J. Trop. Plant Pests Dis.
Vol. 26, No. 2, September 2026
Pages: 290–303

ISSN: 1411-7525
E-ISSN: 2461-0399
DOI : 10.23960/j.hptt.226290-303

RESEARCH PAPER

Effectiveness of entomopathogenic fungal combinations on eggs and larval development of *Spodoptera frugiperda* J.E. Smith (Lepidoptera: Noctuidae) in corn plants

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Manuscript received: 30 July 2025. Revision accepted: 25 November 2025. Available online: 23 April 2026.

ABSTRACT

Spodoptera frugiperda J.E. Smith is an invasive pest of corn, requiring effective and environmentally friendly control strategies. This study aimed to evaluate the effectiveness of three entomopathogenic fungal (EPF) isolates, namely *Beauveria bassiana* WS, *Metarhizium anisopliae* B22C, and *Trichoderma asperellum* A116, tested as single isolates or in combination against *S. frugiperda* eggs and larvae. The experiment used a Completely Randomized Design (CRD) with eight treatments (three single treatments, four combinations, and a control) and four replications. Conidial suspensions were applied by spraying onto eggs and second-instar larvae. Parameters observed included the percentage of unhatched eggs, larval mortality, and pupal and adult development. Chitinase, protease, and lipase activities were qualitatively tested to support the identification of pathogenicity mechanisms. Data were analyzed using analysis of variance (ANOVA), followed by the LSD test at a 5% significance level. The results showed that EPF combinations increased mortality and inhibited the development of *S. frugiperda*. The combination of *B. bassiana* WS + *T. asperellum* A116 was the most effective treatment, inhibiting egg hatching by 85% and reducing pupal and adult formation to 25.95% and 12.96%, respectively. The highest mortality of first-instar larvae was observed in the single treatment of *B. bassiana* WS and the tertiary combination of *B. bassiana* WS + *M. anisopliae* B22C + *T. asperellum* A116, at 24.18% and 22.91%, respectively. Consistent enzymatic activity indicated potential biocontrol synergy through the production of cuticle-degrading enzymes. This combination is recommended for field-scale testing as an environmentally friendly alternative to reduce dependence on chemical insecticides.

Keywords: Biological control, combination, entomopathogenic fungi, ovicides, *Spodoptera frugiperda*

INTRODUCTION

Corn (*Zea mays*) is a major food commodity as a source of carbohydrates after rice, playing a crucial role in agricultural and economic development programs in Indonesia. National corn demand is reported to continue to increase in line with population growth (BPS-Statistics Indonesia, 2021). In Indonesia, food availability is a crucial determinant of food security and national stability (Sandy et al., 2019). Increased demand that is not matched by increased production will impact food availability and market prices. One of the main obstacles in corn farming is pest attack by the armyworm *Spodoptera frugiperda* J.E. Smith (Lepidoptera: Noctuidae). This invasive pest has recently been reported to spread rapidly and cause significant damage to maize production in several regions of Indonesia (Trisyono et al., 2019; Lestari et al., 2024; Ginting et al., 2024).

S. frugiperda larval infestation on plants is characterized by burrow marks in the form of coarse powder resembling sawdust found on the surface or tips of leaves (Nonci et al., 2019). Heavy infestations can cause yield losses of 20–94% (Directorate of Food Crop Protection, 2020; Meilin et al., 2020), and even up to 100% in young corn plants (Trisyono et al., 2019). *S. frugiperda* adults are able to travel long distances and spread rapidly in Indonesia (Nonci et al., 2019). Conventionally, farmers rely on pesticides to control *S. frugiperda* (Kumela et al., 2018), but their use has negative impacts such as health problems (Harrison et al., 2019), death of non-target insects, pollution, pest resistance (Zhang et al., 2021), secondary

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pest outbreaks, resurgence, and ecosystem damage (Adriyani, 2006). Therefore, environmentally friendly control alternatives are needed.

The use of biological agents in the form of entomopathogenic fungi (EPF) is an alternative solution that can reduce the use of synthetic pesticides (Sari et al., 2022). The mechanism of EPF in killing host insects involves the production of metabolites, including cell wall–degrading enzymes and toxins (Peng et al., 2021), proteases, lipases, aminopeptidases (Clarkson & Charnley, 1996), and chitinases (Giridhar et al., 2012), which degrade the endocuticle of pest insects, causing death. Several fungi reported to be effective as entomopathogens include *Beauveria bassiana* (Flawerina et al., 2021; Trizelia et al., 2019), *Metarhizium anisopliae* (Akutse et al., 2019), and *Trichoderma asperellum* (Islam et al., 2022). Previous studies reported that *B. bassiana* and *M. anisopliae* exhibit high pathogenicity against various insect pests and are effective biological control agents (Herlinda et al., 2006; Prayogo, 2013; Effendy et al., 2010). *B. bassiana* and *M. anisopliae* control insect pests through direct infection, where fungal conidia attach to the insect cuticle and penetrate it using chitinase, protease, and lipase enzymes. The conidia then develop in the insect's hemolymph and produce toxins that cause insect death (Vajri et al., 2024). *T. asperellum*, better known as a plant pathogen control agent, affects pests through enzymes that damage eggs or young larvae and is also able to stimulate plant defenses (Bamisile et al., 2014). The combination of these three fungi has the potential to provide a synergistic effect by combining direct infection and indirect mechanisms to increase the effectiveness of biological control of insect pests.

