Journal of Applied Entomology

WILEY

JOURNAL OF APPLIED ENTOMOLOGY

ORIGINAL ARTICLE OPEN ACCESS

Effect of Endophytic Fungi on *Thrips tabaci* Development and Population Dynamics

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Received: 12 November 2025 | **Revised:** 26 March 2026 | **Accepted:** 1 April 2026

Keywords: feeding behaviour | fungal endophytes | onion thrips | oviposition | population development | systemic effects

ABSTRACT

Endophytic fungi are promising biocontrol agents because they colonise healthy plant tissues asymptomatically while inducing systemic resistance that negatively affects herbivorous insects. We investigated whether treatments with the endophytes *Trichoderma harzianum* and *Beauveria bassiana* in two onion cultivars (*Allium cepa* L.; Sturon and Red Baron) induce plant responses that alter *Thrips tabaci* behaviour and population development. Under controlled conditions, seeds were treated with conidial suspensions and plants subsequently received foliar applications; plants were then exposed to *T. tabaci* for 72 h, 4 weeks, or 8 weeks in no-choice assays. Both endophytes reduced thrips host-plant preference: at 72 h post-exposure, inoculated plants had 2.01–2.89-fold fewer feeding punctures and 2.78–3.93-fold fewer eggs than controls. Over longer durations, endophyte treatments also suppressed thrips population growth: after 4 and 8 weeks, significantly more thrips were collected from control plants than from endophyte-colonised plants. Thrips populations did not differ between the two onion cultivars across treatments and time points. We discuss targeted inoculation of onions with specific endophytic fungal strains as a strategy for sustainable thrips management and its prospects for field implementation.

1 | Introduction

Onion thrips, *Thrips tabaci* Lindeman (Thysanoptera: Thripidae), is regarded as the most serious pest of onion (*Allium cepa* L.) and is responsible for economic losses in onion production worldwide (Diaz-Montano et al. 2011; Gill et al. 2015). The damage from *T. tabaci* arises from both the adults and larvae by feeding on the epidermal cells of the plants, resulting in necrotic leaf patches that impair photosynthesis, hinder plant growth, lead to nutrient loss and bulb size reduction, ultimately diminishing onion yield (Diaz-Montano et al. 2010; Fournier et al. 1995). In addition to the direct invasion of the onion plants, *T. tabaci* also inflicts indirect damage by acting as a vector for the transmission of plant pathogens, namely, the Iris yellow spot virus (IYSV) (Gent et al. 2006; Srinivasan et al. 2012; Boateng et al. 2014), Tomato spotted wilt virus (TSWV) (Jacobson et al. 2013) as well as *Alternaria porri* Ellis (McKenzie et al. 1993), which has the potential to devastate an entire onion crop (Gent et al. 2004; Pozzer et al. 1999; Birithia et al. 2021; Chatzivassiliou 2008; Saini et al. 2024). Controlling this key pest insect in onion cultivation poses a significant challenge for several reasons. Onion thrips is characterised by small body size and cryptic lifestyle (Morse and Hoddle 2006), making detection and monitoring difficult, especially at the early stage of infestation. Moreover, due to their adaptability and extensive host range, they can reproduce in spring on many plant species such as cabbage, wheat, oat, barley, lettuce, dandelion, weed vegetation, after overwintering in the residue of onions and other crops before recolonization in the following onion season (North and Shelton 1986; Larentzaki et al. 2007; Szostek and Schwartz 2015). In commercial onion production, conventional pest management strategies for *T. tabaci* have

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depended on multiple applications of synthetic insecticides, which are commonly utilised to control established thrips infestations, even at low population densities. Nonetheless, factors such as oviposition within leaf tissues, larvae being concealed in the narrow crevices of onion leaves, pupae hidden in the soil, and the waxy cuticular surface of onion leaves have led to the low success of the foliar insecticide spray (Salas 1994; Gill et al. 2015). Furthermore, due to their high reproductive rate and multiple overlapping generations (Morse and Hoddle 2006; Nault and Shelton 2010), coupled with prolonged exposure to pesticides, onion thrips have developed insecticide resistance, as evidenced in various countries, including the United States (Shelton et al. 2006; Adesanya et al. 2020), Canada (MacIntyre Allen et al. 2005), and Australia (Herron et al. 2008). Integrated pest management (IPM) practices for controlling thrips on onions have not been very effective due to the lack of active components that successfully diminish *T. tabaci* populations. Apart from the above considerations, apprehensions regarding the impact of using insecticides on the environment, biodiversity, and human health have prompted the search for alternative pest management strategies.

Microbial agents are often utilised as substitutions for chemical pesticides, with entomopathogenic fungi being advocated as a sustainable and environmentally friendly alternative. Regrettably, their practical application as contact biopesticides is limited since the fungus conidia are not only damaged and inactivated by ultraviolet (UV) radiation but also susceptible to low moisture and other environmental factors (Braga et al. 2001; Fernandes et al. 2007, 2015; Jaronski 2010). These issues have led to a growing interest in employing fungal entomopathogens as fungal endophytes, which not only exist naturally but also can be artificially introduced into plants to assess their effects on insect pests and plant pathogens. Fungal endophytes are defined as fungi that at a certain stage in their life cycle live symbiotically within plant tissues without causing adverse effects on the performance of the colonised host plant (Carroll 1988; Wilson 1995; Schulz and Boyle 2006). As demonstrated in previous studies, the interaction between insect herbivores and their host plants can be modulated by microbial associations with the host plants (Shikano et al. 2017; Grunseich et al. 2019). These associations have been shown to confer a range of fitness benefits and ecological adaptations to the colonised plant (Rodriguez et al. 2009). In addition to promotion of plant growth (Mayerhofer et al. 2013), endophytes can also help the host plants in terms of resistance to plant diseases (Bamisile et al. 2018; Muvea et al. 2018; Russo et al. 2018; Kiarie et al. 2020) and insect herbivores (Barelli et al. 2016; Jaber and Ownley 2017).

In recent years, there has been a significant focus on clarifying the role of endophytic fungi in enhancing plant resistance to insect pests, aiming to develop them into bio-insecticides. Numerous studies have demonstrated that endophytes have the capacity to synthesis bioactive ingredients that negatively affect herbivorous insects. However, most of the investigations were short-term studies, which frequently concentrate on immediate pest-feeding behaviour, reproduction and mortality (Akello et al. 2008; Powell et al. 2009; Gurulingappa et al. 2010; Vidal and Jaber 2015; Coppola, Cascone, et al. 2019). Research on the effect of endophytic fungi against sucking insect pests indicates that foliar inoculation of melon plants with strains of the endophytes *Beauveria bassiana* (Bals.) Vuill. and *Metarhizium brunneum* Petch dramatically increased nymph mortality of sweet potato whitefly *Bemisia tabaci* Gennadius (Garrido-Jurado et al. 2017). Rasool et al. (2021) revealed that wheat and bean seed treatment with *Metarhizium robertsii* and *Beauveria bassiana* reduced the population growth of *Rhopalosiphum padi* L and *Aphis fabae* Scopoli after 10 days of infestation. In the context of managing *T. tabaci* on onion, Muvea et al. (2014) showed that several endophytic fungal strains markedly reduce thrips feeding, oviposition, and survival. Building on this work, the present study evaluates the effects and persistence of two endophytic fungi across onion cultivars on *T. tabaci* population dynamics. Using controlled non-choice bioassays, we assessed (i) feeding damage and reproductive output and (ii) population development on two onion cultivars following combined seed and foliar inoculation with two specific endophytes, that is, *Trichoderma harzianum* and *Beauveria bassiana*. Both fungi are known to endophytically colonise diverse plants and to exert detrimental effects on insects (Coppola, Diretto, et al. 2019; Alınç et al. 2022; Zhang et al. 2019; Garrido-Jurado et al. 2017). Additionally, *T. harzianum* has been shown to alter onion thrips behaviour (Muvea et al. 2014, 2015), although its long-term population-level impacts remain unclear, and while *B. bassiana* is a well-established entomopathogen against thrips (Gouli et al. 2009; Ain et al. 2021), its efficacy as an endophyte in onion has been little studied. Our hypothesis is twofold: first, that endophytic colonisation by *T. harzianum* and *B. bassiana* confers a longer-lasting suppressive effect on thrips—persisting from initial exposure through several weeks—manifested as reduced feeding, oviposition, and population growth; and second, that these endophyte-mediated effects are largely independent of onion cultivar. Demonstrating durable, cultivar-independent protection would support sustainable, broadly applicable thrips management in onion production.

2 | Materials and Methods

2.1 | Rearing of Insects

Chives (*Allium schoenoprasum* L. cultivar Grande) were used for stock and synchronised rearings. Plants were grown from seeds (HILD samen GmbH, Marbach, Germany) in 12 cm diameter pots filled with Fruhstorfer soil type P (Hawita Group, Vechta, Germany) and cultivated in the greenhouse nursery at the Section of Phytomedicine (IPP), Institute of Horticultural Production System, Leibniz University Hannover, Germany. *T. tabaci* of the stock rearing were cultivated on 8–10 weeks old chives plants in gauze cages placed in a climate chamber (25°C ± 1°C, relative humidity of 60% ± 5%, photoperiod of 12 h L: 12 h D). To obtain synchronised thrips for the experiments, synchronised rearing was organised in a climate chamber at the same conditions. 25–30 adult thrips were released in a glass jar with chives leaves cutting from 8 to 10 weeks old chives plants inside. Every jar had a hole cut into the lid which was covered with thrips-proof gaze to allow ventilation. After 2 days, adults were removed and egg-infested chives leaves were collected and transferred to new ventilated jars. Fresh chives leaves were added 3 times per weeks to continuously nourish high quality food sources for larval and adult thrips. The synchronised rearing was implemented continuously for timely provision of thrips for the experiments.

