in traps such as the McPhail trap that attracts protein-deprived flies and lure them into the trap where the fly drowns. There are also multiple variations of these traps. However, these traps and the lure used attract flies at very short distances, typically within the canopy (De Faveri et al. 2024).

5.3.2 Male annihilation technique (MAT)

MAT, a ME-based lure-and-kill control strategy (Fig. 2), is widely applied for successful management and eradication (Steiner et al. 1970; Koyama et al. 1984; Chang et al. 2013). This technique carried out using MAT devices such as fibreboard blocks soaked in ME and a toxicant which were successfully deployed in the Australian eradication of *B. papayae* (now *B. dorsalis*) (Hancock et al. 2000; Meats et al. 2008). The California eradication programs spot apply SPLAT-MAT-ME (Specialized Pheromone and Lure Application Technology) to power poles (Manoukis et al. 2019) and other programs apply MAT in a mass trapping program (Mau et al. 2007; Vargas et al. 2008).

Devices or traps are dispensed in the orchard in a standard transect and the densities vary between programs. The most used density of MAT devices is one device/trap every 50 m or 400/km^2 (Hancock et al. 2000; Affandi et al. 2023). Ndlela et al. (2016) applied MAT in Lynfield traps at densities of 5 traps/ha, equivalent to 500/km^2. Manoukis et al. (2019), however determined that higher density rates of SPLAT-MAT-ME resulted in decreasing effectiveness. They found that densities of 110/km^2 were more effective than the higher densities such as 220/km^2 and 440/km^2. Adopting MAT using lower densities results in higher efficacy and savings in products and labour. De Faveri et al. (2024) reduced MAT densities from 4/ha (400/km^2) as reported by Affandi et al. (2023) down to 2/ha (200/km^2) with no reduction in efficacy. This resulted in halving the cost of materials in the MAT program.

5.3.3 Protein bait application technique (BAT)

Fruit flies require protein to realize reproductive potential and forage leaf and fruit surfaces to attain sufficient protein (De Faveri et al. 2024). Steiner (1952) first used protein baits laced with an insecticide to lure and kill immature adult flies. Since then protein baits have been adopted in eradication programs (Hancock et al. 2000; Meats et al. 2008), Area-wide Management (AWM) systems programs (Lloyd et al. 2010; Affandi et al. 2023; De Faveri et al. 2024) and farm level systems approaches (De Faveri et al. 2018). The bait is usually applied to foliage as a spot or band spray (Fig. 2), thus attracting the immature or protein-deprived adults and killing them after feeding (Lloyd et al. 2010; De Faveri et al. 2024). Attraction to protein baits is at short distance, therefore spot sprays are applied to every tree or as a band spray in alternate rows (Lloyd et al. 2010; De Faveri et al. 2024). However, the placement of protein bait can influence the foraging behaviours of fruit flies (Senior et al. 2017). The original protein baits were developed from protein hydrolysates and various formulations have since been developed with improved attraction to fruit flies. The successful Australian eradication program of *B. papayae* (now *B. dorsalis*) in the late 1990s used an autolyzed yeast formulation mixed with malathion (Hancock et al. 2000). A low-cost protein bait was developed from beer yeast waste which is used in several Asian countries (Zhou et al. 2012; Vijaysegaran 2016). Wang et al. (2021) tried to improve the bait with the addition of preservatives, antibiotics and the addition of substances e.g., guava essence, to increase attraction. In the early 2000s, GF-120, a mixture of protein combined with a reduced risk toxicant called Spinosad which is derived from fermentation products of soil actinomycete *Saccharopolyspora spinosa* Mertz & Yao (Stark et al. 2004), was developed, tested in the USA and became commercially available in 2002.

Protein baits have been known to cause a phytotoxic effect on fruit upon contact. Several products were shown to cause damage to varying degrees. De Faveri et al. (2013) examined the effects of several products and determined that they all caused different levels of phytotoxic blemish to mango fruits. The authors trialled the application of protein baits to tree trunks, thus avoiding contact with fruit. The application method was successful in reducing fruit fly populations, however, was labour intensive. Manrakhan et al. (2015) reported the phytotoxic effects of GF-120 NF on green Nadorcott mandarins in South Africa and recommended development of other application methods than ground sprays.

5.4 Cultural control practices

Cultural control methods such as orchard sanitation and crop hygiene involve measures to prevent fruit fly life cycle completion and subsequent reinfestation (Fig. 2). These are labour intensive, but effective and environmentally friendly measures that involve regular collecting, removal, destroying (e.g., crushing in a grinder), sterilising (e.g., exposing to the heat of the sun for a few days within plastic bags), or burying (> 50 cm depth) infested, damaged or fallen fruits (Benjamin et al. 2015; Manrakhan 2020; Viswanath Reddy et al. 2020). In some cases, infestation of the fruits on the ground by *B. dorsalis* can be higher than those on the trees and if left untreated, become breeding sources of pest flies within the orchards (Theron et al. 2017). Instead, these infested fruits are recommended to be placed in augmentorium in orchards (tent-like structures) (Fig. 2) that trap adult flies but increase parasitoid population in orchards (Benjamin et al. 2015; Manrakhan 2020). Although orchards with sanitation measures were shown to have a lower *B. dorsalis* infestation compared to those without sanitation (Pinero et al. 2009), combining sanitation with other measures, such as bait sprays or soil mechanical treatment is recommended as integrated approaches because sanitation alone is insufficient to remove the entire fruit fly population (e.g., Pinero et al. 2009; Adhikari et al. 2020). Sanitation has also been included in eradication programs of *B. dorsalis* in Indonesia, Mauritius and Thailand (Seewooruthun et al. 2000; Orankanok et al. 2007; Affandi et al. 2023).

Other methods involve soil treatment to destroy pupae (e.g., tillage), removal of host plants, crop rotation, early harvesting, pruning, weeding, netting whole plant or bagging individual fruit (Fig. 2). Netting and bagging fruit can give full protection against *B. dorsalis*, but depending on the material used for bagging, fruit quality may change, with paper bags generally recommended (Sarker et al. 2009; Chen et al. 2011; Nasruddin et al. 2020). The timing of these management actions may be critical for their success. Fruit should be bagged at least one month prior to harvest or before fruit colour change (Chen et al. 2011; Benjamin et al. 2015; Secretaria et al. 2022). In chilies, Nasruddin et al. (2020) set up nets when plants started blooming due to potential early infestation of young fruits. In guava, Choudhary et al. (2022) emphasised the importance of timing of pruning for the reduction of fruit fly populations. The measures of host plant removal and soil tillage/treatment can be perceived as safe and effective but less practical and in the case of host plant removal, uneconomic, as in Nepal (Adhikari et al. 2020). Furthermore, in his review focused on Queensland fruit fly (*B. tryoni*), Clarke et al. (2011) argued that calls for removal of feral crop plants may be premature if a high percentage of fruit and fruit fly larvae within are removed by vertebrate frugivores, which remains poorly known for *B. dorsalis*.

Resistance of plants to fruit fly infestation may differ among species, the choice of varieties with different resistance or fruit ripening stage can substantially affect yield loss. Yang et al. (2023) found *B. dorsalis* eggs in 89.23% of exotic passion fruits (*Passiflora* sp.), but only few developed into larvae due to arrestment during embryonic development caused by hydrogen cyanide. This indicates that exotic passion fruit can act as a powerful eco-trap to supress *B. dorsalis* populations.

Syamsudin et al. (2022) showed that chilli varieties with large fruit, high water and carbohydrate content, low fibre and produce volatiles such as β-cis-ocimene were more susceptible to *B. dorsalis* infestation. In mangoes, flesh flavonoid content, physico-biochemical properties of the peel, such as firmness, phenolic content, acidity and tannins are shown to affect the degree of resistance of varieties to *B. dorsalis* (Sison et al. 2020), while in avocados, fruit firmness plays an important role in preventing oviposition puncture and ovulation (Follett 2009). Furthermore, since fruit flies generally prefer to lay eggs in ripe fruits, early harvest reduces fruit fly infestation and some fruits can be considered conditional non-hosts depending on fruit ripeness (Benjamin et al. 2015; Viswanath Reddy et al. 2020). However, this is not the case in all fruit types, and oriental fruit fly is able to infest immature fruits in some cases (Ekesi & Billah 2006). To reduce crop damage, varieties with preferred characteristics or those that mature at the time of low *B. dorsalis* population density can be chosen or new resistant varieties can be developed (Chen et al. 2011). Furthermore, other management measures, such as nitrogen fertilisation can affect plant defence response to fruit fly infestation and should be considered (Li et al. 2023).

5.5 Sterile insect technique (SIT)

SIT is a strategy of insect birth control originally conceived by Knipling in 1955. The process involves breeding large numbers of the target insect pest species, exposing the male insects to irradiation to make them sterile yet sexually competitive, and then releasing the sterile males *en masse* across to the target area in an area-wide manner (Fig. 2) (Dyck et al. 2021). In an appropriate overflooding ratio, the mass release of sterile males is expected to outnumber fertile males in the field and have a higher chance to mate with fertile females, thus producing non-viable offspring and gradually leading

to the eradication of the natural population (Klassen et al. 2021).

The implementation of SIT is most effective when the population density of the target species is low (McCombs & Saul 1995). This is particularly useful as a preventative measure during the early detection of the invasive pest species, the initial stage of establishment of a newly invaded species in a new environment, or when the existing population has been brought down to a low density by other control tactics, as suggested by Suckling et al. (2014). Due to the growing interest in sustainable pest control technology that aims to reduce insecticidal use and fruit damage, there is now a greater push to integrate SIT in fruit fly AW-IPM programs to suppress fruit fly populations instead of eradicating them. This approach has been implemented successfully for *B. dorsalis* and the guava fruit fly, *B. correcta* (Bezzi) in Thailand (Sutantawong et al. 2004; Orankanok et al. 2007).

The success of SIT eradication and suppression of the fruit fly population necessitate the combination of IPM tactics and an efficient surveillance network on an area-wide basis. Key IPM tactics often used synergistically in fruit fly suppression programs are MAT, destruction of infested fruits, and protein bait application (Suckling et al. 2014, 2016).

The fruit fly SIT program usually involves the development of a genetic sexing strain based on sex-linked pupal colour, such as in *B. dorsalis* (McCombs & Saul 1995), to facilitate sex separation in SIT mass rearing. The sterile-male-only releases increase the induced sterility level and higher relative mating success with fertile females, enabling a lower overflooding ratio of sterile to fertile male releases in the absence of sterile females (Rendón et al. 2004; Shelly & Manoukis 2022). The *B. tryoni* SIT program in Australia may be one of the very few countries that release bisexual sterile males and females due to the lack of genetic sexing strain for the species. The effectiveness of the bisexual release of *B. tryoni* was not known. However, it was recommended for commercial stone-fruit orchards as there was no evidence to support the claim that the released sterile females would sting and cause damage, leading to fruit downgrade and reduced marketability (Reynolds et al. 2022). Hence, the bisexual release of *B. dorsalis* could be explored in the future if it could help lower the operational cost, at the same time increase the efficiency of the SIT programs.

Ionizing radiation is commonly used in SIT programs. Gamma radiation from radioisotopes such as cobalt-60 or caesium-137 is often used but there is a growing interest in using X-rays in Lepidopteran and Dipteran SIT, including tephritid fruit flies due to its practicality (Chang et al. 2015; Zhao et al. 2022). However, there are fewer studies on X-ray irradiation on the radiation biology and physiological and molecular genetics of the target pest insects in comparison to gamma irradiation, which is well-developed and documented. Recent studies have shown that X-ray irradiation can induce undesirable changes in protein expression and main energy-generating pathways in *B. dorsalis* at larval and pupal stages, which could impact biological performance such as pheromone signalling and mating competitiveness (Chang et al. 2015).

Chemosterilant is a simpler, more economical method for insect sterilization and does not require genetic modification or regulatory licenses before implementation (Bouyer & Vreysen 2019; Li et al. 2022). However, its use for insect sterilization poses potential health and environmental risks due to their carcinogenic and mutagenic properties (Hayes 1968). Recent advancement on insect genetics and molecular analysis in the past 15 years has made development of a safer, effective and specific chemosterilant possible for use in SIT and reducing insecticide applications (Baxter 2016). In tephritid fruit flies, hexamethylphosphoramide (HMPA) has been shown to be a promising chemosterilant that has a negative impact on male and female reproductive development by altering the levels of acid phosphatase, alkaline phosphatase and vitellogenin. Application of 0.03% HMPA on *Zeugodacus tau* induced high efficacy of male sterility, resulting in less than 10% offspring egg hatch (Li et al. 2022). Future research should focus on the search of a chemosterilant that would be available at low cost, minimal impact on survival and competitiveness of treated males, low toxicity to humans and biodegradable for minimizing environmental hazard and occupational safety concerns.

5.6 Biocontrol

5.6.1 Parasitoids

Parasitoids (Braconidae, Pteromalidae and Figitidae) are among the most studied biocontrol agents for control of fruit flies (Fig. 2) (Dias et al. 2022). Parasitism rates can depend on host fruit and fly species and densities, fruit size (fruit fly larvae can hide deeper into larger fruit), fruit damage, insecticide treatments, as well as parasitoid species and associated traits (age, learning, density), intra- and inter-specific interactions (competition, superparasitism, kleptoparasitism, hyperparasitism) and their interaction with other biocontrol agents (Wang et al. 2004; Montoya et al. 2012; Cai et al. 2020; Dias et al. 2022; Hossain et al. 2023). The life stage attacked may also indirectly play a role in parasitism efficiency, and high parasitism rate of *Fopius arisanus* is hypothesized to be due its attack of host eggs which are exposed closer to the fruit skin compared to larvae (Vargas et al. 2012).

Classical biocontrol is conducted through intentional introduction of an exotic biocontrol agent (Dias et al. 2022). Between 1947 and 1952, the first classical biocontrol program to control *B. dorsalis* was successfully completed in Hawaii. Three parasitoid species *F. arisanus, F. vandenboschi* and *Diachasmimorpha longicaudata* were successfully established by 2012 (out of 32 natural enemies introduced) (Clausen et al. 1965; Vargas et al. 2012). *Fopius arisanus* became dominant and caused 95% decrease in *B. dorsalis* populations (Vargas et al. 2012). Garcia et al. (2020) reported several other parasitoid species that are now suc-

cessfully established on *B. dorsalis* in Hawaii. Starting in the 1950s, parasitoids from Hawaii have been used for introduction in multiple islands in the Pacific (Vargas et al. 2012). Classical biological control of *B. dorsalis* was also successfully conducted in Africa using *F. arisanus* and to the lesser extent *D. longicaudata* (Gnanvossou et al. 2016; Mohamed et al. 2016). *Fopius arisanus* was found to prefer *B. dorsalis* over some indigenous species in Africa (Mohamed et al. 2010) and to spread up to 8 km from the release point over a four-years period (Gnanvossou et al. 2016). Heve et al. (2021) recommended that combined releases of *F. caudatus, D. longicaudata, F. arisanus and Psyttalia cosyrae* in Africa should provide better control of several fruit fly species, including *B. dorsalis*, because negative interspecific interactions are rare and wasps have the ability to discriminate between parasitised and unparasitised hosts.

