Tobacco Growth Promotion by the Entomopathogenic Fungus, *Isaria javanica* pf185

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**ABSTRACT**

*Isaria javanica* pf185 is an important entomopathogenic fungus with potential for use as an agricultural biocontrol agent. However, the effect of *I. javanica* pf185 on plant growth is unknown. Enhanced tobacco growth was observed when tobacco roots were exposed to spores, cultures, and fungal cell-free culture supernatants of this fungus. Tobacco seedlings were also exposed to the volatiles of *I. javanica* pf185 in vitro using I-plates in which the plant and fungus were growing in separate compartments connected only by air space. The length and weight of seedlings, content of leaf chlorophyll, and number of root branches were significantly increased by the fungal volatiles. Heptane, 3-hexanone, 2,4-dimethylhexane, and 2-nonanone were detected, by solid-phase micro-extraction and gas chromatography-mass spectrophotometry, as the key volatile compounds produced by *I. javanica* pf185. These findings illustrate that *I. javanica* pf185 can be used to promote plant growth, and also as a biocontrol agent of insect and plant diseases. Further studies are necessary to elucidate the mechanisms by which *I. javanica* pf185 promotes plant growth.

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Entomopathogenic fungi have potential as biocontrol agents against insect pests [1]. These fungi are commercially available and are used primarily as biopesticides to control arthropod pests in various cropping systems [2]. Recent studies have shown that entomopathogenic fungi positively influence plant health through induction of systemic resistance against plant diseases and abiotic stresses, promotion of crop growth [3,4], and direct inhibition of plant pathogens [5,6]. Consequently, entomopathogenic fungi are attractive candidates for the study of integrated pest management. Their cross-kingdom effects indicate that entomopathogenic fungi might have broader roles in crop protection than just insect control.

Several fungal entomopathogens, including *Beauveria* spp., *Metarhizium* spp., and *Lecanicillium* spp., promote plant growth after colonizing the host plant [3,4,7]. Proteomic analysis of palm colonized by the entomopathogenic fungi *Beauveria bassiana* and *Lecanicillium* spp. showed improvement in photosynthesis, energy metabolism, plant defense, and induction of stress-protective proteins [8]. The mechanisms involved in promoting plant growth might include altered plant growth hormone activity and/or improved nutrition. For example, colonization of soybean by *Metarhizium anisopliae* resulted in the induction of salt tolerance by reduction in abscisic acid production and elevation in jasmonic acid levels under stressed conditions [9]. The entomopathogen *Metarhizium robertsii* secretes siderophores under iron-depleted culture conditions [10], which might improve iron nutrition in a host plant. Altered plant nutrition has been reported in plants colonized by *B. bassiana* [11]. Microbial volatile compounds have also been shown to enhance plant growth. For instance, *Fusarium oxysporum* isolates produce organic volatile compounds that differentially affect plant growth [12]. Furthermore, rhizobacteria, such as *Bacillus subtilis* and *Pseudomonas chlororaphis*, produce 2R,3R-butanediol, which enhances plant growth and induces systemic resistance against biotic and abiotic stresses [13–16].

In this study, we investigated the plant growth-promoting effect of the entomopathogenic fungus, *Isaria javanica* isolate pf185 and its metabolites, which have been established to exhibit biocontrol activity against insects and plant diseases [17]. Tobacco was used to determine whether exposure to the fungal spores and mycelia, or secreted and...
volatile products improved plant growth. We characterized the volatile compounds produced by the fungus and used authenticated products to determine their effects on tobacco growth. To the best of our knowledge, our finding that the pf185 isolate of *I. javanica* and its volatiles promoted tobacco growth is the first demonstration of the importance of volatiles produced by entomopathogenic fungi in inducing beneficial plant responses.

*I. javanica* pf185 (KACC93241P) was obtained from the Korean Agricultural Culture Collection, KACC, National Agrobiodiversity Center, Wanju, South Korea). The pf185 strain was grown and maintained on potato dextrose agar (PDA; Difco Inc. Detroit, MI) as described previously [17]. *Nicotiana tabacum* L. “Xanthi” seeds were surface-sterilized using an ethanol and sodium hypochlorite solution as described previously [18]. The sterilized tobacco seeds were planted in Murashige and Skoog (MS; Sigma) described previously [19]. The sterilized tobacco seeds were planted in Murashige and Skoog (MS; Sigma-Aldrich Inc., St. Louis, MO) salt medium supplemented with 0.5% (w/v) agar and 3% (w/v) sucrose in Petri dishes (SPL Life Science Co., Pocheon, Korea). The tobacco plants were grown for two weeks with a light-dark cycle of 16:8 h under 40-W fluorescent lights (2000 lux, 80 μmol photons m⁻² s⁻¹). The temperature was maintained at 25 ± 3 °C, with a relative humidity of 50–60%.

