Physical Education, Health and Social Sciences

https://journal-of-social-education.org

E-ISSN: 2958-5996

P-ISSN: 2958-5988

Behavioral Ecology and Integrated Management of Fruit Flies (Bactrocera spp.) in Horticultural Crops

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DOI: https://doi.org/10.63163/jpehss.v4i1.1207

Abstract

The genus *Bactrocera* comprises some of the most economically damaging fruit fly pests worldwide, inflicting billions in losses to horticultural crops through direct damage and trade restrictions. This review synthesizes current knowledge on the behavioral ecology and integrated management of *Bactrocera* species, including B. dorsalis, B. *zonata*, and B. *oleae*. It explores their taxonomic complexities, invasion biology, life history traits, and sensory driven behaviors such as visual and olfactory host seeking, pheromone-mediated reproduction, and oviposition preferences influenced by host cues and environmental factors. Economic impacts are detailed across regions, with emphasis on demographic parameters like high reproductive rates and host suitability metrics. Management strategies are evaluated, encompassing cultural practices (sanitation and fruit bagging), push-pull techniques, male annihilation (MAT), sterile insect technique (SIT), and emerging genetic tools like CRISPR-Cas9. Regulatory frameworks under IPPC and EPPO are discussed for quarantine and pest-free areas. The review advocates for climate-smart, area-wide IPM to mitigate invasions and promote sustainable horticulture, highlighting the need for interdisciplinary approaches to counter these adaptive pests.

Keywords: Bactrocera; Fruit Flies; Behavioral Ecology; Integrated Pest Management; Invasion Biology; Semiochemicals; Sterile Insect Technique; CRISPR-Cas9; Host Preference; Economic Impact

Introduction

The global horticulture sector faces an unprecedented challenge from dipterous insects within the family Tephritidae, specifically those belonging to the genus Bactrocera Macquart. These organisms represent some of the most invasive and economically damaging pests in the world, threatening food security and international trade systems (Wan, 2025). Species such as the oriental fruit fly (Bactrocera dorsalis), the peach fruit fly (Bactrocera zonata), and the olive fruit fly

(Bactrocera oleae) possess biological traits that allow them to exploit a vast array of host plants across diverse ecological zones (Ouguas et al., 2025). The economic implications are vast, with potential losses to the citrus industry in China alone estimated at USD 40 billion for B. dorsalis and USD 14 billion for B. correcta (Ullah et al., 2023).

Economic Significance and Global Impact Patterns

The genus Bactrocera is of paramount importance due to the magnitude of direct and indirect damage it inflicts on commercial fruit and vegetable production. Direct damage occurs when female flies puncture the fruit skin to oviposit, followed by larval feeding on the pulp, which leads to internal decay, premature fruit drop, and total crop loss (Amin et al., 2025). Indirect costs arise from the stringent quarantine regulations imposed by importing countries, which often require expensive phytosanitary treatments or result in total trade bans (Hossain et al., 2019).

In tropical and subtropical regions, the impact is particularly severe due to the year-round availability of host plants and favorable climatic conditions. In Pakistan, the annual financial losses associated with Bactrocera infestations are estimated at USD 200 million (Ashfaq et al., 2020). In Egypt and the Near East, the figures reach EUR 190 million and EUR 320 million, respectively. In the United States, the establishment of the Mediterranean fruit fly (a related tephritid) would cause estimated annual losses of USD 1.3 billion to USD 1.8 billion, underscoring the high stakes of managing Bactrocera incursions in fruit-producing states like California and Florida (Papadopoulos et al., 2024).

