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Research Article

Endophytic Entomopathogenic Fungi Negatively Impact on Growth and Development of *Spodoptera frugiperda* J.E. Smith (Lepidoptera: Noctuidae)

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ABSTRACT

An alternative method for controlling *Spodoptera frugiperda* applies entomopathogenic fungi (EPF). The present research aimed to determine the impact of the endophytic EPF on the growth and development of *S. frugiperda*. Twenty molecularly identified isolates of the endophytic EPF were used in seed treatments with the fungal suspension 1×10^{10} conidia.mL^{-1}. The endophytic EPF that colonized corn leaves eaten by the neonate *S. frugiperda* larvae was able to significantly decrease the body weight of the larvae and pupae. The endophytic EPF could prolong the developmental time of all instar larvae and pupae. The endophytic EPF could raise larval and pupal mortality and reduce the ability of adults to emerge from pupae, and decrease egg laying by females. The lowest percentage of adult emergence was observed in the adults from larvae consuming corn leaves colonized with *Beauveria bassiana* JaGiP and JgSPK isolates, which were 34.67% and 24%, respectively. Consequently, a reduced adult emergence could lead to a high cumulative death rate of 76% from larvae to adults. Finally, the endophytic EPFs negatively affect *S. frugiperda* growth and development. *B. bassiana* JaGiP and JgSPK isolates are the most pathogenic fungi in inhibiting the growth and development of *S. frugiperda*. They are promising candidates for controlling *S. frugiperda* in the corn field.

1. Introduction

The fall armyworm (FAW), *Spodoptera frugiperda* J.E. Smith (Lepidoptera: Noctuidae), first attacked corn in West Sumatra, Indonesia, in March 2019 (Sartiami *et al*. 2020). The pest is a migratory herbivorous moth native to South America. The FAW has spread to over 80 countries within six to seven years. It is an imminent menace to the agricultural sector in Southern Europe (Wyckhuys *et al*. 2024). In Indonesia, it has spread to almost every province, such as Bengkulu (Ginting *et al*. 2020), South Sumatra (Herlinda *et al*. 2020), Bali (Supartha *et al*. 2021), and West Java (Russianzi *et al*. 2021). It is polyphagous and attacks various species of plants, including maize (*Zea mays* L) and rice (*Oryza sativa* L.). In Indonesia, two strains of FAW, the corn and rice strains, have been reported (Herlinda *et al*. 2022b). The pest has been reported to cause $9.4 billion in crop losses in Africa (Eschen *et al*. 2021). The larval stage of FAW is very destructive and can destroy shoots, leaves, and growing points of maize (Herlinda *et al*. 2022b). If the pest invades the maize at the beginning of the vegetative stage, its damage can approach 100% (Supartha *et al*. 2021).

Due to the insect's voracious appetite and obvious damage to the foliage, synthetic insecticides are being used excessively (Wyckhuys *et al*. 2024). Most farmers in Indonesia rely on synthetic insecticides to control *S. frugiperda* (Asfiya *et al*.2022). Numerous instances of *S. frugiperda* resistance have been caused by the extensive usage of insecticides (Boaventura *et al*. 2020). The resistance to spinosad, organophosphorus insecticides, and pyrethroid of invaded *S. frugiperda* is at a moderate to high level (Zhang *et al*. 2021). Modes of insecticide entry that are inaccurate are not just deadly to *S. frugiperda* (Silva *et al*. 2020), but also kill its natural enemies, such as chlorpyrifos, which can harm the egg parasitoid, *Telenomus remus* (Nixon) (Hymenoptera: Platygastridae) (Amaro *et al*. 2018). In fact, *S. frugiperda* in the corn field has abundant natural enemies, e.g., *T. remus* and larval parasitoid, *Chelonus formosanus* Sonan (Hymenoptera: Braconidae) (Herlinda *et al*. 2023), and they can be disturbed by spraying the synthetic insecticides. Consequently, alternative strategies for controlling FAW are required, such as using entomopathogenic fungi (EPF).

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Previous studies found that conidia of the EPF adhere topically to larval bodies and can kill *S. frugiperda* larvae effectively (Herlinda *et al*. 2020), but they do not kill the adult egg parasitoid, *T. remus* (Amaro *et al*. 2018). However, the adult longevity of *Trichogramma pretiosum* Riley (Hymenoptera: Trichogrammatidae) developed from host eggs that had been treated with *Metarhizium anisopliae* (Metschn.) Sorokin reduces significantly (Potrich *et al*. 2017). The endophytic EPFs penetrate and colonize within corn leaf tissue through seed treatment is a better option than the fungal topical application (Sari *et al*. 2023a). The use of endophytic EPF for seed treatment was recognized to be the "first line of defense" against *S. frugiperda* (Kinyungu *et al*. 2023). Aside from plant defense, the seed treatment with the endophytic EPFs was addressed specifically to kill the larvae of *S. frugiperda* (Sari *et al*. 2023b) and was not harmful to its parasitoids (Putri *et al*. 2024) or predators due to the endophytic EPF within plant tissue (Akutse *et al*. 2019). Our previous research has found 20 isolates of the endophytic EPF from plant leaves, shoots, and roots, and they were molecularly identified (Herlinda *et al*. 2021). The endophytic EPFs have also been investigated for their potential to decrease the FAW adult emergence and the number of eggs laid (Herlinda *et al*. 2022a). However, limited information is now available regarding how the fungi impact the FAW growth and development. The impact of the endophytic EPF on the growth and development of *S. frugiperda* needed to be investigated. Therefore, the purpose of the present study was to observe the impact of the endophytic EPF on the growth and development of *S. frugiperda*.

2. Materials and Methods

2.1. Preparation of the Endophytic Entomopathogenic Fungi

From May to July 2023, the present experiment was conducted at the Entomology Laboratory, Department of Plant Protection, Faculty of Agriculture, Universitas Sriwijaya, Indonesia. In the present research, there were 20 isolates of the endophytic EPF cultured and used. They were from plants in South Sumatra, Indonesia, and maintained at the Entomology Laboratory. Each isolate was separated into single spores that were used for molecular identification and had been identified molecularly in 2021 (Table 1) (Herlinda *et al*. 2021). Because these EPF could colonize plants as endophytes

Table 1. Isolates and species of endophytic EPF from South Sumatra. Indonesia used in the present research