2.2 | Source of Fungal Endophytes

Two endophytic fungi were compared in the study, *Trichoderma harzianum* ICIPE 709 provided by International Centre of Insect Physiology and Ecology (ICIPE)—Kenya and *Beauveria bassiana* strain ATTC 74040, that is, the commercial product Naturalis supplied by CBC (Europe) S.r.l—BIOGARD Division. The isolates were grown on potato dextrose agar (PDA) (Merck KGaA, Darmstadt, Germany) media at 25°C in complete darkness. Under laminar flow hood, growing conidia of the isolates were collected from 2 weeks-old cultures by flooding the plates with 10 mL of sterile distilled water containing 0.05% Tween 20 and scratching the surface of the culture with a sterile cotton bud, and suspending them in an Erlenmeyer flask containing 20 mL of sterile distilled water containing 0.05% Tween 20. Vortexing for 10 min created a homogeneous conidial suspensions, which was filtered through a sterile cheesecloth to remove hyphae and to obtain the stock suspension. The conidia were quantified using a Thoma haemocytometer (Assistent, Glaswarenfabrik Karl Hecht GmbH & Co KG, Germany) and the suspension was adjusted to a final concentration about 1×10^8 conidia/ml for inoculation steps. To verify the reliability of the experimental process, conidial germination rates were confirmed to be at least 90% in each experiment by counting viable spores under a stereo microscope (Leica DM750, Leica Microsystems) at 400× magnification (Oliveira et al. 2015).

2.3 | Endophytic Establishment in Onion Plants and Growth Conditions

Allium cepa L. seeds (HILD samen GmbH, Marbach, Germany) with two cultivars Sturon, that is, a yellow onion and Red Baron, that is, a red onion, were used for the experiment. In the ventilation flow hood, onion seeds were surface-sterilised by immersing in ethanol 70% for 2 min, followed by 3 min dipping in 2% sodium hypochlorite added 0.05% Tween 20, then rinsed thrice in autoclaved distilled water. The seeds were dried on a sterile paper for about 20 min. To evaluate the successful sterilisation, 100 μL of the last wash water was plated on PDA media, and incubated in the dark for 10 days at 25°C. The absence of fungal growth at the end of the incubation period was an indication of the efficacy of the sterilisation process.

After drying, the seeds were soaked into the selected fungal endophytes suspension as treatments and into the conidia-free solution of 0.05% Tween 20 as control for 8 h before transfer to cultivation pots containing Fruhstorfer soil type P (Hawita Group, Vechta, Germany). The plants were maintained in a climate chamber (25°C ± 1°C, relative humidity of 60% ± 5%, photoperiod of 12 h L: 12 h D) and irrigated regularly. Three weeks after germination, the plants were transplanted to single plants per pot (12 cm diameter size) or three plants per pot (14 cm diameter size) for different purposes of later experiments. All plants were fertilised once a week with 0.2% Wuxal Top N (Aglukon Spezialdünger, Düsseldorf, Germany).

Three weeks after transplanting to new pots, the onion plants were at the stage of having 2–3 fully grown true leaves; the foliar inoculation method was applied. This supplementary inoculation aims to guarantee fungal infection on all treated plants and to promote homogeneous fungal growth of the two fungi on both the onion roots and leaves. It must be ensured that all onion leaves are dry before inoculation. During inoculation, the top of the pots was covered with aluminium foil to avoid conidial runoff to the soil. For the treatments, each onion plant was inoculated by spraying all leaves with 10 mL of conidial suspension using a 50 mL hand pressure sprayer. The control plants were sprayed with 10 mL of 0.05% Tween 20. Following the application of the spray, the plants were enveloped with plastic bags for a duration of 24 h in order to sustain optimal humidity levels, thereby promoting the endophytic colonisation of plant tissues. The plants were kept in the climate chamber until the experiment started (25°C ± 1°C, relative humidity of 60% ± 5%, photoperiod of 12 h L: 12 h D).

2.4 | Confirmation of Endophytically Colonisation

Re-isolation was conducted to ensure that all experimental onion plants were successfully inoculated with the endophytic fungi (modified from Powell et al. 2009). Evaluation time varied for each experiment. Onion plants were uprooted carefully, and soil was removed by gently washing with running tap water. For each plant, two leaves and two root strands were collected. Two parts of each leaf (6 cm length each part) and two parts of each root (6 cm length each part) were collected. Under a laminar flow hood, the plant fragments were surface sterilised by immersing them in 70% ethanol for 30 s, followed by 2% sodium hypochlorite amended with Tween 20 for 3 min and subsequently rinsed three times with sterile distilled water. The surface-sterilised plant parts were dried under the laminar flow hood, then each sample was cut into 1 cm long parts. Five pieces from the identical plant fragment were uniformly distributed on PDA plates supplemented with antibiotics (0.1 g Penicillin + 0.01 g Chlortetracyline + 0.05 g Steptomycinsulfat). In order to evaluate the efficacy of the surface sterilisation procedure, 100 μL of the last rinse water was plated on PDA media. Additionally, randomised extra samples were imprinted into PDA to verify the complete removal of epiphytic microorganisms. All the Petri dishes were incubated in the dark at 25°C and fungal growth was observed during the subsequent 14 days. Only if no fungus had grown in the control Petri dishes which contained last rinse water of tested samples, could the results be used for later analysis. Successful colonisation of sampled plant parts was visually examined after incubation for 3–14 days. Whenever a fungus grew from the leaf discs, a square piece was cut out of the medium overgrown with fungus and placed on a new PDA medium without antibiotics. The newly prepared plate was placed in the incubator until the conidia developed, by which the fungus could be identified by visual morphological comparison with a mother plate.

2.5 | Thrips Feeding and Egg Laying Behaviour Bioassay

The control and fungal inoculated onion plants were cultivated for 8–9 weeks old (3 weeks post leaf inoculation) in the climate chamber before experimental use. One onion plant was placed inside a thrips-proof gauze cage with the size of 45 cm H × 30 cm W × 30 cm L. Female adult thrips were carefully collected with a fine brush from synchronised cultures into 15 individuals per Eppendorf tube containing a wet cotton piece and starved for 22–24 h. Each Eppendorf tube containing starved

thrips with the lid opened was placed at the base of the plant. All the closed cages were kept at 25°C ± 1°C, relative humidity of 60% ± 5%, photoperiod of 12 h L: 12 h D. After 72 h, all alive thrips observed on the plants were recaptured and counted initially (Muvea et al. 2014). The second and fourth true leaves from each plant were collected and cut into four sections of 4 cm. Under a stereo microscope (Leica MZ6), the number of small feeding spots in those sections of leaves was counted and recorded to quantify feeding damage before eggs counting step. Those leaf sections were then stained with the solution of 1 g fuchsin acid per 1 L of Lactoglycerol (85% lactic acid + glycerol + distilled water with the ratio of 1:2:2) at 80°C–85°C for 5 min (modified from Rozenberg et al. 2015). The sections were later gently washed by dipping in warm distilled water 3 times before placing in 90 mm Petri dishes and ready for eggs counting under a stereo microscope (Leica DM750-Leica Microsystems).

The experiment comprised of three treatments (two fungal endophytes and a control) for each onion cultivar were arranged in a completely randomised block design with five cages assigned to each treatment. The experiment was repeated four times, that is, with a total of 20 replicates. The colonisation of onion by the endophytes was confirmed in the remaining plants after the experiment finished. Only endophyte-colonised onion plant recordings were used for statistical analyses.

2.6 | Effect of Endophytically Colonised Onion Plants on Thrips Populations Dynamics

With the aim of investigating how thrips populations develop under the influence of endophytically colonised onion plants, the other bioassays were designed similarly to the one above but with two different durations of 4 and 8 weeks. All the onion plants for both control and inoculated plants were about 11–12 weeks old. Three onion plants treated in the same treatment in one pot were placed in a gauze cage to serve as the food supply for the thrips. 15 female onion thrips that were starved for 24 h were released into the cage. The number of alive thrips for both nymph and adult stages on each pot was assessed after 4 and 8 weeks. At the assessment time, each plant was gently covered by a labelled polythene paper bag, cut at the base of the plant and closed the bag, stored at −4°C for 4–5 h in order to immobilise the thrips for later quantification. The experiment was repeated four times each with five cages, that is, in total 20 replicates every treatment. The colonisation of onion by the endophytes among plants used for the bioassay was confirmed before the experiment started. Only endophyte-colonised onion plant recordings were used for the experiment.

2.7 | Statistical Analysis

In order to evaluate the influence of treatments or onion cultivars (fungal endophytically treated plants and control) on thrips behaviour and population, various parameters were examined, including the count of recaptured alive thrips, feeding punctures, eggs laid in the initial experiment and the number of thrips (both adult and emerged larvae) in the subsequent experiment. The parametric one-way ANOVA test was applied when the data exhibited normal distribution, while the non-parametric Kruskal-Wallis test was utilised for non-normally distributed data (Fox and Weisberg 2023). The post hoc Tukey HSD and Dunn's tests were used to identify the statistically significant differences, with a significance level of 5% (p-value < 0.05). The number of thrips for different treatments, experimental duration (4 weeks and 8 weeks) and onion cultivars were analysed using the generalised linear model (GLM), assuming a negative binomial distribution (count data with overdispersion). The significantly different means were identified by post hoc Tukey HSD, considering a significance level of 5%. All experiments were performed using a completely randomised design, and all data sets were previously checked for normality and homogeneity of variance across the treatments using Shapiro–Wilk and Levene tests. All the analyses were performed using the R statistical software, version 4.2.3 (R Core Team 2023).