Augmentative biocontrol is conducted through release of commercially reared biocontrol agents and largely depends on the ability of the parasitoids to survive, disperse and find hosts (Dias et al. 2022). Moreover, rearing methods and costs, shipping, handling, field exposure, and types of release vessels may have substantial influence on the efficacy and adoption of this method (Messing et al. 1993). Several programs that started as classical biocontrol programs of *B. dorsalis* followed up as augmentative control, as in Hawaii (Garcia et al. 2020). Currently, *D. longicaudata* is a mass-reared species worldwide (Dias et al. 2022), but despite augmentative releases of large numbers of this species against *B. dorsalis*, it may not become dominant (Purcell et al. 1998). In China, the pupal parasitoid *Spalangia endius* (Walker) (Hymenoptera: Pteromalidae) is commercially produced on *Musca domestica* and can be used for *B. dorsalis* control at low population density (Zheng et al. 2021).

Conservation biocontrol approaches aim to enhance natural enemy population in the environment by providing resources and shelter. Native parasitoids are shown to be able to parasitize up to 40% of fruit flies (Dias et al. 2022.) However, not all native species are effective as biological agents. A native parasitoid in Africa, *Psyttalia cosyrae* gets encapsulated within *B. dorsalis*, although it successfully controls several other fruit fly species (Heve et al. 2021). Conservation biocontrol has rarely been investigated in fruit flies, although it shows substantial effects on numerous other insect pest species and benefits for crop production (Dainese et al. 2019). Fruit flies and their parasitoids are likely to frequently move between crops and between crop and non-crop areas, especially in vegetable crops, and better understanding of these movements, locations of fly mating and roosting sites and general habitat-use would facilitate landscape level pest suppression in all three biocontrol approaches.

Bacterial symbionts in *B. dorsalis* may affect host-parasitoid interactions and parasitoid-oriented management strategies, with some positively affecting parasitoids and can be considered for use as probiotics in parasitoid mass rearing (Gwokyalya et al. 2023a). In another study, Gwokyalya et al. (2023b) demonstrated parasitism-induced gut perturbations of microbial communities of *B. dorsalis*. Furthermore, viruses injected by parasitoids, such as *D. longicaudata* can alter the host immune defences and may benefit mass-rearing programs by ensuring successful development of parasitoids (Montoya et al. 2012).

5.6.2 Entomopathogenic fungi (EPF)

Most investigated EPFs for the control of *B. dorsalis* are *Metarhizium anisopliae* Metchnikoff Sorokin (Hypocreales: Clavicipitaceae) and *Beauveria bassiana* (Sordariomycetes: Clavicipitaceae). EPFs typically penetrate insects through the cuticle via mechanical damage (except when spores are orally ingested together with bait spray) and proliferate in the hemolymph to produce blastospores. EPFs can reduce flies' fertility and fecundity, affect their nutrient content by reducing activity of digestive enzymes, while EPFs secondary metabolites, such as destruxins are toxic to fruit flies, or can have antimicrobial properties and affect insects' immune system (Benjamin et al. 2015; Shaurub 2023). *Metarhizium anisopliae* can cause high mortality of fruit fly larvae, pupae and adults, with younger life stages more susceptible, while it generally has no effect on parasitoids, humans or the environment (Heve et al. 2021; Wang et al. 2021). Moreover, it is easily mass-produced and stored and can last in the soil for over one year (Ouna 2010). On the contrary, *Be. bassiana*, although highly effective for control of *B. dorsalis* (Marri et al. 2016; Wang et al. 2021), can cause dermal sensitivity in people who are repeatedly exposed (Shaurub 2023).

Since EPFs cannot search for their hosts, application methods are through foliar sprays, protein baits and auto-dissemination for adult control and soil inoculation (granular, aqueous or oil/aqueous) for pupae control (Benjamin et al. 2015; Viswanath Reddy et al. 2020). In auto-dissemination method, the insect is attracted visually, chemically or by food to the auto-inoculators where they get infected by EPFs. They can spread EPFs through the population mainly through mating and lek formation by males, although the effectiveness of this method can be reduced if it affects their mating behaviour or competitiveness (females can prefer healthy males) (Sookar et al. 2014; Shaurub 2023). Spore concentration, as well as environmental variables, such as climate elements and their interaction (temperature, humidity, solar radiation (UV-A and UV-B)), soil physicochemical properties, texture and microbiota can affect efficacy of EPFs for fruit fly control (Manrakhan 2020; Shaurub 2023). Shaurub (2023) recommends applying EPFs under fruit trees at the onset of fruiting to control fruit fly pupae.

Compatibility of using soil inoculation by *M. anisopliae* and GF-120 spinosad bait spray for control of *B. dorsalis* has been shown in mangoes in Kenya where combined treatment had substantially lowered fruit infestation compared to individual treatments or control (Heve et al. 2021). Using EPFs also appears compatible with parasitoid biocontrol methods, although this is poorly investigated in *B. dorsa-*

lis (Manrakhan 2020). *Metarhizium anisopilae* spores may reduce predatory formicide fauna by killing or interfering in predation by *Oecophylla longinoda*, but the effect of EPFs on other arthropods is poorly investigated (Heve et al. 2021). The usefulness of inoculation of sterile males with EPFs as vectors is still unknown in *B. dorsalis*, while research on other species showed high effectiveness in transmitting the conidia to the wild population although there may be negative effects on quality control parameters of sterile insects (Dias et al. 2018; Manrakhan 2020; Shaurub 2023). Wakil et al. (2022) has demonstrated additive and synergistic effects of combined application of EPNs and EPFs (*Be. bassiana* and *Heterorhabditis bacteriophora*) on *B. dorsalis* under laboratory, glasshouse and field cage conditions. However, both synergistic and antagonistic effects between EPNs and EPFs have been found in other fruit fly species (Heve et al. 2021; Shaurub 2023; Toledo et al. 2023).

5.6.3 Entomopathogenic nematodes (EPNs)

Most investigated EPNs for control of fruit flies are *Steinernema* (Steinernematidae) and *Heterorhabditis* (Heterorhabditidae) (Heve et al. 2021). They are obligate parasites and the only free-living stage are infective juveniles. They are attracted by CO_2 release by the host and can actively search for hosts (cruiser strategist – effective for larvae and pupae control) or sit and wait (more effective for fruit fly larvae control). The *Heterorhabditis* species which have cruiser strategists can kill *B. dorsalis* larvae at up to 20 cm distance Godjo et al. (2018). EPNs enter the host through natural openings or *Heterorhabditis* species can use tooth-like structures to penetrate the cuticle. They form mutualistic relationships with bacteria *Xenorhabdus* spp. and *Photorhabdus* spp. (family Morganellaceae) which produce toxin that can kill the host in one or two days after they are released in the host's hemocoel (Shaurub 2023). EPNs can also cause suppression of host's immune system, enzyme inhibition and nutrient depletion (Shaurub 2023). Experiments on fruit fly suppression in field conditions using EPNs have to date provided promising results and showed that EPNs can even infest fruit fly larvae within the fruit and thus be used as a sanitation method (Shaurub 2023; Toledo et al. 2023). Some EPNs can be reared in vivo or in vitro or obtained from commercial products and mass rearing is already developed in several countries (Heve et al. 2021; Toledo et al. 2023). However, the short shelf-life of the commercial products is one of the major limitations for commercial use (Toledo et al. 2023).

When deciding on EPN use for fruit fly control, factors that should be considered are density (due to potential intraspecific competition at high densities), EPN species (high interspecific competition), origin (exotic species may be less effective due to lack of adaptation to local conditions), fly's species and developmental stage (younger life stages are more susceptible), abiotic factors (temperature, humidity, solar UV radiation, soil texture, pH and depth) (Godjo et al. 2018; Shaurub 2023; Aatif et al. 2023; Toledo et al. 2023). Other organisms, such as fungi, bacteria, mites, insects and earthworms can also affect EPN efficiency for fruit fly control (Toledo et al. 2023). *Solenopsis* ants may kill developing EPNs in cadavers in soil, while they might also be susceptible to EPNs in soil, but these types of interactions are poorly studied (Heve et al. 2021).

In Pakistan, Aatif et al. (2023) found that for control of *B. dorsalis* larvae, *Steinernema asiaticum* was more effective than other EPNs (94.97% mortality) and was most effective at high concentrations, 12% soil moisture, 36 °C temperature and in sandy loam soil. However, other nematodes such as, *H. bacteriophora, H. indica* and *S. carpocapsae* can also show high effectiveness against *B. dorsalis* larvae and pupae (Aatif et al. 2023). In another study in Pakistan, Usman et al. (2021) showed in laboratory, greenhouse and field trials that *H. bacteriophora* was the most efficacious and virulent against *B. dorsalis* although *S. carpocapsae, S. riobrave* and *S. feltiae* showed high virulence. In China, *S. carpocapsae* can cause up to 86.3% *B. dorsalis* larvae and pupae mortality at 300 IJs/cm^2 density and under field conditions (Lin et al. 2005).

It is recommended to apply EPNs under fruit trees as infected cadavers (rather than in water suspension), in the fructification stage and using species that actively search for hosts in soil (Godjo et al. 2021; Shaurub 2023). Using EPNs together with parasitoid biocontrol appears compatible, given that no negative effects on parasitoids have been found to date, although the effects on progeny of parasitoids have not been studied (Heve et al. 2021). EPNs can also be used in combination with insecticides (e.g., spinosad, malathion, spinetoram, acetamiprid, phosmet, and novaluron) and other biocontrol agents as mostly synergistic results were found in control of fruit flies, while some plant extracts (garlic, ginger, ruf leaf, chinaberry fruits) reduced viability and infectivity of EPNs (Shaurub 2023; Toledo et al. 2023). Multiple species of EPNs can produce synergistic, additive or antagonistic effects, but this remains to be investigated in *B. dorsalis* (Heve et al. 2021).

5.6.4 Predators

Predators have not been widely investigated for control of fruit flies (Dias et al. 2022). The main predators that did attract researchers' attention for control of fruit flies are ants (Hymenoptera: Formicidae) which control fruit flies by oviposition deterrence and by predation (Vayssières et al. 2016). Two *Oecophylla* species are typically investigated, the African weaver ant (*O. longinoda*) and the predatory Asian weaver ant (*O. smaragdina*), common in Australia and Asia, although other ant species such as *Solenopsis* spp. are abundant and can be important for control of fruit flies (Van Mele et al. 2007; Heve et al. 2021). *Oecophylla longinoda* may reduce the number of *B. dorsalis* laid eggs by 75% and cause 80% larval mortality (Wong & Wong1988; Van Mele et al. 2007; Cao et al. 2012). Abdulla et al. (2017) showed that *O.*

longinoda can be as effective as imidacloprid insecticide in controlling *B. dorsalis*. The predation rate of *B. dorsalis* by *S. invicta* can also be substantial (70%), although the authors showed that the soil depth (no predation at 6 cm depth) and moisture should be considered (Cao et al. 2012). *Pheidole megacephala* is reported to attack *B. dorsalis* larvae causing 36% mortality (Newell & Haramoto 1968).

The approach in biocontrol of fruit flies by predators is typically through conservation biocontrol. Aggressive behaviour, emission of semiochemicals, intraguild predation and deterrence of other natural enemies by *O. longinoda* may limit its use with augmentative releases (Appiah et al. 2014; Vayssières et al. 2016). Similarly, some *Solenopsis* species are shown to be aggressive, cut plant leaves, buds and seeds, cause pain and discomfort and are typically managed in areas near human activities (Heve et al. 2021). However, conservation biocontrol practices that use sugar solution to attract *Solenopsis* ants for use in *B. dorsalis* control have been recommended (Heve et al. 2021). There are numerous other natural enemy species that remain to be investigated for control of *B. dorsalis* (Liu et al. 2019; Garcia et al. 2020). High larval mortality may be caused by birds, bats and rodents by consuming infested fruits, spiders can predate on fruit fly adults, while other insects (e.g., green mantises, crickets, beetles, earwigs, true bugs) are shown to attack late instar larvae and pupae of *B. dorsalis* (Garcia et al. 2020; Dias et al. 2022).

Generally, compatibility of using predator biocontrol with other management actions is poorly investigated and should be carefully considered given potential for both positive and negative effects. Behavior-modifying chemicals produced by predators can be used in a blend as a pre-harvest spray to prevent *B. dorsalis* oviposition in fruits. Mutual negative effects may happen in the use of *Solenopsis* spp. and EPNs, but this is poorly understood (Heve et al. 2021). Negative effects of ME on predation of *B. dorsalis* by *Gekko monarchus* has been found (Wee & Tan 2001). Irradiated fruit flies may have lower ability to escape from predators as shown for *A. ludens*, but this remains to be investigated in *B. dorsalis* (Dias et al. 2022).

5.6.5 Pathogenic microorganisms

Bacteria and viruses have been poorly researched for control of fruit flies. In the review by Dias et al. (2022) the entomopathogenic bacterium *Bacillus thuringiensis* is the most studied bacteria for control of fruit flies, out of 11 reported (*Klebsiella, Candidatus, Lactobacillus, Pantoea, Providencia, Serratia, Streptomyces, Wolbachia*, and *Zygosaccharomyces*), while viruses were investigated in only one study on medfly. Jaffar et al. (2023) reported that baculoviruses, and in particular nuclear polyhedrosis virus (NPV) has potential to control *B. dorsalis*, but more research is needed before it can be integrated into pest management programs. Protozoa (*Nosema tephritidae*) has been found infecting *B. dorsalis* (Fujii & Tamashiro 1972).

5.7 Integrated Pest Management

The above programs when delivered alone provide limited levels of control. For example, BAT when solely applied will suppress *B. dorsalis* populations to low levels, but will not achieve the same level of control as a program that includes several approaches aimed at suppressing the population (Vijaysegaran 2016). However, when several approaches are applied there can be a cumulative effect on the population suppression. Fruit fly population suppression is most effective when implemented on an area-wide basis (Carlson & Wetzstein 1993) because of the high dispersal capability of the tephritid fruit flies that can disperse between adjacent agroecosystems. The implementation of such programs over much smaller areas is reportedly less likely to be successful against such a mobile pest as shown for other fruit fly species (De Faveri 2018). Affandi et al. (2023) reported on a successful IPM program based at the orchard scale (20–40 ha), but which included interventions in nearby villages. All the programs take a similar approach, with slight differences in technology applications and scale of programs. The SIT programs discussed in 5.5 utilise similar tactics to suppress populations and implement SIT to suppress or eradicate populations (Suckling et al. 2014, 2016). One of the critical components of all programs is the engagement of stakeholders.

The Hawaii AWM program consisted of six components including population monitoring, field sanitation, BAT, MAT, SIT and parasitoid releases. This program targeted *B. dorsalis*, melon fly, *Z. cucurbitae* and the Mediterranean fruit fly, *C. capitata* and was implemented in four farming areas ranging from 400 ha to 3800 ha (Mau et al. 2007; Vargas et al. 2008). In Australia, the incursion of *B. papayae* (now *B. dorsalis*) was eradicated over an area of 78 000 km^2 using monitoring, MAT and protein baiting. The incursion was eradicated within four years (Hancock et al. 2000). The three programs used different levels of techniques, but they were all implemented over large areas, thereby increasing the probability of success. Here, we list two specific cases of IPM against *B. dorsalis* in Southeast Asian countries, including the control methods or options employed for the management in practice and their final outcomes, to better understand the key points of IPM system.

A specific case 1: IPM of B. dorsalis in mangoes or other fruits in Indonesia

This case study describes the area-wide systems approach that has been implemented on smallholder mango farms in Indonesia. Mango is one of the most cultivated fruits in Indonesia. Most of the production is consumed domestically with a small proportion being exported. It is the main or supplementary source of income for many resources poor smallholder farmers. Indonesia is one of the largest producers of mango, typically around 5th in world production. The main fruit fly pests of mango in Indonesia are *B. dorsalis* and *B. carambolae*. Infestation rates as high as 70% are common. Mango farmers in Indonesia typically apply insecti-

cide cover sprays on individual farms to control the pests. An Australian Centre for international Agricultural Research (ACIAR) funded projects trialled an area-wide systems approach to control fruit flies in smallholder mango farms.