One advantage of using EPF for biological control is that they can target various stages of insect development, including eggs, larvae, pupae, and adults (Akutse et al., 2019). Idrees et al. (2021) reported that *B. bassiana* was effective in causing mortality of up to 85.6% in *S. frugiperda* eggs. Idrees et al. (2023) reported that *M. anisopliae* caused mortality of up to 86% and 57% in *S. frugiperda* eggs and neonates, respectively. The use of *Trichoderma* spp. was also reported by Alfasiri et al. (2025) to cause mortality of up to 78.54% and 60.22% in *S. frugiperda* eggs and neonates, respectively. Similar findings indicated that entomopathogenic fungi are capable of infecting early developmental stages of insect pests due to enzymatic degradation of the insect cuticle and toxin production (Rizkie et al., 2017; Prayogo, 2013).

Recent research interest in microbial development has shifted toward the use of microbial consortia consisting of various entomopathogenic strains to improve stability and efficiency in biocontrol activities under diverse environmental conditions (Sarma et al., 2015). Some studies have shown that combinations of EPF can produce synergistic or additive effects, increasing pest mortality compared to single treatments (Půža & Tarasco, 2023). Batool et al. (2020) reported that the combination of *B. bassiana* and *T. asperellum* effectively caused mortality of *Ostrinia furnacalis* up to 98.3%. Nazir et al. (2018) also reported that the binary combination of *B. bassiana* (BB-252) and *Lecanicillium lecanii* (V-4), as well as the tertiary combination of *B. bassiana* (BB-252, BB-253) and V-4, caused mortality of aphids (*Myzus persicae*) of 80% and 78%, respectively. However, interactions between fungi are not always positive. Competition for space, nutrient sources, or secondary metabolites can trigger antagonism and reduce effectiveness (Pauli et al., 2018; Correa-Cuadros et al., 2016). Furthermore, studies specifically investigating the combined treatment of three fungal entomopathogens (*B. bassiana*, *M. anisopliae*, and *T. asperellum*) on *S. frugiperda* eggs are still very limited or have not been reported in the literature over the past five years, even though this phase is vulnerable and crucial in the pest's life cycle. Therefore, a direct evaluation of the effectiveness of the combination of *B. bassiana*, *M. anisopliae*, and *T. asperellum* on *S. frugiperda* eggs is necessary to explore the potential benefits of the biocontrol combination and to test the hypothesis of increased efficacy without laboratory analysis of synergistic or antagonistic interactions.

MATERIALS AND METHODS

Research Site. This research was conducted at the Biological Control Laboratory, Faculty of Agriculture, Andalas University, from April to June 2024.

Research Design. This study used a Completely Randomized Design (CRD) with eight treatments and four replications. Fungal isolates were obtained from the Biological Control Laboratory, Department of Plant Protection, Faculty of Agriculture, Andalas University. The fungal isolates used were *B. bassiana* WS, *M. anisopliae* B22C, and *T. asperellum* A116. The treatment combinations used are presented in Table 1.

Fungal Rejuvenation on SDA Medium. All fungal isolates used in this study were rejuvenated by cutting colonies using a cork borer and transferring them with a spatula onto Sabouraud Dextrose Agar

(SDA; Merck, Germany) medium in Petri dishes. The isolates were incubated at room temperature (±25 ºC) for approximately 15 days for further use. The characteristics of the fungi are shown in Table 2 and Figure 1.

