Strategies for Entomopathogenic Fungi in Mosquito Biocontrol

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Fungal diseases are widespread among insects and play a crucial role in naturally regulating insect populations. Mosquitoes, known as vectors for numerous infectious diseases, pose a significant threat to human health. Entomopathogenic fungi (EPF) have emerged as highly promising alternative agents to chemical mosquitocides for controlling mosquitoes at all stages of their life cycle due to their unique infection pathway through direct contact with the insect’s cuticle.

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1. Introduction

Mosquitoes pose a significant global threat as they serve as vectors for transmitting various infectious diseases, such as malaria, yellow fever, dengue, chikungunya, West Nile fever, and Zika fever [1][2]. According to the data provided by the World Health Organization, malaria presents a substantial risk to approximately half of the global population, with an estimated annual infection rate of 200–300 million individuals and an alarming mortality rate of almost one million per year [3].

So far, chemical insecticides have served as the primary method for controlling and eliminating mosquitoes [4][5]. Nevertheless, the excessive use of synthetic insecticides has resulted in mosquito resistance and poses significant risks to the environment and non-target organisms, including humans [6]. As a result, there has been an increasing focus on exploring chemical-free biocontrol approaches to address these challenges. These approaches include the use of bacteria, viruses, and fungi as more comprehensive vector control interventions [7].

Bacteria and viruses can play a role in the digestive tract when ingested by insects. However, their effectiveness in controlling adult mosquitoes with piercing–sucking mouthparts is limited [7][8]. Entomopathogenic fungi (EPF), on the other hand, can infect mosquitoes through direct contact with the mosquito’s cuticle, without the need for ingestion, making them highly attractive as control agents. These fungi are ecologically safe and have the capacity to target mosquitoes at all stages of their life cycle, including adults, eggs, larvae, and pupae [9][10][11][12][13][14]. Additionally, EPF have long-lasting effects on the developmental parameters of mosquitoes, such as reduced fecundity in subsequent generations [15].

2. Effectiveness of Entomopathogenic Fungi in Mosquito Control

2.1. Effectiveness of Entomopathogenic Fungi on Different Development Stage of Mosquito

Metarhizium and *Beauveria* are two main generalist entomopathogenic fungi that have been widely used in pest control in various insect species, including agricultural pests and mosquitoes [16]. The recent advancements in the application of EPF in mosquito control has been extensively reviewed by Cafarchia et al., focusing on the field application of formulations of *B. bassiana* and *M. anisopliae* and providing detailed information on these two main fungal strains in mosquito control [8]. Additionally, Shen et al. also provide a summary of the application of EPF on mosquito larvae and adults [5]. In recent years, EPF have been found to affect mosquito development and can also effectively control mosquito at the egg and pupal stages.

2.2. Factors That Influence Spore Quality

The efficacy of fungal strains in biocontrol can vary among different mosquito species, and spore quality plays crucial for the biocontrol effectiveness. The choice of culture media also has an impact on the virulence of fungal conidia against *Ae. aegypti* larvae. Conidia produced on rice grains have demonstrated higher virulence compared to those cultivated on artificial media such as RYA and SDA [12]. Furthermore, the *Metarhizium brunneum* blastospores exhibit higher virulence toward *Ae. aegypti* larvae than conidia, due to multiple routes of entry (cuticle and gut) in water [17]. A recent report indicates that *M. anisopliae* blastospores exhibit higher virulence against *Ae. aegypti* adults, larvae and pupae [11][17][18][19]. Supplementation of Riboflavin and $NaNO_3$ in the culture medium has been shown to enhance protease and conidial production, leading to improved larvicidal activity against *Ae. aegypti* [20]. Additionally, mineral oil has been shown to enhance the efficacy of fungal propagules in the aquatic environment, demonstrating its potential as an adjuvant in entomopathogenic fungi [21]. These studies highlight the importance of selecting the appropriate form of inoculum and cultural condition for efficacious control of disease vectors.