The AWM system has been reported by Affandi et al. (2023) and the results were based on the first two years of the program which continued for six years. De Faveri et al. (2024) outline the program and its implementation in a training manual. Results for research between 2021 and 2024 and reported here are based on De Faveri et al. (unpublished data).

Two sites located in East Java, including the villages of Krasak (40 ha) and Sedong Lor (24 ha) were selected to demonstrate the effectiveness of the program. An untreated control site was established at Putat village (45 ha). The Krasak site included mixed farming, with mango the main cash crop. The Sedong Lor site was predominantly mango with some mixed farming which consisted mainly of rice. The Putat site was predominantly mango. All three sites were located adjacent to villages which contained alternate hosts. The components of the program included:

a) Stakeholder engagement
b) Population monitoring with 4 traps/ha
c) MAT based on a grid of MAT wooden blocks every 50 m, but was reduced to 1 every 100 m
d) BAT applied weekly from fruit development stage of approximately golf ball size until all fruit were harvested
e) Sanitation to collect and destroy all fallen and residual fruit including mango and alternate hosts

The goal of the program was to reduce and maintain populations at the suppression level of < 1 fly/ trap/day (FTD) (FAO 2018). The monitoring program included trapping of flies using ME and toxicant baited traps and a fruit damage monitoring program where fruits were collected, held for 5–7 days and cut to determine the infestation levels. The results indicated that the populations were suppressed to < 1 FTD within six months and were maintained at the level. Population levels at the untreated control site peaked at 450 FTD. The infestation levels were maintained below 1% from year 2 onwards, compared to levels up to 67% in the untreated control village. After two years, a further site of 70 ha has been added as well as an extra untreated site at Pawidean, just two kilometres away from the Krasak site. Similar to other IPM sites, population levels were reduced to below 1 FTD within six months and infestation rates maintained below 1%. In contrast, populations at the Pawidean site peaked at 860 FTD and were regularly at levels of > 100 FTD during the fruiting period. The MAT densities and protein bait concentration have been halved, resulting in increased profits, but no adverse effect on efficacy.

The program has been highlighted to be effective in areas as small as 24 ha and adjacent to hotspots such as villages that contain alternate hosts. All components can be implemented by farmers at reasonable costs. Goals can be achieved within months and maintained on an ongoing program. The program uses very small quantities of insecticide in the MAT devices and small amounts in the protein bait that is applied in spot sprays to foliage. The case study demonstrates the application of a highly effective, inexpensive and environmentally sustainable program that can be implemented in areas at least as small as 24 ha in size.

A specific case 2: IPM of B. dorsalis in Thailand and Malaysia

Thailand is one of the world's largest producers and exporters of fruits. Its tropical climate, including tropical rainforest, tropical monsoon and tropical savannah, as well as its unique geography with varying terrain conditions in different regions, allows a high diversification in tropical and subtropical fruit production. *B. dorsalis* and *B. correcta* are the major fruit fly pests affecting fruit and vegetable production and trade in Thailand. Both species are highly polyphagous, with *B. dorsalis* infesting more than 100 species and *B. correcta* infesting at least 62 species of fruits. The major economic important fruits attacked by the two species are mango, rose apple, guava, jujube, sugar apple, jackfruit and sapodilla.

Thailand was the first country within the South and Southeast Asia regions to implement an AW-IPM program to suppress fruit fly population in mango production areas. Prior to the 1980s, fruit fly control in Thailand relied heavily on the use of broad-spectrum insecticides. Mango growers would carry out calendar insecticide cover sprays 7–10 times during the fruiting season. Despite the heavy use of insecticides, growers still lost 30% of their crops. This method was not only expensive but also limited export opportunities due to insecticide residue and the production of low-quality fruits. Moreover, it caused serious environmental pollution, chemical residues, and had a negative impact on biological diversity (Sutantawong et al. 2004). Realizing that insecticidal control is not a sustainable solution for fruit fly pest control, the Department of Agriculture Extension (DOAE) adopted a pilot IPM program with a component of SIT against *B. dorsalis* in a mango production area in the northern Ratchaburi Province in 1987, with technical cooperation from the International Atomic Energy Agency (IAEA).

In 1987, a pilot project was carried out in Paktor District, Ratchaburi Province to combat *B. dorsalis* on a 7.2 km^2 mango production area. The project involved a group of farmer organizations to implement an AW-IPM with SIT component, along with a ME-based surveillance network. This technique was successfully applied in conjunction with other IPM strategies such as MAT, orchard sanitation, and selective protein bait spray to control the population of *B. dorsalis* together with community participation and decision making (Chinviniijkul et al. 2016). Over a period of six years (1988–1993), the fruit fly infestation was reduced from over 82% to 9% (Sutantawong et al. 2004). The same pilot

project was extended from 2000 to 2004 and expanded to cover 34 km^2. The fruit fly infestation was further reduced to 3.6% (Sutantawong et al. 2004; Orankanok et al. 2007), demonstrating the effectiveness of AW-IPM integrated with a SIT component.

Encouraged by the success of the pilot project, a second fruit fly AW-IPM program integrated with SIT component was launched in Pitchit Province. This program, targeting both *B. dorsalis* and *B. correcta* since both species are attracted to ME, covered an area of 36 km^2. The program reduced fruit fly infestation from over 40% to 15.5% in just two years (2003–2004) (Orankanok et al. 2007). The AW-IPM program integrated with a SIT component has been successful in suppressing fruit fly populations since then. The trend of fruit production and export from Thailand has continued to increase, reaching USD 7.8 billion in 2023.

The success of AW-IPM against fruit fly pests requires close cooperation and commitment from small-scale growers and grower organizations. Unfortunately, in Malaysia, there is no proper fruit fly IPM or AW-IPM in place. Most fruit orchards are small-scale and privately owned, and growers commonly practice broad-spectrum insecticide spraying and installation of ME-baited traps for fruit fly trapping, which is done on an orchard basis and not collectively or concurrently. These practices, together with the lack of integration with other IPM tactics, have proven to be ineffective in suppressing fruit fly populations.

While fruit bagging is the most effective pre-harvest strategy for reducing fruit fly infestation, it is often labour-intensive and expensive. Additionally, most Malaysian growers have poor knowledge on the modes of action of insecticides and the ability to identify insect pest species, similar to the findings of Chang et al. (2021). They also lack fundamental biology and ecology knowledge of fruit fly pests, and do not practice orchard sanitation to remove or destroy infested fruits, which would help eliminate breeding grounds for fruit flies. As a result, fruit fly populations continue to increase despite insecticide application and fruit fly trapping.

6 Limitation and challenges of current IPM strategies

Global climate warming significantly shifts the geographical distribution, behaviour, and management of agricultural pests, including *B. dorsalis* (Zeng et al. 2019). Therefore, IPM strategies designed to control *B. dorsalis* should adapt to climate changes to remain effective. Rising temperatures and changing precipitation patterns enable the fruit fly to expand its range into previously unsuitable areas. This geographical shift poses a challenge to current IPM strategies, which are often region-specific (Wang et al. 2023). As a result, monitoring and surveillance need to be intensified and expanded to new potential habitats to detect and manage infestations early (Zhao et al. 2024).

Climate change also affects the life cycle and population dynamics of *B. dorsalis*. Warmer temperatures can accelerate the development and reproduction rates of the fruit flies, leading to increased pest pressure and more frequent outbreaks (Zeng et al. 2019). This necessitates a revision of IPM strategies to include more frequent monitoring and potentially more aggressive control measures. Moreover, climate change can impact the effectiveness of biological control agents used in IPM. Natural enemies of *B. dorsalis*, such as parasitoids and predators, may also be affected by changing climates, potentially reducing their efficacy. Thus, IPM strategies need to incorporate climate-resilient biological control agents or develop new strategies that can withstand changing environmental conditions (Wang et al. 2023).

Changes in temperature and humidity can alter the persistence and activity of pesticides, necessitating adjustments in application rates and schedules. Developing climate-smart pest control technologies and practices becomes crucial to maintain the effectiveness of chemical interventions (Zhao et al. 2024). In a nut shell, climate change presents significant challenges to current IPM strategies against *B. dorsalis*. Continuous research and innovation in pest management practices will be crucial to sustainably manage *B. dorsalis* under changing climatic conditions (Zhao et al. 2023).

7 New concepts and approaches for pest control

7.1 Novel devices in monitoring and control

Monitoring of fruit flies has typically been based on setting traps and checking and servicing them regularly (FAO 2018). Various approaches such as trapping densities, arrays and automation have been researched to minimise these costs without impacting efficiency. For example, Caton et al. (2023) tested several models of novel transect designs compared to the regularly spaced grids for delimitation surveys to reduce the servicing distances. The models indicated that trap-sect designs for single site reduced service distances for mobile insects by 65–89% compared to regular grid designs, resulting in similar detection probabilities to regular grids.

The development of smart traps is another area that has been increasingly researched, and can be employed for population monitoring (Fig. 2). Jiang et al. (2008) and Jiang et al. (2013) developed agro-ecological based systems monitoring. The trap, baited with ME, is equipped with infrared diodes that are paired with photoelectric sensors. The traps provide trap counts but not identification of species. Tariq et al. (2022) designed a smart trap with image capture capability designed to distinguish species. Results are alerted through a mobile telephone app. The trap and monitoring app provide real-time monitoring with 85% diagnostic accuracy. The review by Lello et al. (2023) highlighted the development of smart traps over the last ten years, suggesting the

potential of automatic detection and monitoring techniques in pest management.

7.2 Simultaneous MAT-SIT applications

Traditionally, the fruit fly SIT program is often integrated after MAT application to decrease pest population density. This allows for a lower overflooding ratio in sterile male release while avoiding a large proportion of sterile males being trapped in the male lure-based surveillance network. A mathematical model by Barclay et al. (2014) suggests that simultaneous MAT and SIT applications can be beneficial for ME-responding tephritid fruit fly pests if the sterile males are treated with ME prior to release. This pre-release treatment renders them less responsive to the toxic MAT baits. Wee & Rosli (2024) showed that treating immature *B. dorsalis* males with ME-incorporated yeast-sugar hydrolysate diet for just two days can reduce males' responsiveness to ME for a relatively high percentage and for a more extended period than allowing immature males feeding on ME source (Shelly 2020). Depending on the ME doses administered, feeding ME-incorporated diet to males also enhances mating competitiveness for a certain duration compared to untreated control males without compromising the longevity of the treated males for a significant portion of their lifetime. The simultaneous application of MAT and SIT could be a useful strategy to reduce operational costs such as insect holding time, and shorten the time to eradication (Barclay et al. 2014).

7.3 New insect sterility technologies

Genetic regulation of insect populations is a developing technology for insect control. It is considered a new generation of insect sterility technology based on the concept of traditional technology, which is developed by combining genetics, molecular biology and genetic engineering. To date, the development of insect sterility technology has mainly experienced two stages: SIT in the last century and genetic regulation technique based on genetic transformation established in the early part of this century. Current researches have focused on sex determination pathways and spermatogenesis genes, as well as some genes involved in copulation.

7.3.1 Sex determination genes mediated lethal strain

The application of sex-determining pathway genes in insect population genetic regulation is mainly based on the characteristics of sex-specific splicing, combining tetracycline regulatory system and insect genetic transformation technology to obtain transgenic insects carrying sex-specific lethal complex. At present, the most widely used genes of sex determination pathway are *tra* and *dsx* genes.

In 2007, a female-specific intron of the sex-determining gene *tra* was firstly exploited to engineer female-specific autocidal genetic systems in *C. capitata*. These rely on the insertion of cassette exons from the *C. capitata tra* gene into a heterologous tetracycline-repressible transactivator such that the transactivator transcript is disrupted in male splice variants, but not in the female-specific one (Fu et al. 2007) (Fig. 3A). Ant et al. (2012) used the same system to obtain the OX3097D-Bol transgenic strain in the olive fly, providing highly penetrant female-specific lethality, dominant fluorescent marking, and genetic sterility. Meanwhile, Schetelig et al. (2012) reported that reproductive sterility system for the tephritid fruit fly pest, *Anastrepha suspensa*, is presented, based on lethality primarily limited to embryos heterozygous for a conditional lethal transgene combination. Ogaugwu et al. (2013) combined the female-specific splice system, the embryonic-specific promoter and the tetracycline system to obtain a female-specific embryonal lethal strain in the Mediterranean fruit fly. A sex-specific splicing of *dsx* and the single-component Tet-off system was successfully constructed in silkworm to obtain a female larva lethal strain (Tan et al. 2013), that can be developed in *B. dorsalis* in the future. In addition, the strain is very stable in laboratory breeding, and is expected to be rapidly popu-

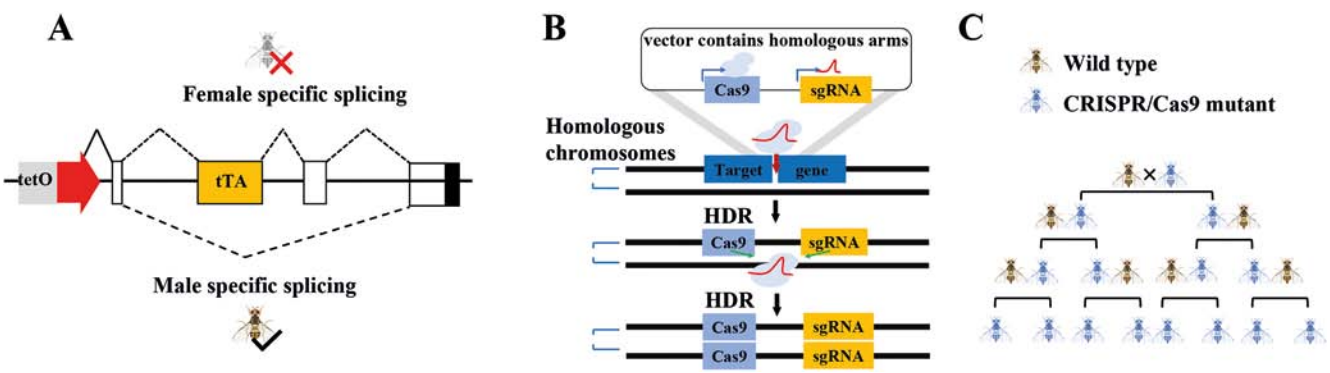

Fig. 3. Genetic regulation of insect populations using molecular technology. (A) Diagram of insect carrying a dominant lethal construct based on "tet-off" system for mass rearing. Expression of tTA is regulated by sex-specific alternative splicing in insects. (B) Global gene drive based on CRISPR/Cas9. (C) Super-Mendelian inheritance for global gene drive (mutant individuals are indicated in blue while wild types are in yellow).

larized in sericulture production and improve the economic value of sericulture. In terms of applied research, the more advanced are mainly disease-carrier insects, such as flies and mosquitoes, and some studies have been put into the field for population control. Cage experiments in olive fruit flies have shown that genetically modified male insects are highly competitive and can effectively control wild population density (Ant et al. 2012). Following the release of the OX513A strain of *Aedes aegypti* in the Cayman Islands, it was found that after a period of time, the number of wild *Aedes aegypti* populations on the islands decreased significantly (Harris et al. 2011). These reports should prove advantageous for the implementation of SIT against *B. dorsalis*.