3 | Results

3.1 | Thrips Feeding and Egg Laying Behaviour Bioassay

The success test for endophytic colonisation conducted at the end of the experiment revealed that both fungal endophytes had colonised 100% of the experimental plants; hence, all 20 replicates were included in the data analysis. In general, after an experimental period of 72 h, both endophytes *T. harzianum* and *B. bassiana* had negative effects on thrips feeding and egg-laying behaviour. Additionally, there was no variability between the two onion cultivars, yellow onion cultivar Sturon and red onion cultivar Red Baron, with regard to thrips behaviour, even on the control plants.

The results of the experiment indicated that the two endophyte treatments had a significant reduction effect on the number of alive thrips collected on the onion plants in both onion cultivars (Sturon $F = 33.89$, $p < 0.001$; Red Baron $\chi^2 = 33.35$, $p < 0.001$). Meanwhile, no difference between the two fungal treatments was noted (Sturon $p = 0.88$; Red Baron $p = 1$). Compared to the control on Sturon cultivar, the survival of onion thrips was reduced by 40.65% and 43.5% on plants inoculated with *T. harzianum* and *B. bassiana*, respectively. A similar trend was observed on the cultivar Red Baron, where the reduction in survival rates of onion thrips was 44.26% on *T. harzianum* treated plants and 45.96% on *B. bassiana* treated plants (Figure 1).

The feeding damage caused by onion thrips was significantly reduced in both endophyte-inoculated plants when compared to the control (Sturon $F = 116.7$, $p < 0.001$; Red Baron $F = 75.97$, $p < 0.001$). In the trial using the cultivar Sturon, onion plants treated with *T. harzianum* and *B. bassiana* showed fewer feeding punctures caused by *T. tabaci*, averaging 22.85 and 16.85 feeding punctures, respectively. These values were 2.1 and 2.9 times lower than those on the control plants. The difference in feeding activity between the two endophyte-treated groups was also statistically significant ($p = 0.02$). Similarly, the number of feeding punctures on control plants was twice as high as on endophyte-treated plants for the cultivar Red Baron (Figure 2).

At 72 h post-exposure, oviposition of onion thrips was adversely affected by endophyte treatments (Sturon $\chi^2 = 39.77$, $p < 0.001$;

Red Baron $\chi^2 = 42.88$, $p < 0.001$). The number of eggs laid on Sturon onion plants across two fungal *T. harzianum* and *B. bassiana* treatments (with means values of 7.7 and 7.3 eggs, respectively) was significantly lower than that on the control plants (mean of 21.35 eggs). In addition, the number of eggs laid on Red Baron control plants was 2.8 and 3.9 times higher than on *T. harzianum* and *B. bassiana* treated plants, despite the absence of statistical significance between these last two treatments (Figure 3).

3.2 | Effect of Endophytically Colonised Onion Plants on Thrips Populations Dynamics

Overall, thrips population development was significantly reduced on endophyte colonised onion plants for both cultivars. The effect of endophytes on thrips population density was still prevalent after 8 weeks. However, only small differences in population development were detected when comparing treatments with the two fungal endophytes *T. harzianum* and *B. bassiana*.

In the trials using the onion cultivar Sturon, both endophytic fungi caused a significant reduction in total number of thrips compared to the control, irrespective of the evaluation time points after 4 and 8 weeks ($F = 79.66$, $p < 0.001$ and $F = 19.51$, $p < 0.001$, respectively). Four weeks after the release of thrips into the experimental cages, the reduction in total thrips numbers on plants inoculated with *T. harzianum* and *B. bassiana* was 56.8% and 39.9%, respectively, compared to the control. While after 8 weeks of experiment, these rates were lower, ranging between 22.69% and 22.43%, respectively (Figure 4A,D). When adults and larvae were assessed independently within the same endophyte treatment, there was also a significant treatment effect on the number of adult thrips (after 4 weeks $\chi^2 = 39.75$, $p < 0.001$; after 8 weeks $F = 7.32$, $p = 0.0015$; Figure 4B,E), and larvae (after 4 weeks $F = 49.57$, $p < 0.001$; after 8 weeks $F = 22.06$, $p < 0.001$; Figure 4C,F) and the population density decreased after 4 weeks for adult up to 64% (*B. bassiana*) and for thrips larvae by 69% (*T. harzianum*). Additionally, there was a notable difference between the effects of the two fungal species. At 4 weeks duration experiment, the total number of onion thrips on plants treated with *B. bassiana* (with means of 45.7 thrips) was significantly

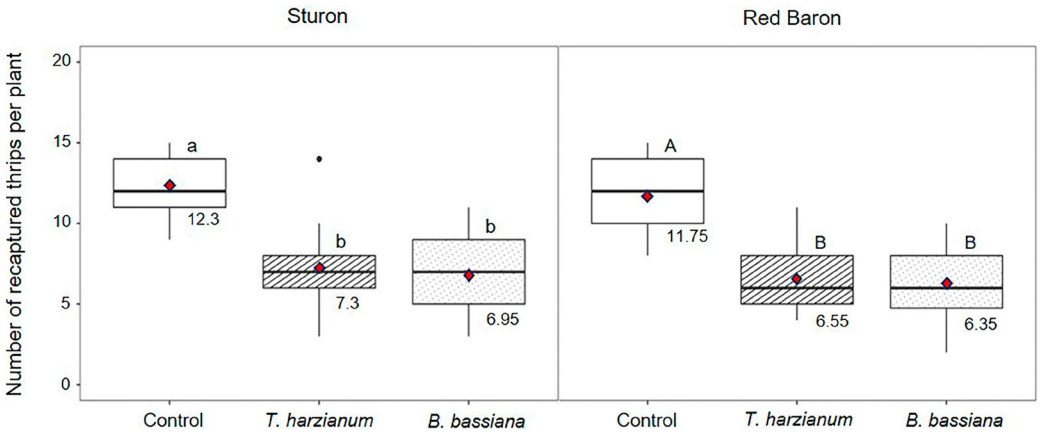


FIGURE 1 | Number of recaptured alive thrips on onion plant from different treatments 72 h after release of 15 female *Thrips tabaci* per cage. The mean values are denoted by red dots accompanied by a numerical value. Different letters show significant differences between the effect of the treatments (ANOVA followed by Tukey's HSD test, $p < 0.05$ for Sturon cultivar, Kruskal–Wallis followed by Dunn's post hoc test for Red Baron cultivar, $p < 0.05$). $n = 20$. [Colour figure can be viewed at wileyonlinelibrary.com]

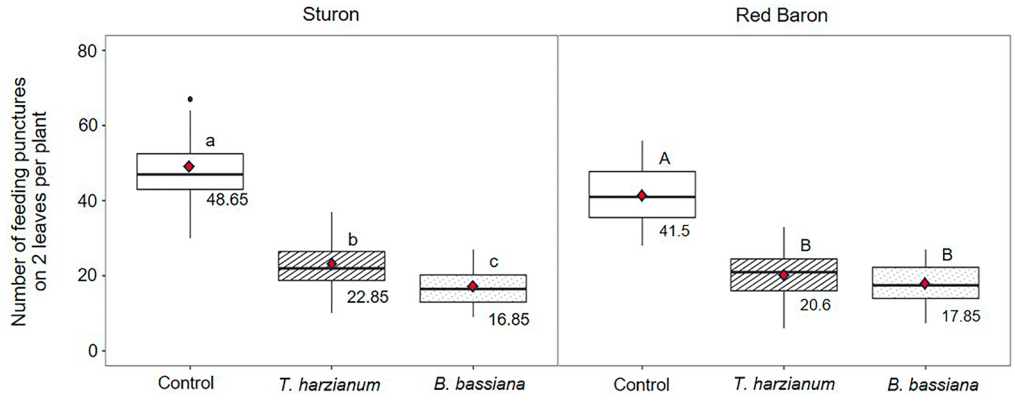


FIGURE 2 | Number of feeding punctured on 2 leaves per onion plant from different treatments 72 h after release of 15 female *Thrips tabaci* per cage. The mean values are denoted by red dots accompanied by a numerical value. Different letters show significant differences between the effect of the treatments (ANOVA followed by Tukey's HSD test, $p < 0.05$). $n = 20$. [Colour figure can be viewed at wileyonlinelibrary.com]

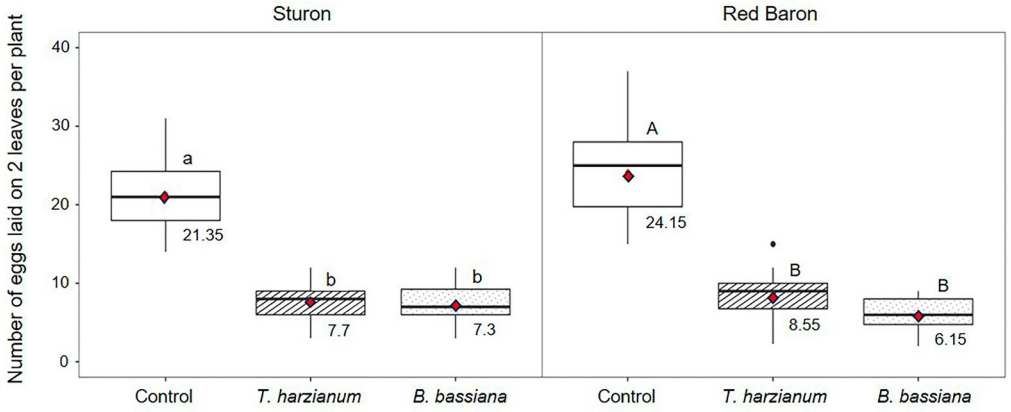


FIGURE 3 | Number of eggs laid on 2 leaves per onion plant from different treatments 72 h after release of 15 female *Thrips tabaci* per cage. The mean values are denoted by red dots accompanied by a numerical value. Different letters show significant differences between the effect of the treatments (Kruskal–Wallis followed by Dunn's post hoc test, $p < 0.05$). $n = 20$. [Colour figure can be viewed at wileyonlinelibrary.com]

higher ($p = 0.0016$) compared to *T. harzianum* treated plants (with means of 32.85 thrips; Figure 4A), which corresponded to a comparable disparity in the number of larvae (Figure 4C). Nevertheless, after the 8-week experiment, the difference disappeared ($p = 0.99$).