Table 1. Combination treatments of fungal isolates used in the experiment

Treatment	Treatment code	Treatment description
Single isolate (1)	BbWS	*Beauveria bassiana* WS
	MaB22C	*Metarhizium anisopliae* B22C
	TaA116	*Trichoderma asperellum* A116
Binary combination (1:1)	BbWS + MaB22C	*B. bassiana* WS + *M. anisopliae* B22C
	BbWS + TaA116	*B. bassiana* WS + *T. asperellum* A116
	MaB22C + TaA116	*M. anisopliae* B22C + *T. asperellum* A116
Tertiary combination (1:1:1)	BbWS + MaB22C + TaA116	*B. bassiana* WS + *M. anisopliae* B22C + *T. asperellum* A116
Control	K	Control (Sterile distilled water)

Table 2. Morphology of entomopathogenic fungi on SDA media

Treatment code	Origin of isolate	Place of origin	Colony surface color	Hyphae	Conidia
BbWS	Infected stink bugs	Padang City, West Sumatra	White Cotton	Partitioned	Round
MaB22C	Oil palm rhizosphere	Pasaman Regency, West Sumatra	Light green	Branching	cylinder
TaA116	Chili root endophytes	Agam Regency, West Sumatra	Dark green	Partitioned	Round

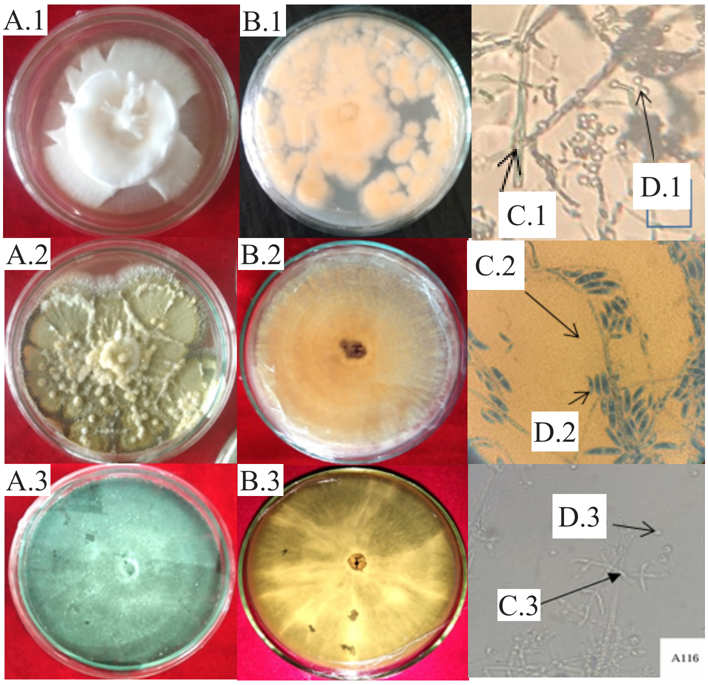

Figure 1. Macroscopic and microscopic characteristics (at 100× magnification) of entomopathogenic fungi on SDAY medium at 15 days after incubation. A. Macroscopic top view; B. Macroscopic bottom view; C. Microscopic hyphal morphology; D. Microscopic conidia morphology; 1. *Beauveria bassiana* WS; 2. *Metarhizium anisopliae* B22C; 3. *Trichoderma asperellum* A116.

Propagation of *S. frugiperda*. *S. frugiperda* larvae were obtained from corn cultivation centers in Kuranji District, Padang City, West Sumatra. The larvae collected were in instar 3 and 4 stages. Each larva was kept individually in a 5 cm × 5 cm × 5 cm plastic box and fed cut corn leaves, which were replaced every 24 hours with fresh leaves. Larvae that entered the pupal phase were transferred into plastic jars lined with filter paper and placed in insect cages measuring 45 cm × 45 cm × 45 cm with cut leaves inside as oviposition substrates. Adults emerging from pupae were fed 10% honey solution soaked in cotton and hung above the cage. Eggs produced by the adults were used as test material in this study.

Preparation of Fungal Suspension. Fifteen-day-old fungal colonies were harvested by adding 10 mL of sterile distilled water and Tween 80 (0.01%) (SmartLab Indonesia) as a surfactant into the Petri dish. The mixture was gently brushed to release conidia, then transferred to a test tube and homogenized using a vortex (Gemmy VM-300, Taiwan). Dilution was performed to obtain a concentration of 10^7 conidia/mL. Conidial density was calculated using a haemocytometer (Improved Neubauer) (Minitub, Germany) (Dhawan & Joshi, 2017).

Application of Fungal Conidia Combination to *S. frugiperda* Eggs. The virulence test of fungal combinations was conducted to determine whether the combinations were able to cause mortality in *S. frugiperda* eggs. The test followed the method of Trizelia (2005). The conidial concentration of each fungal combination used was 10^7 conidia/mL. Treatment application was carried out by spraying 3 mL of fungal conidial suspension onto groups of one-day-old eggs in Petri dishes lined with moist filter paper. The control treatment was sprayed with sterile distilled water at the same volume. The comparison of fungal suspension volumes in each combination is shown in Table 3. Observations were conducted daily until the eggs hatched. The percentage of hatched eggs was calculated using the following formula:

$$T = \frac{X}{Y} \times 100\%$$

T = Percentage of egg hatching;
X = Number of eggs hatched;
Y = Total number of eggs.