7.3.2 Sex-biased genes mediated sterility

Sex-specific sterility gene, in the genetic regulation of an insect population, is mainly based on the use of its sex-specific sterility phenotype combined with insect genetic transformation technology to obtain transgenic insects carrying sex-specific sterility complex. This sex-specific infertility gene is mainly involved in spermatogenesis and ovum development, mating behaviour and other reproductive genes, once these genes are mutated, they will produce sterility related phenotypes. The sex-specific sterility phenotype is transferred to the population by transgene, thus achieving population control. However, the function of many genes is not unilateral, so there aren't many genes that can be applied to population genetic regulation. In *C. capitata*, the researchers developed a dominant lethal genetic system containing a tetracycline-repressible transactivator (tTA) that causes lethality in early developmental stages of the heterozygous progeny (Gong et al. 2005). Subsequently, Schetelig et al. (2009) present a first alternative reproductive sterility system for medfly based on transgenic embryonic lethality. This system is dependent on newly isolated medfly promoter/enhancer elements of cellularization-specifically-expressed genes. In addition, Ogaugwu et al. (2013) effectively establish an early-acting transgenic sexing system in the medfly by using the sex-specifically spliced transformer intron to restrict ectopic mRNA translation of the pro-apoptotic gene *hidAla5* to females only.

In Lepidoptera, CRISPR/Cas9-mediated *serine protease 2* transgene mutation of silkworm and diamondback moth both result in male individual sterility phenotype, which can be inherited by female individuals. Moreover, the mutation does not affect the mating behaviour of the mutants, and the male sterility phenotype can be well transmitted to the offsprings, which is of great significance for the genetic control of the moth (Xu et al. 2020b). The knockout mutation of the ovarian serine protease gene caused abnormal female eggs of silkworm, the eggs produced were sterile, and the mutation did not affect the mating behaviour of the mutant, providing a new method for genetic control of the pest (Xu et al. 2020a). *Sxl* gene is a key upstream gene for sex determination in *Drosophila*, but not in silkworms (Bell et al. 1988; Saccone et al. 2002; Xu et al. 2017). Mutant *sxl* was obtained by CRISPR/Cas9 gene knockout, and it was found that *sxl* mutation caused male mutant sterility, and further studies showed that this phenotype is through affecting spermatogenesis of silkworm, especially the growth and development of non-nucleated sperm (Sakai et al. 2019). *Mael* gene has been reported to be involved in PIWI-mediated inhibition of gonadal transposons in *Drosophila* and *Bactrocera*, but not in silkworms, where it is important for spermatogenesis (Chen et al. 2019). In 2021, Meccariello et al. (2021) enabled X-chromosome-specific sequence repeats knock out line by CRISPR/Cas9 and CRISPR/Cas12a during spermatogenesis of the Mediterranean fruit fly, this yielded a significant and consistent distortion of the sex ratio towards males. Taken together, sex-specific expression genes or sex-biased genes were used for developing transgenic sexing strains, provided potential new target gene selection for the control of *Bactrocera* pests.

7.3.3 Gene drive in insects

Recently, genome editing has been applied efficiently as a loss-of-function approach to explore gene function. As a newly emerged genome editing tool, CRISPR/Cas9 has been widely applied to create genetic modification in diverse tephritid species including *C. capitata* (Aumann et al. 2018), *A. suspensa* (Li et al. 2019), *B. dorsalis* (Wang et al. 2020), *B. tryoni* (Choo et al. 2020), *B. oleae* (Meccariello et al. 2020) and *Z. cucurbitae* (Ward et al. 2021). Due to the powerful and convenient gene editing capabilities of CRSPR/Cas9 technology, Esvelt et al. (2014) proposed a theoretical model of a gene drive system based on this technology. Gene drive refers to the phenomenon that certain genotypes or specific traits in a population are passed on to offspring favourably, this process is also known as ultra-Mendelian inheritance. The sex-determining gene *dsx* combined with CRISPR/Cas9 has resulted in gene-drive strains in *Anopheles gambiae* that can transmit sex-specific sterility phenotypes to offspring to a greater extent and thus achieve better population control (Kyrou et al. 2018), In *C. capitata*, Meccariello et al. (2024) and Carrami et al. (2018) presented a Cas9-based homing gene-drive element targeting the transformer gene and showed its high efficiency for sex conversion from females to males. CRISPR/Cas9 mediated gene drives only need to edit single guide RNAs to bind and cut any site with PAM structure. This greatly expands the scope of application of this system (Fig. 3B and 3C). If the selected target site is a gene that plays an important role in female reproduction or growth and development, it can specifically kill female offspring or make them sterile, and eventually lead to the extinction of the population due to the imbalance of the sex ratio. However, due to its powerful genetic transformation ability and the lack of control measures, this homing strategy is quite invasive and irreversible, which may lead to the extensive spread of transgenic insects in the target species, and even cause the replacement

or extinction of the entire species, resulting in a series of safety and moral problems.

Both the sterile insect technology and gene drive technology mentioned above use transgenic methods to integrate synthetic expression boxes into the insect genome. To be sure, genetically modified insects still need to undergo a rigorous and comprehensive risk assessment, as well as the understanding and support of governments and the public, before they are finally released into the wild. Although the relevant policies and public attitudes vary greatly between countries, the positive interaction between national policies, public attitudes and scientific research and development, based on the research foundation already carried out, will provide unlimited possibilities for the use of mature genetic control technology to control wild pest populations in the future.

7.3.4 RNA interference (RNAi)

Recent advancements in molecular technology have opened up new possibilities for insect sterility in SIT programs by using RNA interference (RNAi) as an alternative to radiation (Darrington et al. 2017). Studies have shown that the ingestion of double-stranded RNA materials (dsRNAs) can silence sequence-specific genes that significantly affect male fertility in *B. dorsalis* and *B. tryoni*. This results in a decrease in the number and viability of spermatozoa produced by the male insects, without affecting their mating ability (Li et al. 2011; Dong et al. 2016; Cruz et al. 2018). The RNAi-based approach has several advantages as it does not require any irradiation or functional foreign protein and only targets sequence-specific genes in the target organisms, which could be a promising strategy for insect management in the future.

8 Conclusion and future outlooks

Bactrocera dorsalis is a highly invasive species, and in recent decades, its geographical distribution has been expanding poleward to temperate regions with the aid of globalization and climate change, posing significant threats to fruit and vegetable production as well as cross-border trade. Targeted to its biological invasion processes, multiple preventative and eradication tactics were adopted and integrated to prevent its spread, outbreak and heavy damage. Our survey feedback highlights the current pest management tends to be biased to chemical spray, and the expectation of local growers emphasizes the demand for more efficient and environmental-friendly programs. Thus, in-depth basic research to improve IPM strategies is urgently needed to develop novel non-chemical control techniques. Lack of knowledge and experience on this pest is the key barrier leading to the failure of IPM, appealing for future initiatives to strengthen growers' education from extension advisors to raise their awareness and cooperation. More efforts are needed for optimizing and integrating the existing IPM strategies. Natural control, i.e., releases and conservation of natural enemies, serves as better alternatives to reduce chemical application. The AWM programs that have been highlighted in this review offer environmentally sustainable solutions, some being more expensive than others. Regional collaboration to implement these programs would reduce the overall risk from this pest. New sterility technologies such as genetic modification offer alternative and possibly cheaper solutions to sterility than the typical SIT programs based on irradiation. This is a quick developing field, with success for other insect pests has the potential to provide lasting solutions to this and other fruit fly pests. Lastly, quarantine interception and phytosanitary treatment are important to curtail the potential entry risk of invasive species.

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References

Aatif, H. M., Afzal, A., Idrees, A., Mansha, M. Z., Hanif, C. M. S., Ali, Y., … Li, J. (2023). Entomopathogenic nematodes for the control of oriental fruit fly *Bacterocera dorsalis* (Diptera: Tephritidae). *Journal of King Saud University. Science, 35*(1), 102428. https://doi.org/10.1016/j.jksus.2022.102428

Abdulla, N. R., Rwegasira, G. M., & Mwatawala, M. W. (2017). Efficacy of African weaver ant, *Oecophylla longinoda* (Hymenoptera: Formicidae) in reducing losses due to frugivorous fruit flies (Diptera: Tephritidae) in smallholder mango production systems in Eastern Tanzania. *Biocontrol Science and Technology, 27*(10), 1205–1219. https://doi.org/10.1080/09583157.2017.1391173

Adhikari, D., Joshi, S. L., Thapa, R. B., Pandit, V., & Sharma, D. R. (2020). Fruit fly management in Nepal: A case from plant clinic. *Journal of Biological Control, 34*(1), 8–14. https://doi.org/10.18311/jbc/2020/22833

Affandi, A., Hendri, Emilda, D., Mansyah, E., De Faveri, S., Shanmugam, V. S., & Jonhson, P. (2023). Implementation of area-wide management for fruit fly control strategy on Mango cv. Gedong Gincu in Indonesia. *2nd International Symposium on Durian and Others Tropical Fruits* (ISoDOTF-2021). At: Solok, West Sumatra, Indonesia. https://doi.org/10.1063/5.0136405

Aketarawong, N., Bonizzoni, M., Thanaphum, S., Gomulski, L. M., Gasperi, G., Malacrida, A. R., & Gugliemino, C. R. (2007). Inferences on the population structure and colonization process of the invasive oriental fruit fly, *Bactrocera dorsalis* (Mendel). *Molecular Ecology, 16*(17), 3522–3532. https://doi.org/10.1111/j.1365-294X.2007.03409.x

Ant, T., Koukidou, M., Rempoulakis, P., Gong, H. F., Economopoulos, A., Vontas, J., & Alphey, L. (2012). Control of the olive fruit fly using genetics-enhanced sterile insect technique. *BMC Biology, 10*(1), 51. https://doi.org/10.1186/1741-7007-10-51

Appiah, E. F., Ekesi, S., Afreh-Nuamah, K., Obeng-Ofori, D., & Mohamed, S. A. (2014). African weaver ant-produced semiochemicals impact on foraging behaviour and parasitism by the Opiine parasitoid, *Fopius arisanus* on *Bactrocera invadens* (Diptera: Tephritidae). *Biological Control, 79*, 49–57. https://doi.org/10.1016/j.biocontrol.2014.08.004

Aumann, R. A., Schetelig, M. F., & Häcker, I. (2018). Highly efficient genome editing by homology-directed repair using Cas9 protein in *Ceratitis capitata. Insect Biochemistry and Molecular Biology, 101*, 85–93. https://doi.org/10.1016/j.ibmb.2018.08.004

Badii, K. B., Billah, M. K., Afreh-Nuamah, K., Obeng-Ofori, D., & Nyarko, G. (2015). Review of the pest status, economic impact and management of fruit-infesting flies (Diptera: Tephritidae) in Africa. *African Journal of Agricultural Research, 10*(12), 1488–1498. https://doi.org/10.5897/ajar2014.9278 https://doi.org/10.5897/AJAR2014.9278

Barclay, H. J., McInnis, D., & Hendrichs, J. (2014). Modeling the area-wide integration of male annihilation and the simultaneous release of methyl eugenol-exposed *Bactrocera* spp. sterile males. *Annals of the Entomological Society of America, 107*(1), 97–112. https://doi.org/10.1603/AN13010

Baxter, R. H. G. (2016). Chemosterilants for control of insects and insect vectors of disease. *Chimia, 70*(10), 715–720. https://doi.org/10.2533/chimia.2016.715

Bell, L. R., Maine, E. M., Schedl, P., & Cline, T. W. (1988). Sex-lethal, a *Drosophila* sex determination switch gene, exhibits sex-specific RNA splicing and sequence similarity to RNA binding proteins. *Cell, 55*(6), 1037–1046. https://doi.org/10.1016/0092-8674(88)90248-6

Benelli, G., Daane, K. M., Canale, A., Niu, C. Y., Messing, R. H., & Vargas, R. I. (2014). Sexual communication and related behaviours in Tephritidae: Current knowledge and potential applications for Integrated Pest Management. *Journal of Pest Science, 87*(3), 385–405. https://doi.org/10.1007/s10340-014-0577-3

Bouyer, J., & Vreysen, M. J. B. (2019). Concerns about the feasibility of using 'precision guided sterile males' to control insects. *Nature Communications, 10*(1), 3954. https://doi.org/10.1038/s41467-019-11616-9

Bushland, R. C., Lindquist, A. W., & Knipling, E. F. (1955). Eradication of screw-worms through release of sterilized males. *Science, 122*(3163), 287–288. https://doi.org/10.1126/science.122.3163.287

Cai, P., Song, Y., Huo, D., Lin, J., Zhang, H., Zhang, Z., … Ji, Q. (2020). Chemical cues induced from fly-oviposition mediate the host-seeking behaviour of *Fopius arisanus* (Hymenoptera: Braconidae), an effective egg parasitoid of *Bactrocera dorsalis* (Diptera: Tephritidae), within a tritrophic context. *Insects, 11*(4), 231. https://doi.org/10.3390/insects11040231

Cai, P., Song, Y., Meng, L., Lin, J., Zhao, M., Wu, Q., … Ji, Q. (2023a). Phenological responses of *Bactrocera dorsalis* (Hendel) to climate warming in China based on long-term historical data. *International Journal of Tropical Insect Science, 43*(3), 881–894. https://doi.org/10.1007/s42690-023-00996-7

Cai, P., Song, Y., Meng, L., Liu, R., Lin, J., Zhao, M., … Ji, Q. (2023b). Climate warming affects phenology of *Bactrocera dorsalis*: A case study of Fujian and Guangxi, China. *Bulletin of Insectology, 76*, 73–81. Retrieved from http://www.bulletinofinsectology.org/pdfarticles/vol76-2023-073-081cai.pdf

Cao, L., Zhou, A., Chen, R., Zeng, L., & Xu, Y. (2012). Predation of the oriental fruit fly, *Bactrocera dorsalis* puparia by the red imported fire ant, *Solenopsis invicta*: Role of host olfactory cues and soil depth. *Biocontrol Science and Technology, 22*(5), 551–557. https://doi.org/10.1080/09583157.2012.668515

Carlson, G. A., & Wetzstein, M. E. (1993). Pesticides and pest management. In G. A. Carlson, D. Zilberman, & J. A. Miranowski (Eds.), *Agriculture and environmental resources economics* (pp. 268–318). Oxford, UK: Oxford University Press.

Carrami, E. M., Eckermann, K. N., Ahmed, H. M., Sánchez, C. H. M., Dippel, S., Marshall, J. M., & Wimmer, E. A. (2018). Consequences of resistance evolution in a Cas9-based sex conversion-suppression gene drive for insect pest management. *Proceedings of the National Academy of Sciences of the United States of America, 115*(24), 6189–6194. https://doi.org/10.1073/pnas.1713825115

Caton, B. P., Fang, H., Pallipparambil, G. R., & Manoukis, N. C. (2023). Transect-based trapping for area-wide delimitation of insects. *Journal of Economic Entomology, 116*(3), 1002–1016. https://doi.org/10.1093/jee/toad059

Chang, Y. Y., Tan, J., & Tan, J. L. (2021). Knowledge and attitude of Malaysian fruit growers on Integrated Pest Management (IPM). *ASM Science Journal, 16*, 1–13. https://doi.org/10.32802/asmscj.2021.804

Chang, C. L., Villalun, M., Geib, S. M., Goodman, C. L., Ringbauer, J., & Stanley, D. (2015). Pupal X-ray irradiation influences protein expression in adults of the oriental fruit fly, *Bactrocera dorsalis. Journal of Insect Physiology, 76*, 7–16. https://doi.org/10.1016/j.jinsphys.2015.03.002

Chang, C. L., Cho, I. K., Li, Q. X., Manoukis, N. C., & Vargas, R. I. (2013). A potential field suppression system for *Bactrocera dorsalis* Hendel. *Journal of Asia-Pacific Entomology, 16*(4), 513–519. https://doi.org/10.1016/j.aspen.2013.08.006

Chailleux, A., Thiao, D. S., Diop, S., Bouvery, F., Ahmad, S., Caceres-Barrios, C., … Diatta, P. (2021). Understanding *Bactrocera dorsalis* trapping to calibrate area-wide management. *Journal of Applied Entomology, 145*(9), 831–840. https://doi.org/10.1111/jen.12897

Chen, J. Y., Cai, P., Zhang, G. B., & Sun, Z. J. (2011). Research progress of occurrence and comprehensive control of Oriental fruit fly *Bactrocera dorsalis* (Hendel). *Plant Diseases and Pests, 2*, 42–47.