Two-week-old tobacco seedlings were planted in pots containing 500 cm³ of sterile soil-less medium (peat moss:vermiculite:perlite, 7:3:3, v/v) with one seedling per pot. The pots were supplied with 10 mL of sterile water every 2 days. After 2 weeks of growth, the seedlings were drenched with fungal products. To obtain intact cultures, *I. javanica* pf185 cells were grown in potato dextrose broth (PDB, Difco Inc.) at 25 °C in a shaking incubator at 150 rpm for 7 days. These cultures were diluted 1:1 v/v with sterile water. To obtain cell-free extracellular metabolites, the 7-day-old fungal cultures were centrifuged at 15,000 g for 10 min to remove fungal debris, and the supernatant was passed through a 0.2 μm filter (Millipore Filter Corp., Bedford, MA). To obtain spores for plant application, fungal colonies from the 7-day-old PDA plates were harvested by suspension in sterile water. The suspension was filtered through two layers of sterile cheese cloth to remove hyphal debris. Spore concentration in the filtrate was determined and adjusted to 1 × 10⁸ spores/mL under a microscope (Olympus BX41, Tokyo, Japan) using a hemocytometer (Marienfeld Superior, Lauda-Königshofen, Germany). The tobacco plants were treated with 15 mL aliquots of the spore suspension or supernatant four times at weekly intervals. The intact culture (20 mL) was applied only once. For the control treatments, sterile water or PDB was used. The experiment was repeated twice with six plants per treatment. The plant growth parameters in the treatment groups were measured one week after the final treatment.

A previous study indicated that chlorophyll meter can be used to evaluate the correlation between chlorophyll content and nitrogen content in tobacco [20]. To determine the effects of treatments on tobacco plants, the leaf chlorophyll content was measured in at least 10 different locations of the third and fourth fully developed tobacco leaves, using a chlorophyll meter (SPAD-502Plus, Minolta Camera Co., Osaka, Japan). Each plant was subsequently harvested. To measure the fresh weight of shoot and root, the seedlings were cut 1 cm above the root with a sterile knife. The fresh weight of the roots and shoots were immediately measured using an analytical balance (A&D Korea Limited, Seoul, Korea). The length and diameter of the plant stems were measured using a digital ruler (Mitutoyo Corp., Kanagawa, Japan). The lateral root density was measured using the image analysis software ASSESS 2.0 (APS Press, St. Paul, MN). The experiment was repeated twice with six plants per treatment. In this study, the experimental data from the assay of plant growth effects of *I. javanica* pf185 preparations were analyzed by Student’s *t*-test using Statistical Package for Social Sciences (SPSS Inc., Armonk, NY), ver. 23. Significance was set at *p* < .05.

In the pot experiments, tobacco plant growth was promoted by the treatment with the fungus and its metabolites. The growth of tobacco seedlings treated with a root drench of *I. javanica* pf185 fungal cultures was significantly higher than that of seedlings treated with non-inoculated half-strength PDB (Figure 1). Treatment with the culture of *I. javanica* pf185 by root drenching significantly enhanced the shoot height (*p* = .001), root length (*p* = .004), and shoot weight (*p* = .02), but there was no significant effect on the root weight at 28 days post-inoculation (dpi). When tobacco plant seedlings were treated with the spore suspension, the shoot weight (*p* = .02) and root weight (*p* = .008) were enhanced (Figure 1). Cell-free supernatants of *I. javanica* pf185 also enhanced shoot growth, shoot height (*p* = .006), and shoot weight (*p* = .003) (Figure 1). These results showed that *I. javanica* pf185 promoted tobacco plant growth.

After 2 weeks, three tobacco seedlings were transplanted to one half of an 1 plate (100 × 15 mm², SPL Life Science Co.) containing solid MS medium. The other half of the plate contained PDA inoculated with 0.1 mL of spore suspension (1 × 10⁷ spores/mL) in sterile water 24 h prior to the experiment. As a control, the PDA was treated with only 0.1 mL sterile water. The inoculated I-plates were sealed with Parafilm and placed in a growth room under fluorescent light for two weeks and used to measure...
the tobacco growth parameters. Root development of the tobacco plants in the treatment and control groups was observed using a microscope at ×40 magnification (M165 FC; Leica Microsystems, Tokyo, Japan).