Table No. 1 Estimated Economic Losses Caused by Major Fruit Fly Species in Key Agricultural Regions

Region	Species	Crop	Economic Impact / Loss Metric
China	Bactrocera dorsalis	Citrus	Estimated potential loss: USD 40 billion
California, USA	Tephritid Complex	Multiple	Estimated annual loss: USD 1.3 - 1.8 billion
Global	Bactrocera oleae	Olive	Estimated annual loss: USD 800 million
Pakistan	Bactrocera zonata	Guava / Peach	Estimated annual loss: USD 200 million
Florida, USA	Bactrocera dorsalis	Mixed Fruit	Outbreak impact: USD 10.2 - 58.5 million
West Java, Indonesia	Bactrocera spp.	Mango / Guava	Yield loss range: 40% to 70%

Taxonomic Architecture and Invasion Biology

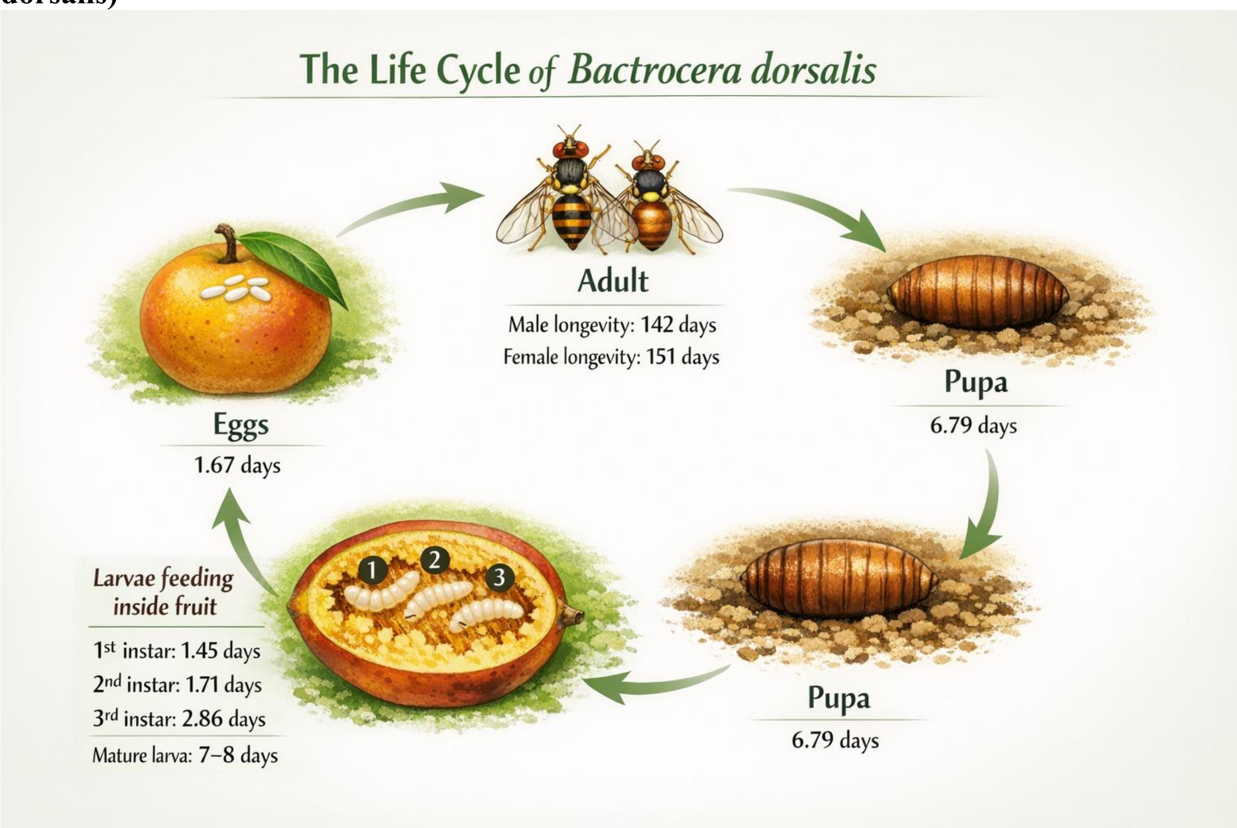
The taxonomy of Bactrocera is characterized by complex species groups, often requiring integrative taxonomic approaches for accurate identification. The Bactrocera dorsalis complex is the most notable, formerly comprising over 70 described species that were later consolidated as the research community recognized high degrees of morphological and genetic overlap (Drew et al., 2022). For example, Bactrocera invadens, which caused widespread devastation in Africa after its detection in Kenya in 2003, and Bactrocera papayae in Southeast Asia, are now recognized as synonymous with B. dorsalis (Wang et al., 2024).

