ORIGINAL RESEARCH ARTICLE

The potential of the entomopathogenic fungus *Beauveria bassiana* to manage insect pests and diseases

Amar Bahadur

College of Agriculture, Tripura, Agartala 799210, India; amarpatel44@rediffmail.com

ABSTRACT

The saprophytic white muscardine fungus *Beauveria bassiana* (Balsamo) Vuillemin is a potential biocontrol agent against varied insect pests, is a commercially available mycopesticide in many countries, and is extensively used for insect pest management. It produces several metabolites, such as antibacterial, antifungal, cytotoxic, and insecticidal compounds that protect against insect pests and plant pathogens, with dual-purpose crop protection, a new concept in plant disease management. This insect pathogen is also beneficial to plant endophytes that are antagonistic to plant diseases and promote rhizosphere colonizers and plant growth, inducing systemic resistance. The induced systemic responses of fungal endophytes enhance genes that are expressed in pathogenesis and increase the production of pathogenesis-related proteins and defense enzymes. The fungus infects the insects by degrading mechanically and chemically their cuticles. It promotes plant growth, provides systemic protection against pests and pathogens in sustainable agricultural crop production, and reduces the usage of chemical pesticides.

Keywords: entomopathogen; mycopesticides; endophytes; growth promotion; induce resistance; pests management

ARTICLE INFO

Received: 16 October 2023 Accepted: 11 December 2023 Available online: 18 December 2023

COPYRIGHT

Copyright © 2023 by author(s). Natural Resources Conservation and Research is published by EnPress Publisher LLC. This work is licensed under the Creative Commons Attribution-NonCommercial 4.0 International License (CC BY-NC 4.0). https://creativecommons.org/licenses/bync/4.0/

1. Introduction

The Italian entomologist Agostino Bassi discovered the causal agent of the pebrine disease of silkworm white mummies^[1]. He first suggested that a fungus caused this "white muscardine" disease, which later was named *Beauveria bassiana* (Balsamo) Vuillemin^[2]. The cadavers are covered with the white powdery layer characteristic of white muscardine disease. This fungal disease is common during the rainy season and has a very high incidence during the winter. Most entomopathogenic fungi infect through the insect cuticle, involving adsorption, adhesion, germination, the development of appressorium, and penetration pegs. They produce enzymes (proteases, chitinases, esterases, and lipases), which digest the insect cuticle and reach the hemocoel, followed by suppressing the host's immune response^[3]. Beauveria bassiana is a natural pathogen for many insects and other invertebrates. Diseases caused by B. bassiana (white muscardine) and Metarhizium anisopliae (Metschnikoff) Sorokin (green) are common in silkworms and frequently appear during winter. Both fungi occur naturally in the soil and infect a wide range of soil insect species. They are best cultivated on Sabouraud agar with 2% glucose. B. bassiana is a most effective biological control agent against a wide range of insect families, including agricultural pests^[4] such as aphids, thrips, whiteflies, weevils, locusts, scarabs, caterpillars, and other larvae, pupae, and adults^[5]. Applied in the field, B. bassiana causes no harm to non-target insects, such as predators, parasitoids, pollinating insects, and useful

insects such as honey bees^[6]. It is widely used as a myco-insecticide for the control of several insect pests as an alternative to synthetic chemical insecticides. It is widely used commercially as a biological control agent, both in agriculture and forestry^[7]. The commercial products BotaniGard and Mycotrol are used widely in the US, the EU, Japan, Mexico, and other countries^[8]. The most common commercial myco-insecticides and myco-acaricides are based on B, bassiana, M. anisopliae, B. brongniartii (Saccardo) Petch, and Isaria (Paecilomyces) fumosorosea Wise^[8]. B. bassiana can be cultured in solid-state fermentation, and formulations of conidia are sprayed on plants as emulsions or wettable powders. It has shown antifungal ability against Rhizoctonia solani Kühn. B. bassiana, a facultative saprophyte, grows as a plant endophyte and interacts with plant roots worldwide^[9]. It grows into plant leaves and becomes dormant there until consumed by insects. Entomopathogenic fungi can colonize plant tissues and serve as biopesticides and biostimulants that promote plant growth and trigger defense mechanisms. B.bassiana protects against insect pests and plant pathogens, but the mechanisms are not yet completely understood^[10]. Plant diseases are directly affected by *Beauveria* sp. By mycoparasitism, competition, antibiosis, and indirect interaction by stimulating induced systemic resistance (ISR) as well as endophytic colonizing behaviour^[11-14]. A recent study on endophytic strains of *B. bassiana* highlighted their ability to promote plant growth and provide systemic protection against pests and pathogens^[15,16]. Endophytes have been identified in several commercially important plant species^[17,18], and promote plant growth^[19], beneficial rhizosphere colonizers^[20], and can be used as biofertilizers^[17]. Inoculating B. bassiana on numerous plants by various methods has demonstrated its colonizing capability^[21]. It effectively controls pest and fungal diseases, triggering physiological mechanisms that promote nutrient uptake and plant growth and increase tolerance to abiotic stress and drought^[15,16,22,23]. The positive effect of endophytic strains of *B. bassiana* on plant growth and yield is documented in several crops viz., $coffee^{[24]}$, $tomato^{[25]}$, $cotton^{[19]}$, broad bean^[26], soybean^[27], maize^[28], barley^[29], grapevine^[30], and tobacco^[31].