Isolate origin	Location (village, district/ciy)	Fungal isolate	Fungal spesies	Gen bank acc. no.	References
Bananas	Tanjung Pering. Ogan Ilir	PsgTjPr	*Aspergillus niger*	MZ242060	(Herlinda *et al.* 2021)
Maize	Banyuurip. Banyuasin	JgByU	*Aspergillus niger*	MZ242059	(Herlinda *et al*. 2021)
Maize	Banyuurip. Banyuasin	JaBuBys	*Aspergillus niger*	MZ242058	(Herlinda *et al*. 2021)
Maize	Purwosari. Banyuasin	JgPWSR	*Aspergillus flavus*	MZ359829	(Herlinda *et al*. 2021)
	Simpang Padang Karet. Pagar Alam				
Maize	Gunung Ibul. Prabumulih	JgSPK	*Beauveria bassiana*	MZ356494	(Herlinda *et al*. 2021)
	Simpang Padang Karet. Pagar Alam				
Maize	Curup Jare. Pagar Alam	JaGiP	*Beauveria bassiana*	MZ356495	(Herlinda *et al*. 2021)
Maize	Tanjung Pering. Ogan Ilir	JaSpkPGA(2)	*Beauveria bassiana*	MZ356496	(Herlinda *et al.* 2021)
Maize	Tanjung Pering. Ogan Ilir	JgCrJr	*Beauveria bassiana*	MZ356497	(Herlinda *et al*. 2021)
Maize	Tanjung Pering. Ogan Ilir	JaTpOi (1)	*Beauveria bassiana*	MZ356498	(Herlinda *et al*. 2021)
Ridged gourd	Curup Jare. Pagar Alam	GaTpeOi	*Chaetomium* sp.	MZ359734	(Herlinda *et al*. 2021)
Maize					
Bananas	Curup Jare. Pagar Alam	JgTjPr	*Chaetomium* sp.	MZ359736	(Herlinda *et al*. 2021)
Red chilies	Gunung Ibul. Prabumulih	PiCrPga	*Chaetomium* sp.	MZ359735	(Herlinda *et al.* 2021)
Maize	Tanjung Payang. Pagar Alam	CaCjPga	*Chaetomium* sp.	MZ359737	(Herlinda *et al*. 2021)
Red chilies	Mulia Sari. Banyuasin	JaGiPRB	*Curvularia lunata*	MZ359815	(Herlinda *et al.* 2021)
Maize	Simpang Padang Karet.	CMTJP	*Curvularia lunata*	MZ359816	(Herlinda *et al*. 2021)
Maize	Pagar Alam	JaMsBys	*Curvularia lunata*	MZ359819	(Herlinda *et al*. 2021)
Maize	Telang Sari. Banyuasin	JaSpkPga(3)	*Curvularia lunata*	MZ359818	(Herlinda *et al*. 2021)
	Tanjung Payang. Pagar Alam	JgTgSr	*Curvularia lunata*	MZ359817	(Herlinda *et al*. 2021)
Red chilies		CaTpPga	*Metarhizium anisopliae*	MZ242073	(Herlinda *et al*. 2021)
Maize	Tanjung Pering. Ogan Ilir	JaTpOi(2)	*Penicillium citrinum*	MZ359812	(Herlinda *et al*. 2021)

and kill host insects as entomopathogens, so it was determined that they were endophytic EPF (Herlinda *et al*. 2022a). They were cultured on agar medium (SDA, Sabouraud Dextrose Agar). Prior to fungal culture, the SDA (65 g of SDA in 1 L of sterile distilled water) was boiled to dissolve it thoroughly, and then autoclaved at 121°C for 20 min. The fungal culture (Ø 10 mm) was added to Petri dishes in a laminar flow cabinet and incubated for 14 days at 25°C. In order to obtain a higher fungal conidia concentration, the agar fungal culture was regrown in the Sabouraud Dextrose Broth (SDB) and incubated for 14 days with fermentation in a shaker for 7 days (at 120 rpm) and 7 days without shaking (Sari *et al*. 2023a). The fungal concentration of spores for this experiment was determined using a hemocytometer.

2.2. Preparation of the Experimental *Spodoptera frugiperda*

The mass-rearing of the FAW was carried out in the laboratory with room temperature (25-26°C) and 82-83% of relative humidity, following the method of Herlinda *et al*. (2020). The photoperiod of the room was managed by using 12 hours of light and 12 hours of dark. *S. frugiperda* larvae were kept individually because of their cannibalistic behaviour. The larvae were fed with artificial food, and the food was changed every two days. In order for the adult insects to lay their eggs, all pupae that emerged from the larvae were put within a cage (50 × 50 × 50 cm^3) with wire mesh, and in the cage, there was sterile soil for the pupal habitat and a young corn plant for the habitat where eggs were laid. To gain a homogeneous FAW culture, the mass-rearing was carried out for over 10 generations. The eggs laid and larvae hatched were collected to be used in the bioassay of the present research.

2.3. Seed Inoculation and Confirmation of Endophytic EPF Colonization

Bonanza' (yellow) sweet corn (*Zea mays* Linn. var. Saccharata Sturt) was used for the present experiment. Corn seeds (N = 75 seeds per isolate) were surface sterilised in a laminar flow cabinet with 70% alcohol for 3 min and dipped for 2 min in 1.5% NaOCl (sodium hypochlorite), and flushed three times with sterile distilled water, finally dried on sterile filter paper until the residual water vaporized (Elfita *et al*. 2019). The third flush water was also cultured into agar medium (SDA) in order to ensure the success of the surface

sterilization process (Inglis *et al*. 2012). Subsequently, the sterilized seeds were immersed for 24 hours in 10 mL of the fungal suspension, which contained 1 × 1010 conidia mL^{-1} of each fungal isolate, and the control sterilized seeds were submerged in 10 mL of sterile distilled water. To observing the fungal colonization and distribution within corn seedling, this experiment used method of Sari *et al*. (2022) by cutting tip leaves of 14-day-old corn and culturing them onto the SDA medium to detect the mycelia of the endophytic fungi and also used Fluorescein Diacetate (FDA) following method of Wei and Liu (2021) were mixed in a 1:1 ratio. The seeds inoculated with the endophytic EPF and control seeds (uninoculated) were incubated for 2 weeks in a hydroponic medium following the method of Novianti *et al*. (2020) and maintained in laboratory conditions (12 Light: 12 Dark). The plant tissue samples (inoculated or uninoculated seedlings) were examined under a fluorescence microscope (450-490 nm) to detect fungal colonization within corn seedlings.

2.4. Growth and Development Observation of *Spodoptera frugiperda*

The inoculated and uninoculated corn seedlings were fed to neonates (first instar larvae or larvae hatching within 24 hours). The treated larvae (N = 75 per isolate) were allowed to consume fungus-inoculated seedlings for a period of 12 hours, while the untreated larvae (the control) were fed uninoculated seedlings. The larvae were maintained separately in a container (height 3.9 cm, Ø 5.6 cm). Then, the larvae were provided with an artificial diet, which was changed every day for a fresh one. The artificial diet was created in accordance with the method described by Sreelakshmi and Mathew (2017). This experiment was conducted using a completely randomized design (CRD) and This experiment was tried three times for each isolate and carried out in a controlled environment with consistent relative humidity and temperature of 25°C and 97%. The growth variables observed were colonization of fungi within leaves, weight and length of *S. frugiperda* larvae and pupae, larval mortality, pupal emergence, and pupae becoming adults, sex ratio, and number of eggs laid by a female of *S. frugiperda*. The developmental variables observed were the developmental time of larvae and pupae and adult longevity. The morphology of unhealthy larvae, pupae, and adults, and the dead larvae and pupae, were recorded daily. The behavior of unhealthy larvae was also observed every day.