Invasion biology plays a critical role in the global spread of these pests. The "bridgehead effect" describes a scenario where a newly invaded region serves as the source for subsequent secondary introductions, effectively accelerating the rate of global expansion (Blumenfeld et al., 2021). The speed and scale of these invasions are unprecedented, driven by the increasing volume of transcontinental trade and the movement of infested produce. Bactrocera dorsalis has invaded at least 70 countries, while B. oleae is present in over 34, demonstrating the genus's capacity to adapt to diverse climates ranging from Mediterranean to tropical zones (Jaffar et al., 2023).

Life History and Demographic Parameters

The success of Bactrocera species is largely attributed to their high reproductive potential and plastic life-history traits. A comprehensive understanding of developmental parameters is essential for predicting population outbreaks and designing management schedules (Rahman et al., 2023). For Bactrocera latifrons, a major pest of solanaceous crops, the generation time is relatively short, allowing for rapid population build-up under favorable conditions (Amin et al., 2025).

Figure 1: The Developmental Stages and Longevity of the Oriental Fruit Fly (Bactrocera dorsalis)



The developmental duration of B. latifrons on eggplant highlights the efficiency of its life cycle. The intrinsic rate of increase (r) for this species is 0.097 per day, with a net reproductive rate (R0) of 73.4. This high R0 indicates that a single female can significantly contribute to the next generation, making early detection critical. The average lifespan of adults, exceeding 100 days for both sexes, further extends the window for mating and oviposition (Amin et al., 2025).

Table No. 2 Stage-Wise Developmental Period, Survival, and Adult Longevity of the Fruit Fly

Development Stage	Duration (Days)	Survival / Success Rate (%)
Egg Stage	4.3 plus/minus 0.1	96% (Hatching)
Larval Stage	11.3 plus/minus 0.2	88% (Survival)
Pupal Stage	9.3 plus/minus 0.1	84% (Emergence)

Adult Female Lifespan	101.0 plus/minus 5.4	N/A
Adult Male Lifespan	102.0 plus/minus 4.8	N/A
Average Generation Time	43.96	N/A

For polyphagous species like B. dorsalis, the Host Reproduction Number (HRN) provides a metric for host suitability, defined as the number of adults emerged per kilogram of fruit (Wan, 2025). This metric varies widely across its vast host range, which includes over 613 plant species. High HRN values are observed in "very good" hosts like Terminalia catappa (tropical almond) and Psidium guajava (guava), while others like Citrus species may serve as "moderately good" or "poor" hosts depending on the variety and region (Chawla, 2022).

Behavioral Ecology: Sensory Perception and Host Seeking

Bactrocera species utilize a sophisticated array of visual, olfactory, and contact cues to navigate their environment, locate hosts, and find mates. This sensory ecology is exploited in the development of monitoring and management tools (Ouguas et al., 2025).

Visual Stimuli and Attraction

Visual cues are primary drivers of long-range attraction and short-range host acceptance. Studies on colored traps have revealed significant preferences among different Bactrocera species. In experiments using open pans, white and yellow colors were found to be most attractive to B. dorsalis, B. correcta, and B. zonata (Mohd Nor et al., 2018). Recent advancements have shown that ultraviolet (UV) and green stimuli enhance the attractiveness of colored traps for B. dorsalis, suggesting that light wavelength specifically modulates behavioral responses (Zhang & Liu, 2025).