2. Mode of action

Entomopathogens are evidence of their large antagonistic potential against plant pathogens. Possible mechanisms of plant disease suppression of fungal entomopathogens by direct mechanisms such as mycoparasitism, competition, and antibiosis, indirect interaction by stimulating induced systemic resistance as well as promotion of plant growth^[17]. The Mycoparasitic involves four major steps, chemotrophic growth, recognition, attachment, and cell wall degradation by the pathogen by enzymes, viz., chitinases, and β -1, 3 glucanases followed by penetration by appressoria-like structures. The endophytic B. bassiana strain 11-98 has been observed coiling around larger hyphae of *Pythium myriotylum* by hydrolyzing β -1,3 and β -1,4 glucanases on chitin-based medium and has suggested its hyperparasitic activity against oomycetes fungi^[32]. Fungal biocontrol entomopathogens compete for food and space endophytically in colonised plants as well as colonize the rhizosphere^[33]. Colonization of grapevine plants by an endophytic strain of *B. bassiana* has reduced the incidence and severity of *Plasmopara viticola* causing downy mildew of grapes^[12]. The antagonistic activity of entomopathogenic fungi against insects and plant diseases, in addition to their beneficial effect on nutrient uptake, would be highly beneficial to develop a method for their use in sustainable agriculture. The mechanism involved by fungal entomopathogens is the production of various secondary metabolites viz., antibiotics, bioactive volatile organic compounds, lytic agents, enzymes, as well as toxic substances conferring protection against disease-causing plant pathogens^[17]. Production of various enzymes by entomopathogenic fungi governs various physiological processes such as morphogenesis, pathogenesis, parasitism, and growth regulation, as well as immunity and its antagonistic behaviour against a wide range of phytopathogens. The antagonistic ability of B. bassiana against Fusarium oxysporum causes tomato wilt^[34]. and Gaeumannomyces graminis var. tritici^[35], causing take-all of wheat reduced by the production of hydrolytic enzymes mainly chitinases and β -glucanases. The protease enzyme (Pr1) activity has been widely exploited against various groups of phytopathogenic fungi viz., *R. solani* and *F. oxysporum* on tomato due to its effective antifungal nature^[11,32].

Entomopathogenic fungi direct action against insect pests, may induce systemic immunity in plants and disease resistance by directly activating defense mechanisms of the host plants. Induction of immunity is assessed by oxygen-reactive species in response to fungal and bacterial elicitors, and by examining defense gene expression by the treatment of entomopathogenic fungi^[36]. Plant growth is enhanced as observed in colonized plants by entomopathogenic fungi to produce bioactive compounds^[37,38]. Entomopathogenic fungi are important biocontrol agents that infect a wide range of arthropods and play an important role in reducing pests' populations and of crop disease^[39]. *Beauveria bassiana* can induce systemic immunity and disease resistance against several fungal and bacterial phytopathogens and promote plant growth. A wide diversity of entomopathogenic fungi that are abundant in agricultural plant species as endophytes, exchange nutrients from the healthy host plants without causing any visible symptoms^[40]. Endophytic fungi have the potential to colonize and grow within plants systemically, and provide prolonged persistence and continuous protection^[44,45]. The colonization of plant tissues by endophytes fungi reduces as well the damage caused by herbivores and fungal disease^[46,47].

Beauveria bassiana endophytic colonization in tomato and cotton plants has increased resistance against the plant pathogens Rhizoctonia solani and Pythium myriotylum, and has had activity against insect pests and bacterial pathogens^[10,11,48]. These entomopathogenic fungi induce photosynthesis and energy metabolism as responses to stress, which enhance plant growth and stimulate disease resistance^[49]. Plant growth has been enhanced when colonized by the entomopathogenic fungi B. bassiana, B. brongniartii, and M. brunneum, from the production of bioactive compounds^[10]. Living plants exhibit various mechanisms of defense against parasites and pathogens, age-related resistance, organ-specific resistance, and induced resistance, a resistance triggered by the activation of genetically programmed pathways in plants to diminish the effect of consecutive pathogen attacks^[50]. Plants display two types of induced resistance, systemic acquired resistance (SAR), and induced systemic resistance (ISR). In comparison to SAR acting by protein accumulation and the salicylic acid pathway, ISR relies on pathways regulated by jasmonate and ethylene^[51]. Entomopathogenic fungi act as endophytes to improve nutrient uptake and plant growth^[52,53]. Entomopathogenic fungi were shown to form mycorrhiza-like interactions in response to biotic and abiotic stress and absorption of water and nutrients^[53]. Bean seeds treated with conidial suspensions of B. bassiana and M. robertsii have produced improved plant growth, more leaves and greater fresh and dry root weight in comparison to the control^[54]. B. bassiana-treated plants evidence an influence in metabolism by increasing the level of total alkaloids^[55]. Iron availability has improved in the presence of endophytic B. bassiana and M. brunneum, leading to an increase in leaf chlorophyll content and the length of roots^[56]. Analysis of *B. bassiana* infected grapevine tissue has found significantly increased calcium and magnesium^[57]. Entomopathogenic fungi also support plants to improve their resistance to disease and survival under stress conditions^[58], as seen with biocontrol agents *B. bassiana* and *M. anisopliae* activity against *Myzus persicae* and *Botrytis cinerea*^[59]. *B. bassiana* produces secondary metabolites such as beauvericin, bassianolides, oosporein, cyclosporin A, and oxalic acid and have cytotoxic, antibacterial, and antifungal activities^[17]. B. bassiana effect is also induced through volatile compounds in melon and cotton^[60]. Entomopathogenic fungi used as insect pathogens colonize endophytically a wide array of host plant tissues and subsequently confer benefits such as plant growth enhancement and suppression of disease pathogens as found for *B. bassiana*. Plant growth mediated by the endophytic colonization by diverse fungal genera of entomopathogens has resulted from inoculated seed treatment, foliar spray, and root drench^[19,26,61-63]. B. bassiana has been reported to suppress the soil-borne pathogens caused by damping off by Rhizoctonia solani and Pythium myriotylum in tomato^[33]. and cotton^[11]; bacterial blight caused by *Xanthomonas axonopodis* pv. *malvacearum* in cotton^[11], the Zucchini yellow mosaic virus in squash^[23], downy mildew caused by *Plasmopara viticola* in grapevines^[12], and sheath blight caused by *Rhizoctonia solani* in rice^[64].