2.4. Data Analysis

Data analysis for comparing colonization of fungi within leaves, weight and length of *S. frugiperda* larvae and pupae, larval mortality, pupal emergence, and pupae becoming adults, sex ratio, number of eggs, developmental time of larvae and pupae, and adult longevity among treatments was ANOVA (analysis of variance). To determine the differences among treatments (isolates and control) at P = 5% was used Tukey's test (HSD). The calculation was conducted by using the SAS University Edition 2.7 9.4 M5 software.

3. Results

3.1. Confirmation of Endophytic Colonization

After seed soaking procedure, the percentage of fungal colonization in the leaves started to rise between 7 and 14 days later. At 14 days after inoculation, the percentage of fungal colonization of all isolates (66.67-100%) was significantly different from the control ($P<0.0001$) (Table 2). The percentage of colonization were not significantly different among fungal isolates. The seed immersion treatment resulted in the tip leaves of treated maize grown on the SDA medium being overgrown with the endophytic EPF isolates. Therefore, all fungal isolates (Table 1) used in the present research were proven to be endophytic EPFs.

3.2. Endophytic EPF Impact on *Spodoptera frugiperda* Growth

FAW neonate larvae fed on the maize leaves inoculated with the endophytic EPF significantly induced the 1st, 4th, and 5th instar weight reduction. However, the weight of 2nd, 3rd, and 6th larvae fed on the fungal inoculated corn was not significantly different from those of untreated fungal treatment or control ($P<0.0001$) (Table 3). The lightest body of the 5th larvae (35.10 mg) have occurred on the larvae treated with *Beauveria bassiana* (Bals.) Vuill. JaGiP isolate. All instars fed on young maize colonized with endophytic EPF had significantly shorter body length compared to the control ($P<0.0001$) (Table 4). Similarly, the length and weight of pupae treated with the endophytic EPF were lower than untreated pupae ($P<0.0001$) (Table 5). The smallest pupae of *S. frugiperda* came from the neonate larvae consuming leaves inoculated with *B. bassiana* JaGiP isolate. Therefore, the larvae consuming leaves inoculated with the endophytic EPF had a negative effect on the larval and pupal *S. frugiperda* growth.

Table 2. Mean colonization of fungi within leaves treated with endophytic EPF at 7 and 14 days after inoculation

Fungal species	Fungal isolate	Mean colonization (%)	
		7 days after inoculation	14 days after inoculation
Control	-	0.00^{d}	0.00^{b}
Aspergillus niger	PsgTjPr	40.00^{abc}	86.67^{a}
Aspergillus niger	JgByU	20.00^{cd}	73.33^{a}
Aspergillus niger	JaBuBys	53.33^{abc}	80.00^{a}
Aspergillus flavus	JgPWSR	40.00^{abc}	80.00^{a}
Beauveria bassiana	JgSPK	90.00^{a}	93.33^{a}
Beauveria bassiana	JaGiP	73.33^{abc}	93.33^{a}
Beauveria bassiana	JaSpkPGA(2)	66.67^{abc}	93.33^{a}
Beauveria bassiana	JgCrJr	80.00^{ab}	100.00^{a}
Beauveria bassiana	JaTpOi (1)	53.33^{abc}	100.00^{a}
Chaetomium sp.	GaTpeOi	40.00^{abc}	86.67^{a}
Chaetomium sp.	JgTjPr	33.33^{bcd}	66.67^{a}
Chaetomium sp.	PiCrPga	26.67^{bcd}	73.33^{a}
Chaetomium sp.	CaCjPga	26.67^{bcd}	80.00^{a}
Curvularia lunata	JaGiPRB	20.00^{cd}	73.33^{a}
Curvularia lunata	CMTJP	26.67^{bcd}	66.67^{a}
Curvularia lunata	JaMsBys	40.00^{abc}	73.33^{a}
Curvularia lunata	JaSpkPga(3)	26.67^{bcd}	93.33^{a}
Curvularia lunata	JgTgSr	20.00^{cd}	66.67^{a}
Metarhizium anisopliae	CaTpPga	46.67^{abc}	73.33^{a}
Penicillium citrinum	JaTpOi(2)	46.67^{abc}	66.67^{a}
F-value		5.62*	6.92*
P-value		1.82×10^{-6}	1.20×10^{-7}
HSD value		2.03	210.45

* : significantly different; values within a column followed by the different letters were significantly different at P<0.05 according to Tukey's test (HSD)

Table 3. Weight of *Spodoptera frugiperda* larvae fed on young maize colonized with endophytic EPF

Fungal species	Fungal isolate	Larval weight (mg larvae^{-1})					
		1st larvae	2nd larvae	3rd larvae	4th larvae	5th larvae	6th larvae
Control	-	7.23^{abc}	15.67	39.00	73.73^{a}	152.14^{a}	264.53
Aspergillus niger	PsgTjPr	6.01^{bc}	19.56	38.28	65.84^{ab}	81.80^{bc}	119.08
Aspergillus niger	JgByU	8.78^{abc}	18.51	45.46	67.43^{ab}	89.62^{b}	110.96
Aspergillus niger	JaBuBys	10.44^{abc}	17.23	32.40	56.26^{abc}	90.27^{b}	109.71
Aspergillus flavus	JgPWSR	8.48^{a}	18.74	36.14	58.89^{abc}	74.82^{bc}	109.65
Beauveria bassiana	JgSPK	4.92^{c}	10.96	27.68	47.42^{abc}	70.94^{bc}	104.81
Beauveria bassiana	JaGiP	5.05^{c}	6.67	14.18	20.83^{c}	35.10^{c}	108.97
Beauveria bassiana	JaSpkPGA(2)	6.26^{ab}	9.71	13.63	38.36^{abc}	62.97^{bc}	94.29
Beauveria bassiana	JgCrJr	7.28^{bc}	12.62	16.87	28.16^{bc}	64.27^{bc}	429.46
Beauveria bassiana	JaTpOi (1)	5.93^{abc}	9.41	16.15	33.86^{abc}	67.03^{bc}	119.66
Chaetomium sp.	GaTpeOi	6.00^{bc}	10.21	19.84	52.65^{abc}	77.80^{bc}	112.85
Chaetomium sp.	JgTjPr	7.11^{abc}	13.01	19.75	42.25^{abc}	68.93^{bc}	114.30
Chaetomium sp.	PiCrPga	6.80^{abc}	18.48	25.83	34.74^{abc}	47.27^{bc}	91.93
Chaetomium sp.	CaCjPga	7.29^{ab}	11.41	14.01	18.99^{c}	64.79^{bc}	103.50
Curvularia lunata	JaGiPRB	7.39^{abc}	11.19	15.29	23.62^{abc}	64.76^{bc}	119.60
Curvularia lunata	CMTJP	6.26^{abc}	9.71	13.63	38.36^{c}	62.97^{bc}	94.29
Curvularia lunata	JaMsBys	9.00^{abc}	13.40	23.82	35.24^{abc}	82.63^{bc}	112.00
Curvularia lunata	JaSpkPga(3)	9.33^{bc}	21.07	33.98	37.22^{abc}	81.86^{bc}	115.26
Curvularia lunata	JgTgSr	6.62^{abc}	14.46	31.32	52.70^{abc}	84.96^{bc}	106.09
Metarhizium anisopliae	CaTpPga	7.44^{bc}	11.91	19.91	34.11^{abc}	59.18^{bc}	89.49
Penicillium citrinum	JaTpOi(2)	6.44^{abc}	11.32	18.52	27.95^{bc}	52.34^{bc}	94.07
F-value		3.65**	1.39^{ns}	2.18^{ns}	4.24**	5.72**	1.05^{ns}
P-value		2.01×10^{-4}	0.18	0.02	4.01×10^{-5}	1.03×10^{-6}	0.43
HSD value		3.92			41.09	51.24	-

ns : not significantly different; * = significantly different; values within a column followed by the different letters were significantly different at P<0.05 according to Tukey's test (HSD)