Mortality increase wass calculated using the formula:

$$E = \frac{P - K}{P} \times 100\%$$

E = Effectiveness or increased mortality;
P = Mortality in treatment;
K = Mortality in control.

Larvae that emerged from hatched eggs were counted and fed with fresh corn leaves to observe their development until the adult stage. First-instar larvae obtained from egg development after fungal application were counted and observed daily until they reached the second instar. Observations were also conducted on larvae showing symptoms of entomopathogenic fungal infection. The percentage of first-instar larval mortality was calculated using the following formula:

$$T = \frac{X}{Y} \times 100\%$$

T = Percentage of mortality of first-instar larvae;
X = Number of first instar larvae that died;
Y = Total number of first-instar larvae.

The percentage of pupae formed was determined by calculating the number of pupae formed from all eggs that hatched into first-instar larvae. The percentage of pupae formed was calculated using the formula of Saputra et al. (2016):

$$Pp = \frac{P}{N} \times 100\%$$

Pp = Percentage of pupae formed;
p = Number of pupae formed;
N = Number of eggs that hatched into first-instar larvae.

The percentage of adult (imago) formation was determined by counting the number of adults formed from all eggs that hatched in each treatment. The percentage of adult formation was calculated using the

Table 3. Comparison of volumes of combined fungal suspensions used in the virulence test against *S. frugiperda* eggs at a concentration of 10^7 conidia/mL

Treatment	Ratio of fungal suspension volumes	Total volume
Single isolate	1	3 mL
Binary combination (2 isolates)	1 : 1	3 mL
Tertiary combination (3 isolates)	1 : 1 : 1	3 mL
Control (sterile distilled water)	0	3 mL

formula from Saputra et al. (2016):

$$Pi = \frac{i}{N} \times 100\%$$

Pi = Percentage of adult formed;
i = Number of adult formed;
N = Number of eggs that hatched into first-instar larvae.

Fungal Combination Enzymatic Activity Test. Various fungal extracellular enzymes are capable of degrading the cuticle and tissues of host insects. Enzymatic activity tests were conducted using the method of Stuart et al. (2020). The enzymatic activities tested were chitinase, protease, and lipase. A total of 10 µL of conidial suspension containing a fungal combination at a concentration of 10^7 conidia/mL was placed in each Petri dish containing specific enzyme media, namely chitinase medium (colloidal chitin, 1%; MgSO4 7H2O, 0.5 g; K2HPO4, 0.7 g; KH2PO4, 0.3 g; FeSO4.7H2O, 0.01 g; ZnSO4, 0.001 g; MnCl2, 0.001 g in 1000 mL of distilled water), protease medium (yeast extract, 2.5 g; dextrose, 1 g; NaCl, 2.5 g; agar, 15 g; peptone, 5 g; skim milk, 100 mL in 1000 mL of distilled water), or lipase medium (Tween 80, 10 mL; peptone, 10 g; NaCl, 5 g; CaCl2-2H2O, 0.1 g; agar, 20 g in 1000 mL distilled water), and then incubated for 3 days. The presence of a halo or clear zone around the colony indicates enzymatic activity.

RESULTS AND DISCUSSION

Egg Hatchability and First-Instar Larval Mortality of *S. frugiperda*. The results showed that fungal combinations applied to the eggs significantly affected the development of *S. frugiperda* eggs. The binary combination treatment of BbWS+TaA116 showed the highest effectiveness in inhibiting egg hatching, up to 85%, followed by the single treatment of BbWS at 82.53% and the binary combination of BbWS+MaB22C at 78%. In contrast, the tertiary combination treatment of BbWS+MaB22C+TaA116 showed the lowest effectiveness among the fungal treatments, namely 43%, although this value was still higher than the control (8.94%). Data on *S. frugiperda* egg development are presented in Table 4 and Figure 2.

In addition, observations of first-instar larval mortality showed that the application of

Table 4. Development of *S. frugiperda* eggs after application of entomopathogenic fungal combinations at the egg stage

Treatment code	Number of eggs (eggs)	Egg hatching (%) ± LSD	Eggs not hatching (%) ± LSD	Effectiveness of non-hatching eggs (%)
BbWS + TaA116	116.50	15.00 ± 3.2 e	85.00 ± 3.5 e	83.54
BbWS	130.25	17.47 ± 3.3 e	82.53 ± 3.5 e	80.81
BbWS + MaB22C	113.75	22.00 ± 3.4 e	78.00 ± 3.5 e	75.84
TaA116	142.75	32.57 ± 3.7 d	67.43 ± 3.5 d	64.23
MaB22C	116,.00	33.41 ± 3.7 d	66.59 ± 3.5 d	63.31
MaB22C + TaA116	124.25	46.00 ± 3.6 c	54.00 ± 3.5 c	49.48
BbWS + MaB22C + TaA116	134.00	57.00 ± 3.5 b	43.00 ± 3.5 b	37.40
Control	117.50	91.06 ± 2.8 a	8.94 ± 3.5 a	-

Values followed by the same letter in the same column are not significantly different at the 5% level according to the LSD test.

