Understanding Invasion, Ecological Adaptations, Management of Bactrocera dorsalis

Subjects: Entomology

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Bactrocera dorsalis (Hendel, 1912) (Diptera: Tephritidae), commonly known as the oriental fruit fly, is a highly destructive pest that globally infests fruits and vegetables, resulting in significant annual economic losses. Initially detected in Taiwan Island, it has rapidly expanded its distribution range to various regions in mainland China since the 1980s, with a continuous northward spread. To mitigate the damage caused by this pest, extensive efforts have been undertaken to comprehend its ecological and physiological adaptations and develop management strategies.

Keywords: *B. dorsalis* ; oriental fruit fly ; pest management ; fruit fly ; Invasion and dispersion ; tolerance ; risistance

1. Introduction

Tephritid fruit flies are an economically significant pest species globally, including mainland China [1]. They exhibit endophagous feeding behavior, which causes both quantitative and qualitative yield reductions. As a result, they pose significant threats to global fruit and vegetable production [2][3]. The pest affects a broad array of fruit and fleshy vegetable crops in tropical and subtropical regions. The presence of these pests was first observed in Taiwan Island, China, in 1912 [4][5]. The genus *Bactrocera*, which comprises a minimum of 440 species [6], is primarily distributed throughout tropical Asia, Australia, and the South Pacific [7][8]. The wide host range, great climate tolerance, and strong dispersing capacities of these species have led to their spread over the Asia Pacific region in the last century, covering all of South-East Asia from India to Hawaii [7]. The oriental fruit fly, *Bactrocera dorsalis* (Hendel) (Diptera: Tephritidae), is recognized as a destructive and persistent fruit fly pest. *B. dorsalis* has been documented to infest over 250 host plant species [9][10], including mango (*Mangifera indica* L., Anacardiaceae), banana (*Musa* spp., Musaceae), guava (*Psidium guajava* L., Myrtaceae), orange (*Citrus* spp., Rutaceae), papaya (*Carica papaya* L., Caricaceae), peach (*Prunus persica* (L.) Batsch, Rosaceae), grape (*Vitis* spp., Vitaceae), pomegranate (*Punica granatum* L., Lythraceae), lychee (*Litchi chinensis* Sonn., Sapindaceae), and longan (*Dimocarpus longan* Lour., Sapindaceae) [11][12]. Numerous studies have documented the economic damage caused by *B. dorsalis*. For instance, a study carried out in Thailand found that *B. dorsalis* infestation in mango farms caused an average annual yield loss of 15.5% [13]. Similarly, in India, fruit fly infestation led to a reduction in the marketable yield of mango by 25–30% [14]. According to an estimate, guava, sapota, citrus fruits, and mango in India, incurred losses equivalent to USD 356 million [15]. This significant economic loss is attributed to the fruit damage caused by *B. dorsalis*, which can affect 30% to 100% of fruits, depending on the season [16].

In addition to yield reduction, *B. dorsalis* also leads to the quality degradation of fruits, causing phytosanitary issues and triggering trade restrictions, thereby aggravating economic losses. A study conducted in Taiwan revealed that the infestation of fruit flies resulted in trade restrictions on the export of guava to the United States and Japan, leading to an estimated economic loss of USD 2.5 million per year [17]. These studies demonstrate the substantial economic losses caused by *B. dorsalis* and emphasize the necessity for implementing effective management strategies to mitigate the impact of this insect pest on horticultural crops. In China, the economic losses caused by the fruit fly pest species in citrus orchards have been widely reported, especially in Guangdong [18] and Fujian Provinces of China [1]. *B. dorsalis* exhibits three to eleven generations per year in China, with the majority of areas experiencing four to eight generations [8][19]. In the near future, there is the potential for *B. dorsalis* to expand into temperate northern and southern areas of China [20] (**Figure 1**).