Table 4. Length of *Spodoptera frugiperda* larvae fed on young maize colonized with endophytic EPF

Fungal species	Fungal isolate	Larval length (mm)					
		1st larvae	2nd larvae	3rd larvae	4th larvae	5th larvae	6th larvae
Control	-	2.56^{def}	7.67^{cdef}	13.85^{bcde}	19.28^{ab}	23.05^{a}	24.96^{a}
Aspergillus niger	PsgTjPr	2.50^{ef}	5.89^{defg}	12.11^{abcde}	14.89^{bcde}	22.39^{a}	24.30^{a}
Aspergillus niger	JgByU	5.45^{a}	12.16^{a}	18.56^{a}	20.53^{a}	23.23^{a}	24.89^{a}
Aspergillus niger	JaBuBys	5.88^{a}	11.55^{ab}	17.33^{ab}	19.58^{ab}	23.16^{a}	24.31^{a}
Aspergillus flavus	JgPWSR	4.71^{abc}	10.94^{abc}	14.18^{abcde}	16.47^{abcd}	21.85^{ab}	23.73^{a}
Beauveria bassiana	JgSPK	2.07^{f}	5.52^{defg}	10.71^{cde}	12.19^{def}	12.79^{de}	13.84^{b}
Beauveria bassiana	JaGiP	2.45^{bcdef}	7.77^{cdef}	10.64^{ef}	11.94^{def}	12.60^{de}	13.79^{b}
Beauveria bassiana	JaSpkPGA(2)	3.05^{cdef}	4.18^{fg}	5.82^{gh}	9.31^{fg}	11.82^{ef}	13.05^{b}
Beauveria bassiana	JgCrJr	3.03^{cdef}	3.67^{g}	4.53^{h}	8.02^{fg}	10.42^{ef}	13.10^{b}
Beauveria bassiana	JaTpOi (1)	2.79^{cdef}	3.63^{g}	4.13^{h}	6.36^{g}	8.05^{f}	10.25^{c}
Chaetomium sp.	GaTpeOi	2.58^{def}	7.48^{cdef}	14.23^{abcde}	18.82^{ab}	21.94^{ab}	23.79^{a}
Chaetomium sp.	JgTjPr	2.62^{def}	6.49^{defg}	11.52^{ef}	19.82^{ab}	22.72^{a}	23.57^{a}
Chaetomium sp.	PiCrPga	3.22^{bcdef}	12.29^{a}	15.52^{abcd}	17.0^{3abcd}	18.56^{bc}	24.88^{a}
Chaetomium sp.	CaCjPga	5.07^{ab}	10.57^{abc}	13.76^{bcde}	15.80^{abcd}	21.26^{ab}	23.19^{a}
Curvularia lunata	JaGiPRB	4.72^{a}	8.49^{bcde}	16.24^{abcd}	20.95^{a}	23.09^{a}	24.88^{a}
Curvularia lunata	CMTJP	3.05^{abc}	4.18^{bcde}	5.82^{abc}	9.31^{a}	11.82^{a}	13.05^{a}
Curvularia lunata	JaMsBys	4.19^{abcde}	8.47^{bcde}	13.96^{abcde}	17.55^{abc}	21.16^{ab}	23.67^{a}
Curvularia lunata	JaSpkPga(3)	4.36^{abcde}	8.68^{abcd}	11.22^{def}	16.14^{abcd}	23.88^{a}	24.47^{a}
Curvularia lunata	JgTgSr	4.49^{abcde}	10.19^{abc}	17.28^{ab}	18.20^{abc}	21.05^{ab}	24.73^{a}
Metarhizium anisopliae	CaTpPga	3.09^{cdef}	4.96^{efg}	7.45^{fgh}	10.10^{efg}	10.86^{ef}	11.85^{bc}
Penicillium citrinum	JaTpOi(2)	2.52^{ef}	6.37^{defg}	10.22^{efg}	13.05^{cdef}	15.89^{cd}	24.06^{a}
F-value		10.96**	15.83**	23.47**	20.15**	58.04**	160.60**
P-value		6.89×10^{-11}	1.36×10^{-13}	$<2 \times 10^{-16}$	1.82×10^{-15}	$<2 \times 10^{-16}$	$<2 \times 10^{-16}$
HSD value		1.93	3.66	4.61	5.34	3.77	2.32

* : significantly different; values within a column followed by the different letters were significantly different at P<0.05 according to Tukey's test (HSD)

Table 5. Weight and length of *Spodoptera frugiperda* pupae from larvae fed on young maize colonized with endophytic EPF

Fungal species	Fungal isolate	Pupal weight (mg pupae^{-1})	Pupal length (mm)
Control	-	281.33^{ab}	14.77^{abc}
Aspergillus niger	PsgTjPr	299.00^{a}	13.60^{cdef}
Aspergillus niger	JgByU	285.33^{ab}	13.90^{bcdef}
Aspergillus niger	JaBuBys	293.67^{ab}	13.60^{cdef}
Aspergillus flavus	JgPWSR	276.67^{abc}	13.83^{bcdef}
Beauveria bassiana	JgSPK	169.00^{defg}	13.00^{ef}
Beauveria bassiana	JaGiP	160.67^{efg}	12.93^{f}
Beauveria bassiana	JaSpkPGA(2)	140.00^{g}	13.40^{def}
Beauveria bassiana	JgCrJr	140.00^{g}	13.30^{def}
Beauveria bassiana	JaTpOi (1)	133.00^{g}	13.23^{def}
Chaetomium sp.	GaTpeOi	240.67^{abc}	13.53^{cdef}
Chaetomium sp.	JgTjPr	223.00^{abcde}	14.87^{ab}
Chaetomium sp.	PiCrPga	236.33^{abcd}	15.17^{a}
Chaetomium sp.	CaCjPga	204.33^{cdef}	13.80^{bcdef}
Curvularia lunata	JaGiPRB	237.00^{abc}	14.00^{abcdef}
Curvularia lunata	CMTJP	232.33^{abcd}	14.20^{abcde}
Curvularia lunata	JaMsBys	253.33^{abc}	14.17^{abcdef}
Curvularia lunata	JaSpkPga(3)	232.00^{abcd}	13.77^{bcdef}
Curvularia lunata	JgTgSr	219.00^{bcde}	14.27^{abcd}
Metarhizium anisopliae	CaTpPga	150.10^{fg}	13.30^{def}
Penicillium citrinum	JaTpOi(2)	292.67^{ab}	14.33^{abcd}
F-value		19.02*	6.60*
P-value		5.15×10^{-15}	1.47×10^{-07}
HSD value		2.37	0.12