3. Formulations

Formulation of microbial pesticides for the control of plant pathogens and insect pests is important in sustainable agriculture crop production. Several biopesticides are registered and can manage insect pests. B. bassiana is commercially available and widely used against insect pests. It can control the damping-off of tomatoes caused by Rhizoctonia solani and can protect against cotton seedling disease by soil-borne fungal pathogens. The development of biopesticides can control both plant pathogens and insect pests for plant protection in agriculture. The formulations of B. bassiana on shelf-life and entomopathogenic activity are introduced as a biocontrol agent of insect pests. The fungal entomopathogens are a potential bio-control agent that requires mass production of infective spores by solid-substrate, liquid culture and solid-state fermentation for conidia and blastospores at an adequate pH, temperature, nitrogen, carbohydrates, oxygen and carbon dioxide for fungal growth^[65]. During the fermentation process, blastospores are produced and the aerial spores are produced on the conidiogenous cells of the infected insects. Solid-substrate fermentation involves the mass production of conidia on an agar-based medium or natural substrate, viz., barley, rice, wheat, sorghum for B. bassiana, and maize for B. brongniartii^[65]. The formulations are commonly used as granules, wettable powders, dust as solid formulations and water-disposable powders, liquids (suspension concentrates) or oils (emulsifiable) as liquid formulations^[66]. Carriers use paraffin oil, mineral oil and vegetable oils for M. anisopliae and B. bassiana spore adhesion, germination, penetration, shelf life and efficacy in field conditions^[67]. Granular-based formulations of *B. bassiana* contain clay minerals (attapulgite, bentonite) as inert carriers for uniform spread and persistence^[68]. The formulations are commonly used as dipping plant roots into spore suspension for soil-borne pathogens, foliar spray of liquid suspension with spreading agent, soil treatment with a granular form of fungal spore and vectors for indirect transfer^[69]. Entomopathogenic fungi formulation of B. bassiana is BotaniGard, Naturalis-L, Mycotrol, Bio-Power, Beauvericin, Boverol, Betal, Ostrinol, Beevicide, and Racer-BB for management of various biotic stresses.

4. Induction of resistance in plants

Entomopathogenic fungi act as insect control agents, either through a plant-mediated response or by exerting a direct insecticidal effect. In a recent study, entomopathogenic fungi, often considered insect pathogens, play extra roles in nature, such as endophytes, plant disease antagonism, plant growth promotion, rhizosphere colonization, and management of diverse abiotic stresses^[70]. Beauveria bassiana can be a colonizing endophyte in a broad range of host plants and promotes their growth and defense^[71,72]. Endophytic fungi can improve growth and plant resistance to herbivores, pathogens, and various abiotic stresses that affect populations of pests and natural enemies^[73,74]. Beauveria bassiana has been found to endophyte colonization diverse plants, viz., maize (Zea mays L.), Poaceae, potato (Solanum tuberosum L.), Solanaceae, soybean (Glycine max L.), Fabaceae, faba beans (Vicia faba L.), Fabaceae, and tomato (Solanum lycopersicum L.), Solanaceae, with positive effects on plant growth^[52]. The growth-promoting effect of *B. bassiana* in tomatoes has resulted from increased nutrient bioavailability, production of iron siderophores, and phosphate solubilization^[71]. The defense responses have been classified as either pattern-triggered, or effect-triggered immunity^[75]. Pattern-triggered immunity is the sensing of pathogen-associated molecular patterns by the plant, triggering a defense response, such as callose deposition and induction of salicylic acid (SA), jasmonic acid (JA) or ethylene (ET) pathways^[76]. Beauveria bassiana has been shown to induce plant defense responses in date palm (Phoenix dactylifera L.), Arecaceae, and grapevine (Vitis vinifera L.), Vitaceae^[77]. Root colonization by B. bassiana strains caused strain-specific changes in the expression of genes encoding pathogenesis-related proteins, phytoalexins, jasmonate, and salicylic acid pathways^[78]. Fungal entomopathogens stimulate the production of various defense-related enzymes against phytopathogens viz., phenylalanine ammonia-lyase (PAL), peroxidases (POX), phenylperoxidse (PPO), catalase, chitinase and phenolic compounds. *B. bassiana* strain can control tomato damping off disease through the production of defense-related enzymes viz., phenylalanine ammonia-lyase (PAL), peroxidases (POX) and phenol compounds^[13]. The ISR stimulation by fungal entomopathogens is an important biocontrol mechanism leading to the reduction of disease symptoms by the production of bioactive secondary metabolites^[79]. *B. bassiana* strain 11–98 has inoculated cotton seedlings that resulted in a significant reduction in disease severity for bacterial blight (*Xanthomonas campestris* pv. *malvacearum*) through induction of resistance systemic in cotton^[32]. Fungal entomopathogens, viz, *B. bassiana* and *Lecanicillium* spp. have caused greater accumulation of induced proteins related to photosynthesis and energy metabolism-enhancing plant growth, as well as stimulated disease resistance in plants^[49].