Olfactory Ecology and Kairomones

Olfaction is perhaps the most critical sense for host selection. Female fruit flies detect Volatile Organic Compounds (VOCs) emitted by ripening fruits. In Bactrocera oleae, the attraction to olive fruits is mediated by specific compounds such as alpha-pinene, limonene, and nonanal (Giunti et al., 2020). Interestingly, the responsiveness to these compounds is highly temperature-dependent. Peak landings and egg production in B. oleae occur at 30 degrees Celsius, while activity effectively ceases at extreme temperatures of 15 degrees Celsius and 35 degrees Celsius (Kokkari et al., 2024). The relationship between fruit volatiles and physiology is profound. For B. oleae, exposure to certain VOCs favors ovarian maturation, meaning the fruit itself acts as a chemical signal that prepares the female for reproduction (Ogah et al., 2025). Similarly, in B. latifrons, the preference for Capsicum species over Solanum is believed to be influenced by total phenolic content and specific volatile profiles that signal host quality for larval development (Mohd Nor et al., 2018).

Reproductive Behavior and Chemical Ecology

Reproduction in Bactrocera involves complex social interactions, including lekking and pheromone-mediated communication. These behaviors often exhibit distinct circadian rhythms (Zhang & Liu, 2025).

Mating Rhythms and Pheromone Synthesis

Mating activity in many species, such as B. correcta and B. dorsalis, occurs primarily at dusk. During this period, males engage in wing fanning, which aids in the dispersal of pheromones and the production of a high pitched buzzing sound (Clark, 2024). The pheromonal chemistry of Bactrocera is unique; males of many species sequester chemicals from the environment specifically methyl eugenol (ME) or cue-lure (CL) and convert them into components of their sex pheromones. This sequestration not only attracts females but also enhances the male's competitive advantage in leks. (Muhammad et al., 2024).

The perception of these chemicals is mediated by specific proteins. In B. dorsalis, an odorant binding protein (BdorOBP56f-2) is critical for detecting methyl eugenol; disruptions to the gene encoding this protein significantly impair foraging and mating behaviors. This highlights a potential vulnerability that can be exploited through genetic or behavioral interference (Chen et al., 3021)

Lekking and Competitive Interaction

Lekking behavior involves males aggregating on host or non-host plants to display. In these aggregations, visual characteristics and physical displays are vital for female acceptance (Shelly, 2024) Research comparing wild, sterile, and mass reared males has shown that while mass reared males may display more frequent mounting behavior toward other males, their overall mating success in competitive environments can be comparable to wild flies, provided that rearing and sterilization protocols are optimized (Parker et al., 2021).

Host Selection and Oviposition Preference

The selection of an oviposition site is a critical decision that directly impacts offspring fitness. This is governed by the "preference-performance hypothesis," which suggests that females will choose hosts that maximize larval survival and growth (Amin et al., 2025).

Host Specificity and Preference Hierarchies

While many Bactrocera species are polyphagous, they exhibit clear hierarchies in host preference. In laboratory choice tests, B. dorsalis consistently preferred mango and papaya over guava, although guava is often heavily invested in the field due to its high abundance and susceptibility (Mohd Nor et al., 2018). In solanaceous crops, B. latifrons favors bird chili and banana pepper, while turkey berry (Solanum torvum) is the least preferred host (Rattanapun et al., 2021).

The physical characteristics of the fruit, such as hardness, firmness, and skin thickness, are crucial. Bactrocera latifrons infestations are higher in overripe eggplants that have turned yellow, as the fruit structure becomes easier to penetrate. For B. dorsalis, fruit characteristics like chewiness and gumminess are also evaluated by the female before committing to oviposition (Theron et al., 2023).