* : significantly different; values within a column followed by the different letters were significantly different at P<0.05 according to Tukey's test (HSD)

3.3. Endophytic EPF Impact on the Development of *Spodoptera frugiperda*

FAW neonate larvae feeding maize leaves inoculated with the endophytic EPF could induce significantly higher larval mortality compared to the control ($P<0.05$) (Table 6). Higher mortality occurred on larvae consuming leaves inoculated with *B. bassiana* JgSPK isolate and JaGiP isolate. The emergence of pupae and adults treated with the endophytic EPF decreased significantly compared to the control ($P<0.0001$). The sex ratio of *S. frugiperda* was not influenced by the endophytic EPF ($P>0.05$). Eggs laid by females treated with the endophytic EPF could decrease significantly compared to the control ($P<0.0001$). The developmental time of all instar larvae ($P<0.05$) (Table 7) and pupae ($P<0.0001$) could be prolonged by the endophytic EPF. However, the endophytic EPF did not affect the adult longevity of *S. frugiperda* ($P>0.05$). The total lifespan of *S. frugiperda* treated with the endophytic EPF was longer than that of the control ($P<0.0001$) (Table 8). Therefore, the larvae fed on fungal colonized corn leaves had a negative effect on the *S. frugiperda* development.

The FAW larvae consuming leaves colonized with the endophytic EPF could induce unhealthy and abnormal larvae. The unhealthy larval body became hardened like mummies, brown in color, shriveled, and smaller than the body of the control (Figure 1). However, the healthy larval body of the control had normal symptoms, namely a bendable body and a bigger size, with a green color. The unhealthy larvae usually died with their bodies covered with conidia and mycelia. The unhealthy larvae infected by the endophytic EPF that were able to become pupae could produce abnormal pupae with a small body, hardened, and shriveled (Figure 2). Finally, the unhealthy pupae infected by the endophytic EPF that were able to become adults could induce malformed adults with shrunken and small bodies, and folded wings, and some adults failed to emerge from the pupae (Figure 3).

4. Discussion

In the present research, all fungal isolates of the EPFs used in this study were able to colonize leaves of young maize when inoculated by seed immersion

Table 6. Percentage of larval mortality, pupal and adult emergence, sex ratio, eggs laid by a female, and viable eggs of *Spodoptera frugiperda* from larvae fed on young maize colonized with endophytic EPF

Fungal species	Fungal isolate	Larval mortality (%)	Pupal emergence (%)	Adult emergence (%)	Sex ratio	Eggs laid per female
Control	-	2.67^{d}	97.33^{a}	97.33^{a}	0.88	72.11^{a}
Aspergillus niger	PsgTjPr	9.33^{bcd}	90.67^{ab}	85.33^{ab}	0.82	19.09^{bcde}
Aspergillus niger	JgByU	9.33^{abcd}	89.33^{abcd}	89.33^{ab}	0.86	19.08^{bcde}
Aspergillus niger	JaBuBys	6.67^{bcd}	93.33^{ab}	92.00^{a}	0.93	17.94^{bcde}
Aspergillus flavus	JgPWSR	9.33^{bcd}	90.67^{ab}	90.67^{a}	0.85	17.61^{bcde}
Beauveria bassiana	JgSPK	36.00^{a}	44.00^{f}	24.00^{e}	0.44	9.44^{de}
Beauveria bassiana	JaGiP	30.67^{ab}	53.33^{ef}	34.67^{de}	0.41	8.89^{de}
Beauveria bassiana	JaSpkPGA(2)	17.33^{abcd}	74.67^{bcdef}	61.33^{bcd}	0.85	29.19^{b}
Beauveria bassiana	JgCrJr	26.67^{abc}	57.33^{def}	41.33^{cde}	0.67	9.44^{de}
Beauveria bassiana	JaTpOi (1)	22.67^{abcd}	62.67^{cdef}	46.67^{cde}	0.62	10.74^{cde}
Chaetomium sp.	GaTpeOi	6.67^{bcd}	90.67^{abc}	84.00^{ab}	0.74	24.24^{bc}
Chaetomium sp.	JgTjPr	12.00^{abcd}	85.33^{abcde}	77.33^{abc}	0.85	18.36^{bcde}
Chaetomium sp.	PiCrPga	8.00^{abcd}	89.33^{abcd}	86.67^{ab}	0.79	21.73^{bcd}
Chaetomium sp.	CaCjPga	5.33^{cd}	93.33^{ab}	92.00^{ab}	0.77	20.75^{bcde}
Curvularia lunata	JaGiPRB	8.00^{abcd}	92.00^{ab}	89.33^{ab}	0.78	19.19^{bcde}
Curvularia lunata	CMTJP	5.33^{bcd}	94.67^{ab}	94.67^{a}	0.65	18.23^{bcde}
Curvularia lunata	JaMsBys	4.00^{cd}	93.33^{ab}	92.00^{ab}	0.70	14.10^{cde}
Curvularia lunata	JaSpkPga(3)	5.33^{bcd}	92.00^{abc}	90.67^{ab}	1.04	7.08^{e}
Curvularia lunata	JgTgSr	10.67^{abcd}	89.33^{abcd}	88.00^{ab}	1.01	17.35^{bcde}
Metarhizium anisopliae	CaTpPga	13.33^{abcd}	78.67^{abcdef}	74.67^{abc}	0.67	6.98^{e}
Penicillium citrinum	JaTpOi(2)	14.67^{abcd}	80.00^{abcde}	78.67^{abc}	0.63	15.28^{bcde}
F-value		3.84**	7.82**	12.10**	0.51**	24.84**
P-value		1.46×10^{-4}	1.29×10^{-8}	1.34×10^{-11}	0.97	$<2 \times 10^{-16}$
HSD value		21.68	21.74	23.20	-	14.58

* : significantly different; values within a column followed by the different letters were significantly different at $P<0.05$ according to Tukey's test (HSD)

Table 7. Developmental time of larvae fed on young maize colonized with endophytic EPF