5. Management of insect pests and diseases

Fungal entomopathogens contribute to plant protection against various abiotic and biotic stresses, including plant diseases, by increasing nutrient uptake, enhancing plant growth, and production of phytohormones and iron-chelating compounds^[80,81]. B. bassiana can colonize several plant species to manage pests and pathogens^[11,18,82,83]. The antagonistic abilities of entomopathogenic fungi have been extensively deliberated in a wide array of seed, foliar as well as soil-borne plant pathogens. Entomopathogenic fungi act as insect pathogens, and have additional roles in plant disease management viz., endophytic, antagonism, rhizosphere colonization and plant growth promotion^[12,26,59]. However, the mechanisms involved are not yet completely understood^[10]. The potential of *B. bassiana* has recently drawn attention worldwide for its beneficial roles as a plant disease antagonist, beneficial rhizosphere colonizer, plant growth promoter and endophyte. B. bassiana harbours plant tissues from its endophytic ability without causing any visible symptoms^[84]. Endophytic colonization by *B. bassiana* has reduced the severity of damping-off caused by *R.* solani and Pythium myriotylum. B.bassiana can colonise hosts systemically and be transmitted by seed, seed coats or rhizomes^[85]. As a naturally occurring endophyte or established through artificial inoculation in agricultural and horticultural crops, including wheat, maize, sorghum, tomato, potato, bean, banana, pumpkin, cotton and jute^[17]. The dual-purpose biocontrol abilities of *B. bassiana* against insect pests and plant pathogens^[17], have indicated fungal interactions in the host plant^[82,86]. Indirect mechanisms are growth promotion and vigour in plants through solubilization of essential macro and micronutrients, induction of systemic resistance by the endophyte colonization of the plant, and regulation of defence enzymes such as peroxidase, and phenol ammonia-lyase^[32,62]. The entomopathogen fungus produces various metabolites such as antibiotics, enzymes, and bioactive volatile compounds^[87]. These secondary metabolites show various insecticidal, antimicrobial, anticancer and antioxidant properties^[88]. Endophytic B. bassiana pre-treatment of cotton seedlings resulted in lower severity of *Xanthomonas* bacterial blight disease^[11]. The establishment of *B*. bassiana has been successful in squash, and protected it from the Zucchini yellow mosaic virus^[18]. Entomopathogenic fungi are promising antagonists against various plant pathogens, viz., Rhizoctonia solani, Fusarium oxysporum, Pythium spp., Botrytis cinerea, Hemileiavastatrix, Sphaerotheca fuliginea, Phytopthora megasperma, Alternariaporri, Colletotrichum falcatum, Plasmopara viticola, Xanthomonas campestris pv. malvacaerum, etc.^[10,12-14,59,89]. Beauveria is an effective bioagent against the codling moth, Colorado potato beetle, termites, American bollworm, and Helicoverpa armigera^[90].

6. Conclusions

The negative effects of synthetic chemical pesticides have prompted attention toward developing ecofriendly pest management alternatives. Bio-pesticides are replacing synthetic compounds and are a component of environment-friendly insect pests and disease management. The beneficial microorganisms are being successfully adopted in agriculture to promote plant growth and crop yield. Various insect-pathogenic endophyte fungi function as biocontrol agents and are now being considered in sustainable pest management. The potential of biopesticides as alternatives to chemical pesticides is based on evidence; most entomopathogenic fungi pesticides are relatively safe and represent alternatives to synthetic pesticides. It is necessary to conduct pathogenic/toxicity-related tests in non-target organisms as well as on vertebrates to avoid any kind of risk and ensure that precautionary measures during production and application are taken to avoid harmful reactions. Bioproducts based on fungal biocontrol agents are necessary because of the numerous advantages of these microorganisms.