When using Red Baron onion cultivar, the influence of fungal endophytes was also recorded by the remarkably lower total number of thrips on endophyte inoculated onion plants compared to the control (after 4 weeks $\chi^2 = 39.45$, $p < 0.001$; after 8 weeks $F = 31.66$, $p < 0.001$; Figure 5A,D). Regarding the effect of the two endophytes, at 4 weeks post-exposure, both endophyte treatments resulted in a comparable total number of thrips. Meanwhile, the number of thrips on plants treated with *B. bassiana* was slightly lower compared to plants treated with *T. harzianum*, but this difference was not significant ($p = 0.069$) after the 8 weeks experiment. Similarly, the effect of the endophytic fungi was again evident in the various stages of thrips after both experimental periods. The endophyte treatments significantly affected the populations of adult (after 4 weeks $\chi^2 = 43.32$, $p < 0.001$; after 8 weeks $F = 14.4$, $p < 0.001$; Figure 5B,E) and larval thrips (after 4 weeks $\chi^2 = 41.88$, $p < 0.001$; after 8 weeks $F = 31.86$, $p < 0.001$; Figure 5C,F).

Overall, thrips population densities were similar on the two different onion cultivars for both treatments and the control for both periods. Only in the treatment with *B. bassiana*, the onion cultivar Red Baron showed an increased thrips resistance compared to the cultivar Sturon (4-week experiment $p < 0.001$, 8-week experiment $p = 0.045$). Population increase over the first 4 weeks differed markedly between the control and the two fungal treatments (Sturon: $\chi^2 = 15.6$, $p < 0.001$; Red Baron: $\chi^2 = 15.4$, $p < 0.001$). From Weeks 4 to 8, total thrips numbers rose further within each treatment. For Sturon ($\chi^2 = 52.0$, $p < 0.001$), densities increased by 28.1% ($p < 0.001$) in the control, compared with 129.2% ($p < 0.001$) and 65.3% ($p < 0.001$) under *T. harzianum* and *B. bassiana*, respectively. For Red Baron, the effect of experimental period was also significant ($\chi^2 = 52.3$, $p < 0.001$): control populations grew by 26.4% ($p < 0.001$), whereas increases of 127.4% ($p < 0.001$) and 108.7% ($p < 0.001$) were observed under *T. harzianum* and *B. bassiana*, respectively. Although relative growth between Weeks 4 and 8 was greater under *T. harzianum* than under *B. bassiana*, thrips densities on endophyte-colonised plants remained below control levels at Week 8, indicating a more persistent, longer-lasting suppressive effect—particularly for *B. bassiana*.

4 | Discussion

The systemic impact of endophytic fungi on *T. tabaci* was investigated in terms of oviposition activity, feeding damage and population dynamics. The results of this study indicate that the behaviour and population development of the onion thrips were significantly negatively affected by artificial inoculation of onion plants with *T. harzianum* as well as *B. bassiana*, irrespective of the onion cultivar. This remains valid for the hypothesis we proposed, despite the different mode of action of the two fungi. Indeed, *Trichoderma* is well-known acting as endophyte in the rhizosphere. However, several studies have demonstrated that many *Trichoderma* species have the capacity to colonise diverse aboveground plant components (Bailey et al. 2009; Bandeira et al. 2023; Natsiopoulos et al. 2024). When colonising and establishing in the host plant as an endophytic fungus, *Trichoderma* strains were reported to enhance indirect plant defence barriers against insects (Macías-Rodríguez et al. 2020; Natsiopoulos et al. 2024; Coppola, Diretto, et al. 2019). Meanwhile, the entomopathogenic fungus *B. bassiana* is a broad-spectrum biocontrol agent effective against numerous herbivore species and plant pathogens (Blond et al. 2018; Mascarin and Jaronski 2016). Recent research has evidenced the efficiency of *B. bassiana* colonisation in enhancing host plant defences against pest attack (Castillo-Lopez et al. 2014; Gurulingappa et al. 2010; Powell et al. 2009), including *Frankliniella occidentalis* Pergande (Mantzoukas et al. 2022; Zhou et al. 2025). Herein, our finding provides evidence that *B. bassiana* also induced negative effects on onion thrips behavioural performance which were comparable to those of *T. harzianum*.

Endophytic fungi protect plants from herbivorous insects through multiple mechanisms, including antixenosis, which refers to the plant trait that deter herbivores from feeding (Vega 2018), oviposition (Lopez and Sword 2015) or remaining on the host plant (Akello and Sikora 2012). In the initial

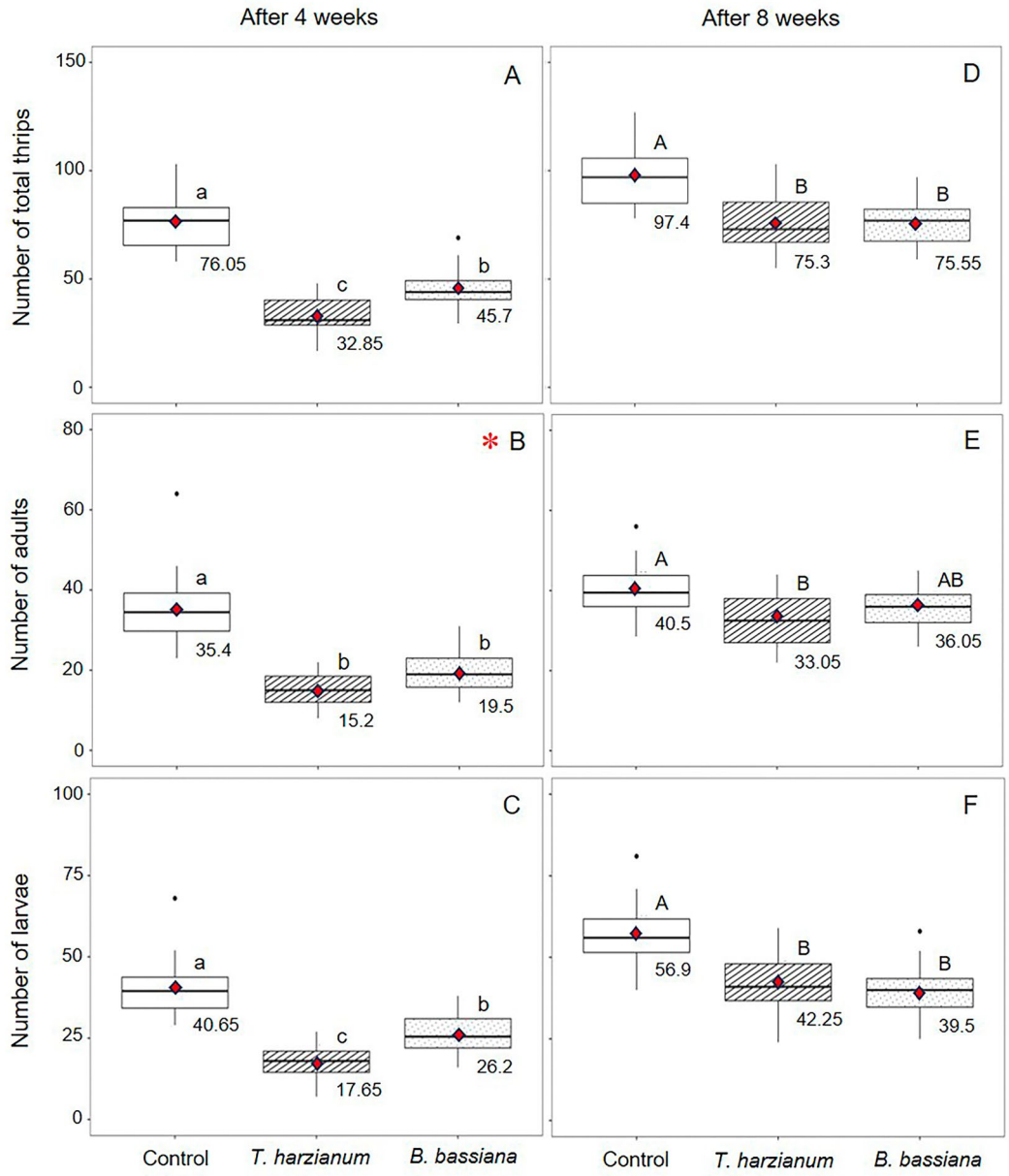


FIGURE 4 | Number of total thrips, adults and hatched larvae on onion plants Sturon cultivar under 2 different treatments 4 weeks and 8 weeks post-exposure to 15 released female *Thrips tabaci*. The mean values are denoted by red dots accompanied by a numerical value. Different letters show significant differences between the effect of the treatments (ANOVA followed by Tukey's HSD test, $p < 0.05$; boxplot tables with red asterisks indicate data analysed by Kruskal–Wallis followed by Dunn's post hoc test, $p < 0.05$). $n = 20$. [Colour figure can be viewed at wileyonlinelibrary.com]