Fungal species	Fungal isolate	Development time of larvae (days)					
		1st larvae	2nd larvae	3rd larvae	4th larvae	5th larvae	6th larvae
Control	-	2.68^{ab}	3.30^{efg}	2.35^{e}	2.23^{c}	3.24^{bc}	2.99^{c}
Aspergillus niger	PsgTjPr	2.59^{ab}	3.71^{b}	4.00^{c}	4.45^{a}	2.96^{c}	3.72^{abc}
Aspergillus niger	JgByU	2.69^{a}	3.59^{bcde}	4.56^{b}	3.65^{b}	3.65^{ab}	3.60^{abc}
Aspergillus niger	JaBuBys	2.67^{ab}	3.14^{gh}	2.65^{e}	3.74^{b}	3.24^{bc}	3.54^{abc}
Aspergillus flavus	JgPWSR	2.63^{ab}	3.16^{fgh}	3.61^{cd}	4.26^{a}	3.28^{bc}	4.01^{ab}
Beauveria bassiana	JgSPK	2.63^{ab}	3.68^{bc}	2.66^{e}	3.71^{b}	3.65^{ab}	3.51^{abc}
Beauveria bassiana	JaGiP	2.60^{ab}	4.28^{a}	5.46^{a}	4.45^{a}	3.28^{bc}	3.18^{bc}
Beauveria bassiana	JaSpkPGA(2)	2.57^{ab}	3.42^{bcdefg}	2.45^{e}	2.21^{c}	3.55^{ab}	3.37^{abc}
Beauveria bassiana	JgCrJr	2.58^{ab}	3.42^{bcdefg}	2.58^{e}	2.53^{c}	3.57^{ab}	3.43^{abc}
Beauveria bassiana	JaTpOi (1)	2.56^{ab}	3.44^{bcdefg}	2.46^{e}	2.58^{c}	3.56^{ab}	3.44^{abc}
Chaetomium sp.	GaTpeOi	2.67^{ab}	3.67^{bc}	5.52^{a}	3.63^{b}	3.68^{ab}	3.71^{abc}
Chaetomium sp.	JgTjPr	2.63^{ab}	3.71^{b}	3.63^{cd}	4.60^{a}	3.69^{ab}	4.28^{a}
Chaetomium sp.	PiCrPga	2.65^{ab}	3.64^{bcd}	3.62^{cd}	4.63^{a}	3.37^{abc}	3.57^{abc}
Chaetomium sp.	CaCjPga	2.68^{ab}	3.29^{efg}	2.34^{e}	2.25^{c}	3.26^{bc}	2.94^{c}
Curvularia lunata	JaGiPRB	2.65^{ab}	3.32^{defg}	2.35^{e}	2.24^{c}	3.24^{bc}	3.09^{bc}
Curvularia lunata	CMTJP	2.65^{ab}	3.35^{cdefg}	2.70^{e}	2.55^{c}	3.66^{ab}	3.41^{abc}
Curvularia lunata	JaMsBys	2.56^{ab}	3.43^{bcdefg}	2.56^{e}	2.49^{c}	3.54^{ab}	3.41^{abc}
Curvularia lunata	JaSpkPga(3)	2.54^{b}	3.44^{bcdefg}	2.46^{e}	2.22^{c}	3.56^{ab}	3.45^{abc}
Curvularia lunata	JgTgSr	2.57^{ab}	2.92^{h}	4.00^{c}	4.61^{a}	3.87^{a}	3.31^{abc}
Metarhizium anisopliae	CaTpPga	2.55^{ab}	3.49^{bcdef}	2.73^{e}	3.38^{b}	2.41^{d}	3.30^{abc}
Penicillium citrinum	JaTpOi(2)	2.55^{ab}	3.50^{bcde}	3.39^{e}	3.52^{b}	3.27^{bc}	3.60^{abc}
F-value		3.29**	18.3**	103.50**	114.50**	12.12**	2.86**
P-value		5.69×10^{-4}	1.03×10^{-14}	$<2 \times 10^{-16}$	$<2 \times 10^{-16}$	1.31×10^{-11}	2.03×10^{-3}
HSD value		0.04	0.08	0.13	0.12	0.13	0.25

* = significantly different; values within a column followed by the different letters were significantly different at P<0.05 according to Tukey's test (HSD)

treatment. The leaves of maize inoculated with the EPFs were overgrown with the fungal mycelia, but no fungal mycelia were found on the leaves of untreated seeds (control). The finding showed that the EPFs from seed treatment could colonize the leaves. So, it confirmed that the EPFs colonized the maize leaves were endophytic. We also found that the leaf tissues that had received a fungal inoculation emitted a fluorescent signal by FDA detection. According to Wei and Liu (2021), the FDA can emit a fluorescent signal only when the plant epidermis combines with fungus. The fungus metabolizes and hydrolyzes the FDA to create products with bright green fluorescence detected by fluorescence microscopy. In the the present research, the percentage of fungal colonization in the maize leaves varied from 66.67% to 100% among 20 isolates at 14 days after seed inoculation. However, the endophytic fungi could live in the tissue for more than 14 days; for example, they were still detected on tomato leaves for up to 30 days following inoculation (Carolina *et al*. 2020). The endophytic EPF could survive in the tissue for a few months (Shikano 2018).

The endophytic EPF could significantly decrease the body weight of the larvae. The larvae consuming leaves inoculated with the *B. bassiana* JaGiP isolate became the smallest ones. Similarly, the tiniest pupae can be produced by larvae consuming the leaves that were inoculated with the *B. bassiana* JaGiP isolate. Thus, the neonate larvae feeding on leaves inoculated with the endophytic EPF negatively affected *S. frugiperda* larval and pupal growth. Furthermore, the larvae that fed on maize leaves inoculated with the fungi could have a higher mortality rate than the control. Larvae had a higher mortality rate when their neonate larvae consumed leaves inoculated with *B. bassiana* JgSPK and JaGiP isolates. It took 3 to 4 days after the neonate larvae were treated with the endophytic EPF, the larvae began to die, which also accorded with the previous study (Sari *et al*. 2023a). Boomsma *et al*. (2014) reported that the hyphae of the endophytic EPF within leaf tissues enter the oral cavity of larvae. Then, the hyphae produce blastospores or conidia in the larval hemolymph, and the secondary metabolites produced by blastospores kill the larvae (Mancillas-Paredes *et al*. 2019). When the larvae the fungus continue to develop saprophytically by taking up the corpse's bodily fluids by taking up the corpse's bodily fluids (Gabarty *et al*. 2014). The fungi have the ability to cause mycosis (Russo *et al*. 2020) and can produce asexual conidia and sexual ascospores

Table 8. Developmental time of *Spodoptera frugiperda* pupae and adult longevity from larvae fed on young maize colonized with endophytic EPF