Conflict of interest

The author declares no conflict of interest.

References

- 1. Lord JC. From Metchnikoff to Monsanto and beyond: The path of microbial control. *Journal of Invertebrate Pathology* 2005; 89(1): 19–29. doi: 10.1016/j.jip.2005.04.006
- 2. Steinhaus EA. Insect pathology, introduction. In: Steinhaus EA (editor). *Insect Pathology, An Advanced Treatise*. Academic Press; 1963.
- Götz P. Invertebrate immune response to fungal cell wall components. In: Latgé JP, Boucias D (editors). *Fungal Cell Wall and Immune Response*. Springer Berlin Heidelberg; 1991. pp. 317–329. doi: 10.1007/978-3-642-76074-7 24
- 4. Tanada Y, Kaya HK. Insect Pathology. Academic Press; 1993. pp. 319–385.
- 5. Keller S. Use of *Beauveria brongniartii* in Switzerland and its acceptance by farmers. In: Proceedings of Integrated Control of Soil Pest Subgroup "Melolontha"; 19–21 October 1998; Sion, Switzerland.
- Goettel MS, Hajek AE. Evaluation of non-target effects of pathogens used for management of arthropods. In: Wajnberg E, Scott JK, Quimby PC (editors). Evaluating Indirect Ecological Effects of Biological Control. Key Papers from the Symposium 'Indirect Ecological Effects in Biological Control', Montpellier, France, 17–20 October 1999. CABI Publishing; 2001. pp. 81–97. doi: 10.1079/9780851994536.0081
- Meyling NV, Eilenberg J. Ecology of the entomopathogenic fungi *Beauveria bassiana* and *Metarhizium* anisopliae in temperate agroecosystems: Potential for conservation biological control. *Biological Control* 2007; 43(2): 145–155. doi: 10.1016/j.biocontrol.2007.07.007
- de Faria MR, Wraight SP. Mycoinsecticides and mycoacaricides: A comprehensive list with worldwide coverage and international classification of formulation types. *Biological Control* 2007; 43(3): 237–256. doi: 10.1016/j.biocontrol.2007.08.001
- Klingen I, Eilenberg J, Meadow R. Effects of farming system, field margins and bait insect on the occurrence of insect pathogenic fungi in soils. *Agriculture, Ecosystems & Environment* 2002; 91(1–3): 191–198. doi: 10.1016/S0167-8809(01)00227-4
- 10. Jaber LR, Ownley BH. Can we use entomopathogenic fungi as endophytes for dual biological control of insect pests and plant pathogens? *Biological Control* 2018; 116: 36–45. doi: 10.1016/j.biocontrol.2017.01.018
- 11. Ownley BH, Griffin MR, Klingeman WE, et al. *Beauveria bassiana*: Endophytic colonization and plant disease control. *Journal of Invertebrate Pathology* 2008; 98(3): 267–270. doi: 10.1016/j.jip.2008.01.010
- 12. Jaber LR. Grapevine leaf tissue colonization by the fungal entomopathogen *Beauveria bassiana s.l.* and its effect against downy mildew. *BioControl* 2015; 60: 103–112. doi: 10.1007/s10526-014-9618-3
- 13. Azadi N, Shirzad A, Mohammadi H. A study of some biocontrol mechanisms of *Beauveria bassiana* against Rhizoctonia disease on tomato. *Acta Biologica Szegediensis* 2016; 60(2): 119–127.
- 14. Lozano TMD, Garrido JI, Quesada ME. *M. brunneum* and *B. bassiana* release secondary metabolites with antagonistic activity against *V. dahlia* and *P. megasperma* olive pathogens. *Crop Protect* 2017; 100: 186–195.
- 15. Sinno M, Ranesi M, Di Lelio I, et al. Selection of endophytic *Beauveria bassiana* as a dual biocontrol agent of tomato pathogens and pests. *Pathogens* 2021; 10(10): 1242. doi: 10.3390/pathogens10101242
- 16. Gupta R, Keppanan R, Leibman-Markus M, et al. The entomopathogenic fungi *Metarhizium brunneum* and *Beauveria bassiana* promote systemic immunity and confer resistance to a broad range of pests and pathogens in tomato. *Phytopathology* 2022; 112(4): 784–793. doi: 10.1094/PHYTO-08-21-0343-R
- 17. Ownley BH, Gwinn KD, Vega FE. Endophytic fungal entomopathogens with activity against plant pathogens: Ecology and evolution. *BioControl* 2010; 55: 113–128. doi: 10.1007/s10526-009-9241-x