Table No. 3 Host Preference and Primary Attraction Cues of Economically Important Tephritid Fruit Fly Species

Pest Species	Highly Preferred Hosts	Least Preferred / Non-Hosts	Primary Cues
Bactrocera dorsalis	Mango, Guava, Tropical Almond	Zucchini, Bitter Gourd	ME-like volatiles, fruit firmness
Bactrocera latifrons	Bird Chili, Banana Pepper	Turkey Berry	Solanaceous VOCs, phenolic content
Bactrocera zonata	Banana, Orange, Peach	Pumpkin, Apple	ME-like volatiles, sugar content
Zeugodacus cucurbitae	Sponge Gourd, Bitter Gourd	Pumpkin, Orange	Cue-lure, cucurbitacin signals
Bactrocera carambolae	Starfruit	Papaya	Host-specific VOCs

The Role of Temperature and Ripening

Temperature significantly influences host suitability. For B. carambolae and B. papayae (dorsalis), seasonal variations in host availability and climate create shifting windows of dominance. High temperatures can accelerate fruit ripening, increasing the emission of VOCs and the vulnerability of the fruit skin, and thereby attracting higher densities of fruit flies (Ouguas et al., 2025). Conversely, extreme heat can lead to fruit abortion and a subsequent crash in the local fly population (Wan, 2025).

Integrated Management: Conventional and Cultural Tactics

The management of Bactrocera species requires a multifaceted approach that minimizes reliance on synthetic insecticides while maintaining economic thresholds (Maqsood et al., 2025).

Field Sanitation and Cultural Control

Sanitation is the first line of defense in any IPM program. It involves the systematic removal and destruction of fallen and infested fruits to break the pest's life cycle. Larvae in infested fruit typically drop to the soil to pupate; by collecting these fruits and burying them deep (at least 10 to 12 inches) or treating them with heat, growers can significantly reduce the next generation's population (Singh et al., 2023).

Physical Barriers: The Role of Fruit Bagging

Fruit bagging is a physical exclusion technique that has shown remarkable efficacy, particularly for high-value crops like mango and apple. In Bangladesh, bagging mangoes with double-layer brown paper bags 42 days before harvest reduced B. dorsalis infestation to zero (Hossain et al., 2019). Beyond pest protection, bagging also improves fruit quality by managing surface temperature, moisture, and sunlight, leading to better skin color and reduced mechanical damage (Ali et al., 2021).

Table No. 4 Comparative Assessment of Bagging Materials on Infestation Levels, Physicochemical Fruit Quality, and Benefit Cost Ratio

Bagging Material	Impact on Infestation	Impact on Fruit Quality	Economic Benefit
Double-layer Brown Paper	Reduced to 0%	Best skin color, high market price	2x BCR vs. Pesticides
Non-woven Fabric	Minimum infestation (2.13%)	Highest Ascorbic Acid, high TSS	High durability
Polythene Bags	Significant reduction	Risk of high moisture / rot	Low cost
Cloth Bags	Moderate protection	Natural ventilation	Reusable

The economic return from bagging can be nearly twice as high as conventional pesticide management, despite the high labor costs associated with bag application. In organic production systems, bagging is often the only viable method for achieving zero-infestation levels required for export markets (Ignacio et al., 2023).

Push-Pull Strategy and Repellent Plants

An innovative behavioral management approach is the push-pull strategy, which utilizes chemical and visual signals to divert pests away from the main crop. In tomato cultivation, lemongrass (Cymbopogon nardus) acts as a repellent ("push") while basil (Ocimum basilicum) and yellow sticky traps serve as attractants ("pull") (Siddiqui et al., 2017). Lemongrass can suppress fruit fly populations by 40% to 60%, providing a sustainable and eco-friendly alternative to synthetic sprays (Hulwani et al., 2025).

Integrated Management: Semiochemical and Genetic Tools

Modern IPM programs increasingly leverage the biological vulnerabilities of Bactrocera through semiochemicals and genetic manipulation (Magar et al., 2024).