The use of I plates enabled the measurement of the tobacco plant responses to the volatiles produced by *I. javanica* pf185 (Figure 2). Compared with that of the seedlings grown in the absence of the fungus (control), the seedlings grown with the fungal volatiles showed significantly enhanced growth ($p < .000001$). The shoot height and root length both increased by approximately 1.5-fold when the seedlings were grown with the volatiles, compared with those of the controls, whereas the shoot and root weights increased by more than two-
fold (Figure 2). These changes correlated with the increase in leaf chlorophyll content \( p = 0.00001 \) and stem diameter \( p = 0.00001 \). When the seedlings were grown with the fungal volatiles, both lateral root and root hair formation were enhanced when compared with those of the control. These results suggest that the volatiles from *I. javanica* pf185 have growth-promoting effects that are accompanied by altered root architecture and increased fresh weight biomass in tobacco.

Spores of *I. javanica* pf185 (20 μL suspension) were cultured on 1 mL of PDA at 28 °C for 36 h in closed 20 mL glass headspace bottles (Supelco, Bellefonte, PA) before the collection of volatiles.

Commercioally available solid phase microextraction (SPME) fiber (50/30 μm DVB/Carboxen/PDMS; Supelco, Bellefonte, PA) was used to analyze the volatiles produced by *I. javanica* pf185. The volatiles were analyzed by headspace SPME and gas chromatography-mass spectrophotometry (GC-MS) as described previously [21], with minor modifications. The volatile organic compounds (VOCs) from the airspace of the bottles containing 1 mL of PDA without inoculation were used as the control. After extraction, the SPME fiber was desorbed at 30 °C for 30 min in the injection port of an Agilent 6890 GC Plus (Agilent Technologies, Santa Clara, CA) coupled to Pegasus HT (GC-TOF-MS) equipped

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**Figure 2.** Effect of fungal volatiles on tobacco plant growth. The data shown are of plants 2 weeks after treatment in I plates. (A) Images of tobacco seedlings and tobacco root hair formation after co-inoculation with spore suspension of *Isaria javanica* pf185. Images of root hair formation were captured under a microscope. (B) Mean growth parameters of tobacco cultivated with or without *I. javanica* pf185 (potato dextrose broth) in I plates. A significant difference in responses between treatments and controls, as assessed by Student’s t-test \( (\alpha < 0.01) \), are indicated with three asterisks. Means and standard errors of two independent experiments are shown, with six seedlings per replicate.
with a Combi-Pal Autosampler. The chromatographic separation was performed with a DB-WAX (30 m × 0.25 μm, 0.25 μm film thickness) column using helium as the carrier gas at a constant flow rate of 1 mL/min. The column was held at 45°C for 3 min, and then the temperature was increased to 240°C using the program; (3 min) → 5°C/min → 80°C → 20°C/min → 150°C (5 min) → 30°C/min → 240°C (15 min). The LECO Pegasus 4D-TOFMS detector (LECO Corp., Saint Joseph, MI) was programmed with an electron ion (EI) source operating at 70 eV, and the acquisition range was between m/z 50 and 500 (Supplemental Table 1). The temperature of the transfer line and ion trap was 230°C. The volatile compounds were identified by comparing them with those in the GC-MS system data banks [National Institute of Standards and Technology (NIST) Main El MS Library, 2014]. Each sample was tested twice.

The GC-MS analysis of the volatile compounds produced by *I. javanica* pf185 showed the presence of several compounds (Table 1 and Figure 3). Volatiles were also detected in the headspace of the non-inoculated PDA bottles. However, fungal growth changed the composition of the volatiles. The level of 5-(carboxymethyl) hydroxylamine, 2-methyl propanal, 3-methyl-furan, and hexamethyl-disiloxane was 5–25 times higher in the fungus inoculated PDA bottles than in the non-inoculated PDA bottles. Additionally, four volatiles (heptane, 3-hexanone, 2,4-dimethyl-hexane, and 2-nonanone) were only present in the headspace of *I. javanica* pf185 inoculated PDA bottles (Table 1 and Figure 3).

This study extends the documented of the growth-promoting effects of fungal genera to include an entomopathogenic strain of *I. javanica* and establishes a role for the metabolites that are volatile. The findings add to similar findings in isolates of *Aspergillus*, *Fusarium*, *Penicillium*, and *Trichoderma* [12,22–25], as well as other genera of entomopathogenic fungi such as *Beauveria*, *Metarhizium*, *Purpureocillium*, and *Lecanicillium* [3,4,26]. For example, *B. bassiana*, *I. fumosorosea*, and *M. brunneum* stimulated cabbage growth under water stress [27], and foliar applications of the endophytes *B. bronniarttii* and *M. brunneum* increased *Vicia faba* growth [4].