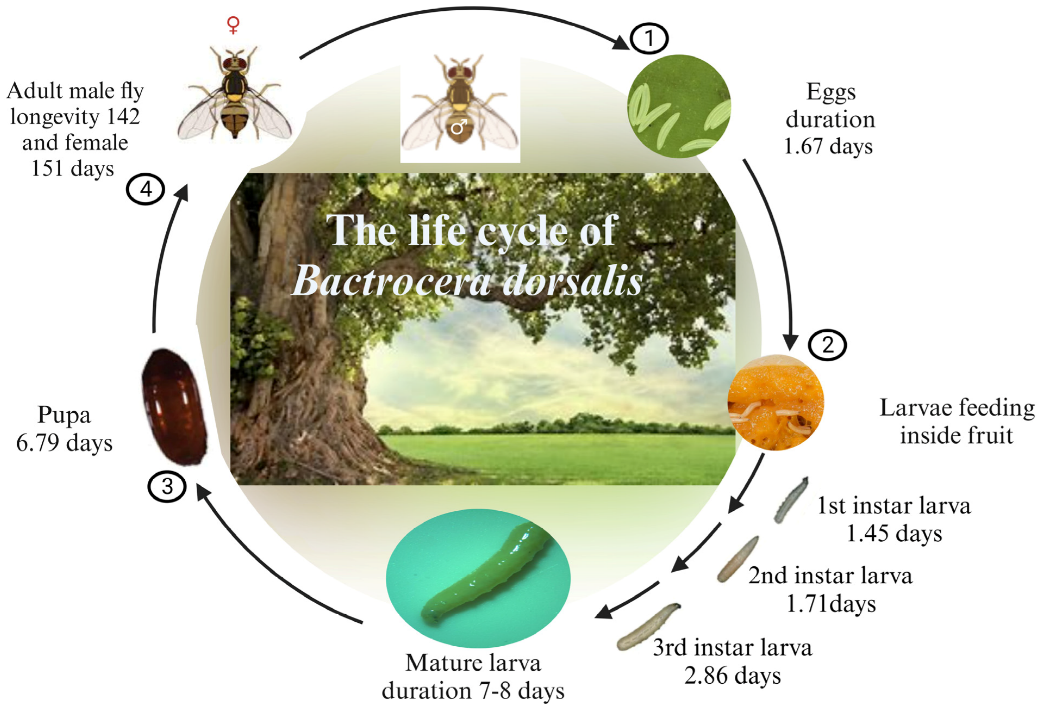

Figure 1. The life cycle of *B. dorsalis*.

2. Pest Management of *Bactrocera dorsalis*

2.1. Mass Trapping

B. dorsalis could be mass-trapped using pheromone and food-based baits. Various pheromones and scent-based compounds, including synthetic para-pheromones or male lures such as methyl eugenol (ME), have been developed to attract and control *B. dorsalis.* These compounds mimic the natural pheromones produced by melon and oriental fruit flies. These pheromones are used to attract and trap male flies, allowing for population monitoring and infestation assessment [21]. E-coniferyl alcohol (E-CF) has also been found to be effective in attracting female *B. dorsalis* [22]. A comprehensive investigation on current resistance and lure tolerance to fruit flies [23] assessed the response of *B. dorsalis* males to non-ME lures. The experiment evaluated the mating and lure response of non-ME-responding (NMR) and non-responding lines (NRLs) of *B. dorsalis* males. Results showed that NMR males had higher mating success rates compared to NRL males and exhibited a greater attraction to non-ME lures, which have been implicated in the development of tolerance mechanisms among *B. dorsalis* populations [23][24].

Another research revealed that *B. dorsalis* causes significant economic losses in the fruit and vegetable industry by laying eggs inside hosts. Chemical controls are not very effective due to the pest's cryptic feeding habits, strong flight ability, and resistance to insecticides. Olfaction-based trapping using ME has been the most cost-effective tool for monitoring and controlling *B. dorsalis* populations for seven decades [22][25]. However, laboratory selection for ME responsiveness has resulted in the non-responsiveness of *B. dorsalis*, which may lead to the recolonization of the pest in some areas [26]. The study aimed to determine the levels of ME responsiveness in *B. dorsalis* field populations in China [23][24]. Results showed that the field populations had lower ME sensitivity compared to the susceptible strain, possibly due to odorant binding protein (BdorOBP2, BdorOBP83b), and P450 gene expressions in olfactory organs [24]. Protein-based baits and food odors, such as yeast, vinegar, and fermentation products, can also attract both male and female oriental fruit flies. These baits can be combined with pheromones to increase trap efficacy [27]. Visual attractants, such as brightly colored sticky traps, can also be used to attract oriental fruit flies, and they can complement other attractants for a more comprehensive monitoring and control approach [28][29]. It is important to note that attractants can be species-specific, and the most effective ones for *B. dorsalis* may vary based on environmental conditions and other factors. Following are the steps involved in bait-based physical control techniques for managing *B. dorsalis* infestations: (a) Monitoring: It includes observations and record-keeping of the presence, distribution, and abundance of *B. dorsalis* in affected areas. (b) Selection of bait material: It includes selection of appropriate bait material, such as food-based baits (fishmeal or yeast hydrolysates, ME, raspberry ketone, cue lure, honey, or molasses) that have been successful in attracting fruit fly species. (c) Formulation of bait: It includes formulating the selected bait material into an attractive and easily dispersible form by adding a food-grade preservative for shelf-life extension and a hydroscopic agent to maintain its moisture content. (d) Deployment of baits: It involves deployment of the baits using various methods, including bait stations, bait trees, or spray applications, depending on the specific circumstances of each situation. (e) Collection and disposal of captured fruit flies:

It involves regular monitoring to assess the effectiveness of the bait and removing and disposing of captured fruit flies to prevent escape and further spread. (f) Evaluation: It includes assessing the success of the bait-based physical control technique by monitoring oriental fruit fly population levels over time and comparing pre- and post-treatment populations to determine the reduction in the number of fruit flies.

2.2. Biological Control

Parasitoids, hymenopteran wasps, lay their eggs inside hosts, consuming them from the inside and leading to their death. *Fopius arisanus* (Sonan), a species of egg parasitoid, targets *B. dorsalis* [8]. As a potential biological control agent, *F. arisanus* effectively parasitizes the host eggs and reduces the pest population [30]. It is well-adapted to tropical and subtropical environments, distributed throughout Asia, Africa, and the Pacific region [31]. Utilizing *F. arisanus* offers advantages over chemical pest control, including specificity to the target pest, conservation of beneficial insects, and long-term sustainability [32]. In order to effectively utilize *F. arisanus* for biological control, it is important to understand its biology, behavior, and life cycle, as well as its interactions with the host and other factors that may affect its efficacy. Researchers have also developed mass rearing for *F. arisanus* to produce large numbers of individuals for release into the field. *F. arisanus* is a promising biological control agent for the oriental fruit fly, offering a sustainable and environmentally friendly approach to managing this destructive pest [33]. Another parasitoid, *Spalangia endius* (Walker) (Hymenoptera: Pteromalidae) is a solitary endoparasitoid that attacks fruit fly pupae, including *B. dorsalis.* This wasp lays its eggs inside the pupae, and the emerging larvae consume the host pupae from within, killing the fruit fly [34]. Using *S. endius* for the biological control of *B. dorsalis* has advantages over other methods. It is highly specific in targeting fruit fly pests and does not harm beneficial insects. Field trials have shown that this parasitoid can effectively reduce the number of *B. dorsalis* adults, thereby minimizing crop damage [35][36]. To effectively use *S. endius* for biological control, understanding the biology and behavior of both the wasp and the fruit fly is crucial. The timing of wasp releases is critical in achieving maximum parasitism rates. In general, releases should coincide with the emergence of fruit fly pupae, which is the stage at which *S. endius* lays its eggs. Releasing large numbers of parasitoids can help control fruit fly populations in a targeted area [37][38] (**Table 1**). Viruses, bacteria, and fungi can also infect and be lethal to the fruit fly adult and larvae [39]. Among the pathogens studied for use against *B. dorsalis*, viruses, especially baculoviruses, have been found to be highly virulent to fruit fly species. They have demonstrated effectiveness in reducing fruit fly populations in both laboratory and field studies.

Baculoviruses are insect-specific viruses that replicate within the insect host and cause death. Among the baculovirus isolates identified and characterized, the nuclear polyhedrosis virus (NPV) has been found to be highly virulent to several insect species [40][41]. NPV studies have demonstrated its ability to reduce the number of fruit fly individuals in laboratory and field settings, thereby decreasing the damage caused by this pest. Moreover, NPV is safe for the environment and non-target organisms, making it a promising option for fruit fly management [42]. However, it is important to note that using pathogenic microorganisms, including viruses, for insect pest management is still in its early stages, and more research is needed to fully understand their potential and limitations. Baculoviruses, particularly NPV, have shown potential for controlling *B. dorsalis*, and further research is needed to integrate them into pest management programs effectively. The entomophagous fungus *Beauveria bassiana* (Sordariomycetes: Clavicipitaceae) is an entomopathogenic fungus that is known to be an effective biological control agent against *B. cucurbitae*. This fungus infects the insects and causes mortality [43]. In China, *B. bassiana* effectively controlled *B. dorsalis*, achieving a mortality rate of over 80% in laboratory experiments. Similarly, another study showed that *B. bassiana* effectively reduced the population density of *B. dorsalis* in the field [44][45]. *B. bassiana* can be used as a biological control agent in several ways: (1) Inoculative releases: This involves releasing large numbers of fungal spores (conidia) into the environment, which then infect the insects. This approach is most effective when used in conjunction with other management strategies, such as the use of pheromones or host-plant resistance. (2) Injection or spraying: This process involves injecting or spraying a suspension of conidia directly onto the insects, causing them to become infected. (3) Formulations: *B. bassiana* can also be formulated into granules or dusts that can be applied to the host plants or environment, where they will encounter the insects. The entomopathogenic bacterium *Bacillus thuringiensis* (Bt) is a naturally occurring soil bacterium that produces a toxic crystal protein effective against many insect pests, including *B. dorsalis* [46]. Entomopathogenic nematodes are parasitic roundworms that can infect and kill fruit fly larvae [47]. Further research and understanding of biology will improve their integration into pest management programs (**Table 1**).