Fungal species	Fungal isolate	Development time of larvae (days)					
		Prepupae	Pupae	Female adult	Male adult	Egg	Total lifespan
Control	-	2.65^{ab}	6.95^{cde}	3.98	4.40^{ab}	3.00	33.37^{f}
Aspergillus niger	PsgTjPr	2.94^{ab}	10.24^{a}	4.14	4.30^{ab}	3.00	41.75^{ab}
Aspergillus niger	JgByU	3.60^{a}	8.68^{abc}	3.72	3.31^{d}	3.00	40.75^{ab}
Aspergillus niger	JaBuBys	3.60^{a}	6.88^{de}	3.99	4.20^{ab}	3.00	36.45^{de}
Aspergillus flavus	JgPWSR	3.31^{ab}	9.86^{ab}	4.21	4.04^{bc}	3.00	41.34^{ab}
Beauveria bassiana	JgSPK	2.71^{ab}	7.43^{cde}	3.95	4.35^{ab}	3.00	36.94^{cd}
Beauveria bassiana	JaGiP	2.29^{b}	10.58^{a}	4.09	4.42^{ab}	3.00	43.21^{a}
Beauveria bassiana	JaSpkPGA(2)	3.47^{a}	6.53^{e}	3.85	3.63^{cd}	3.00	34.42^{def}
Beauveria bassiana	JgCrJr	3.38^{ab}	6.63^{e}	4.03	4.26^{ab}	3.00	35.15^{def}
Beauveria bassiana	JaTpOi (1)	3.53^{a}	6.75^{de}	4.03	4.39^{ab}	3.00	35.35^{def}
Chaetomium sp.	GaTpeOi	2.29^{b}	9.71^{ab}	4.45	4.43^{ab}	3.00	42.32^{ab}
Chaetomium sp.	JgTjPr	2.47^{ab}	9.85^{ab}	3.62	3.28^{d}	3.00	41.48^{ab}
Chaetomium sp.	PiCrPga	2.29^{b}	9.49^{ab}	3.80	3.98^{bc}	3.00	40.06^{b}
Chaetomium sp.	CaCjPga	3.47^{a}	6.93^{de}	4.35	4.38^{ab}	3.00	34.52^{def}
Curvularia lunata	JaGiPRB	3.37^{ab}	7.08^{cde}	3.62	3.40^{d}	3.00	33.96^{ef}
Curvularia lunata	CMTJP	3.41^{ab}	6.81^{de}	4.23	4.31^{ab}	3.00	35.77^{def}
Curvularia lunata	JaMsBys	3.38^{ab}	6.98^{cde}	3.39	3.42^{d}	3.00	34.75^{def}
Curvularia lunata	JaSpkPga(3)	3.45^{a}	6.62^{e}	3.64	3.34^{d}	3.00	34.39^{def}
Curvularia lunata	JgTgSr	2.85^{ab}	8.66^{abc}	3.83	3.52^{d}	3.00	39.61^{bc}
Metarhizium anisopliae	CaTpPga	3.48^{a}	8.36^{bcd}	4.15	4.32^{ab}	3.00	36.86^{d}
Penicillium citrinum	JaTpOi(2)	3.30^{ab}	9.75^{ab}	4.16	4.58^{a}	3.00	40.06^{b}
F-value		4.89**	18.91**	0.87^{ns}	29.73**	1.00^{ns}	42.15**
P-value		7.46×10^{-6}	5.74×10^{-15}	0.62	$<2 \times 10^{-16}$	0.48	$<2 \times 10^{-16}$
HSD value		0.31	0.30	-	0.11	-	0.22

ns : not significantly different; * = significantly different; values within a column followed by the different letters were significantly different at P<0.05 according to Tukey's test (HSD)

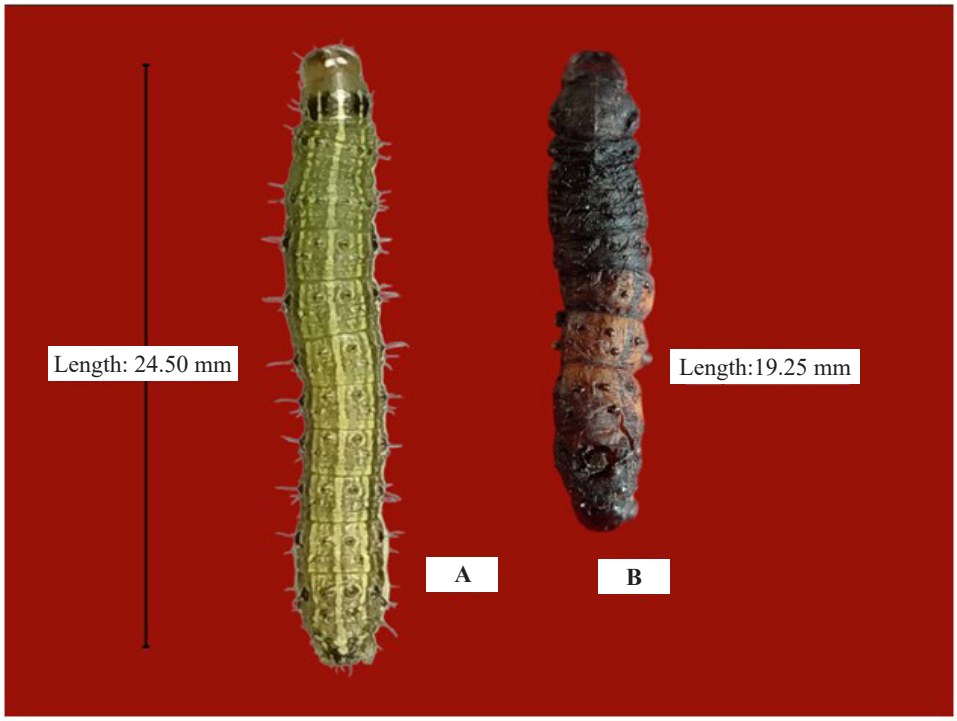

Figure 1. Morphology of *Spodoptera frugiperda* larvae: healthy larvae of control (A) and dead larvae infected by endophytic fungi (B)

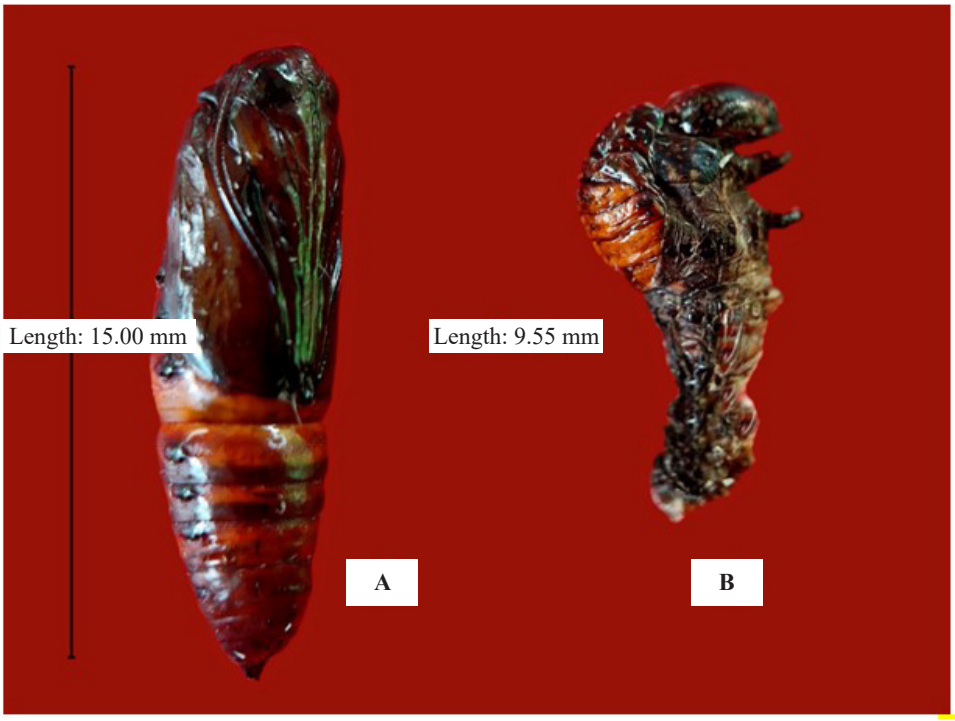

Figure 2. Morphology of *Spodoptera frugiperda* pupae: healthy pupae of control (A) and unhealthy pupae with malformation infected by endophytic fungi (B)