Male Annihilation Technique (MAT)

MAT involves the mass-trapping or baiting of males using powerful attractants (ME or CL) combined with a toxicant. This strategy aims to reduce the male population to such low levels that females are unable to find mates, leading to population collapse (Souder et al., 2020). In Pakistan, ME-baited traps collected significantly higher numbers of B. zonata and B. dorsalis compared to CL-baited traps, reflecting the dominance of ME-responding species in the region (ul Haq et al., 2024).

Recent research suggests that lower density applications of MAT dispensers (e.g., 110 to 220 sites per square kilometer) may be more effective than higher densities. High-density sources can cause "olfactory interference," where the sheer volume of attractant in the air makes it difficult for males to pinpoint individual traps (Wan, 2025).

Sterile Insect Technique (SIT) and Synergistic Integration

SIT is a biological control method where millions of sterile males are released to compete with wild males. The success of SIT was famously demonstrated in the eradication of B. cucurbitae from Okinawa, Japan, where billions of sterile flies were released (Hendrichs et al., 2021).

The simultaneous application of MAT and SIT is a major area of research. Traditionally, MAT was used before SIT to lower the wild population. However, by treating mass-reared males with specific compounds or diets (such as extracts from Terminalia fruit) that render them temporarily non-responsive to ME, SIT and MAT can be integrated simultaneously (Babarinde et al., 2021). This "male enhancement" approach increases the sterile-to-wild male overflooding ratio and significantly improves the cost-effectiveness of eradication programs (Kouloussis et al., 2013).

Genetic Frontiers: CRISPR-Cas9 and pgSIT

The advent of CRISPR-Cas9 genome editing has opened new possibilities for the precision management of Bactrocera. By targeting specific genes, researchers can develop new genetic sexing strains and suppression systems (Nguyen et al., 2025).

Table No 5. Genetic Targets and Associated Phenotypic Outcomes Relevant to Fruit Fly Management

Gene Target	Species	Phenotypic / Biological Result	Management Application
transformer (tra)	*Bactrocera dorsalis*	Male-biased sex ratio, female sterility	Population suppression
white (w)	*Bactrocera spp.*	White eyes, loss of pigmentation	Genetic marker for SIT
white pupae (wp)	*Bactrocera spp.*	White puparium (normally brown)	Genetic sexing systems
yellow (y)	*Bactrocera dorsalis*	Yellow body color, reduced longevity	Fitness reduction

BdorOBP56f-2	*Bactrocera dorsalis*	Impaired perception of Methyl Eugenol	Behavioral disruption

Regulatory Landscape and Quarantine Protocols

Given the high invasive potential of Bactrocera species, international trade is strictly governed by phytosanitary stanSdards. The International Plant Protection Convention (IPPC) provides the framework for International Standards for Phytosanitary Measures (ISPMs) (Gupta et al., 2022)