Table 1. Natural enemies *of B. dorsalis*.

Bio-Control Agents	Name of Species	Host Stages	Reference
Predator	*Oecophylla longinoda*	Pupa/larva	[48]
	Pachycrepoideus vindemmiae	Larva/pupa	[49]

Bio-Control Agents	Name of Species	Host Stages	Reference
Parasitoids	***Fopius arisanus***	**Egg**	[50]
	Psyttalia cosyrae	**Larva-pupal**	[51]
	Diachasmimorpha longicaudata	**Larva**	[51]
Nematodes	***Heterorhabditis taysearae***	**Larva/pupa**	[49]
	H. indica	**Larva/pupa**	[52]
	***Steinernema* sp**	**Larva/pupa**	[53]

2.3. Sterile Insect Technique (SIT)

The sterile insect technique is a promising biological control for *Bactrocera* species, with a proven track record of success in various countries worldwide. It is a sustainable and eco-friendly method of pest management that complements other control strategies, providing long-term control of this economically important insect pest. The technique has been used for decades to manage various insect pests, including *B. dorsalis*, commonly known as the oriental fruit fly. SIT involves mass-rearing and sterilization of male insects, which are then released into the wild to mate with females. Mating with sterilized males leads to the laying of eggs by female insects that do not hatch, ultimately leading to a decline in the pest population [8][54]. This technique was first employed in the 1950s to control the screwworm, *Cochliomyia hominivorax*, in the southern United States and has since been effectively utilized against various other insect pests worldwide. Fruit flies, including *B. dorsalis*, have been successfully managed using SIT in several countries, such as China, Australia, and Hawaii [55][56]. For instance, in Hawaii, SIT was implemented in the early 2000s to manage oriental fruit fly outbreaks in the state's agriculture industry. The program's success resulted in a significant decline in the pest population [57]. In Australia, SIT has been incorporated into integrated pest management to control Mediterranean fruit fly *C. capitata* populations in the country's horticulture industry [58]. The genetic sexing strain is a technique utilized to manipulate the sex ratios of a population, leading to more effective and efficient pest management. It has been successfully applied worldwide, including China, to manage *B. dorsalis*. This technique employs a genetic marker to distinguish between male and female fruit flies. By releasing only sterilized males into the environment, the population growth of the pest can be suppressed without the need for chemical insecticides [59].

In China, researchers have developed a genetic sexing strain for *B. dorsalis* using the temperature-sensitive lethal (tsl) mutation. This mutation causes the death of females at a certain temperature, enabling the separation of male and female fruit flies [60]. The genetic sexing strain has been proven effective in suppressing the population growth of several fruit fly species in field trials [61]. This technique has also been applied to manage fruit flies in other countries, including Australia and Thailand [13][58][62][63]. These studies demonstrate the potential of the genetic sexing strain as an integrated pest management tool for managing tephritid fruit flies.

2.4. Molecular Control

The management of *B. dorsalis* is challenging due to its high resistance to insecticides. To overcome this challenge, it is crucial to identify new targets for insect pest control. Transient receptor potential (TRP) channels play a crucial role in various physiological processes in insects, including nociception, thermo-sensation, and olfaction [64][65]. In recent years, there have been extensive studies on the identification and characterization of TRP channels in various insect species, including *B. dorsalis*. In one study [65], 15 TRP channel genes were identified in the genome of *B. dorsalis*. The expression patterns of these genes were analyzed in different tissues, such as the antennae, brain, midgut, Malpighian tubules, and fat body. The results revealed that TRP channels were differentially expressed across various tissues, with some TRP genes being predominantly expressed in specific tissues. Additionally, another study [66] investigated the role of TRP channels in insecticide resistance in insects. They used RNA interference (RNAi) to knock down the expression of TRP channels in *B. dorsalis*. The findings showed that knockdown of TRP channels significantly reduced insecticide resistance in *B. dorsalis*, suggesting the potential utilization of TRP channels as targets for insect pest control [67][68]. The identification, characterization, and expression analysis of TRP channel genes in the oriental fruit fly will provide crucial information for the development of new and effective strategies for the management and control of this pest.