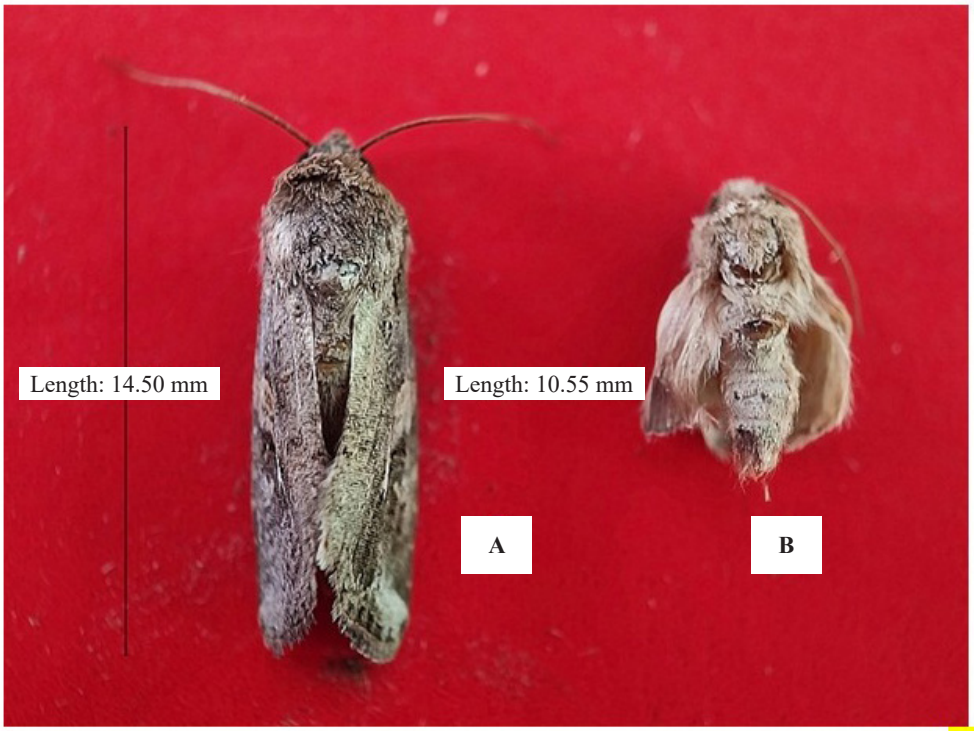

Figure 3. Morphology of *Spodoptera frugiperda* adults: healthy adults of control (A) and unhealthy adults with malformation infected by endophytic fungi (B)

(Boomsma *et al*. 2014). Afterwards, the fungi expand, resulting in the mycelia and spores covering the cadaver corpse, causing mycosis (Sari *et al*. 2022).

Additionally, specific genes present in endophytic EPF can induce the expression of defense mechanisms in the host plants, such as the synthesis of siderophores, competitive exclusion, lytic enzyme release, then, antibiosis and systemic acquired resistance (SAR) and induced systemic resistance (ISR) are examples of indirect defensive mechanisms (Akram *et al*. 2023). The secondary metabolites secreted by the EPFs in plants exert deterring or antifeedant and antibiosis effects on *S. frugiperda* larvae (Jaber and Ownley 2018). The EPFs can also produce terpenoid concentrations against *S. frugiperda* larvae, and after ingesting toxic protein or metabolites, the larvae are killed (Russo *et al*. 2020).

The symptoms of mycosis detected on the deceased larvae in the present research were comparable to those observed in a previous study, where the bodies became dry, shriveled, rigid, and coated in mycelium and fungal spores (Lestari *et al*. 2022). The mycosis just occurred on the FAW larvae treated with the endophytic EPFs, we did not find mycosis on untreated (control) fungal larvae. Mycosis can be found on *S. frugiperda* larvae feeding on plants colonized by endophytic EPFs (Russo *et al*. 2020). In the present study, the abnormal pupae and adults could lead to a higher cumulative mortality rate. Because the deformed pupae's short, folded, or asymmetrical wings obstructed the adults, they could develop into abnormal adults. Consequently, the abnormal adults and pupae treated with the endophytic EPF could increase cumulative mortality and decrease FAW population densities in the field.

In the present research, the endophytic EPF inoculated within maize leaves could prolong the larval and pupal developmental time, and consequently, the total lifespan of the fungal-treated larvae was longer than that of the control. Previous studies have also revealed that the EPF could prolong the insect developmental time (Lopez and Sword 2015) because the fungi decrease the larval ability to digest and ingest the food, causing the larvae to grow slower than usual (Hussain *et al*. 2009). Moreover, the endophytic EPF could significantly decrease the pupal and adult emergence. *S. frugiperda* adults from larvae treated with *B. bassiana* JgSPK and JaGiP isolates had the lowest emergence percentage, namely 24% and 34.67%, respectively. This indicated that the success of adult emergence was very low, and thus, the cumulative mortality from larvae to adults became high, reaching 76%. Therefore, the neonate larvae feeding on leaves inoculated with the endophytic EPF negatively affected *S. frugiperda* development. *B. bassiana* JaGiP and JgSPK isolates were pathogenic in inhibiting the growth and development of *S. frugiperda*. These two isolates of *B. bassiana* were promising candidates for managing the *S. frugiperda* population in the corn field. The seed treatment with the endophytic EPF could act as the first line of maize defense against *S. frugiperda* larvae in the fields, which needs to be confirmed in future research. Furthermore, the endophytic EPFs could kill the FAW larvae concealed within maize midribs (Herlinda *et al*. 2021) because the fungal inoculated plants could produce deterring or antifeedant and antibiosis effects on *S. frugiperda* larvae (Jaber and Ownley 2018). Therefore, the susceptible young maize plant (Supartha *et al*. 2021) could be protected by seed treatment using the endophytic EPFs to be a first line defense against *S. frugiperda* larvae (Sari *et al*. 2022).

Finally, these findings highlight that the *S. frugiperda* growth and development can be inhibited by the endophytic EPF. The endophytic EPF inoculated within corn leaves eaten by the neonate larvae of *S. frugiperda* can increase larval and pupal mortality. The endophytic EPF can decrease the ability of adult eclosion and egg laying, which can decrease the ability of adult eclosion and egg laying. *B. bassiana* JgSPK and JaGiP isolates are the most pathogenic fungi that inhibit the growth and development of *S. frugiperda*. These two isolates of *B. bassiana* are promising candidates for managing *S. frugiperda* in the corn field. The seed treatment using the endophytic EPF could act as a first line of defense for maize against *S. frugiperda* larvae in the fieldsneed it, which needs to be confirmed in future research. It was necessary to protect young maize plants earlier using the fungal seed treatment.

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