3. Combination of Entomopathogenic Fungi with Other Strategies in Mosquito Control

A singular method or intervention is often insufficient to effectively control vector-borne diseases, and therefore a holistic and integrated approach is necessary. Integrated vector management (IVM) is a comprehensive approach for mosquito control that combines multiple vector control methods and approaches in a coordinated manner. This includes source reduction, as well as larvicidal and adulticidal applications to control mosquitoes at different life stages [22]. IVM offers several advantages by integrating multiple control strategies, resulting in effective prevention and measures. Consequently, it is well-suited for large-scale mosquito- and insect-control efforts. EPF have increasingly been employed for effective field control of mosquitoes, targeting eggs, larvae, pupae, and adults [8][18]. The utilization of EPF in conjunction with other mosquito control strategies has demonstrated a synergistic effect and have the potential to further increase the efficacy of IVM program for mosquito control.

3.1. Combined with Chemical Insecticides

Chemical insecticides often have specific targets, making mosquitoes prone to developing resistance [23][24]. Mosquito resistance is typically associated with the induction of detoxification enzymes,, including cytochrome P450 monooxygenases, acetylcholinesterase (AChE), glutathione S-transferase (GST), esterase (EST), acid phosphatases (ACP), and alkaline phosphatases (ALP) [24][25][26]. Fungal insecticides, on the other hand, can diminish the immune defenses and reduce the activity of detoxification enzymes in mosquitoes. Studies have shown that *M. anisopliae* and *B. bassiana* can suppress the enzymatic activities of ACP in chlorpyrifos-resistant *Cx. quinquefasciatus* [25]. *Metarhizium anisopliae* is compatible with diflubenzuron at lower concentrations and combined applications have shown to enhance *Cx. pipiens* management [27]. Furthermore, the combination of *M. anisopliae* with the insecticide Imidacloprid (IMI) increases virulence against *Ae. aegypti* when ultra-low concentrations of IMI are used [28]. Hence, fungal mosquitocides effectively combat mosquito populations that have developed resistance to certain chemicals or drastically reduce the consumption of chemical pesticides.

3.2. Combined with Microbial Metabolites or Microbial Organisms

Many microbial metabolites, such as avermectins, a type of neurotoxic insecticide, and Asperaculane B, which can inhibit the acetylcholinesterase enzyme, have been extensively employed as effective biocontrol insecticides [29][30][31]. Combining insect pathogenic fungi with microbial metabolites represents a promising approach to mosquito control. The co-application of *M. robertsii* and avermectins lead to a synergistic effect on *Ae. aegypti* larvae mortality [30][32]. Avermectins can reduce the relative abundance of antagonist in mosquito gut, favoring the fungus [32]. *Metarhizium robertsii* significantly reduces the activity of detoxification enzymes, such as esterases, proteases, and phenoloxidase in mosquitoes, disrupting the immune and detoxifying systems and promoting fungal infection [30][32]. *Bacillus thuringiensis* (Bt) has been extensively studied and commercially applied in pest control due to the high pesticidal activity of Bti endotoxins [33][34]. The combined application of the mosquito larvae pathogen *Leptolegnia chapmanii* with Bt produce a synergistic larvicidal effect on *Ae. aegypti* [33]. Additionally, many EPF have been found to produce metabolites toxic to mosquitoes. Twelve metabolites from *Penicillium toxicarium* extracts exhibited high toxicity to mosquito larvae and adults [35]. *P*-orlandin, a nontoxic metabolite from *A. niger*, can target mosquito FREP1, which is a critical protein for parasite infection in *Anopheles gambiae* and could block malaria transmission [36]. Several fungal cell culture filtrates have displayed mortality against mosquito [37]. Recent research on fungal metabolites in mosquito control is summarized in Supplementary Table S1. Consequently, the combination of fungal pathogens with microbial metabolites or other microbes producing toxic metabolites demonstrates a synergistic effect and reduces the reliance on chemicals in mosquito management.