bioassay, the number of recaptured alive thrips on endophyte-treated plants 72 h after infestation was already significantly lower compared to those on control plants on both onion cultivars. This result is consistent with the previous findings of Muvea et al. (2014), who reported that onion thrips proportion was negatively impacted by several strains of endophytic fungi, including *T. harzianum*. The reason for the behavioural avoidance of thrips from fungal-inoculated plants might possibly be the result of the endophyte-mediated impact through olfactory cues (Jallow et al. 2008; Ludwaba et al. 2024). Recent studies indicated that endophytic fungi can modulate important phytohormones such as jasmonic acid (JA) and salicylic acid (SA) (Martínez-Medina et al. 2017; Zhang et al. 2025), which are signalling pathways in host plants, thereby triggering the induced systemic resistance (ISR) via enhancing the production of defensive metabolites and volatile compounds (Jallow et al. 2008; Agbessenou et al. 2022; Saikkonen et al. 2013). Therefore, endophytic fungi play a crucial role in host plant selection (George et al. 2024). Before colonising a plant, adult thrips have to determine a potential suitable host plant, which includes pre-landing and post-landing activities. The approach and subsequent landing of the thrips on the potential host are influenced by several factors, such as the olfactory (Koschier et al. 2007) and/or visual cues (Lopez-Reyes et al. 2022). In choice situations, before landing, Muvea et al. (2015) revealed the involvement of volatile emissions in the context of host plant selection by onion thrips in Y-tube olfactometer trials, demonstrating a repellent effect of plants colonised by the endophyte *Hypocrea lixii*. Similarly, the colonisation of kidney bean plants by *Lecanicillium attenuatum*

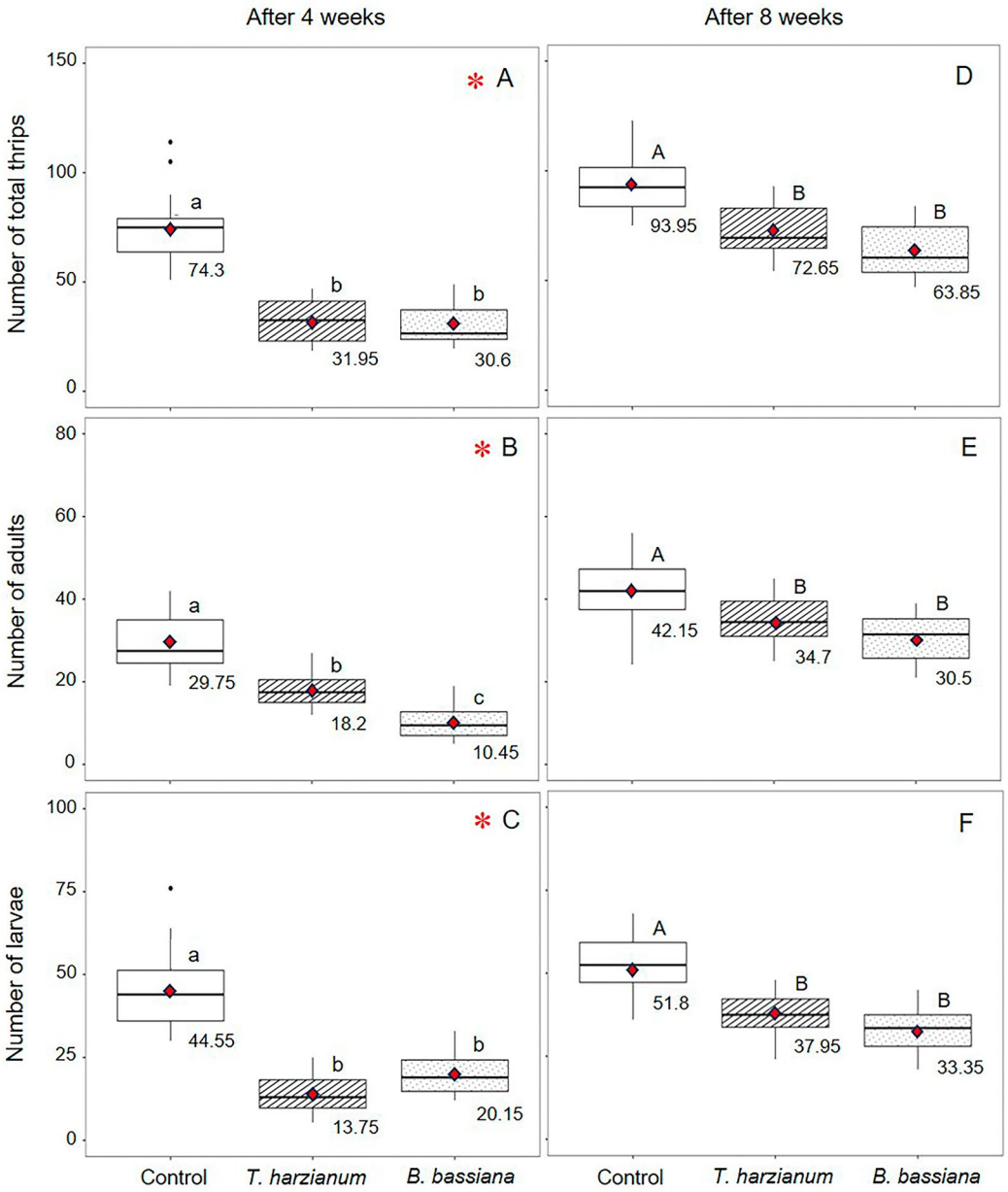


FIGURE 5 | Number of total thrips, adults and hatched larvae on onion plants Red Baron cultivar under 2 different treatments 4 weeks and 8 weeks post-exposure to 15 released female *Thrips tabaci*. The mean values are denoted by red dots accompanied by a numerical value. Different letters show significant differences between the effect of the treatments (ANOVA followed by Tukey's HSD test, $p < 0.05$; boxplot tables with red asterisks indicate data analysed by Kruskal–Wallis followed by Dunn's post hoc test, $p < 0.05$). $n = 20$. [Colour figure can be viewed at wileyonlinelibrary.com]

and *L. cauligalbarum* was found to repel *F. occidentalis* (Zhou et al. 2025). In contrast, our current experiments were conducted under a no-choice scenario, which excludes dispersal to alternative resources. Nevertheless, thrips seem to avoid colonisation of endophyte inoculated onion plants underlining a strong repellent effect by volatiles (Vu and Meyhöfer in prep.). The number of thrips remaining on the fungal-inoculated plants was significantly lower than on the control plants. In cages containing endophyte treated plants, in addition to the alive thrips recorded on the plants, many thrips were observed crawling on the mesh at the top of the cage, indicating a strong deterrent impact of the endophytes. The effects were further emphasised by a decrease in feeding and oviposition activity. Activities that occur after landing on a potential host plant, in contrast to the habitat finding step, require thrips to be directly exposed to the secondary metabolites to assess plants' suitability for feeding and/or oviposition, with nutritional contents and defences of the plant playing a crucial role in their host acceptance (Brown et al. 2002; Pobożniak and Koschier 2013). Our findings are in line with those reported in the study of Zhou et al. (2025), who demonstrated that the application of *L. attenuatum* and *L. cauligabarum* led to a reduction in feeding behaviour and oviposition capacity of western flower thrips. Moreover, similar studies have also reported the negative systemic impact of endophytic fungi on the behaviour of different pest insects. *B. bassiana* induced a reduction in

damage caused by the aphid *Aphis gossypii* Glover on cotton plant (Gurulingappa et al. 2010), a reduction in the number of eggs and nymphs of greenhouse whiteflies *Trialeurodes vaporariorum* Westwood (Barra-Bucarei et al. 2020); *Vicia faba* L. seeds treated with *B. bassiana* and *Trichoderma asperellum* M2RT4 were found to limit the offspring development and reproductive fitness of aphids *Acyrthosiphon pisum* Harris and *Aphis fabae* Scopoli (Akello and Sikora 2012). Our research revealed that fungi-inoculated plants still served as oviposition substrate, implying that at least some females, if not all, considered inoculated plants appropriate for reproduction. It is unclear whether only single or multiple individuals fed and/or laid eggs on the fungi-inoculated plants, behavioural tracking of individuals would be necessary to unravel the potential relevance of close-range and gustatory cues.

Extending the study duration enabled a more comprehensive assessment of the long-term impact of fungal endophytes on thrips population development and to get initial insights about their biocontrol potential on the field. Despite our inability to record the mortality of thrips due to the small size of both adults and larvae as well as their possibility of being buried in the soil, the significantly lower number of thrips collected from fungal treated plants compared to the control at the two time points of the experiments still clearly demonstrates the effectiveness of studied endophytic fungi on the population dynamics of *T. tabaci*. Endophytic fungi protect plants against herbivorous insects through antibiosis, a mechanism involving toxic secondary metabolite compounds, affecting insect survival, growth and reproduction (Vega et al. 2008, 2009). Recent studies indicate that *T. harzianum* and *B. bassiana* boost plant growth while enhancing mainly ethylene, SA- and JA-dependent defences, thereby reducing herbivore damage (Van Hee et al. 2023; Yousef-yousef et al. 2024) as well as their population density (Marassatto et al. 2025). In our experiments, with an extended experimental period we expected an increase in the effect of endophytic fungi on the thrips population. However, it is evident that the number of thrips, including both adults and larvae, developing on fungal inoculated plants was significantly lower than that on control plants after the different treatment periods. But with continued exposure, the detrimental effect of endophytic fungi seemed to be less pronounced while thrips population density started to increase. This was observed similarly with both endophytic treatments and on both onion cultivars. Thus, the effect of the endophytes on herbivores seems to diminish over time. Although the underlying reason remains unclear, it is possible that reduced endophyte impact over time as well as adaptation by thrips (Zhang et al. 2019) may contribute to the observed effects. According to the initial experiment, small numbers of thrips eggs were still found on inoculated plants after the first 72 h. In the later test, thrips populations doubled or tripled from the initial 15 individuals after 4 weeks, depending on the treatment and onion cultivar. Plant quality can influence insect reproduction and their adaptability to the host plants. Once insects find a suitable site to feed and survive, they will continue to lay eggs and maximise their offspring (Brown et al. 2002; Fu et al. 2019). Furthermore, the mutualistic association between endophytic fungi and their host plants may be transient, as not all fungi have the ability for prolonged colonisation, especially if they cannot adapt to the plant physiology (Mercado-Blanco and Lugtenberg 2014). Moreover, under detrimental environmental conditions or host stress, certain endophytes may even switch from mutualistic to parasitic behaviour (Sieber and Grünig 2006; Galindo-Solís and Fernández 2022). Nevertheless, Mantzoukas et al. (2022) also demonstrated that strawberry plants (*Fragaria* sp.) inoculated two times with *B. bassiana* effectively reduced *F. occidentalis* populations for a period of up to 4 months under field conditions. Our experiments were conducted at constant environmental conditions in a climate chamber, excluding the impact of natural fluctuations on the interaction between endophytic fungi, onion plants and thrips. Therefore, validation of the long-term effects of endophytic fungi on herbivorous insects under variable environmental conditions should be the next step to achieve an accurate assessment of their efficacy in praxis.