Chen, K., Chen, S., Xu, J., Yu, Y., Liu, Z., Tan, A., & Huang, Y. (2019). Maelstrom regulates spermatogenesis of the silkworm, *Bombyx mori. Insect Biochemistry and Molecular Biology, 109*, 43–51. https://doi.org/10.1016/j.ibmb.2019.03.012

Chen, X. F., Xu, L., Zhang, Y. X., Wei, D., Wang, J. J., & Jiang, H. B. (2019). Genome-wide identification and expression profiling of odorant binding proteins in the oriental fruit fly, *Bactrocera dorsalis. Comparative Biochemistry and Physiology. Part D, Genomics & Proteomics, 31*, 100605. https://doi.org/10.1016/j.cbd.2019.100605

Chen, X. F., Yang, H., Wu, S., Zhao, W., Hao, G., Wang, J. J., & Jiang, H. B. (2022). BdorOBP69a is involved in the perception of the phenylpropanoid compound methyl eugenol in oriental fruit fly (*Bactrocera dorsalis*) males. *Insect Biochemistry and Molecular Biology, 147*, 103801. https://doi.org/10.1016/j.ibmb.2022.103801

Chieng, A. C. T., Hee, A. K. W., & Wee, S. L. (2018). Involvement of the antennal and maxillary palp structures in detection and response to methyl eugenol by male *Bactrocera dorsalis* (Diptera: Tephritidae). *Journal of Insect Science, 18*(5), 19. https://doi.org/10.1093/jisesa/iey104

Chinvinijkul, S., Sittilob, P., Limopassmanee, W., & Orankanok, W. (2016). Fruit fly area-wide integrated control program in Thailand success or failure? In R. C. Periera, & W., Orankanok (Eds.), *Proceedings of the Ninth International Symposium on Fruit Flies of Economic Importance,* (pp. 2–20).

Choo, A., Fung, E., Chen, I. Y., Saint, R., Crisp, P., & Baxter, S. W. (2020). Precise single base substitution in the *shibire* gene by CRISPR/Cas9-mediated homology directed repair in *Bactrocera tryoni. BMC Genetics, 21*(S2, Suppl 2), 127. https://doi.org/10.1186/s12863-020-00934-3

Choudhary, S. M., Musmade, A. M., Datkhile, R. V., Bodkhe, V. A., & Guru, P. N. (2022). Effect of pruning time on fruit fly infestation in guava (*Psidium guajava* L.). *The Journal of Phytopharmacology, 11*(1), 47–50. https://doi.org/10.31254/phyto.2022.11109

Clarke, A. R. (2019). *Biology and management of Bactrocera and related fruit flies. CABI*. Wallingford, UK: Centre for Agriculture and Biosciences International.

Clarke, A. R., Powell, K. S., Weldon, C. W., & Taylor, P. W. (2011). The ecology of *Bactrocera tryoni* (Diptera: Tephritidae): what do we know to assist pest management? *Annals of Applied Biology, 158*(1), 26–54. https://doi.org/10.1111/j.1744-7348.2010.00448.x

Clarke, A. R., Armstrong, K. F., Carmichael, A. E., Milne, J. R., Raghu, S., Roderick, G. K., & Yeates, D. K. (2005). Invasive phytophagous pests arising through a recent tropical evolutionary radiation: The *Bactrocera dorsalis* complex of fruit flies. *Annual Review of Entomology, 50*(1), 293–319. https://doi.org/10.1146/annurev.ento.50.071803.130428

Clarke, A. R., Leach, P., & Measham, P. F. (2022). The fallacy of year-round breeding in polyphagous tropical fruit flies (Diptera: Tephritidae): evidence for a seasonal reproductive arrestment in *Bactrocera* species. *Insects, 13*(10), 882. https://doi.org/10.3390/insects13100882

Clarke, A. R., Li, Z.-H., Qin, Y.-J., Zhao, Z. H., Liu, L.-J., & Schutze, M. K. (2019). *Bactrocera dorsalis* (Hendel) (Diptera: Tephritidae) is not invasive through Asia: It's been there all along. *Journal of Applied Entomology, 143*(8), 797–801. https://doi.org/10.1111/jen.12649

Clausen, C. P., Clancy, D. W., & Chock, Q. C. (1965). Biological control of the oriental fruit fly (*Dacus dorsalis* Hendel) and other fruit flies in Hawaii. *Technical Bulletin, No 1322*. https://doi.org/10.22004/ag.econ.171232

Cornelius, M. L., Nergel, L., Duan, J. J., & Messing, R. H. (2000). Responses of female oriental fruit flies (Diptera: Tephritidae) to protein and host fruit odors in field cage and open field tests. *Environmental Entomology, 29*(1), 14–19. https://doi.org/10.1603/0046-225X-29.1.14

Cruz, C., Tayler, A., & Whyard, S. (2018). RNA Interference-mediated knockdown of male fertility genes in the Queensland fruit fly *Bactrocera tryoni* (Diptera: Tephritidae). *Insects, 9*(3), 96. https://doi.org/10.3390/insects9030096

Dainese, M., Martin, E. A., Aizen, M. A., Albrecht, M., Bartomeus, I., Bommarco, R., … Steffan-Dewenter, I. (2019). A global synthesis reveals biodiversity-mediated benefits for crop production. *Science Advances, 5*(10), eaax0121. https://doi.org/10.1126/sciadv.aax0121

Darrington, M., Dalmay, T., Morrison, N. I., & Chapman, T. (2017). Implementing the sterile insect technique with RNA interference – a review. *Entomologia Experimentalis et Applicata, 164*(3), 155–175. https://doi.org/10.1111/eea.12575

De Faveri, S., Vijaysegaran, S., & Cheesman, J. (2024). *Area-wide management of methyl eugenol-attracted fruit flies in mango: A systems approach. ACIAR Monograph No. 222*. Canberra: Australian Centre for International Agricultural Research.

De Faveri, S. G. (2013). Farm-wide fruit fly management systems for the east coast of Australia. *Horticulture Innovation Australia Limited Final Report, MT12050*, 75.

De Faveri, S. G. (2018). Integrated pest management and biological pest control strategies in mango cultivation. In V. G. Sauco & P. Lu (Eds.), *Achieving sustainable cultivation of mangoes* (pp. 511–542). London: Burleigh Dodds Science Publishing; https://doi.org/10.19103/AS.2017.0026.21

Deschepper, P., Vanbergen, S., Zhang, Y., Li, Z. H., Hassani, I. M., Patel, N. A., … Delatte, H. (2023). *Bactrocera dorsalis* in the Indian Ocean: A tale of two invasions. *Evolutionary Applications, 16*(1), 48–61. https://doi.org/10.1111/eva.13507

Dias, N. P., Montoya, P., & Nava, D. E. (2022). A 30-year systematic review reveals success in tephritid fruit fly biological control research. *Entomologia Experimentalis et Applicata, 170*(5), 370–384. https://doi.org/10.1111/eea.13157

Dias, N. P., Zotti, M. J., Montoya, P., Carvalho, I. R., & Nava, D. E. (2018). Fruit fly management research: A systematic review of monitoring and control tactics in the world. *Crop Protection (Guildford, Surrey), 112*, 187–200. https://doi.org/10.1016/j.cropro.2018.05.019

Dong, Y. C., Wang, Z. J., Chen, Z. Z., Clarke, A. R., & Niu, C. Y. (2016). *Bactrocera dorsalis* male sterilization by targeted RNA interference of spermatogenesis: Empowering sterile insect technique programs. *Scientific Reports, 6*(1), 35750. https://doi.org/10.1038/srep35750

Drew, R. A. I., Tsuruta, K., & White, I. M. (2005). A new species of pest fruit fly (Diptera: Tephritidae: Dacinae) from Sri Lanka and Africa. *African Entomology, 13*, 149–154. Retrieved from https://hdl.handle.net/10520/EJC32620

Drew, R. A. I., & Hancock, D. L. (1994). The *Bactrocera dorsalis* complex of fruit flies (Diptera: Tephritidae: Dacinae) in Asia. *Bulletin of Entomological Research Supplement Series, 2*, 1–68. https://doi.org/10.1017/S1367426900000278

Drew, R. A. I., & Yuval, B. (2000). The evolution of fruit fly feeding behavior. In M. Aluja & A. Norrbom (Eds.), *Fruit flies (Tephritidae) Phylogeny and Evolution of Behavior* (pp. 731–750). Boca Raton: CRC Press; https://doi.org/10.1201/9781420074468

Duyck, P. F., David, P., & Quilici, S. (2004). A review of relationships between interspecific competition and invasions in fruit flies (Diptera: Tephritidae). *Ecological Entomology, 29*(5), 511–520. https://doi.org/10.1111/j.0307-6946.2004.00638.x

Dyck, V. A., Reyes Flores, J., Vreysen, M. J. B., Regidor Fernández, E. E., Barnes, B. N., Loosjes, M., … Lindquist, D. (2021). Management of area-wide pest management programmes that

integrate the sterile insect technique. In V. A. Dyck, J. Hendrichs & A. S. Robinson (Eds.), *Sterile Insect Technique: principles and practice in area wide Integrated pest management* Second Edition (pp. 781–814). IAEA. CRC Press, Boca Raton, Florida, USA. https://doi.org/10.1201/9781003035572-24

Ekesi, S., Nderitu, P. W., & Rwomushana, I. (2006). Field infestation, life history and demographic parameters of the fruit fly *Bactrocera invadens* (Diptera: Tephritidae) in Africa. *Bulletin of Entomological Research, 96*(4), 379–386. https://doi.org/10.1079/BER2006442

Esvelt, K. M., Smidler, A. L., Catteruccia, F., & Church, G. M. (2014). Concerning RNA-guided gene drives for the alteration of wild populations. *eLife, 3*, e03401. https://doi.org/10.7554/eLife.03401

EPPO (2024). *Bactrocera dorsalis*. EPPO datasheets on pests recommended for regulation. Available online. https://gd.eppo.int

FAO/IAEA (2018). Trapping guidelines for area-wide fruit fly programmes, Second Edition, by Enkerlin WR and Reyes-Flores J (Eds), Rome, Italy.

Fletcher, B. S. (1987). The biology of Dacine fruit flies. *Annual Review of Entomology, 32*(1), 115–144. https://doi.org/10.1146/annurev.en.32.010187.000555

Fletcher, B. S. (1989). Life history strategies of tephritid fruit flies. In A. S. Robinson, & G. Hooper (Eds.), *World Crop Pests. Fruit flies their biology, natural enemies and control* Vol. 3B (pp. 195–208). Elsevier Science Publishing Company Inc., New York.

Follett, P. A. (2009). Puncture resistance in 'Sharwil' avocado to Oriental fruit fly and Mediterranean fruit fly (Diptera: Tephritidae) oviposition. *Journal of Economic Entomology, 102*(3), 921–926. https://doi.org/10.1603/029.102.0309

Fu, G., Condon, K. C., Epton, M. J., Gong, P., Jin, L., Condon, G. C., … Alphey, L. (2007). Female-specific insect lethality engineered using alternative splicing. *Nature Biotechnology, 25*(3), 353–357. https://doi.org/10.1038/nbt1283

Fujii, J. K., & Tamashiro, M. (1972). *Nosema tephrititae* sp. n., a microsporidian pathogen of the oriental fruit fly, *Dacus dorsalis* Hendel. *Proceedings of the Hawaiian Entomological Society, 21*(2), 191–203. Retrieved from https://core.ac.uk/reader/5100260

Garcia, F. R. M., Ovruski, S. M., Suarez, L., Cancino, J., & Liburd, O. E. (2020). Biological control of Tephritid fruit flies in the Americas and Hawaii: A review of the use of parasitoids and predators. *Insects, 11*(10), 662. https://doi.org/10.3390/insects11100662

Gnanvossou, D., Hanna, R., Bokonon-Ganta, A. H., Ekesi, S., & Mohamed, S. A. (2016). Release, establishment and spread of the natural enemy *Fopius arisanus* (Hymenoptera: Braconidae) for control of the invasive oriental fruit fly *Bactrocera dorsalis* (Diptera: Tephritidae) in Benin, West Africa. In S. Ekesi, S. A. Mohamed, & M. De Meyer (Eds.), *Fruit Fly Research and Development in Africa – Towards a Sustainable Management Strategy to Improve Horticulture* (pp. 575–600). Cham: Springer; https://doi.org/10.1007/978-3-319-43226-7_26

Godjo, A., Chabi, N., Zadji, L., Dossou, P., Batcho, O., Baimey, H., … Afouda, L. (2021). Evaluation of the ability of indigenous nematode isolates of *Heterorhabditis taysearae* and *Steinernema kandii* to control mango fruit fly *Bactrocera dorsalis* under laboratory, semi-field and field conditions in Northern Benin. *Crop Protection (Guildford, Surrey), 149*, 105754. https://doi.org/10.1016/j.cropro.2021.105754

Godjo, A., Zadji, L., Decraemer, W., Willems, A., & Afouda, L. (2018). Pathogenicity of indigenous entomopathogenic nematodes from Benin against mango fruit fly (*Bactrocera dorsalis*) under laboratory conditions. *Biological Control, 117*, 68–77. https://doi.org/10.1016/j.biocontrol.2017.10.009

Gong, P., Epton, M. J., Fu, G., Scaife, S., Hiscox, A., Condon, K. C., … Alphey, L. (2005). A dominant lethal genetic system for autocidal control of the Mediterranean fruitfly. *Nature Biotechnology, 23*(4), 453–456. https://doi.org/10.1038/nbt1071

Grechi, I., Preterre, A. L., Lardenois, M., & Ratnadass, A. (2022). *Bactrocera dorsalis* invasion increased fruit fly incidence on mango production in Reunion Island. *Crop Protection (Guildford, Surrey), 161*, 106056. https://doi.org/10.1016/j.cropro.2022.106056

Gui, S. Y., Yuval, B., Engl, T., Lu, Y. Y., & Cheng, D. F. (2023). Protein feeding mediates sex pheromone biosynthesis in an insect. *eLife, 12*, e83469. https://doi.org/10.7554/eLife.83469

Gutierrez, A. P., Ponti, L., Neteler, M., Suckling, D. M., & Cure, J. R. (2021). Invasive potential of tropical fruit flies in temperate regions under climate change. *Communications Biology, 4*(1), 1141. https://doi.org/10.1038/s42003-021-02599-9

Gwokyalya, R., Herren, J. K., Weldon, C. W., Ndlela, S., Gichuhi, J., Ongeso, N., Wairimu, A. W., Ekesi, S., & Mohamed, S. A. (2023a). Multitrophic effects: a tale of microbiome shifts in the oriental fruit. *Research Square,* Preprint v1. https://doi.org/10.21203/rs.3.rs-3672275/v1

Gwokyalya, R., Weldon, C. W., Herren, J. K., Gichuhi, J., Makhulu, E. E., Ndlela, S., & Mohamed, S. A. (2023b). Friend or foe: Symbiotic bacteria in *Bactrocera dorsalis*-parasitoid associations. *Biology (Basel), 12*(2), 274. https://doi.org/10.3390/biology12020274

Han, P., Wang, X., Niu, C. Y., Dong, Y. C., Zhu, J. Q., & Desneux, N. (2011). Population dynamics, phenology, and overwintering of *Bactrocera dorsalis* (Diptera: Tephritidae) in Hubei Province, China. *Journal of Pest Science, 84*(3), 289–295. https://doi.org/10.1007/s10340-011-0363-4

Hancock, D. L., Osborne, R., Broughton, S., & Gleeson, P. (2000). Eradication of *Bactrocera papaya* (Diptera: Tephritidae) by male annihilation and protein baiting in Queensland, Australia. In K. Hong, & T. Penang (Eds.), *Area wide control of fruit flies and other pests* (pp. 381–388). Penerbit Universiti Sains Malaysia.