3.3. Combined with Mosquito Attractants

The utilization of volatile compounds and semiochemicals that attract mosquitoes has been incorporated into complementary vector control strategies to enhance the effectiveness of fungal mosquitocides [20]. Numerous volatile organic compounds (VOCs) with mosquito attractant properties have been identified and analyzed, including natural hosts, chemical compounds, synthetic blends of compounds, and plant odors [38][39][40]. Studies have demonstrated that the emission of volatiles by *B. bassiana* can attract *Anopheles stephensi* mosquitoes [41]. Furthermore, deploying black cloths impregnated with *M. anisopliae* or *B. bassiana* in mosquito traps has shown significant reductions in the survival rates of female *Ae. aegypti*, and the inclusion of attractive lures to these traps can further enhance their effectiveness [42].

Hydrogel, a substrate for a granular formulation of fungal conidia, has been shown to attract gravid females under field conditions [43]. Methyl benzoate, derived from plants, acts as an insect semiochemical and exhibits larvicidal activity against mosquitoes [44]. The combination of *M. anisopliae* with Schinusole essential oil has demonstrated a synergistic effect against *Ae. aegypti* larvae [45]. Yeast volatiles are known to attract many insect species [46]. Inactivated yeast tablets lure have shown attractiveness to both *Ae. aegypti* and *Ae. albopictus* females and have been utilized in yeast-bait ovitraps [47]. Supplementation of sugar to *B. bassiana* conidia formulation can increase the attraction of *Ae. aegypti* and enhance their viability, resulting in a three-fold reduction in population [48]. Combining the oviposition attractant and larvicidal agents *B. thuringiensis israelensis* and *Bacillus sphaericus* in a single formulation can result in higher larval mosquito mortality [49]. Additionally, some bacterial or fungal secretions act as attractants and can affect mosquito behavior, such as oviposition strategy, egg hatching, development rate, and larval or pupa survival [50]. For example, Bt affects the oviposition strategy of *Ae. aegypti* and *Ae. albopictus* [51]. A sesquiterpene alcohol, cedrol, produced by *Fusarium falciforme* can affect the oviposition behavior of *An. gambiae* [52]. Therefore, combining oviposition attractants with fungal biopesticides can synergistically control mosquito adults as well as their aquatic larval offspring. The growing understanding and application of these mosquito attractants would contribute to optimizing lure-and-kill strategies and play a crucial role in integrated mosquito management programs.

3.4. Combined with Predators

The use of predators that feed on aquatic organisms has been demonstrated to be effective in controlling mosquito larvae [53]. Insects that have predatorial capacity to mosquito prey have been identified in the Orders Odonata, Coleoptera, Diptera (primarily aquatic predators), and Hemiptera (primarily surface predators) [54]. Among them, *Toxorhynchites* and copepods are the two most effective predatory organisms against mosquitoes [55]. It has been reported that many EPF have either no or very low impact on aquatic predators [56]. However, combined predator-parasite treatments have shown enhanced efficacy against mosquito compared to single-agent treatments. For example, the combination of *Metarhizium* with *Toxorhynchites* treatments drastically reduce lethal times of *Ae. aegypti* mosquitos compared to individual treatments [20][56][57]. The survival of adult *An. gambiae* exposed to *B. bassiana* after larval pre-exposure to a predator, namely nymphs of the dragonfly *Pantala favescens,* has been shown to increase the susceptibility of mosquito to fungal parasitism at the adult stage [58]. However, *A. flavus* displays a mortality rate of over 80% at dosage of 2×10^{16} (two-fold-higher dosage used in larval assays) when tested against two aquatic predators, *Alpheus bouvieri* and *Toxorhynchites splendens*, indicating that it cannot be directly applied directly to the aquatic region [59].

4. Engineering Manipulation of EPF to Improve Their Mosquitocidal Efficacy

With the advancement of genetic engineering techniques, genetic control methods have emerged as promising alternative strategies for enhancing the biological control capabilities of entomopathogenic fungi against mosquito vectors of disease [4]. Three strategies have been reported for modifying EPF.