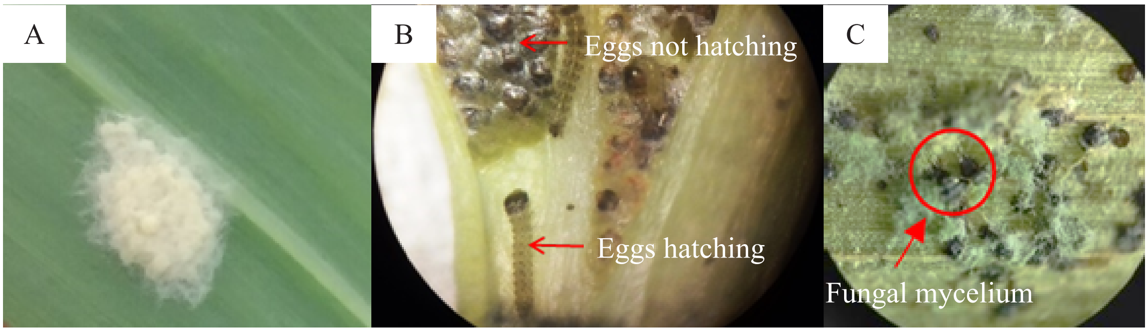

Figure 2. *S. frugiperda* eggs after application of entomopathogenic fungal combination. A. Normal eggs after spraying; B. Hatched and unhatched eggs (MaB22C+TaA116); C. Mycelial growth after application of the fungal isolate.

entomopathogenic fungi to eggs significantly affected the mortality of newly hatched larvae, ranging from 17% to 24.18%. The single treatment of BbWS resulted in the highest mortality (24.18%), followed by the tertiary combination of BbWS+MaB22C+TaA116 and the binary combination of BbWS+TaA116, at 22.91% and 22.86%, respectively. Larvae emerging from the eggshells were observed consuming the remaining shells contaminated with the fungal combination after treatment. Larval mortality was observed on the second day after hatching, with symptoms including stiffening and blackening of the larval body. In contrast, the binary combination treatment of BbWS+MaB22C showed the lowest effectiveness (17%), although still higher than the control (8.4%). Data on first-instar larval mortality and death symptoms of *S. frugiperda* are presented in Table 5 and Figure 3.

The binary combination treatment of *B. bassiana* and *T. asperellum* (BbWS+TaA116), as well as the single treatment of *B. bassiana* (BbWS), showed the best results in suppressing *S. frugiperda* egg hatching by more than 80%. This is consistent with the characteristics of *B. bassiana* as a virulent entomopathogenic fungus against various insect pests (Vajri et al., 2024). Entomopathogenic fungi are ovicidal, infecting eggs directly or disrupting embryonic development. Prayogo (2010) reported that insect eggs consist of an exochorion layer containing carbohydrates and endocrine components, and a crystalline layer containing protein. The high virulence of the BbWS+TaA116 combination is supported by the ability of *B. bassiana* to produce embryotoxic toxins (such as beauvericin and bassianolide) as well as protease and chitinase enzymes (Wang et al., 2021). *T. asperellum* is also known to produce glucanase and chitinase, which enhance the penetration ability of *B. bassiana*, thus exhibiting a synergistic effect (Batool et al., 2020). Furthermore, the activity of hydrolytic enzymes (chitinase, protease, and lipase) also plays an important role in pathogenicity (Deb & Dutta, 2021). Qualitative confirmation through biochemical assays of hydrolytic enzyme production in this study showed that the BbWS+TaA116 combination actively produced all three enzymes compared to other combinations (Table 6; Figure 4), which is suspected to be the main contributing to the high inhibition of *S. frugiperda* egg development.

The tertiary combination of

Table 5. First-instar larval mortality of *S. frugiperda* following application of entomopathogenic fungal combinations at the egg stage

Treatment code	First-instar larval mortality (%) ± LSD	Mortality effectiveness (%)
BbWS	24.18 ± 2.0 d	17.23
BbWS + MaB22C + TaA116	22.91 ± 2.0 c	15.84
BbWS + TaA116	22.86 ± 2.0 c	15.79
TaA116	20.97 ± 2.0 c	13.72
MaB22C	18.06 ± 2.0 b	10.55
MaB22C + TaA116	17.90 ± 2.0 b	10.37
BbWS + MaB22C	17.00 ± 2.0 b	09.39
Control	8.40 ± 2.0 a	-

Values followed by the same letter in the same column are not significantly different at the 5% level according to the LSD test.