Hardy, D. E., & Adachi, M. (1956). Insects of micronesia Diptera: Tephritdae. *Insects of Micronesia, 14*, 1–28. http://hbs.bishopmuseum.org/pubs-online/pdf/iom14-1.pdf

Hardy, D. E. (1973). The fruit flies (Tephritidae-Diptera) of Thailand and bordering countries. *Pacific Insects Monographs, 31*, 1–353. http://hbs.bishopmuseum.org/pim/pdf/pim31.pdf

Harris, A. F., Nimmo, D., McKemey, A. R., Kelly, N., Scaife, S., Donnelly, C. A., … Alphey, L. (2011). Field performance of engineered male mosquitoes. *Nature Biotechnology, 29*(11), 1034–1037. https://doi.org/10.1038/nbt.2019

Hayes, W. J., Jr. (1968). Toxicology aspects of chemosterilants. In G. C. Labecque & C. N. Smith (Eds.), *Principles of insect chemosterilization* (pp. 315–347). New York, USA: Appleton-Century-Crofts.

Hee, A. K. W., Ooi, Y. S., Wee, S. L., & Tan, K. H. (2015). Comparative sensitivity to methyl eugenol of four putative *Bactrocera dorsalis* complex sibling species – further evidence that they belong to one and the same species *B. dorsalis*. *ZooKeys, 540*, 313–321. https://doi.org/10.3897/zookeys.540.6099

Hendel, F. (1912). H. Sauter's Formosa-Ausbeute. Genus Dacus, Fabricius (1805) (Diptera). *Supplementa Entomologica, 1*, 13–24.

Heve, W. K., Adjadeh, T. A., & Billah, M. K. (2021). Overview and future research needs for development of effective biocontrol strategies for management of *Bactrocera dorsalis* Hendel (Diptera: Tephritidae) in sub-Saharan Africa. *Pest Management Science, 77*(10), 4224–4237. https://doi.org/10.1002/ps.6485

Hossain, M. F., Hossain, M. A., Seheli, K., & Leblanc, L. (2023). Response of the braconid parasitoid *Diachasmimorpha longicaudata* (Ashmead) to fruits infested by oriental fruit fly, *Bactrocera dorsalis* (Hendel). *Journal of Entomology and Zoology Studies, 11*(1), 194–198. https://doi.org/10.22271/j.ento.2023.v11.i1c.9156

Hossain, M. S., Sarkar, B. C., Hossain, M. M., Mian, M. Y., Rajotte, E. G., Muniappan, R. O., & O'Rourke, M. E. (2020). Comparison of biorational management approaches against mango fruit fly (*Bactrocera dorsalis* Hendel) in Bangladesh. *Crop Protection (Guildford, Surrey), 135*, 104807. https://doi.org/10.1016/j.cropro.2019.05.001

Howlett, F. M. (1912). The effects of oil of *Citronella* on two species of *Dacus. Transactions of the Royal Entomological Society of London, 60*(2), 412–418. https://doi.org/10.1111/j.1365-2311.1912.tb03101.x

Jaffar, S., Rizvi, S. A. H., & Lu, Y. Y. (2023). Understanding the invasion, ecological adaptations, and management strategies of *Bactrocera dorsalis* in China: A review. *Horticulturae, 9*(9), 1004. https://doi.org/10.3390/horticulturae9091004

Jiang, J. A., Tseng, C. L., Lu, F. M., Yang, E. C., Wu, Z. S., Chen, C. P., … Liao, C. H. (2008). A GSM-based remote wireless automatic monitoring system for field information: A case study for ecological monitoring of oriental fruit fly, *Bactrocera dorsalis* (Hendel). *Computers and Electronics in Agriculture, 62*(2), 243–259. https://doi.org/10.1016/j.compag.2008.01.005

Jiang, J. A., Lin, T. S., Yang, E. C., Tseng, C. L., Chen, C. P., Yen, C. W., … Chuang, C. L. (2013). Application of a web-based remote agro-ecological monitoring system for observing spatial distribution and dynamics of *Bactrocera dorsalis* in fruit orchards. *Precision Agriculture, 14*(3), 323–342. https://doi.org/10.1007/s11119-012-9298-x

Jiang, J. J., Zhou, K., Liang, G. W., Zeng, L., & Wen, S. Y. (2014). A novel point mutation of acetylcholinesterase in a trichlorfon-resistant strain of the oriental fruit fly (Diptera: Tephritidae). *Applied Entomology and Zoology, 49*(1), 129–137. https://doi.org/10.1007/s13355-013-0232-0

Jin, T., Zeng, L., Lin, Y. Y., Lu, Y. Y., & Liang, G. W. (2011). Insecticide resistance of the oriental fruit fly, *Bactrocera dorsalis* (Hendel) (Diptera: Tephritidae), in mainland China. *Pest Management Science, 67*(3), 370–376. https://doi.org/10.1002/ps.2076

Klassen, W., Curtis, C. F., & Hendrichs, J. (2021). History of the sterile insect technique. In V. A. Dyck, J. Hendrichs, & A. S. Robinson (Eds.), *Sterile Insect Technique: Principles and Practice in Area-Wide Integrated Pest Management* (2nd ed., pp. 1–44). Boca Raton, FL, USA: CRC Press; https://doi.org/10.1201/9781003035572-1

Knipling, E. F. (1955). Possibilities of insect control or eradication through the use of sexually sterile males. *Journal of Economic Entomology, 48*(4), 459–462. https://doi.org/10.1093/jee/48.4.459

Koyama, J., Teruya, T., & Tanaka, K. (1984). Eradication of the oriental fruit fly (Diptera; Tephritidae) from the Okinawa island by a male annihilation method. *Journal of Economic Entomology, 77*(2), 468–472. https://doi.org/10.1093/jee/77.2.468

Kyrou, K., Hammond, A. M., Galizi, R., Kranjc, N., Burt, A., Beaghton, A. K., & Crisanti, A. (2018). A CRISPR-Cas9 gene drive targeting *doublesex* causes complete population suppression in caged *Anopheles gambiae* mosquitoes. *Nature Biotechnology, 36*(11), 1062–1066. https://doi.org/10.1038/nbt.4245

Lello, F., Dida, M., Mkiramweni, M., Matiko, J., Akol, R., Nsabagwa, M., & Katumba, A. (2023). Fruit fly automatic detection and monitoring techniques: A review. *Smart Agricultural Technology, 5*, 100294. https://doi.org/10.1016/j.atech.2023.100294

Li, B. S., Zhan, G. P., Wang, Y. J., Ren, L. L., Liu, B., & Li, T. X. (2013). Thermal death kinetics of fruit flies *Bactrocera dorsalis, B. papayae* and *B. correcta* (Diptera: Tephritidae). [in Chinese]. *Acta Entomologica Sinica, 56*, 1404–1412.

Li, H., Li, Z., & Zhao, Z. H. (2023). Egg-associated germs induce salicylate defenses but not render plant against a global invasive fruit fly effectively. *Journal of Agricultural and Food Chemistry, 71*, 6023–6031. https://doi.org/10.1021/acs.jafc.3c00427

Li, H., Zhang, Y., Li, H., Reddy, G. V. P., Li, Z. H., Chen, F. J., … Zhao, Z. H. (2023). The nitrogen-dependent GABA pathway of tomato provides resistance to a globally invasive fruit fly. *Frontiers in Plant Science, 14*, 1252455. https://doi.org/10.3389/fpls.2023.1252455

Li, J., & Handler, A. M. (2019). CRISPR/Cas9-mediated gene editing in an exogenous transgene and an endogenous sex determination gene in the Caribbean fruit fly, *Anastrepha suspensa. Gene, 691*, 160–166. https://doi.org/10.1016/j.gene.2018.12.055

Li, X. X., Zhang, M. Y., & Zhang, H. Y. (2011). RNA interference of four genes in adult *Bactrocera dorsalis* by feeding their dsRNAs. *PLoS One, 6*(3), e17788. https://doi.org/10.1371/journal.pone.0017788

Li, X., Wu, Q., Wu, J., Zeng, L., Cheng, D., Xian, J., & Lu, Y. (2022). Effects of four chemosterilants on *Bactrocera tau. Ecotoxicology and Environmental Safety, 243*, 114028. https://doi.org/10.1016/j.ecoenv.2022.114028

Li, X. L., Li, D. D., Cai, X. Y., Cheng, D. F., & Lu, Y. Y. (2024). Reproductive behavior of fruit flies: Courtship, mating, and oviposition. *Pest Management Science, 80*(3), 935–952. https://doi.org/10.1002/ps.7816

Li, M., Yang, T., Bui, M., Gamez, S., Wise, T., Kandul, N. P., … Akbari, O. S. (2021). Suppressing mosquito populations with precision guided sterile males. *Nature Communications, 12*(1), 5374. https://doi.org/10.1038/s41467-021-25421-w

Lin, J. T., Zeng, L., Liang, G. W., Lu, Y. Y., & Bin, S. Y. (2005). Effects of entomopathogenic nematodes on the oriental fruit fly, *Bactrocera* (*Bactrocera*) *dorsalis* (Hendel) [In Chinese] [in Chinese]. *Acta Entomologica Sinica, 48*(5), 736–741.

Lin, K. W., Lin, H. L., Shiesh, C. C., Hsu, Y. L., Lin, C. H., Chen, S. C., & Yeh, W. B. (2020). Cold treatment for guava fruits infested with oriental fruit fly, *Bactrocera dorsalis* (Diptera: Tephritidae). *Applied Entomology and Zoology, 55*(1), 37–44. https://doi.org/10.1007/s13355-019-00651-z

Liu, H., Zhao, X. F., Fu, L., Han, Y. Y., Chen, J., & Lu, Y. Y. (2017). *BdorOBP2* plays an indispensable role in the perception of methyl eugenol by mature males of *Bactrocera dor-*

salis (Hendel). *Scientific Reports, 7*(1), 15894. https://doi.org/10.1038/s41598-017-15893-6

Liu, H., Chen, Z. S., Zhang, D. J., & Lu, Y. Y. (2018). *BdorOR88a* modulates the responsiveness to methyl eugenol in mature males of *Bactrocera dorsalis* (Hendel). *Frontiers in Physiology, 9*, 987. https://doi.org/10.3389/fphys.2018.00987

Liu, H., Zhang, D. J., Xu, Y. J., Wang, L., Cheng, D. F., Qi, Y. X., … Lu, Y. Y. (2019). Invasion, expansion, and control of *Bactrocera dorsalis* (Hendel) in China. *Journal of Integrative Agriculture, 18*(4), 771–787. https://doi.org/10.1016/S2095-3119(18)62015-5

Lloyd, A., Hamacek, E., Kopittke, R., Peek, T., Wyatt, P., Neale, C., … Gu, H. (2010). Area-wide management of fruit flies (Diptera: Tephritidae) in the central Burnett district of Queensland, Australia. *Crop Protection (Guildford, Surrey), 29*(5), 462–469. https://doi.org/10.1016/j.cropro.2009.11.003

Lux, S. A., Copeland, R. S., White, I. M., Manrakhan, A., & Billah, M. K. (2003). A new invasive fruit fly species from the *Bactrocera dorsalis* (Hendel) group detected in East Africa. *International Journal of Tropical Insect Science, 23*(4), 355–361. https://doi.org/10.1017/S174275840001242X

Manoukis, N. C., Vargas, R. I., Carvalho, L., Fezza, T., Wilson, S., Collier, T., & Shelly, T. E. (2019). A field test on the effectiveness of male annihilation technique against *Bactrocera dorsalis* (Diptera: Tephritidae) at varying application densities. *PLoS One, 14*(3), e0213337. https://doi.org/10.1371/journal.pone.0213337

Manrakhan, A., Stephen, P. R., & Cronje, P. J. R. (2015). Phytotoxic effect of GF-120 NF fruit fly bait on fruit of mandarin (*Citrus reticulata* Blanco cv. Nadorcott): Influence of bait characteristics and fruit maturity stage. *Crop Protection (Guildford, Surrey), 78*, 48–53. https://doi.org/10.1016/j.cropro.2015.08.015

Manrakhan, A. (2020). Pre-harvest management of the oriental fruit fly. *Perspectives in Agriculture, Veterinary Science, Nutrition and Natural Resources, 15*, 1–13. https://doi.org/10.1079/PAVSNNR202015003

Marri, D., Gomez, D. A. M. A., Wilson, D. D., Billah, M. K., Yeboah, S., & Osae, M. (2016). Evaluation of the efficacy of a commercial formulation of *Beauveria bassiana* for the control of the invasive fruit fly *Bactrocera dorsalis* (Diptera: Tephritidae). *Biopesticides International, 12*(1), 9–18. http://0973-483X/12.01/9-18.