4.1. Introducing Insecticidal Molecules into Mosquito

The insertion of insecticide expression genes into EPF can significantly enhance their mortality activity. For example, the genetic modification of *B. bassiana* expressing the Bt toxin *Cyt2Ba*, leads to a substantial improvement in its efficacy in killing mosquitoes [14]. Insecticidal activity can also be enhanced by expressing mosquito-inhibitory molecules. The *B. bassiana* strain expressing an *Ae. aegypti* trypsin-modulating oostatic factor (TMOF), which inhibits food digestion in the guts of adult and larval mosquitoes, exhibited increased virulence against *An. gambiae* compared to the wild-type strain [60]. By using specific fungal promoters to drive the expression of mosquito-killing genes in insect tissue, EPF can target and eliminate mosquitoes more accurately and efficiently [61]. The expression of ion channel blockers under the control of a hemolymph-specific promoter *Mcl1* in *Metarhizium* resulted in increased fungal lethality to mosquitoes at very low spore dosages, even as low as one conidium per mosquito [62]. In a semi-field assay conducted in Burkina Faso, an engineered *Metarhizium* strain expressing an insect-specific toxin (Hybrid) exhibited enhanced fungal lethality and a prolonged mortality effect compared to the wild-type strain, demonstrating its potential to synergistically manage insecticide-resistant mosquitoes in an endemic malaria area [63][64].

Another approach to increase mosquito-killing efficacy is by suppressing the host immunity. Expression of host miRNAs in *B. bassiana* has been shown to significantly enhance fungal virulence against insecticide-resistant mosquitoes. Engineered fungal entomopathogen *B. bassiana,* that produces host immunosuppressive miRNAs, can effectively suppress the host Toll immune response and facilitate fungal infection [65]. This pathogen-mediated RNAi (pmRNAi)-based approach provides an innovative strategy not only to enhance the efficacy of fungal insecticides but also to minimize the possibility of resistance development. Another alternative strategy for mosquito control is the combination of EPF and bacteria that express immune suppressive dsRNA. This combination has been shown to enhance the toxicity of EPF in leaf beetles by inhibiting host immunity [66]. In this strategy, microbiota in the mosquito gut can be modified and serve as a molecular adjuvant and immunomodulator against parasites when in combined application with EPF [67].

4.2. Introducing Antipathogen Effector to Block Vector Disease Transmission

To target the pathogen in mosquitoes is another strategy in genetic manipulation of EPF [68][69]. Genetically modified EPF strains can express antimalarial effector molecules and antimicrobial peptides. Recombinant *M. anisopliae* strains have been engineered to produce antimalarial effector molecules that inhibit the attachment of sporozoites to salivary glands, agglutinate sporozoites, or exhibit antimicrobial toxic activity to inhibit *Plasmodium* development. This approach resulted in a decrease of up to 98% in the malarial sporozoite count in mosquito salivary glands [70]. A similar strategy has also been achieved using midgut symbiont in mosquitoes. The paratransgenic control strategy, which involves expressing an antiplasmodial effector driven by blood meal induced (BMI) promoters, has proven to be effective in inhibiting pathogen infection [7][38][69][71].

4.3. Increasing the Fungal Tolerance to Adverse Environmental Conditions

For application in water, UV-B has no detrimental effect for sedimented conidia even no overlay of water [72]. However, when exposure of fungus-treated mosquito adults to sunlight, UV-B radiation can affect activity of conidia applied on the mosquito's surface [73]. To enhance the efficacy of EPF, increasing their UV tolerance through genetic manipulation is another viable strategy. For instance, the expression of a photolyase from archaea in *M. robertsii* and *B. bassiana* has been shown to enhance their resistance to sunlight while maintaining their virulence against the malaria vector *An. gambiae* [74]. Genetic manipulation of other stress-tolerance-related genes, such as heat shock protein 25, can also improve thermal tolerance [75].

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