- Jaber LR, Salem NM. Endophytic colonisation of squash by the fungal entomopathogen *Beauveria bassiana* (Ascomycota: Hypocreales) for managing *Zucchini yellow mosaic virus* in cucurbits. *Biocontrol Science and Technology* 2014; 24(10): 1096–1109. doi: 10.1080/09583157.2014.923379
- 19. Lopez DC, Sword GA. The endophytic fungal entomopathogens *Beauveria bassiana* and *Purpureocillium lilacinum* enhance the growth of cultivated cotton (*Gossypium hirsutum*) and negatively affect survival of the cotton bollworm (*Helicoverpa zea*). *Biological Control* 2015; 89: 53–60. doi: 10.1016/j.biocontrol.2015.03.010
- 20. Bruck DJ. Fungal entomopathogens in the rhizosphere. In: Roy HE, Vega FE, Chandler D, et al. (editors). *The Ecology of Fungal Entomopathogens*. Springer; 2010. pp. 103–112. doi: 10.1007/978-90-481-3966-8_8
- 21. Mantzoukas S, Eliopoulos PA. Endophytic entomopathogenic fungi: A valuable biological control tool against plant pests. *Applied Sciences* 2020; 10(1): 360. doi: 10.3390/app10010360
- 22. Bamisile BS, Dash CK, Akutse KS, et al. Fungal endophytes: Beyond herbivore management. *Frontiers in Microbiology* 2018; 9: 544. doi: 10.3389/fmicb.2018.00544
- 23. Quesada Moraga E. Entomopathogenic fungi as endophytes: Their broader contribution to IPM and crop production. *Biocontrol Science and Technology* 2020; 30(9): 864–877. doi: 10.1080/09583157.2020.1771279
- Posada F, Vega FE. Inoculation and colonization of coffee seedlings (*Coffea arabica* L.) with the fungal entomopathogen *Beauveria bassiana* (Ascomycota: Hypocreales). *Mycoscience* 2006; 47: 284–289. doi: 10.1007/s10267-006-0308-6
- 25. Prabhukarthikeyan R, Saravanakumar D, Raguchander T. Combination of endophytic *Bacillus* and *Beauveria* for the management of *Fusarium* wilt and fruit borer in tomato. *Pest Management Science* 2014; 70(11): 1742–1750. doi: 10.1002/ps.3719
- Jaber LR, Enkerli J. Effect of seed treatment duration on growth and colonization of *Vicia faba* by endophytic Beauveria bassiana and Metarhizium brunneum. Biological Control 2016; 103: 187–195. doi: 10.1016/j.biocontrol.2016.09.008
- Russo ML, Pelizza SA, Vianna MF, et al. Effect of endophytic entomopathogenic fungi on soybean *Glycine max* (L.) Merr. growth and yield. *Journal of King Saud University-Science* 2019; 31(4): 728–736. doi: 10.1016/j.jksus.2018.04.008
- 28. Russo ML, Scorsetti AC, Vianna MF, et al. Endophytic effects of *Beauveria bassiana* on corn (*Zea mays*) and its herbivore, *Rachiplusia nu* (Lepidoptera: Noctuidae). *Insects* 2019; 10(4): 110. doi: 10.3390/insects10040110
- 29. Veloz-Badillo GM, Riveros-Ramírez J, Angel-Cuapio A, et al. The endophytic capacity of the entomopathogenic fungus *Beauveria bassiana* caused inherent physiological response in two barley (*Hordeum vulgare*) varieties. *3 Biotech* 2019; 9: 12. doi: 10.1007/s13205-018-1548-9
- 30. Mantzoukas S, Lagogiannis I, Mpousia D, et al. *Beauveria bassiana* endophytic strain as plant growth promoter: The case of the grape vine *Vitis vinifera*. *Journal of Fungi* 2021; 7(2): 142. doi: 10.3390/jof7020142
- 31. Qin X, Zhao X, Huang S, et al. Pest management via endophytic colonization of tobacco seedlings by the insect fungal pathogen *Beauveria bassiana*. *Pest Management Science* 2021; 77(4): 2007–2018. doi: 10.1002/ps.6229
- 32. Griffin MR. *Beauveria Bassiana, A Cotton Endophyte with Biocontrol Activity against Seedling Disease* [PhD thesis]. The University of Tennessee; 2007.
- 33. Ownley BH, Pereira RM, Klingeman WE, et al. *Beauveria bassiana*, a dual purpose biocontrol organism, with activity against insect pests and plant pathogens. In: Lartey RT, Caesar AJ (editors). *Emerging Concepts in Plant Health Management*. Research Signpost; 2004. pp. 255–269.
- 34. Culebro-Ricaldi JM, Ruíz-Valdiviezo VM, Rodríguez-Mendiola MA, et al. Antifungal properties of *Beauveria* bassiana strains against *Fusarium oxysporum* f. sp. *lycopersici* race 3 in tomato crop. *Journal of Environmental* Biology 2017; 38(5): 821–827. doi: 10.22438/jeb/38/5/MRN-412
- 35. Renwick A, Campbell R, Coe S. Assessment of in vivo screening systems for potential biocontrol agents of *Gaeumannomyces graminis. Plant Pathology* 1991; 40(4): 524–532. doi: 10.1111/j.1365-3059.1991.tb02415.x
- Pizarro L, Leibman-Markus M, Gupta R, et al. A gain of function mutation in *SlNRC4a* enhances basal immunity resulting in broad-spectrum disease resistance. *Communications Biology* 2020; 3: 404. doi: 10.1038/s42003-020-01130-w
- 37. Rasool S, Cárdenas PD, Pattison DI, et al. Isolate-specific effect of entomopathogenic endophytic fungi on population growth of two-spotted spider mite (*Tetranychus urticae* Koch) and levels of steroidal glycoalkaloids in tomato. *Journal of Chemical Ecology* 2021; 47: 476–488. doi: 10.1007/s10886-021-01265-y
- 38. Cachapa JC, Meyling NV, Burow M, et al. Induction and priming of plant defense by root-associated insectpathogenic fungi. *Journal of Chemical Ecology* 2021; 47(1): 112–122. doi: 10.1007/s10886-020-01234-x
- 39. Xu YJ, Luo F, Li B, et al. Metabolic conservation and diversification of *Metarhizium* species correlate with fungal host-specificity. *Frontiers in Microbiology* 2016; 7: 2020. doi: 10.3389/fmicb.2016.02020
- 40. Saikkonen K, Lehtonen P, Helander M, et al. Model systems in ecology: Dissecting the endophyte–grass literature. *Trends in Plant Science* 2006; 11(9): 428–433. doi: 10.1016/j.tplants.2006.07.001
- 41. Tefera T, Vidal S. Effect of inoculation method and plant growth medium on endophytic colonization of sorghum by the entomopathogenic fungus *Beauveria bassiana*. *BioControl* 2009; 54: 663–669. doi: 10.1007/s10526-009-9216-y