Mau, R. F. L., Jang, E. B., & Vargas, R. I. (2007). The Hawaii area-wide fruit fly pest management partnerships and a good education programme. In M. J. B. Vreysen, A. S. Robinson & J. Hendrichs (Eds.), *Area-wide control of insect pests: From research to field implementation* (pp. 671–683). Springer, Dordecht. https://doi.org/10.1007/978-1-4020-6059-5_62

McCombs, S. D., & Saul, S. H. (1995). Translocation-based genetic sexing system for the oriental fruit fly (Diptera: Tephritidae) based on pupal color dimorphism. *Annals of the Entomological Society of America, 88*(5), 695–698. https://doi.org/10.1093/aesa/88.5.695

Meats, A., Fay, H. A. C., & Drew, R. A. I. (2008). Distribution and eradication of an exotic tephritid fruit fly in Australia: Relevance of invasion theory. *Journal of Applied Entomology, 132*(5), 406–411. https://doi.org/10.1111/j.1439-0418.2008.01290.x

Meccariello, A., Krsticevic, F., Colonna, R., Corsano, G. D., Fasulo, B., Papathanos, P. A., & Windbichler, N. (2021). Engineered sex ratio distortion by X-shredding in the global agricultural pest *Ceratitis capitata. BMC Biology, 19*(1), 78. https://doi.org/10.1186/s12915-021-01010-7

Meccariello, A., Tsoumani, K. T., Gravina, A., Primo, P., Buonanno, M., Mathiopoulos, K. D., & Saccone, G. (2020). Targeted somatic mutagenesis through CRISPR/Cas9 ribonucleoprotein complexes in the olive fruit fly, *Bactrocera oleae. Archives of Insect Biochemistry and Physiology, 104*(2), e21667. https://doi.org/10.1002/arch.21667

Meccariello, A., Hou, S., Davydova, S., Fawcett, J. D., Siddall, A., Leftwich, P. T., … Windbichler, N. (2024). Gene drive and genetic sex conversion in the global agricultural pest *Ceratitis capitata. Nature Communications, 15*(1), 372. https://doi.org/10.1038/s41467-023-44399-1

Messing, R. H., Klungness, L. M., Purcell, M., & Wong, T. T. Y. (1993). Quality control parameters of mass-reared Opiine parasitoids used in augmentative biological control of Tephritid fruit flies in Hawaii. *Biological Control, 3*(2), 140–147. Retrieved from https://doi.org/https://doi.org/10.1006/bcon.1993.1021 https://doi.org/10.1006/bcon.1993.1021

Mohamed, S., Ekesi, S., & Hanna, R. (2010). Old and new host-parasitoid associations: Parasitism of the invasive fruit fly *Bactrocera invadens* (Diptera: Tephritidae) and five African fruit fly species by *Fopius arisanus*, an Asian opiine parasitoid. *Biocontrol Science and Technology, 20*(2), 183–196. https://doi.org/10.1080/09583150903447794

Mohamed, S. A., Ramadan, M. M., & Ekesi, S. (2016). In and out of Africa: parasitoids used for biological control of fruit flies. In S. Ekesi, S. A. Mohamed, & M. De Meyer (Eds.), *Fruit fly research and development in Africa – towards a sustainable management strategy to improve horticulture* (pp. 325–368). Cham: Springer; https://doi.org/10.1007/978-3-319-43226-7_16

Montoya, P., Perez-Lachaud, G., & Liedo, P. (2012). Superparasitism in the fruit fly parasitoid *Diachasmimorpha longicaudata* (Hymenoptera: Braconidae) and the implications for mass rearing and augmentative release. *Insects, 3*(4), 900–911. https://doi.org/10.3390/insects3040900

Moquet, L., Payet, J., Glenac, S., & Delatte, H. (2021). Niche shift of tephritid species after the oriental fruit fly (*Bactrocera dorsalis*) invasion in La Réunion. *Diversity & Distributions, 27*(1), 109–129. https://doi.org/10.1111/ddi.13172

Nasruddin, A. D., Nurariaty, A., & Melina, M. (2020). Effectiveness of nylon exclusion net for preventing chili fruit damage by the oriental fruit fly, *Bactrocera dorsalis* Hendel (Diptera: Tephritidae). *IOP Conference Series. Earth and Environmental Science, 486*(1), 012152. https://doi.org/10.1088/1755-1315/486/1/012152

Navarro-Llopis, V., Ayala, I., Sanchis, J., Primo, J., & Moya, P. (2015). Field Efficacy of a -Based Attractant-Contaminant Device to Control (Diptera: Tephritidae). *Journal of Economic Entomology, 108*(4), 1570–1578. https://doi.org/10.1093/jee/tov157

Navarro-Llopis, V., Primo, J., & Vacas, S. (2013). Efficacy of attract-and-kill devices for the control of *Ceratitis capitata. Pest Management Science, 69*(4), 478–482. https://doi.org/10.1002/ps.3393

Ndlela, S., Mohamed, S., Ndegwa, P. N., Ong'Amo, G. O., & Ekesi, S. (2016). Male annihilation technique using methyl eugenol for field suppression of *Bactrocera dorsalis* (Hendel) (Diptera: Tephritidae) on mango in Kenya. *African Entomology, 24*(2), 437–447. https://doi.org/10.4001/003.024.0437

Newell, I. M., & Haramoto, F. H. (1968). Biotic factors influencing populations of *Dacus dorsalis* in Hawaii. *Proceedings of the Hawaiian Entomological Society, 20*(1), 81–139. Retrieved from https://core.ac.uk/reader/5100208

Ogaugwu, C. E., Schetelig, M. F., & Wimmer, E. A. (2013). Transgenic sexing system for *Ceratitis capitata* (Diptera: Tephritidae) based on female-specific embryonic lethality. *Insect Biochemistry and Molecular Biology, 43*(1), 1–8. https://doi.org/10.1016/j.ibmb.2012.10.010

Ono, H., Hee, A. K. W., & Jiang, H. (2021). Recent advancements in studies on chemosensory mechanisms underlying detection of semiochemicals in *Dacini* fruit flies of economic importance (Diptera: Tephritidae). *Insects, 12*(2), 106. https://doi.org/10.3390/insects12020106

Orankanok, W., Chinvinijkul, S., Thanaphum, S., Sitilob, P., & Enkerlin, W. (2007). Area-wide integrated control of oriental fuit fly *Bactrocera dorsalis* and guava fruit fly *Bactrocera correcta* in Thailand. In M. J. B. Vreysen, A. S. Robinson, & J. Hendrichs (Eds.), *Area-Wide Control of Insect Pests* (pp. 517–526). Dordrecht, Netherlands: Springer; https://doi.org/10.1007/978-1-4020-6059-5_48

Ouna, E. A. (2010). *Entomopathogenicity of Hyphomycetes fungi to fruit fly Bactrocera invadens (Diptera, Tephritidae) and their potential for biological control on mango, Thesis research in entomology-microbiology*. Nairobi: Kenyatta University; https://ir-library.ku.ac.ke/handle/123456789/682

Pieterse, W., Terblanche, J. S., & Addison, P. (2017). Do thermal tolerances and rapid thermal responses contribute to the invasion potential of *Bactrocera dorsalis* (Diptera: Tephritidae)? *Journal of Insect Physiology, 98*, 1–6. https://doi.org/10.1016/j.jinsphys.2016.11.004

Pinero, J. C., Mau, R. F., & Vargas, R. I. (2009). Managing oriental fruit fly (Diptera: Tephritidae), with spinosad-based protein bait sprays and sanitation in papaya orchards in Hawaii. *Journal of Economic Entomology, 102*(3), 1123–1132. https://doi.org/10.1603/029.102.0334

Purcell, M. F., Herr, J. C., Messing, R. H., & Wong, T. T. Y. (1998). Interactions between augmentatively released *Diachasmimorpha longicaudata* (Hymenoptera: Braconidae) and a complex of Opiine parasitoids in a commercial guava orchard. *Biocontrol Science and Technology, 8*(1), 139–151. https://doi.org/10.1080/09583159830504

Qin, Y. J., Krosch, M. N., Schutze, M. K., Zhang, Y., Wang, X. X., Prabhakar, C. S., … Li, Z. H. (2018). Population structure of a global agricultural invasive pest, *Bactrocera dorsalis* (Diptera: Tephritidae). *Evolutionary Applications, 11*(10), 1990–2003. https://doi.org/10.1111/eva.12701

Ranaweeera, P. H., & Hee, A. K. W. (2024). Attractancy of a sesquiterpene, β-caryophyllene to males of the oriental fruit fly, *Bactrocera dorsalis* (Diptera: Tephritidae). *Journal of Chemical Ecology*. https://doi.org/10.1007/s10886-024-01480-3

Rendón, P., McInnis, D., Lance, D., & Stewart, J. (2004). Medfly (Diptera: Tephritidae) genetic sexing strain: large-scale field comparison of males-only and bisexual sterile fly releases in Guatamela. *Journal of Economic Entomology, 97*(5), 1547–1553. https://doi.org/10.1603/0022-0493-97.5.1547

Reynolds, O. L., Collins, D., Dominiak, B. C., & Osborne, T. (2022). No sting in the tail for sterile bisex Queensland fruit fly (*Bactrocera tryoni* Froggatt) release programs. *Insects, 13*(3), 269. https://doi.org/10.3390/insects13030269

Saccone, G., Pane, A., & Polito, L. C. (2002). Sex determination in flies, fruit flies and butterflies. *Genetica, 116*(1), 15–23. https://doi.org/10.1023/A:1020903523907

Sakai, H., Oshima, H., Yuri, K., Gotoh, H., Daimon, T., Yaginuma, T., … Niimi, T. (2019). Dimorphic sperm formation by sex-lethal. *Proceedings of the National Academy of Sciences of the United States of America, 116*(21), 10412–10417. https://doi.org/10.1073/pnas.1820101116

Sarker, D., Rahman, M. M., & Barman, J. C. (2009). Efficacy of different bagging materials for the control of mango fruit fly. *Bangladesh Journal of Agricultural Research, 34*(1), 165–168. https://doi.org/10.3329/bjar.v34i1.5766

Schetelig, M. F., Caceres, C., Zacharopoulou, A., Franz, G., & Wimmer, E. A. (2009). Conditional embryonic lethality to improve the sterile insect technique in *Ceratitis capitata* (Diptera: Tephritidae). *BMC Biology, 7*(1), 4. https://doi.org/10.1186/1741-7007-7-4

Schetelig, M. F., & Handler, A. M. (2012). Strategy for enhanced transgenic strain development for embryonic conditional lethality in *Anastrepha suspensa. Proceedings of the National Academy of Sciences of the United States of America, 109*(24), 9348–9353. https://doi.org/10.1073/pnas.1203352109

Schutze, M. K., Aketarawong, N., Amornsak, W., Armstrong, K. F., Augustinos, A. A., Barr, N., … Clarke, A. R. (2015a). Synonymization of key pest species within the *Bactrocera dorsalis* species complex (Diptera: Tephritidae): taxonomic changes based on a review of 20 years of integrative morphological, molecular, cytogenetic, behavioural and chemoecological data. *Systematic Entomology, 40*(2), 456–471. https://doi.org/10.1111/syen.12113

Schutze, M. K., Mahmood, K., Pavasovic, A., Bo, W., Newman, J., Clarke, A. R., … Cameron, S. L. (2015b). One and the same: integrative taxonomic evidence that *Bactrocera invadens* (Diptera: Tephritidae) is the same species as the Oriental fruit fly *Bactrocera dorsalis. Systematic Entomology, 40*(2), 472–486. https://doi.org/10.1111/syen.12114

Secretaria, L, B., Bayogan, E. R. V., Urquiola, M. A. J., Esconde, R. T., De Faveri, S. G., & Johnson, P. (2022) Carabao' mango quality is affected by preharvest bagging at two maturity stages and subsequent hot water treatment. *V Asia Symposium on Quality Management in Postharvest Systems,* 1336, 159–166. https://doi.org/10.17660/ActaHortic.2022.1336.21

Senior, L. J., Wright, C. L., Missenden, B., & DeFaveri, S. (2017). Protein feeding of Queensland fruit fly *Bactrocera tryoni* and cucumber fly *Zeugodacus cucumis* (Diptera: Tephritidae) on non-host vegetation: effect of plant species and bait height. *Austral Entomology, 56*(3), 296–301. https://doi.org/10.1111/aen.12231

Seewooruthun, S. I., Permalloo, S., Sookar, P., & Soonnoo, A. R. (2000). The oriental fruit fly, *Bactrocera dorsalis* eradicated from Mauritius. In N. S. Price, & S. I. Seewooruthun (Eds.), Proceedings of the Indian Ocean Commission, *Regional Fruit Fly Symposium* (pp. 207–210). Mauritius: Flic En Flac.

Shaurub, E. S. H. (2023). Review of entomopathogenic fungi and nematodes as biological control agents of tephritid fruit flies: Current status and a future vision. *Entomologia Experimentalis et Applicata, 171*(1), 17–34. https://doi.org/10.1111/eea.13244

Shelly, T., Kurashima, R., Mosser, L., Martin, R. M., & Bazelet, C. (2022). Weathering of methyl eugenol solid dispensers: effects on residual amount, release rate, and field capture of *Bactrocera*

dorsalis males (Diptera: Tephritidae). *The Florida Entomologist, 105*(3), 219–224. https://doi.org/10.1653/024.105.0307

Shelly, T. E. (2020). Evaluation of a genetic sexing strain of the oriental fruit fly as a candidate for simultaneous application of male annihilation and sterile insect techniques (Diptera: Tephritidae). *Journal of Economic Entomology, 113*(4), 1913–1921. https://doi.org/10.1093/jee/toaa099

Shelly, T. E., & Manoukis, N. C. (2022). Mating competitiveness of *Bactrocera dorsalis* (Diptera: Tephritidae) males from a genetic sexing strain: effects of overflooding ratio and released females. *Journal of Economic Entomology, 115*(3), 799–807. https://doi.org/10.1093/jee/toac027

Shelly, T., Edu, J., & McInnis, D. (2010). Pre-release consumption of methyl eugenol increases the mating competitiveness of sterile males of the oriental fruit fly, *Bactrocera dorsalis*, in large field enclosures. *Journal of Insect Science, 10*(8), 8. https://doi.org/10.1673/031.010.0801

Sison, M. L. J., Cortaga, C. Q., Barcos, A. K. S., Laurel, N. R., Mateo, J. M. C., & dela Cueva, F. M. (2020). Resistance screening and influence of fruit physico-biochemical properties of "Carabao" and other mango varieties against oriental fruit fly, *Bactrocera dorsalis* (Diptera: Tephritidae), in the Philippines. *Philippine Journal of Science, 149*(4), 1175–1187. https://doi.org/10.56899/149.04.16

Sookar, P. (2014). Study of two potential entomopathogenic fungi, *Metarhizium anisoplia* and *Beauveria bassianaa* for the biocontrol of fruit flies (Diptera: Tephritidae) of economic importance in Mauritius. PhD thesis, Fac. Science. Mauritius University.