Finally, several studies have revealed the presence of fungal spores/hyphae in insects exposed to fungal-infected plants, particularly those treated with *B. bassiana* (Akello et al. 2009; Garrido-Jurado et al. 2017). Therefore, although the number of dead thrips could not be quantified, several thrips carcasses, along with several surviving individuals, were randomly collected after the 4-week and 8-week periods to assess the potential infection with fungal spores. But unfortunately, no mycelial growth was detected in the examined dead thrips. This indicates that thrips are most likely influenced by endophyte-triggered plant defence mechanism, involving alterations in bioactive secondary metabolites, rather than direct effects of entomopathogenic fungi.

Currently, no onion cultivar with a high resistance to *T. tabaci* has been identified so far (Gill et al. 2015), but several cultivars show moderate resistance or may withstand certain damage inflicted by thrips, primarily due to morphology, physical and chemical attributes of the host plants (Diaz-Montano et al. 2010; Silva et al. 2015; Pobożniak et al. 2021). Nevertheless, onions are a rich source of antioxidants, with red onions containing higher levels of flavonoids in comparison to yellow onions (Cheng et al. 2013; Chernukha et al. 2022). Silva et al. (2015) revealed that there was a negative correlation between the phenolic concentration in a red onion cultivar and the level of thrips damage. Therefore, red onion was expected to show higher resistance to *T. tabaci* even when inoculated with the endophytic fungi. However, between the yellow onion cultivar Sturon and the red onion cultivar Red Baron, there was no immediate difference in thrips feeding and oviposition behaviour within the same endophyte treatments, including the two controls. A trait of onion cultivars, known as antixenosis, involving plant morphological features, for example, leaf colour, leaf angle, and a waxy outer layer, that disrupt insect behaviour and contribute to resistance against *T. tabaci* (Diaz-Montano et al. 2010, 2012; Birithia et al. 2014). For example, Birithia et al. (2014) showed that more thrips were observed on blue–green non-glossy onion leaves, while fewer thrips were found on light green glossy leaves. In our study, under controlled experimental conditions of the climate chamber, no obvious difference in morphological characteristics and plant growth between the two onion cultivars, including fungal inoculated and control plants, were observed. Nevertheless two onion cultivars were evaluated, and the results of this study also provide positive signals about the ability of endophytic fungi to colonise multiple onion cultivars while enhancing host plant resistance to thrips damage.

In conclusion, *T. harzianum* and *B. bassiana* treated onion plants exert a negative impact not only on pest survival, feeding behaviour and fecundity rates but also on the population dynamics of onion thrips, subsequently showing the potential endophytic fungi as promising biocontrol agents for the management of *T. tabaci* on onion crops. Notably, the combination of seed and foliar inoculation has shown high reliability in enhancing these effects, further supporting its practical application in pest management. Nonetheless, because fungal conidia are highly sensitive to direct sunlight, further research is required to develop methods that enhance conidia and hyphae persistence, thereby ensuring the efficacy of foliar inoculation process. Testing fungal spore suspension formulations containing natural UV-protective additives to evaluate the colonisation and establishment ability of fungi in plant tissue under practical conditions should be prioritised. Moreover, it is essential to note that the interaction between the host plant, the endophytic fungi and the insect pest can be influenced by climate factors, soil conditions and plant stress levels. Understanding these endophytic fungi's physiological and ecological mechanisms in different host plants and environmental conditions can ensure their consistent performance under practical cultivation conditions. Consequently, the successful commercialization of endophytic fungi-based biopesticides has to be investigated and validated under real agricultural conditions.

Author Contributions

Sevgan Subramanian: methodology, writing – review and editing, resources, conceptualization. **Rainer Meyhöfer:** conceptualization, supervision, funding acquisition, writing – review and editing, project administration, resources, visualization. **Ngoc Anh Vu:** investigation, validation, formal analysis, writing – original draft, methodology, data curation, conceptualization, visualization.

Acknowledgements

We would like to thank Birgit Milde and Timo Michel for their technical support, Sina Rogge and Nilupuli Thushangi for the helpful discussion. The fungal endophyte strain *Trichoderma harzianum* was kindly provided by the International Centre of Insect Physiology and Ecology (icipe) (Kenya). Open Access funding enabled and organized by Projekt DEAL.

Funding

The project was supported by the fund of the Ministry of Agriculture and Environment of Vietnam.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data presented in this study are openly available in the LUH Data Repository at LUIS. https://doi.org/10.25835/ivm37tff (Anh Vu et al. 2025).

References

Adesanya, A. W., T. D. Waters, M. D. Lavine, D. B. Walsh, L. C. Lavine, and F. Zhu. 2020. "Multiple Insecticide Resistance in Onion Thrips Populations From Western USA." *Pesticide Biochemistry and Physiology* 165: 104553. https://doi.org/10.1016/j.pestbp.2020.104553.

Agbessenou, A., K. S. Akutse, A. A. Yusuf, and F. M. Khamis. 2022. "The Endophyte Trichoderma asperellum M2RT4 Induces the Systemic Release of Methyl Salicylate and (Z)-jasmone in Tomato Plant Affecting Host Location and Herbivory of Tuta absoluta." *Front. Plant Sci* 13: 860309. https://doi.org/10.3389/fpls.2022.860309.

Ain, Q., A. U. Mohsin, M. Naeem, and G. Shabbir. 2021. "Effect of Entomopathogenic Fungi, *Beauveria bassiana* and *Metarhizium anisopliae*, on *Thrips tabaci* Lindeman (Thysanoptera: Thripidae) Populations in Different Onion Cultivars." *Egyptian Journal of Biological Pest Control* 31: 97. https://doi.org/10.1186/s41938-021-00445-y.

Akello, J., T. Dubois, D. Coyne, and S. Kyamanywa. 2008. "Effect of Endophytic *Beauveria bassiana* on Populations of the Banana Weevil, *Cosmopolites sordidus*, and Their Damage in Tissue-Cultured Banana Plants." *Entomologia Experimentalis et Applicata* 129: 157–165. https://doi.org/10.1111/j.1570-7458.2008.00759.x.

Akello, J., T. Dubois, D. Coyne, and S. Kyamanywa. 2009. "Effect of Endophytic *Beauveria bassiana* Dose and Exposure Duration on Colonization and Growth of Tissue Cultured Banana (Musa sp.) Plants." *Biological Control* 49, no. 1: 6–10. https://doi.org/10.1016/j.biocontrol.2008.06.002.

Akello, J., and R. Sikora. 2012. "Systemic Acropedal Influence of Endophyte Seed Treatment on *Acyrthosiphon pisum* and *Aphis fabae* Offsprings Development and Reproductive Fitness." *Biological Control* 61: 215–221. https://doi.org/10.1016/j.biocontrol.2012.02.007.

Alınç, T., A. Agbessenou, K. S. Akutse, A. A. Yusuf, and F. M. Khamis. 2022. "The Endophyte *Trichoderma asperellum* M2RT4 Induces the Systemic Release of Methyl Salicylate and (Z)-Jasmone in Tomato Plant Affecting Host Location and Herbivory of *Tuta absoluta*." *Frontiers in Plant Science* 13: 860309. https://doi.org/10.3389/fpls.2022.860309.

Anh Vu, N., S. Subramanian, and R. Meyhöfer. 2025. "Effect of Endophytic Fungi on *Thrips tabaci* Development and Population Dynamics [Data Set]." LUIS. https://doi.org/10.25835/ivm37tff.

Bailey, B. A., M. D. Strem, and D. Wood. 2009. "*Trichoderma* Species Form Endophytic Associations Within *Theobroma cacao* Trichomes." *Mycological Research* 113, no. 12: 1365–1376. https://doi.org/10.1016/j.mycres.2009.09.004.

Bamisile, B. S., C. K. Dash, K. S. Akutse, R. Keppanan, and L. Wang. 2018. "Fungal Endophytes: Beyond Herbivore Management." *Frontiers in Microbiology* 9: 544. https://doi.org/10.3389/fmicb.2018.00544.

Bandeira, J. B., J. N. Rodrigues, R. S. de Oliveira, et al. 2023. "Endophytic Colonization of Five *Trichoderma* Species and Their Effects on Growth of a *Eucalyptus* Hybrid." *Brazilian Journal of Microbiology* 54: 3113–3125. https://doi.org/10.1007/s42770-023-01112-0.