2.5. RNA Interference (RNAi)

RNA interference (RNAi) is a highly effective technique for gene silencing through the use of double-stranded RNA (dsRNA) [69]. It has shown promise in knocking down insect pests as a more environmentally friendly option. Previous studies have demonstrated successful silencing of genes rpl19, v-ATPase-D, noa, and rab11 in adult *B. dorsalis* through the feeding of corresponding dsRNA. Other potential target genes involved in midgut digestion and detoxification have also been identified [70][71]. However, using RNAi for controlling the oriental fruit fly faces challenges, including effectively delivering dsRNA to the insect and potential risks to non-target organisms. The delivery of dsRNA has not been fully implemented yet, and the possible impacts on non-target organisms and host fruits and vegetables must be carefully considered. There is a risk of reducing the expression of genes in natural enemies and other beneficial insects due to the high similarity in rpl19 sequences between these insects and *B. dorsalis*. Therefore, minimizing the impact of dsRNA on non-target insects and host fruits and vegetables is a priority in ongoing efforts to use RNAi for controlling *B. dorsalis*. In a research article addressing the problem of insecticide resistance in *B. dorsalis*, a global pest affecting various crops, researchers focused on the role of UDP-glycosyltransferases (UGTs) in resistance development [72]. These enzymes are involved in metabolically processing both plant secondary metabolites and synthetic insecticides. The study identified 31 UGT genes in the genome of *B. dorsalis*, with 12 of them highly expressed in key tissues such as the antennae, midgut, Malpighian tubules, and fat body. Furthermore, exposure to four different insecticides caused a significant upregulation of 17 UGT genes. To investigate further, RNA interference was used to knock down five selected UGT genes, resulting in reduced oriental fruit fly mortality in response to insecticides from 9.29% to 27.22% [73].

2.6. CRISPR-Cas9

The clustered regularly interspaced palindromic repeat (CRISPR-Cas9) system is a revolutionary tool for precise and efficient genome editing in various organisms [74]. In a study of *B. dorsalis*, researchers targeted a specific gene known as the Sex Peptide Receptor (*Bdspr*) using CRISPR/Cas9 technology [75]. The *Bdspr* gene plays a critical role in the regulation of female reproduction, including ovary development and egg laying. By introducing mutations into this gene, the researchers aimed to examine its effects on female fecundity and reproductive functions in *B. dorsalis*. Several research experiments showed that CRISPR/Cas9-mediated disruption of the *Bdspr* gene, when the insects were fed with the ds-spr gene, led to significant changes in the number and size of ovarioles, a reduction in the number of eggs laid, and a decrease in overall female fecundity. This indicated the importance of the *Bdspr* gene in the normal functioning of the female reproductive system in *B. dorsalis*. The study also demonstrated that the CRISPR/Cas9 system is an effective tool for studying gene function and disrupting specific genes in insects. In the future, this information could potentially be used to develop new strategies for controlling the population of oriental fruit flies, a major agricultural pest causing significant damage to crops worldwide [75][76][77][78]. The CRISPR/Cas9-induced mutation of the *Bdspr* gene in the oriental fruit fly underscores the significance of this gene in female reproduction and highlights the potential of genome editing technology for advancing the field of insect pest management.

In another study focused on understanding the functional role of the white gene in pigmentation in *B. dorsalis*, the white gene was cloned, and knockout strains were created using the CRISPR/Cas9 genome editing system. The results revealed that the mutants lost pigmentation in the compound eye and their head spots. Further analysis using quantitative reverse-transcription PCR showed lower expression levels of the Bd-yellow1 gene in the head of mutants compared to the wild-type strain, while there were no significant differences in the expression of the other six genes. As the yellow gene is crucial for melanin biosynthesis, the reduced expression of Bd-yellow1 in mutants led to a decrease in dark pigmentation in the head spots. This study provides evidence for the first time that the white gene may play a role in cuticle pigmentation by affecting the expression of the yellow gene [79].

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