Figure 3. First-instar *S. frugiperda* larvae after application of entomopathogenic fungal combinations. A. Normal larvae; B. Died larvae showing mycosis after application.

BbWS+MaB22C+TaA116 showed the lowest suppression of *S. frugiperda* egg hatching compared to single or binary treatments. This may be due to competitive interactions occurring during the initial colonization phase among fungi (Quesada-Moraga et al., 2022). Gómez-Valderrama et al. (2022) stated that combinations of three or more entomopathogens often result in non-additive or antagonistic interactions depending on spatial relationships, inoculum ratios, and metabolites produced. Meanwhile, the control showed the highest hatching rate (91.51%), indicating that fungal treatments contributed substantially to inhibiting embryo development or egg penetration.

The combination treatments applied to *S. frugiperda* eggs also affected first-instar larval mortality. The single treatment of BbWS, the tertiary combination of BbWS+MaB22C+TaA116, and the binary combination of BbWS+TaA116 showed the best results in causing first-instar larval mortality of more than 20%. Although relatively low, this value demonstrates that the combination treatment of entomopathogenic fungi applied to eggs successfully impacted the early phase of insect development (Ramatsitsi et al., 2025). The single treatment of *B. bassiana* showed the highest effectiveness in causing first-instar larval mortality. Interestingly, the tertiary combination of BbWS+MaB22C+TaA116 provided an effect almost equivalent to the single isolate and higher than other combinations, although it showed the lowest suppression of egg hatching. Idrees et al. (2021) stated that several entomopathogenic fungi, such as *B. bassiana* and *M. anisopliae*, can cause a "post-oviposition effect" or latent infection, resulting in delayed mortality after hatching. Fungal conidia adhere to the egg surface without immediately killing the embryo. After hatching, pathogenic spores or metabolites remain on the neonate larvae and subsequently infect them, causing post-hatch mortality (da Silva et al., 2025).

The pathogenic processes of *B. bassiana* and *M. anisopliae* follow the classic mechanisms of entomopathogenic fungi. Initially, conidia adhere to the host cuticle through hydrophobic interactions and adhesins, then germinate and form infection structures such as appressoria or penetration pegs (Harith-Fadzilah et al., 2020). During penetration, both fungi secrete hydrolytic enzymes such as proteases, chitinases, and lipases that break down the cuticle layer

Table 6. Biochemical test of hydrolytic enzyme production by combinations of *B. bassiana*, *M. anisopliae,* and *T. asperellum*

Treatment	Enzymatic activity (+/-)		
	Chitinase	Protease	Lipase
BbWS	+	-	+
MaB22C	+	+	-
TaA116	-	+	+
BbWS + MaB22C	+	-	+
BbWS + TaA116	+	+	+
MaB22C + TaA116	-	+	-
BbWS + MaB22C + TaA116	+	+	-
Control	-	-	-

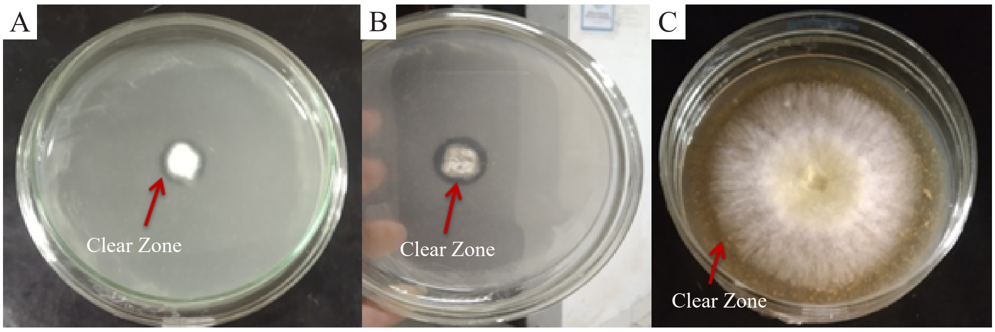

Figure 4. Enzymatic activity of fungal combinations showing clear zones. A. Chitinase activity (BbWS); B. Protease activity (BbWS+TaA116); C. Lipase activity (BbWS+MaB22C).

and allow hyphal invasion into the insect body (Golzan et al., 2023; Saciloto-de-Oliveira et al., 2023). After penetration, the fungus develops in the hemolymph as blastosporic bodies or branching hyphae, producing secondary toxins such as destruxins (in *M. anisopliae*) and other mycotoxins (in *B. bassiana*) that suppress the host immune system and accelerate death (Wang et al., 2023; Oberti et al., 2025). Systemic infection continues with colonization of tissues, including the fat body, trachea, and muscles, before hyphae emerge on the body surface for external sporulation (Sharma & Sharma, 2021). This pathogen–host interaction aligns with the results of this study, where high mortality and inhibition of pupal and adult development were observed, likely driven by a combination of cuticle-degrading enzymes and internal toxicity.