Barelli, L., S. Moonjely, S. W. Behie, and M. J. Bidochka. 2016. "Fungi With Multifunctional Lifestyles: Endophytic Insect Pathogenic Fungi." *Plant Molecular Biology* 90: 657–664. https://doi.org/10.1007/s11103-015-0413-z.

Barra-Bucarei, L., M. G. González, A. F. Iglesias, G. S. Aguayo, M. G. Peñalosa, and P. V. Vera. 2020. "*Beauveria bassiana* Multifunction as an Endophyte: Growth Promotion and Biologic Control of *Trialeurodes vaporariorum*, (Westwood) (Hemiptera: Aleyrodidae) in Tomato." *Insects* 11, no. 9: 591. https://doi.org/10.3390/insects11090591.

Birithia, R. K., S. Subramanian, and D. K. Kuria. 2021. "Farmers' Preference for Onion Varieties and Implications of Knowledge of Iris Yellow Spot Disease in Kenya." *African Crop Science Journal* 29, no. 2: 229–239. https://doi.org/10.4314/acsj.v29i2.4.

Birithia, R. K., S. Subramanian, J. W. Muthomi, and R. D. Narla. 2014. "Resistance to *Iris Yellow Spot Virus* and Onion Thrips Among Onion

Varieties Grown in Kenya." *International Journal of Tropical Insect Science* 34: 73–79. https://doi.org/10.1017/S1742758414000289.

Blond, C. L. H., H. J. Ridgway, M. Brownbridge, et al. 2018. "Non-Host Larvae Negatively Impact Persistence of the Entomopathogen *Beauveria bassiana* in Soil." *Journal of Invertebrate Pathology* 156: 19–28. https://doi.org/10.1016/j.jip.2018.07.001.

Boateng, C. O., H. F. Schwartz, M. J. Havey, and K. Otto. 2014. "Evaluation of Onion Germplasm for Resistance to Iris Yellow Spot (Iris Yellow Spot Virus) and Onion Thrips, *Thrips tabaci*." *Southwestern Entomologist* 39, no. 2: 237–260. https://doi.org/10.3958/059.039.0218.

Braga, G. U., S. D. Flint, C. D. Miller, A. J. Anderson, and D. W. Roberts. 2001. "Both Solar UVA and UVB Radiation Impair Conidial Culturability and Delay Germination in the Entomopathogenic Fungus *Metarhizium anisopliae*." *Photochemistry and Photobiology* 74, no. 5: 734–739.

Brown, A. S., M. S. J. Simmonds, and W. M. Blaney. 2002. "Relationship Between Nutritional Composition of Plant Species and Infestation Levels of Thrips." *Journal of Chemical Ecology* 28: 2399–2409. https://doi.org/10.1023/A:1021471732625.

Carroll, G. 1988. "Fungal Endophytes in Stems and Leaves: From Latent Pathogen to Mutualistic Symbiont." *Ecology* 69, no. 1: 2–9. https://doi.org/10.2307/1943154.

Castillo-Lopez, D., K. Zhu-Salzman, M. J. Ek-Ramos, and G. A. Sword. 2014. "The Entomopathogenic Fungal Endophytes *Purpureocillium lilacinum* (Formerly *Paecilomyces lilacinus*) and *Beauveria bassiana* Negatively Affect Cotton Aphid Reproduction Under Both Greenhouse and Field Conditions." *PLoS One* 9: e103891. https://doi.org/10.1371/journal.pone.0103891.

Chatzivassiliou, E. K. 2008. "Management of the Spread of Tomato Spotted Wilt Virus in Tobacco Crops With Insecticides Based on Estimates of Thrips Infestation and Virus Incidence." *Plant Disease* 92: 1012–1020. https://doi.org/10.1094/PDIS-92-7-1012.

Cheng, A., X. Chen, Q. Jin, W. Wang, J. Shi, and Y. Liu. 2013. "Comparison of Phenolic Content and Antioxidant Capacity of Red and Yellow Onions." *Czech Journal of Food Sciences* 31, no. 5: 501–508. https://doi.org/10.17221/566/2012-CJFS.

Chernukha, I., N. Kupaeva, E. Kotenkova, and D. Khvostov. 2022. "Differences in Antioxidant Potential of *Allium cepa* Husk of Red, Yellow, and White Varieties." *Antioxidants (Basel)* 11, no. 7: 1243. https://doi.org/10.3390/antiox11071243.

Coppola, M., P. Cascone, I. Di Lelio, et al. 2019. "*Trichoderma atroviride* P1 Colonization of Tomato Plants Enhances Both Direct and Indirect Defense Barriers Against Insects." *Frontiers in Physiology* 10: 813. https://doi.org/10.3389/fphys.2019.00813.

Coppola, M., G. Diretto, M. C. Digilio, et al. 2019. "Transcriptome and Metabolome Reprogramming in Tomato Plants by *Trichoderma harzianum* Strain T22 Primes and Enhances Defense Responses Against Aphids." *Frontiers in Physiology* 10: 745.

Diaz-Montano, J., J. Fail, M. Deutschlander, B. A. Nault, and A. M. Shelton. 2012. "Characterization of Resistance, Evaluation of the Attractiveness of Plant Odors, and Effect of Leaf Color on Different Onion Cultivars to Onion Thrips (Thysanoptera: Thripidae)." *Journal of Economic Entomology* 105: 632–641.

Diaz-Montano, J., M. Fuchs, B. A. Nault, J. Fail, and A. M. Shelton. 2011. "Onion Thrips (Thysanoptera: Thripidae): A Global Pest of Increasing Concern in Onion." *Journal of Economic Entomology* 104, no. 1: 1–13. https://doi.org/10.1603/EC10269.

Diaz-Montano, J., M. Fuchs, B. A. Nault, and A. M. Shelton. 2010. "Evaluation of Onion Cultivars for Resistance to Onion Thrips (Thysanoptera: Thripidae) and Iris Yellow Spot Virus." *Journal of Economic Entomology* 103, no. 3: 925–937. https://doi.org/10.1603/EC09263.

Fernandes, É. K. K., D. E. N. Rangel, G. U. L. Braga, and D. W. Roberts. 2015. "Tolerance of Entomopathogenic Fungi to Ultraviolet Radiation: A Review on Screening of Strains and Their Formulation." *Current Genetics* 61: 427–440.

Fernandes, É. K. K., D. E. N. Rangel, Á. M. L. Moraes, V. R. E. P. Bittencourt, and D. W. Roberts. 2007. "Variability in Tolerance to UV-B Radiation Among *Beauveria* spp. Isolates." *Journal of Invertebrate Pathology* 96, no. 3: 237–243. https://doi.org/10.1016/j.jip.2007.05.007.

Fournier, F., G. Boivin, and R. K. Stewart. 1995. "Effect of *Thrips tabaci* (Thysanoptera: Thripidae) on Yellow Onion Yields and Economic Thresholds for Its Management." *Journal of Economic Entomology* 88, no. 5: 1401–1407. https://doi.org/10.1093/jee/88.5.1401.

Fox, J., and S. Weisberg. 2023. "car: Companion to Applied Regression." [R package]. https://cran.r-project.org/package=car.

Fu, B., Q. Li, H. Qiu, L. Tang, D. Zeng, and K. Lu. 2019. "Oviposition, Feeding Preference, and Biological Performance of *Thrips hawaiiensis* on Four Host Plants With and Without Supplemental Foods." *Arthropod-Plant Interactions* 13: 441–452. https://doi.org/10.1007/s11829-018-9647-4.

Galindo-Solís, J. M., and F. J. Fernández. 2022. "Endophytic Fungal Terpenoids: Natural Role and Bioactivities." *Microorganisms* 10, no. 2: 339. https://doi.org/10.3390/microorganisms10020339.

Garrido-Jurado, I., G. Resquín-Romero, S. P. Amarilla, A. Ríos-Moreno, L. Carrasco, and E. Quesada-Moraga. 2017. "Transient Endophytic Colonization of Melon Plants by Entomopathogenic Fungi After Foliar Application for the Control of *Bemisia tabaci* Gennadius (Hemiptera: Aleyrodidae)." *Journal of Pest Science* 90: 319–330. https://doi.org/10.1007/s10340-016-0767-2.

Gent, D. H., L. J. du Toit, S. F. Fichtner, S. K. Mohan, H. R. Pappu, and H. F. Schwartz. 2006. "Iris Yellow Spot Virus: An Emerging Threat to Onion Bulb and Seed Production." *Plant Disease* 90, no. 12: 1468–1480. https://doi.org/10.1094/PD-90-1468.

Gent, D. H., H. F. Schwartz, and R. Khosla. 2004. "Distribution and Incidence of Iris Yellow Spot Virus in Colorado and Its Relation to Onion Plant Population and Yield." *Plant Disease* 88: 446–452. https://doi.org/10.1094/PDIS.2004.88.5.446.

George, J., J. P. Glover, O. P. Perera, and G. V. P. Reddy. 2024. "Role of Endophytic Entomopathogenic Fungi in Mediating Host Selection, Biology, Behavior, and Management of Tarnished Plant Bug, *Lygus lineolaris* (Hemiptera: Miridae)." *Plants (Basel)* 13, no. 15: 2012. https://doi.org/10.3390/plants13152012.

Gill, H. K., H. Garg, A. K. Gill, J. L. Gillett-Kaufman, and B. A. Nault. 2015. "Onion Thrips (Thysanoptera: Thripidae) Biology, Ecology, and Management in Onion Production Systems." *Journal of Integrated Pest Management* 6, no. 1: 6. https://doi.org/10.1093/jipm/pmv006.