Sookar, P., Patel, N., & Ramkalawon, P. (2021). *Bactrocera dorsalis*, an invasive fruit fly species in Mauritius. *Fruits, 76*(6), 269–275. https://doi.org/10.17660/th2021/76.6.2

Srimartpirom, M., Rakkrai, C., Phankum, S., Intarakamhang, R., Sonsiri, C., Buchatian, P., … Follett, P. A. (2023). Vapor heat treatment for quarantine control of the oriental fruit fly (Diptera: Tephritidae) in papaya fruit from Thailand. *Journal of Asia-Pacific Entomology, 26*(2), 102049. https://doi.org/10.1016/j.aspen.2023.102049

Stark, J. D., Vargas, R. I., & Miller, N. (2004). Toxicity of spinosad in protein bait to three economically important tephritid fruit fly species (Diptera: Tephritidae) and their parasitoids (Hymenoptera: Braconidae). *Journal of Economic Entomology, 97*(3), 911–915. https://doi.org/10.1093/jee/97.3.911

Steiner, L. F. (1952). Fruit fly control in Hawaii with poison-bait sprays containing protein hydrolysates. *Journal of Economic Entomology, 45*(5), 838–843. https://doi.org/10.1093/jee/45.5.838

Steiner, L. F., Hart, W. G., Harris, E. J., Cunningham, R. T., Ohinata, K., & Kamakahi, D. C. (1970). Eradication of the oriental fruit fly from the Mariana islands by the methods of male annihilation and sterile insect release. *Journal of Economic Entomology, 63*(1), 131–135. https://doi.org/10.1093/jee/63.1.131

Suckling, D. M., Kean, J. M., Stringer, L. D., Cáceres-Barrios, C., Hendrichs, J., Reyes-Flores, J., & Dominiak, B. C. (2016). Eradication of tephritid fruit fly pest populations: Outcomes and prospects. *Pest Management Science, 72*(3), 456–465. https://doi.org/10.1002/ps.3905

Suckling, D. M., Stringer, L. D., Stephens, A. E., Woods, B., Williams, D. G., Baker, G., & El-Sayed, A. M. (2014). From integrated pest management to integrated pest eradication: Technologies and future needs. *Pest Management Science, 70*(2), 179–189. https://doi.org/10.1002/ps.3670

Sutantawong, M., Orankanok, W., Enkerlin, W. R., Wornoayporn, V., & Cáceres, C. E. (2004). The sterile insect technique for control of the oriental fruit fly, *Bactrocera dorsalis* (Hendel), in mango orchards in Ratchaburi Province, Thailand. In: B. N. Barnes, (Ed.) *Proceedings of the 6th International Symposium on Fruit Flies of Economic Importance* (pp. 223–232). Isteg Scientific Publications, Irene, South Africa. https://nucleus.iaea.org/sites/naipc/twd/Documents/6thISFFEI_Proceedings/SUTANTAWONG.pdf

Syamsudin, T. S., Kirana, R., Karjadi, A. K., & Faizal, A. (2022). Characteristics of chili (*Capsicum annuum* L.) that are resistant and susceptible to oriental fruit fly (*Bactrocera dorsalis* Hendel) infestation. *Horticulturae, 8*(4), 314. https://doi.org/10.3390/horticulturae8040314

Tan, A. J., Fu, G. L., Jin, L., Guo, Q. H., Li, Z. Q., Niu, B. L., … Huang, Y. P. (2013). Transgene-based, female-specifica lethality system for genetic sexing of the silkworm, *Bombyx mori. Proceedings of the National Academy of Sciences of the United States of America, 110*(17), 6766–6770. https://doi.org/10.1073/pnas.1221700110

Tan, K. H., & Nishida, R. (2012). Methyl eugenol: Its occurrence, distribution, and role in nature, especially in relation to insect behavior and pollination. *Journal of Insect Science, 12*(1), 56. https://doi.org/10.1673/031.012.5601

Tan, K. H., & Nishida, R. (1996). Sex pheromone and mating competition after methyl eugenol comsumption in the *Bactrocera dorsalis* complex. In B. A. McPheron & G. J. Steck (Eds.), *Fruit Fly Pests* (pp. 147–153). Florida: St. Lucie; https://doi.org/10.1201/9780367812430-23

Tan, K. H., & Nishida, R. (2000). Mutual reproductive benefits between a wild orchid, *Bulbophyllum patens* and *Bactrocera* fruit flies via a floral synomone. *Journal of Chemical Ecology, 26*(2), 533–546. https://doi.org/10.1023/A:1005477926244

Tariq, S., Hakim, A., Siddiqi, A. A., & Owais, M. (2022). An image dataset of fruitfly species (*Bactrocera zonata* and *Bactrocera dorsalis*) and automated species classification through object detection. *Data in Brief, 43*(8), 108366. https://doi.org/10.1016/j.dib.2022.108366

Theron, C. D., Manrakhan, A., & Weldon, C. W. (2017). Host use of the oriental fruit fly, *Bactrocera dorsalis* (Hendel) (Diptera: Tephritidae), in South Africa. *Journal of Applied Entomology, 141*(10), 810–816. https://doi.org/10.1111/jen.12400

Toledo, J., Moran-Aceves, B. M., Ibarra, J. E., & Liedo, P. (2023). Can entomopathogenic nematodes and their symbiotic bacteria suppress fruit fly pests? a review. *Microorganisms, 11*(7), 1682. https://doi.org/10.3390/microorganisms11071682

Usman, M., Wakil, W., & Shapiro-Ilan, D. I. (2021). Entomopathogenic nematodes as biological control agent against *Bactrocera zonata* and *Bactrocera dorsalis* (Diptera: Tephritidae). *Biological Control, 163*, 104706. https://doi.org/10.1016/j.biocontrol.2021.104706

Van Mele, P., Vayssières, J.-F., Van Tellingen, E., & Vrolijks, J. (2007). Effects of an African weaver ant, *Oecophylla longinoda*, in controlling mango fruit flies (Diptera: Tephritidae) in Benin. *Journal of Economic Entomology, 100*(3), 695–701. https://doi.org/10.1603/0022-0493(2007)100[695:EOAAWA]2.0.CO;2

Vargas, R. I., Leblanc, L., Putoa, R., & Piñero, J. C. (2012). Population dynamics of three *Bactrocera* spp. fruit flies (Diptera: Tephritidae) and two introduced natural enemies, *Fopius arisanus* (Sonan) and *Diachasmimorpha longicaudata* (Ashmead) (Hymenoptera: Braconidae), after an invasion by *Bactrocera*

dorsalis (Hendel) in Tahiti. *Biological Control, 60*(2), 199–206. https://doi.org/10.1016/j.biocontrol.2011.10.012

Vargas, R. I., Piñero, J. C., Mau, R. F. L., Jang, E. B., Klungness, L. M., Mclnnis, D. O., … Wong, L. (2010). Area-wide suppression of the Mediterranean fruit fly, *Ceratitis capitata*, and the Oriental fruit fly, *Bactrocera dorsalis*, in Kamuela, Hawaii. *Journal of Insect Science, 10*(1), 135. https://doi.org/10.1673/031.010.13501

Vargas, R. I., Mau, R. F. L., Jang, E. B., Faust, R. M., & Wong, L. (2008). The Hawaii fruit fly areawide pest management programme. In O. Koul, G. Cuperus & N. Elliott (Eds.), *Areawide Pest Management: Theory and Implementation* (pp. 300–325). Publications from USDA-ARS / UNL Faculty, U.S. Department of Agriculture: Agricultural Research Service, Lincoln, Nebraska. https://digitalcommons.unl.edu/usdaarsfacpub/656 https://doi.org/10.1079/9781845933722.0300

Vayssières, J. F., Offenberg, J., Sinzogan, A., Adandonon, A., Wargui, R., Anato, F., … VanMele, P. (2016). The use of weaver ants in the management of fruit flies in Africa. In S. Ekesi, S. A. Mohamed, & M. De Meyer (Eds.), *Fruit Fly Research and Development in Africa – Towards a Sustainable Management Strategy to Improve Horticulture* (pp. 389–434). Cham: Springer; https://doi.org/10.1007/978-3-319-43226-7_18

Vijaysegaran, S. (2016). Bait manufactured from beer yeast waste and its use for fruit fly management. In B. Sabater-Munoz, T. Vera, R. C. Periera, & W. Orankanok (Eds.), *Proceedings of the Ninth International Symposium on Fruit Flies of Economic Importance,* 12–16 May 2014, Bangkok, Thailand.

Viswanath Reddy, K., Devi, Y. K., & Komala, G. (2020). Management strategies for fruit flies in fruitcrops – a review. *Journal of Emerging Technologies and Innovative Research, 7*, 1472–1480. Retrieved from http://www.jetir.org/papers/JETIR2012193.pdf

Wakil, W., Usman, M., Pinero, J. C., Wu, S., Toews, M. D., & Shapiro-Ilan, D. I. (2022). Combined application of entomopathogenic nematodes and fungi against fruit flies, *Bactrocera zonata* and *B. dorsalis* (Diptera: Tephritidae): laboratory cups to field study. *Pest Management Science, 78*(7), 2779–2791. https://doi.org/10.1002/ps.6899

Wang, B., Huang, Z., Yang, D., Ji, Q., & Cai, P. (2021). Improvement of protein bait produced from beer yeast waste for controlling *Bactrocera dorsalis* (Diptera: Tephritidae) in China. *Journal of Asia-Pacific Entomology, 24*(3), 573–579. https://doi.org/10.1016/j.aspen.2021.04.017

Wang, D., Liang, Q., Chen, M., Ye, H., Liao, Y., Yin, J., … He, Y. (2021). Susceptibility of oriental fruit fly, *Bactrocera dorsalis* (Diptera: Tephritidae) pupae to entomopathogenic fungi. *Applied Entomology and Zoology, 56*(2), 269–275. https://doi.org/10.1007/s13355-021-00734-w

Wang, Y. D., Li, Z. H., & Zhao, Z. H. (2023). Population mixing mediates the intestinal flora composition and facilitates invasiveness in a globally invasive fruit fly. *Microbiome, 11*(1), 213. https://doi.org/10.1186/s40168-023-01664-1

Wang, Y., Gao, B., Zhang, G., Qi, X., Cao, S., Akami, M., … Niu, C. (2020). Mutation of *Bdpaired* induces embryo lethality in the oriental fruit fly, *Bactrocera dorsalis. Pest Management Science, 76*(3), 944–951. https://doi.org/10.1002/ps.5602

Wang, Y. H., Fang, G. Q., Xu, P. H., Gao, B. L., Liu, X. J., Qi, X. W., … Zhan, S. (2022). Behavioral and genomic divergence between a generalist and a specialist fly. *Cell Reports, 41*(7), 111654. https://doi.org/10.1016/j.celrep.2022.111654

Ward, C. M., Aumann, R. A., Whitehead, M. A., Nikolouli, K., Leveque, G., Gouvi, G., … Schetelig, M. F. (2021). White pupae phenotype of tephritids is caused by parallel mutations of a MFS transporter. *Nature Communications, 12*(1), 491. https://doi.org/10.1038/s41467-020-20680-5

Wee, S. L., & Tan, K. H. (2000). Sexual maturity and intraspecific mating success of two sibling species of the *Bactrocera dorsalis* complex. *Entomologia Experimentalis et Applicata, 94*(2), 133–139. https://doi.org/10.1046/j.1570-7458.2000.00613.x

Wee, S. L., & Tan, K. H. (2001). Allomonal and hepatotoxic effects following methyl eugenol consumption in *Bactrocera papayae* male against Gekko monarchus. *Journal of Chemical Ecology, 27*(5), 953–964. https://doi.org/10.1023/A:1010387020135

Wee, S. L., Hee, A. K. W., & Tan, K. H. (2002). Comparative sensitivity to and consumption of methyl eugenol in three *Bactrocera dorsalis* (Diptera: Tephritidae) complex sibling species. *Chemoecology, 12*(4), 193–197. https://doi.org/10.1007/PL00012668

Wee, S. L., & Rosli, N. Q. A. (2024). Evaluation of methyl eugenol-supplemented diet as pre-release treatment for simultaneous application of male annihilation and sterile insect techniques against *Bactrocera dorsalis*. *Journal of Pest Science*. https://doi.org/10.1007/s10340-024-01789-8

Wei, D., Dou, W., Jiang, M., & Wang, J. (2017). Oriental fruit fly *Bactrocera dorsalis* (Hendel). In F. H. Wan, M. Jiang, & A. Zhan (Eds.) *Biological invasions and its management in China* (pp. 267–283). Invading Nature – Springer Series in Invasion Ecology, vol 11. Springer, Dordrecht. https://doi.org/10.1007/978-94-024-0948-2_15

Wong, M. A., & Wong, T. (1988). Predation of the Mediterranean fruit fly and the Oriental fruit fly (Diptera: Tephritidae) by the fire ant (Hymenoptera: Formicidae) in Hawaii. *Proceedings of the Hawaiian Entomological Society, 28*, 169–177. Retrieved from http://hdl.handle.net/10125/11228

Wong, T. T. Y., McInnis, D. O., & Nishimoto, J. I. (1989). Relationship of sexual maturation rate to response of oriental fruit fly strains (Diptera: Tephritidae) to methyl eugenol. *Journal of Chemical Ecology, 15*(4), 1399–1405. https://doi.org/10.1007/BF01014839

Xu, J., Chen, S., Zeng, B., James, A. A., Tan, A., & Huang, Y. (2017). *Bombyx mori* P-element somatic inhibitor (BmPSI) is a key auxiliary factor for silkworm male sex determination. *PLOS Genetics, 13*(1), e1006576. https://doi.org/10.1371/journal.pgen.1006576

Xu, X., Bi, H., Wang, Y., Li, X., Xu, J., Liu, Z., … Huang, Y. (2020a). Disruption of the ovarian serine protease (*Osp*) gene causes female sterility in *Bombyx mori* and *Spodoptera litura. Pest Management Science, 76*(4), 1245–1255. https://doi.org/10.1002/ps.5634

Xu, X., Wang, Y., Bi, H., Xu, J., Liu, Z., Niu, C., … Huang, Y. (2020b). Mutation of the seminal protease gene, serine protease 2, results in male sterility in diverse lepidopterans. *Insect Biochemistry and Molecular Biology, 116*, 103243. https://doi.org/10.1016/j.ibmb.2019.103243

Yang, J., Zheng, L., Liao, Y., Fu, Y., Zeng, D., Chen, W., & Wu, W. (2023). HCN-induced embryo arrest: Passion fruit as an ecological trap for fruit flies. *Pest Management Science, 79*(6), 2172–2181. https://doi.org/10.1002/ps.7396

Zeng, Y., Reddy, G. V. P., Li, Z., Qin, Y., Wang, Y., Pan, X., … Zhao, Z. H. (2019). Global distribution and invasion pattern of oriental fruit fly, *Bactrocera dorsalis* (Diptera: Tephritidae).

Journal of Applied Entomology, 143(3), 165–176. https://doi.org/10.1111/jen.12582

Zhang, J., Liu, W., Chang, H., Wang, Q., Yuan, J., Liu, L., … Wang, G. (2024). Methyl eugenol regulates mating behavior in oriental fruit flies by enhancing lek attractiveness. *National Science Review,* nwae294. https://doi.org/10.1093/nsr/nwae294

Zhang, Y., Liu, S. L., De Meyer, M., Liao, Z. X., Zhao, Y., Virgilio, M., … Li, Z. H. (2023). Genomes of the cosmopolitan fruit pest *Bactrocera dorsalis* (Diptera: Tephritidae) reveal its global invasion history and thermal adaptation. *Journal of Advanced Research, 53*, 61–74. https://doi.org/10.1016/j.jare.2022.12.012

Zhao, J., Li, S., Xu, L., Li, C., Li, Q., Dewer, Y., & Wu, K. (2022). Effects of X-ray irradiation on biological parameters and induced sterility of *Ephestia elutella*: Establishing the optimum irradiation dose and stage. *Frontiers in Physiology, 13*, 895882. https://doi.org/10.3389/fphys.2022.895882

Zhao, Z. H., Carey, J. R., & Li, Z. H. (2024). The global epidemic of *Bactrocera* pests: Mixed-species invasions and risk assessment. *Annual Review of Entomology, 69*(1), 219–237. https://doi.org/10.1146/annurev-ento-012723-102658

Zhao, Z. H., Hui, C., Peng, S., Yi, S., Li, Z., Reddy, G. V. P., & van Kleunen, M. (2023). The world's 100 worst invasive alien insect species differ in their characteristics from related non-invasive species. *Journal of Applied Ecology, 60*(9), 1929–1938. https://doi.org/10.1111/1365-2664.14485

Zheng, W., Zhu, C., Peng, T., & Zhang, H. (2012). *Odorant receptor co-receptor Orco* is upregulated by methyl eugenol in male *Bactrocera dorsalis* (Diptera: Tephritidae). *Journal of Insect Physiology, 58*(8), 1122–1127. https://doi.org/10.1016/j.jinsphys.2012.05.011

Zheng, Y., Song, Z.-W., Zhang, Y.-P., & Li, D.-S. (2021). Ability of *Spalangia endius* (Hymenoptera: Pteromalidae) to parasitize *Bactrocera dorsalis* (Diptera: Tephritidae) after switching hosts. *Insects, 12*(7), 613. https://doi.org/10.3390/insects12070613

Zhou, X. W., Niu, C. Y., Han, P., & Desneux, N. (2012). Field evaluation of attractive lures for the fruit fly *Bactrocera minax* (Diptera: Tephritidae) and their potential use in spot sprays in Hubei Province (China). *Journal of Economic Entomology, 105*(4), 1277–1284. https://doi.org/10.1603/EC12020

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Questionnaire Form on IPM of *Bactrocera dorsalis*