Although strong synergism was not observed in the tertiary combination, the use of fungal combinations still showed significant potential for suppressing early pest populations through egg infection. Previous studies by Idrees et al. (2021) and Idrees et al. (2023) reported that *B. bassiana* and *M. anisopliae* were effective in infecting eggs and early larvae of *S. frugiperda*, causing mortality of 40% and 25.9% (for *B. bassiana*) and 40% and 23.3% (for *M. anisopliae*), respectively. Alfasiri et al. (2025) also reported that *T. asperellum* caused mortality of 78.54% and 60.22% in eggs and early larvae, respectively. However, these studies did not use a combination approach. This finding therefore opens new opportunities for developing biological control agents based on combinations of entomopathogenic fungi for early pest control from the egg stage.

Pupal and Adult Formation of *S. frugiperda*. The results showed that combination treatments of entomopathogenic fungi significantly affected pupal and adult formation of *S. frugiperda*. The best treatment was the combination of BbWS+TaA116, which resulted in the lowest percentages of pupae and adults, at 38.89% and 12.96%, respectively. This was followed by the single treatment of BbWS, the tertiary combination of BbWS+MaB22C+TaA116, and the binary combination of MaB22C+TaA116, which were significantly different from the control. Other treatments were not significantly different from the control (pupae >50%, adults >30%). In the control treatment, pupae and adults were formed at 75.26% and 55.10%, respectively. Data on the percentage of pupal and adult formation of *S. frugiperda* are presented in Tables 7 and 8.

Larvae that successfully developed into pupae and adults showed both normal and abnormal development. Abnormal pupae were identified by failure of the prepupal stage to transform into pupae, followed by death and body blackening (Figure 5). Abnormal adults were identified by damaged wings or death during emergence from the pupal case (Figure 6).

Larval mortality affected pupal formation. High mortality rates and the presence of prepupae that failed to develop into pupae resulted in low pupal and adult formation. In this study, the binary combination treatment of BbWS+TaA116 demonstrated the best results in suppressing pupal and adult formation.

Mortality of *S. frugiperda* pupae and adults caused by *B. bassiana* and *M. anisopliae* has been previously reported. Fungal treatment suppressed adult formation of *S. frugiperda* by 86% using *B. bassiana* (Faddilah et al., 2022) and 57.67% using *M. anisopliae* (Lestari et al., 2022). Alfasiri et al. (2025) also reported

Table 7. Pupal formation of *S. frugiperda* following application of entomopathogenic fungal combinations at the egg stage

Treatment code	Pupal formation (%) ± LSD		
	Normal	Abnormal	Total
Control	73.98 ± 3.0 a	1.28 ± 3.0 c	75.26 ± 3.5 a
BbWS + MaB22C	40.96 ± 3.0 bcd	27.71 ± 3.0 a	68.67 ± 3.5 ab
TaA116	55.78 ± 3.0 ab	7.48 ± 3.0 bc	63.27 ± 3.5 abc
MaB22C	47.24 ± 3.0 bc	8.66 ± 3.0 bc	55.91 ± 3.5 abcd
MaB22C + TaA116	40.43 ± 3.0 cde	12.77 ± 3.0 b	53.19 ± 3.5 bcd
BbWS + MaB22C + TaA116	31.49 ± 3.0 cde	13.62 ± 3.0 b	45.11 ± 3.5 cde
BbWS	28.99 ± 3.0 de	11.59 ± 3.0 bc	39.13 ± 3.5 de
BbWS + TaA116	25.93 ± 3.0 f	12.96 ± 3.0 b	38.89 ± 3.5 de

Values followed by the same letter in the same column are not significantly different at the 5% level according to the LSD test.