- 42. Russo ML, Pelizza SA, Cabello MN, et al. Endophytic colonisation of tobacco, corn, wheat and soybeans by the fungal entomopathogen *Beauveria bassiana* (Ascomycota, Hypocreales). *Biocontrol Science and Technology* 2015; 25(4): 475–480. doi: 10.1080/09583157.2014.982511
- 43. Greenfield M, Gómez-Jiménez MI, Ortiz V, et al. *Beauveria bassiana* and *Metarhizium anisopliae* endophytically colonize cassava roots following soil drench inoculation. *Biological Control* 2016; 95: 40–48. doi: 10.1016/j.biocontrol.2016.01.002
- Allegrucci N, Velazquez MS, Russo M L, et al. *Endophytic colonisation* of tomato by the entomopathogenic fungus *Beauveria bassiana*: The use of different inoculation techniques and their effects on the tomato leafminer *Tuta absoluta* (Lepidoptera: Gelechiidae). *Journal of Plant Protection Research* 2017; 54(2): 205–211. doi: 10.1515/jppr-2017-0045
- 45. Sword GA, Tessnow A, Ek-Ramos MJ. Endophytic fungi alter sucking bug responses to cotton reproductive structures. *Insect Science* 2017; 24(6): 1003–1014. doi: 10.1111/1744-7917.12461
- 46. Gothandapani S, Boopalakrishnan G, Prabhakaran N, et al. Evaluation of entomopathogenic fungus against *Alternaria porri* (Ellis) causing purple blotch disease of onion. *Archives of Phytopathology and Plant Protection* 2015; 48(2): 135–144. doi: 10.1080/03235408.2014.884532
- Kuzhuppillymyal-Prabhakarankutty L, Tamez-Guerra P, Gomez-Flores R, et al. Endophytic *Beauveria bassiana* promotes drought tolerance and early flowering in corn. *World Journal of Microbiology and Biotechnology* 2020; 36: 47. doi: 10.1007/s11274-020-02823-4
- 48. Griffin MR, Ownley BH, Klingeman WE, Pereira RM. Evidence of induced systemic resistance with *Beauveria* bassiana against Xanthomonas in cotton. *Phytopathology* 2006; 96(6).
- Gómez-Vidal S, Salinas J, Tena M, Lopez-Llorca LV. Proteomic analysis of date palm (*Phoenix dactylifera* L.) responses to endophytic colonization by entomopathogenic fungi. *Electrophoresis* 2009; 30(17): 2996–3005. doi: 10.1002/elps.200900192
- 50. Eyles A, Bonello P, Ganley R, Mohammed C. Induced resistance to pests and pathogens in trees. *New Phytologist* 2010; 185(4): 893–908. doi: 10.1111/j.1469-8137.2009.03127.x
- 51. Vallad GE, Goodman RM. Systemic acquired resistance and induced systemic resistance in conventional agriculture. *Crop Science* 2004; 44(6): 1920–1934. doi: 10.2135/cropsci2004.1920
- 52. Vega FE. The use of fungal entomopathogens as endophytes in biological control: A review. *Mycologia* 2018; 110(1): 4–30. doi: 10.1080/00275514.2017.1418578
- 53. Dara SK. Non-entomopathogenic roles of entomopathogenic fungi in promoting plant health and growth. *Insects* 2019; 10(9): 277. doi: 10.3390/insects10090277
- 54. Canassa F, Tall S, Moral RA, et al. Effects of bean seed treatment by the entomopathogenic fungi *Metarhizium robertsii* and *Beauveria bassiana* on plant growth, spider mite populations and behavior of predatory mites. *Biological Control* 2019; 132: 199–208. doi: 10.1016/j.biocontrol.2019.02.003
- 55. Espinoza F, Vidal S, Rautenbach F, et al. Effects of *Beauveria bassiana* (Hypocreales) on plant growth and secondary metabolites of extracts of hydroponically cultivated chive (*Allium schoenoprasum* L.[Amaryllidaceae]). *Heliyon* 2019; 5: e03038. doi: 10.1016/j.heliyon.2019.e03038
- Raya-Díaz S, Sánchez-Rodríguez AR, Segura-Fernández JM, et al. Entomopathogenic fungi-based mechanisms for improved Fe nutrition in sorghum plants grown on calcareous substrates. *PloS One* 2017; 12(10): e0185903. doi: 10.1371/journal.pone.0185903
- 57. Moloinyane S, Nchu F. The effects of endophytic *Beauveria bassiana* inoculation on infestation level of *Planococcus ficus*, growth and volatile constituents of potted greenhouse grapevine (*Vitis vinifera* L.). *Toxins* 2019; 11(2): 72. doi: 10.3390/toxins11020072
- 58. Dong C, Wang L, Li Q, Shang Q. Epiphytic and endophytic fungal communities of tomato plants. *Horticultural Plant Journal* 2021; 7(1): 38–48. doi: 10.1016/j.hpj.2020.09.002
- 59. Yun HG, Kim DJ, Gwak WS, et al. Entomopathogenic fungi as dual control agents against both the pest *Myzus persicae* and phytopathogen *Botrytis cinerea*. *Mycobiology* 2017; 45(3): 192–198. doi: 10.5941/MYCO.2017.45.3.192
- 60. González-Mas N, Gutiérrez-Sánchez F, Sánchez-Ortiz A, et al. Endophytic colonization by the entomopathogenic fungus *Beauveria bassiana* affects plant volatile emissions in the presence or absence of chewing and sap-sucking insects. *Frontiers in Plant Science* 2021; 12: 660460. doi: 10.3389/fpls.2021.660460
- 61. Gurulingappa P, Sword GA, Murdoch G, McGee PA. Colonization of crop plants by fungal entomopathogens and their effects on two insect pests when in planta. *Biological Control* 2010, 55(1): 34–41. doi: 10.1016/j.biocontrol.2010.06.011
- 62. Jaber LR, Enkerli J. Fungal entomopathogens as endophytes: Can they promote plant growth? *Biocontrol Science* and *Technology* 2017; 27(1): 28–41. doi: 10.1080/09583157.2016.1243227
- 63. Jaber LR, Araj SE. Interactions among endophytic fungal entomopathogens (Ascomycota: Hypocreales), the green peach aphid *Myzus persicae* Sulzer (Homoptera: Aphididae), and the aphid endoparasitoid *Aphidius colemani* Viereck (Hymenoptera: Braconidae). *Biological Control* 2018; 116: 53–61. doi: 10.1016/j.biocontrol.2017.04.005