In this study, the importance of volatiles produced by the insect pathogen *I. javanica* pf185 in promoting tobacco plant growth was demonstrated. The ability of microbial metabolites, including volatiles, to directly and indirectly promote plant health is well-documented [13–15,28–32]. In this study, we detected four new volatiles produced by *I. javanica* pf185 grown on PDA medium. However, we are yet to confirm which of the identified volatile compounds from *I. javanica* pf185 cells were responsible for the improvement in plant growth. The active metabolites secreted or released as volatiles by *I. javanica* pf185 are currently under investigation.

The volatiles produced by *I. javanica* pf185 increased root branching and root hair formation. Changes in root morphology have also been observed with entomopathogenic *Metarhizium* isolates; for instance, *M. robertii* stimulated root hair development [26], and *M. anisopliae* improved root development [33]. A recent study showed that pathogenic strains of *Fusarium oxysporum* produced organic volatiles that can enhance plant growth and lateral root development [12], while volatiles from a nonpathogenic strain of *F. oxysporum* also promoted plant growth [34]. Root colonization and changes in lateral root development promoted by *I. javanica* pf185 can enhance its rhizosphere competency by acting as a competitor, limiting both penetration of fungal pathogens and their access to nutrients. It is known that the primary and lateral roots are the main penetration sites for several soil-borne fungal pathogens [35].

In the present study, the volatiles produced by *I. javanica* pf185 grown on PDA were identified as heptane, 3-hexanone, 2,4-methyl-hexane, and 2-nonanone. Although their biological function is largely uncharacterized, such volatiles are known to have varied effects on plants and microbes. Production of 2-nonanone by the root-colonizing bacterium, *Paenibacillus polymyxa*, inhibited nematode growth.

### Table 1. GC/MS analysis of the volatiles produced by *Isaria javanica* pf185 grown on potato dextrose agar.

| Identified compound                        | Retention time (mins) | Mass | Relative area |
|-------------------------------------------|-----------------------|------|--------------|
| 5-(Carboxymethyl) hydroxylamine            | 1:24                  | 45   | 7.9          |
| 2-Methyl propanal                         | 1:54                  | 72   | 4.7          |
| 3-Methyl-furan                            | 2:02                  | 81   | 24.8         |
| Hexamethyl-disiloxane (peak 1)            | 2:33                  | 147  | 5.5          |
| Heptane (peak 2)                          | 2:50                  | 57   | -            |
| 3-Hexanone (peak 3)                       | 4:24                  | 57   | -            |
| 2,4-Dimethyl-hexane (peak 3)              | 4:46                  | 85   | -            |
| 2-Nonanone (peak 4)                       | 12:22                 | 58   | -            |

*Relative area values of each compound detected in the head space of *I. javanica* pf185-inoculated potato dextrose agar (PDA) bottles versus non-inoculated PDA bottles. These values are from one of the two repetitions that showed similar results (Supplemental Figure 1). Four volatiles (*) were detected only when the fungus was present. The peak numbers refer to the compounds separated by GC (see Figure 3).
Heptane produced by *Burkholderia ambifaria* promoted plant growth and productivity [36–38]. The 2,4-dimethyl hexane extracted from the leaves of *Tragia involucrata* exhibited weak in vitro antibacterial activity against *Staphylococcus aureus* [39]. 2-Nonanone is a male-specific pheromone for niptidulid beetles and mealworms [40,41]. Other cocktails of volatiles that improve plant growth are also reported for other fungi [42].

Our previous study indicated that dibutyl succinate, also produced by *I. javanica* pf185, was an aphicide and inhibited growth of *Colletotrichum acutatum* causing anthracnose disease in red-pepper [43]. We are currently monitoring the insecticidal or insect-repellent activities of the volatiles produced by *I. javanica* pf185 using an olfactometer, following previously described protocols with aphids, mites, and root-knot nematodes as targets [44]. These studies will be complemented by using single or mixed application(s) of the authenticated volatiles to compare the potency of the array of metabolites derived from the fungus.

Our findings that *I. javanica* pf185 produces plant-active volatiles *in vitro* are the first steps in our understanding of the beneficial effects of this entomopathogen on plants. Diverse microbial groups exist in the rhizosphere, which serves as a battleground for soil-borne plant pathogens and beneficial microbes [45]. The rhizosphere competency of biocontrol microbes is promoted by biocontrol mechanisms for acquisition of space and the nutrients required for growth and production of active metabolites. The emerging concept that microbial volatiles are part of the successful plant root-microbe interaction will lead to development of these products as eco-friendly chemicals for aiding plant health and productivity [46]. Our findings expand our knowledge of probiotic microbes, particularly when fungal studies are scarcer than those on bacteria. The ability of *I. javanica* pf185 to promote crop growth, as well as biocontrol for plant damage by microbial pathogens and insects, makes this strain an attractive candidate for inclusion in integrated crop protection measures.

**Disclosure statement**

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