Table 8. Adult formation of *S. frugiperda* following application of entomopathogenic fungal combinations at the egg stage

Treatment code	Imago formation (%) ± LSD		
	Normal	Abnormal	Total
Control	54.08 ± 3.0 a	1.02 ± 3.0 e	55.10 ± 3.0 a
BbWS + MaB22C	31.33 ± 3.0 ab	9.64 ± 3.0 ab	40.96 ± 3.0 ab
TaA116	29.93 ± 3.0 abc	2.72 ± 3.0 cde	32.65 ± 3.0 ab
MaB22C	21.26 ± 3.0 bcd	11.02 ± 3.0 a	32.28 ± 3.0 abc
MaB22C + TaA116	25.53 ± 3.0 abc	4.79 ± 3.0 bcde	30.32 ± 3.0 bc
BbWS + MaB22C + TaA116	22.13 ± 3.0 bcd	5.96 ± 3.0 abcd	28.09 ± 3.0 bc
BbWS	18.84 ± 3.0 bcde	7.25 ± 3.0 abc	26.09 ± 3.0 bc
BbWS + TaA116	11.11 ± 3.0 cde	1.85 ± 3.0 de	12.96 ± 3.0 cd

Values followed by the same letter in the same column are not significantly different at the 5% level according to the LSD test.

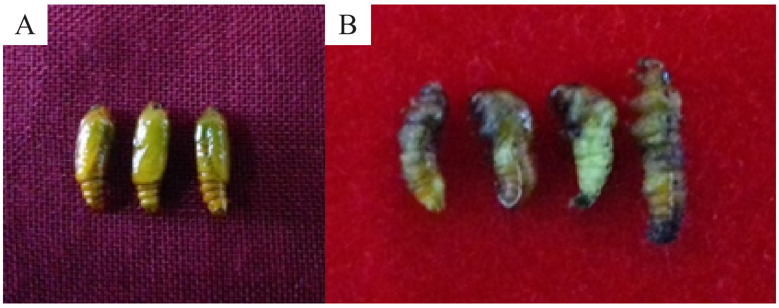

Figure 5. *S. frugiperda* pupae after application of entomopathogenic fungal combinations. A. Normal pupae; B. Abnormal pupae.

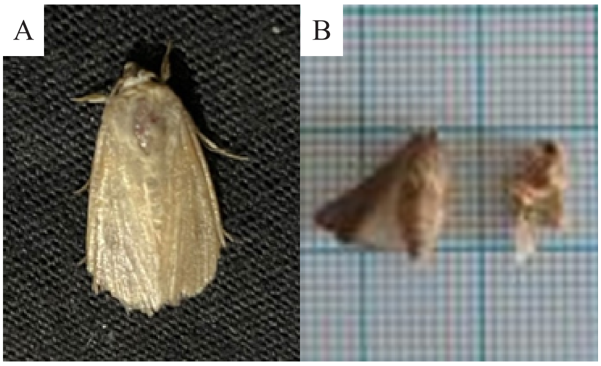

Figure 6. Imago of *S. frugiperda* after application of entomopathogenic fungal combinations. A. Normal imago; B. Abnormal imago.

that *T. asperellum* suppressed pupal and adult formation by 58.51% and 45.13%, respectively. Pupal and adult malformations were associated with decreased pupal weight and length, as well as abnormal wing formation in *S. frugiperda* (Sari et al., 2023).

However, these studies did not use a combination approach. Therefore, this study is among the first to test a combination of three entomopathogenic fungi on egg hatching, first-instar larval mortality, and inhibition of pupal and adult formation. This research opens new opportunities for developing multimicrobial-based biological control.

CONCLUSION

The results showed that the combination of the entomopathogenic fungi *B. bassiana*, *M. anisopliae* and *T. asperellum* was effective in suppressing the development of *S. frugiperda* eggs and first-instar larvae, as well as inhibiting pupal and adult formation. The fungal combinations also produced hydrolytic enzymes, namely chitinase, lipase, and protease, as demonstrated by qualitative assays based on the formation of clear zones on specific media. These clear zones visually indicated enzymatic activity without providing quantitative measurements. The binary combination of *B. bassiana* WS and *T. asperellum* A116 was the most effective treatment in suppressing egg hatching (82.53%), increasing first-instar larval mortality (22.86%), and reducing pupal (25.95%) and adult (12.96%) formation of *S. frugiperda*. This combination also showed the clearest zone in the enzymatic assay, supporting its role in degrading the insect cuticle through chitinase, protease, and lipase activities. Overall, the combination of *B. bassiana* WS and *T. asperellum* A116 has strong potential as a multimicrobial biocontrol agent and offers opportunities for the development of more effective and sustainable biological control strategies.

ACKNOWLEDGMENTS

The authors sincerely thank the Biological Control Laboratory, Faculty of Agriculture, Andalas University, for providing the facilities and support necessary for conducting this research

FUNDING

The authors declare that no funds, grants, or other support were received during the preparation of this manuscript.

AUTHORS' CONTRIBUTIONS

All authors contributed to the completion of this article. IYV, T, HR, and Y contributed to the refinement of the research flow, data analysis, interpretation, and structure of the manuscript. All authors have read and approved the final version of the manuscript.

COMPETING INTEREST

The authors declare no conflict of interest regarding the publication of this manuscript.

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