- 64. Deb L, Dutta P, Mandal MK, et al. Antimicrobial traits of *Beauveria bassiana* against Rhizoctonia solani, the causal agent of sheath blight of rice under field conditions. *Plant Disease* 2023; 107(6). doi: 10.1094/PDIS-04-22-0806-RE
- 65. Vega FE, Nicolai VM, Luangsa JJ, Blackwell M. Fungal entomopathogens. In: Vega FE, Kaya HK (editors). *Insect Pathology*, 2nd ed. Academic Press; 2012. pp. 171–220.
- 66. Copping LG. *The Manual of Biocontrol Agents: A World Compendium*, 3rd ed. British Crop Protection Council; 2004.
- 67. Bateman RP, Carey M, Moore D, et al. The enhanced infectivity of *Metarhizium flavoviride* in oil formulations to desert locusts at low humidities. *Annals of Applied Biology* 1993; 122(1): 145–152. doi: 10.1111/j.1744-7348.1993.tb04022.x
- 68. Staples JA, Milner RJ. A laboratory evaluation of the repellency of *Metarhizium anisopliae* conidia to *Coptotermes lacteus* (Isoptera: Rhinotermitidae). *Sociobiology* 2000; 36(1): 133–148.
- Skinner M, Parker BL, Kim JS. Role of entomopathogenic fungi in integrated pest management. In: Abrol DP (editor). *Integrated Pest Management Current Concepts and Ecological Perspective*. Academic Press; 2014. pp. 169–191. doi: 10.1016/B978-0-12-398529-3.00011-7
- 70. Vidal S, Jaber LR. Entomopathogenic fungi as endophytes: Plant–endophyte–herbivore interactions and prospects for use in biological control. *Current Science* 2015; 109(1): 46–54.
- Barra-Bucarei L, France Iglesias A, Gerding González M, et al. Antifungal activity of *Beauveria bassiana* endophyte against *Botrytis cinerea* in two solanaceae crops. *Microorganisms* 2019; 8(1): 65. doi: 10.3390/microorganisms8010065
- 72. Wei QY, Li YY, Xu C, et al. Endophytic colonization by *Beauveria bassiana* increases the resistance of tomatoes against *Bemisia tabaci*. *Arthropod-Plant Interactions* 2020; 14: 289–300. doi: 10.1007/s11829-020-09746-9
- 73. Preszler RW, Gaylord ES, Boecklen WJ. Reduced parasitism of a leaf-mining moth on trees with high infection frequencies of an endophytic fungus. *Oecologia* 1996; 108: 159–166. doi: 10.1007/BF00333227
- 74. Saikkonen K, Faeth SH, Helander M, Sullivan TJ. Fungal endophytes: A continuum of interactions with host plants. *Annual review of Ecology and Systematics* 1998; 29: 319–343. doi: 10.1146/annurev.ecolsys.29.1.319
- 75. Jones JDG, Dangl JL. The plant immune system. *Nature* 2006; 444: 323–329. doi: 10.1038/nature05286
 76. Garcia-Brugger A, Lamotte O, Vandelle E, et al. Early signaling events induced by elicitors of plant defenses.
- Molecular Plant-Microbe Interactions 2006; 19(7): 711–724. doi: 10.1094/MPMI-19-0711
 77. Rondot Y, Reineke A. Endophytic *Beauveria bassiana* activates expression of defence genes in grapevine and
- 77. Rondot Y, Reineke A. Endophytic *Beauveria bassiana* activates expression of defence genes in grapevine and prevents infections by grapevine downy mildew *Plasmopara viticola*. *Plant Pathology* 2019; 68(9): 1719–1731. doi: 10.1111/ppa.13089
- 78. Raad M, Glare TR, Brochero HL, et al. Transcriptional reprogramming of *Arabidopsis thaliana* defence pathways by the entomopathogen *Beauveria bassiana* correlates with resistance against a fungal pathogen but not against insects. *Frontiers in Microbiology* 2019; 10: 615. doi: 10.3389/fmicb.2019.00615
- 79. Bourgaud F, Gravot A, Milesi S, Gontier E. Production of plant secondary metabolites: A historical perspective. *Plant Science* 2001; 161(5): 839–851. doi: 10.1016/S0168-9452(01)00490-3
- 80. Elena GJ, Beatriz PJ, Alejandro P, Roberto LE. *Metarhizium anisopliae* (Metschnikoff) Sorokin promotes growth and has endophytic activity in tomato plants. *Advances in Biological Research* 2011; 5(1): 22–27.
- 81. Liao X, O'Brien TR, Fang W, St. Leger RJ. The plant beneficial effects of Metarhizium species correlate with their association with roots. *Applied Microbiology and Biotechnology* 2014; 98: 7089–7096. doi: 10.1007/s00253-014-5788-2
- 82. Wagner BL, Lewis LC. Colonization of corn, *Zea mays*, by the entomopathogenic fungus *Beauveria bassiana*. *Applied and Environmental Microbiology* 2000; 66(8): 3468–3473. doi: 10.1128/AEM.66.8.3468-3473.2000
- Akello J, Dubois T, Coyne D, Kyamanywa S. Endophytic *Beauveria bassiana* in banana (*Musa* spp.) reduces banana weevil (*Cosmopolites sordidus*) fitness and damage. *Crop Protection* 2008; 27(11): 1437–1441. doi: 10.1016/j.cropro.2008.07.003
- 84. Stone JK, Bacon CW, White JF. An overview of endophytic microbes: Endophytism defined. In: White JF, Bacon CW (editors). *Microbial Endophytes*. CRC Press; 2000. pp. 3–29.
- 85. Arnold AE. Understanding the diversity of foliar endophytic fungi: Progress, challenges, and frontiers. *Fungal Biology Reviews* 2007; 21(2–3): 51–66. doi: 10.1016/j.fbr.2007.05.003
- 86. Landa BB, López-Díaz C, Jiménez-Fernández D, et al. *In-planta* detection and monitorization of endophytic colonization by a *Beauveria bassiana* strain using a new-developed nested and quantitative PCR-based assay and confocal laser scanning microscopy. *Journal of Invertebrate Pathology* 2013; 114(2): 128–138. doi: 10.1016/j.jip.2013.06.007
- 87. Vega FE, Posada F, Aime MC, et al. Entomopathogenic fungal endophytes. *Biological Control* 2008; 46(1): 72–82. doi: 10.1016/j.biocontrol.2008.01.008
- Shin TY, Bae SM, Kim DJ, et al. Evaluation of virulence, tolerance to environmental factors and antimicrobial activities of entomopathogenic fungi against two-spotted spider mite. *Tetranychus urticae. Mycoscience* 2017; 58(3): 204–212. doi: 10.1016/j.myc.2017.02.002

- 89. Sanivada SK, Challa M. Mycolytic effect of extracellular enzymes of entomopathogenic fungi to Colletotrichum *falcatum*, red rot pathogen of sugarcane. *Journal of Biopesticides* 2014; 7: 33–37.
 90. Thakur R, Sandhu SS. Distribution, occurrence and natural invertebrate hosts of indigenous entomopathogenic
- fungi of Central India. Indian Journal of Microbiology 2010; 50: 89-96. doi: 10.1007/s12088-010-0007-z