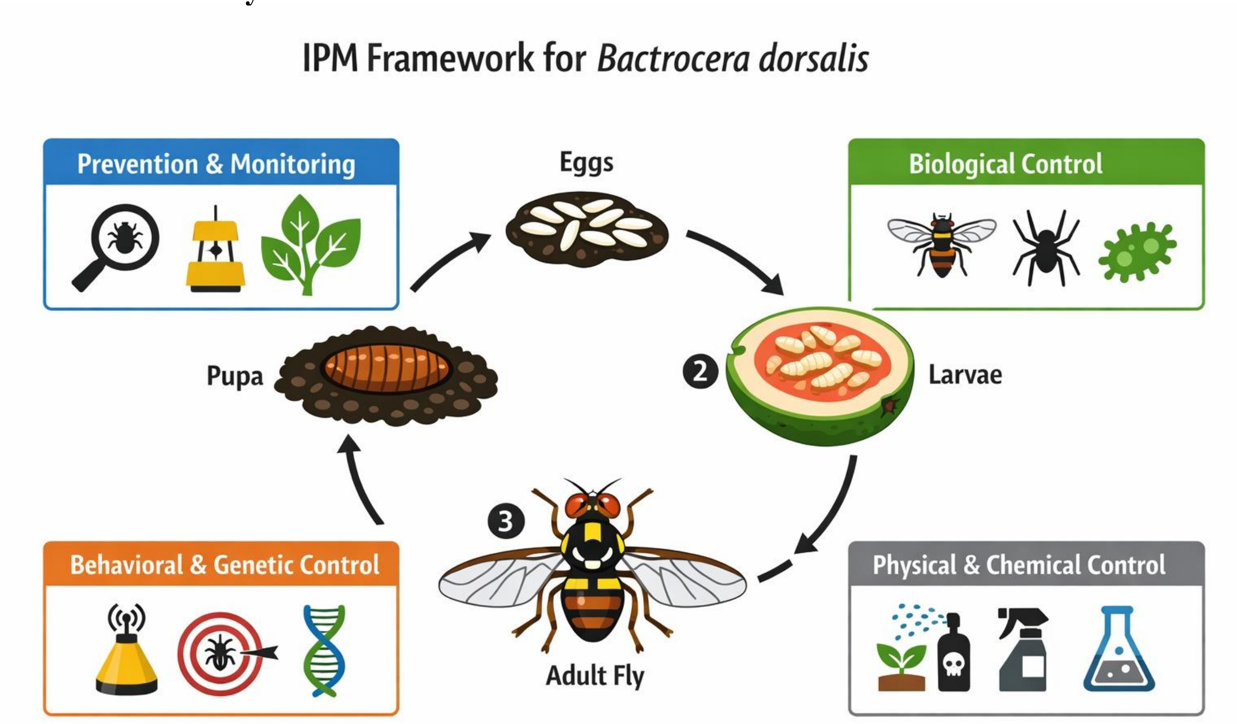
ISPM No. 26 outlines the requirements for establishing and maintaining Pest Free Areas (PFAs). This requires continuous surveillance for at least 12 months with no detections (Ogah et al., 2025). If a detection occurs, the PFA status is suspended, and a degree-day model is used to determine when the quarantine can be safely lifted typically after three generation cycles without further captures (Papadopoulos et al., 2024).

Regional organizations like EPPO (European and Mediterranean Plant Protection Organization) maintain lists of quarantine pests. Bactrocera zonata, for instance, is a regulated pest for which EPPO provides detailed diagnostic protocols to ensure rapid identification at ports of (Jaffar et al., 2023).

Synthesis of Integrated Pest Management Framework

The transition toward a sustainable IPM for Bactrocera involves the integration of behavioral insights with technological advancements (Kokkari et al., 2024). The future of Bactrocera management lies in "climate-smart" pest control, which accounts for shifting ecological niches and utilizes non-chemical tactics like CRISPR-based suppression and optimized push-pull systems to safeguard global horticulture (Ouguas et al., 2025).

Figure 2: Integrated Pest Management (IPM) Framework Mapping Control Strategies to the Bactrocera Life Cycle



Conclusion

The genus Bactrocera represents a group of highly adaptable and ecologically versatile pests with significant economic implications for global horticulture. Their complex behavioral ecology, including sophisticated sensory perception, host selection, and reproductive strategies, underpins their success as invasive species across diverse climates and agricultural systems. The combination of high reproductive rates, polyphagy, and rapid dispersal amplifies their potential to cause severe crop losses and disrupt trade. Integrated management approaches, spanning cultural practices, physical barriers, semiochemical strategies, and advanced genetic tools such as CRISPR-Cas9, provide a multifaceted framework for mitigating these pests. The efficacy of area-wide and climate-smart strategies highlights the importance of combining ecological understanding with technological innovation. Future management success will depend on the continuous integration of behavioral insights, genetic interventions, and international collaboration to develop sustainable, adaptive, and economically viable control measures. By leveraging such interdisciplinary approaches, it is possible to safeguard horticultural production, minimize economic losses, and maintain global trade standards in the face of these resilient fruit fly invaders.

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