Gouli, V. V., S. Y. Gouli, M. Skinner, and M. V. Shternshis. 2009. "Effect of the Entomopathogenic Fungi on Mortality and Injury Level of Western Flower Thrips, *Frankliniella occidentalis*." *Archives of Phytopathology and Plant Protection* 42, no. 2: 118–123. https://doi.org/10.1080/03235400600951829.

Grunseich, J. M., M. N. Thompson, N. M. Aguirre, and A. M. Helms. 2019. "The Role of Plant-Associated Microbes in Mediating Host-Plant Selection by Insect Herbivores." *Plants (Basel)* 9, no. 1: 6.

Gurulingappa, P., G. A. Sword, G. Murdoch, and P. A. McGee. 2010. "Colonization of Crop Plants by Fungal Entomopathogens and Their Effects on Two Insect Pests When in Planta." *Biological Control* 55: 34–41. https://doi.org/10.1016/j.biocontrol.2010.06.011.

Herron, G. A., T. M. James, J. Rophail, and J. Mo. 2008. "Australian Populations of Onion Thrips, *Thrips tabaci* Lindeman (Thysanoptera: Thripidae), are Resistant to Some Insecticides Used for Their Control."

Australian Journal of Entomology 47, no. 4: 361–364. https://doi.org/10.1111/j.1440-6055.2008.00669.x.

Jaber, L. R., and B. H. Ownley. 2017. "Can We Use Entomopathogenic Fungi as Endophytes for Dual Biological Control of Insect Pests and Plant Pathogens?" *Biological Control* 116: 36–45. https://doi.org/10.1016/j.biocontrol.2017.01.018.

Jacobson, A. L., W. Booth, E. L. Vargo, and G. G. Kennedy. 2013. "*Thrips tabaci* Population Genetic Structure and Polyploidy in Relation to Competency as a Vector of Tomato Spotted Wilt Virus." *PLoS One* 8, no. 1: e54484. https://doi.org/10.1371/journal.pone.0054484.

Jallow, M. F. A., D. Dugassa-Gobena, and S. Vidal. 2008. "Influence of an Endophytic Fungus on Host Plant Selection by a Polyphagous Moth via Volatile Spectrum Changes." *Arthropod-Plant Interactions* 2: 53–62. https://doi.org/10.1007/s11829-008-9033-8.

Jaronski, S. T. 2010. "Ecological Factors in the Inundative Use of Fungal Entomopathogens." *BioControl* 55: 159–185. https://doi.org/10.1007/s10526-009-9248-3.

Kiarie, S., J. O. Nyasani, L. S. Gohole, N. K. Maniania, and S. Subramanian. 2020. "Impact of Fungal Endophyte Colonization of Maize (*Zea mays* L.) on Induced Resistance to Thrips- and Aphid-Transmitted Viruses." *Plants* 9, no. 4: 416. https://doi.org/10.3390/plants9040416.

Koschier, E. H., D. Hoffmann, and J. Riefler. 2007. "Influence of Salicylaldehyde and Methyl Salicylate on Post-Landing Behaviour of *Frankliniella occidentalis* Pergande." *Journal of Applied Entomology* 131, no. 5: 362–367. https://doi.org/10.1111/j.1439-0418.2007.01191.x.

Larentzaki, E., A. M. Shelton, F. R. Musser, B. A. Nault, and J. Plate. 2007. "Overwintering Locations and Hosts for Onion Thrips (Thysanoptera: Thripidae) in the Onion Cropping Ecosystem in New York." *Journal of Economic Entomology* 100, no. 4: 1194–1200. https://doi.org/10.1093/jee/100.4.1194.

Lopez, D. C., and G. A. Sword. 2015. "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* 89: 53–60. https://doi.org/10.1016/j.biocontrol.2015.03.010.

Lopez-Reyes, K., K. F. Armstrong, D. A. J. Teulon, et al. 2022. "Colour Response in Western Flower Thrips Varies Intraspecifically." *Insects* 13, no. 6: 538.

Ludwaba, B., M. O. Jimoh, C. P. Laubschera, and F. Nchu. 2024. "Insecticidal and Antioxidant Potential of Volatile Compounds and Nanoparticles From *Tulbaghia violacea* Harv. Inoculated With Endophytic Fungus *Beauveria bassiana* (Bals.-Criv.) Vuill." *South African Journal of Botany* 165: 246–256. https://doi.org/10.1016/j.sajb.2023.12.028.

Macías-Rodríguez, L., H. A. Contreras-Cornejo, S. G. Adame-Garnica, E. Del-Val, and J. Larsen. 2020. "The Interactions of *Trichoderma* at Multiple Trophic Levels: Inter-Kingdom Communication." *Microbiological Research* 240: 126552. https://doi.org/10.1016/j.micres.2020.126552.

MacIntyre Allen, J. K., C. D. Scott-Dupree, J. H. Tolman, and C. R. Harris. 2005. "Resistance of *Thrips tabaci* to Pyrethroid and Organophosphorus Insecticides in Ontario, Canada." *Pest Management Science* 61, no. 8: 809–815. https://doi.org/10.1002/ps.1068.

Mantzoukas, S., E. Daskalaki, F. Kitsiou, et al. 2022. "Dual Action of *Beauveria bassiana* (Hypocreales; Cordycipitaceae) Endophytic Stains as Biocontrol Agents Against Sucking Pests and Plant Growth Biostimulants on Melon and Strawberry Field Plants." *Microorganisms* 10: 2306. https://doi.org/10.3390/microorganisms10112306.

Marassatto, C., L. Ferreira, J. Couceiro, M. de Oliveira, A. Guidolin, and I. Delalibera. 2025. "*Beauveria bassiana* Triggers Soybean Systemic Resistance and Causes Sublethal Effects in *Spodoptera frugiperda*." *Entomologia Experimentalis et Applicata* 174: 236–250. https://doi.org/10.1111/eea.70045.

Martínez-Medina, A., F. V. W. Appels, and S. C. M. van Wees. 2017. "Impact of Salicylic Acid- and Jasmonic Acid-Regulated Defences on Root Colonization by *Trichoderma harzianum* T-78." *Plant Signaling & Behavior* 12: e1345404. https://doi.org/10.1080/15592324.2017.1345404.

Mascarin, G. M., and S. T. Jaronski. 2016. "The Production and Uses of *Beauveria bassiana* as a Microbial Insecticide." *World Journal of Microbiology and Biotechnology* 32: 177. https://doi.org/10.1007/s11274-016-2131-3.

Mayerhofer, M. S., G. Kernaghan, and K. A. Harper. 2013. "The Effects of Fungal Root Endophytes on Plant Growth: A Meta-Analysis." *Mycorrhiza* 23: 119–128.

McKenzie, C. L., B. Cartwright, M. E. Miller, P. Perkins-Veazie, and J. V. Edelson. 1993. "Injury to Onions by *Thrips tabaci* (Thysanoptera: Thripidae) and Its Role in the Development of Purple Blotch." *Environmental Entomology* 22, no. 6: 1266–1277. https://doi.org/10.1093/ee/22.6.1266.

Mercado-Blanco, J., and B. Lugtenberg. 2014. "Biotechnological Application of Bacterial Endophytes." *Current Biotechnology* 3: 60–75. https://doi.org/10.2174/2211550113026660038.

Morse, J. G., and M. S. Hoddle. 2006. "Invasion Biology of Thrips." *Annual Review of Entomology* 51: 67–89. https://doi.org/10.1146/annurev.ento.51.110104.151044.

Muvea, A. M., R. Meyhöfer, N. K. Maniania, H. M. Poehling, S. Ekesi, and S. Subramanian. 2015. "Behavioral Responses of *Thrips tabaci* Lindeman to Endophyte-Inoculated Onion Plants." *Journal of Pest Science* 88: 555–562. https://doi.org/10.1007/s10340-015-0645-3.

Muvea, A. M., R. Meyhöfer, S. Subramanian, H. M. Poehling, S. Ekesi, and N. K. Maniania. 2014. "Colonization of Onions by Endophytic Fungi and Their Impacts on the Biology of *Thrips tabaci*." *PLoS One* 9, no. 9: e108242. https://doi.org/10.1371/journal.pone.0108242.

Muvea, A. M., S. Subramanian, N. K. Maniania, H. Poehling, S. Ekesi, and R. Meyhöfer. 2018. "Endophytic Colonization of Onions Induces Resistance Against Viruliferous Thrips and Virus Replication." *Frontiers in Plant Science* 9: 382594. https://doi.org/10.3389/fpls.2018.01785.

Natsiopoulos, D., E. Topalidou, S. Mantzoukas, and P. A. Eliopoulos. 2024. "Endophytic *Trichoderma*: Potential and Prospects for Plant Health Management." *Pathogens* 13, no. 7: 548. https://doi.org/10.3390/pathogens13070548.

Nault, B. A., and A. M. Shelton. 2010. "Impact of Insecticide Efficacy on Developing Action Thresholds for Pest Management: A Case Study of Onion Thrips (Thysanoptera: Thripidae) on Onion." *Journal of Economic Entomology* 103, no. 4: 1315–1326. https://doi.org/10.1603/EC10096.

North, R. C., and A. M. Shelton. 1986. "Overwintering of the Onion Thrips, *Thrips tabaci* (Thysanoptera: Thripidae), in New York." *Environmental Entomology* 15, no. 3: 695–699. https://doi.org/10.1093/ee/15.3.695.

Oliveira, D. G. P., G. Pauli, G. M. Mascarin, and I. Delalibera. 2015. "A Protocol for Determination of Conidial Viability of the Fungal Entomopathogens *Beauveria bassiana* and *Metarhizium anisopliae* From Commercial Products." *Journal of Microbiological Methods* 119: 44–52. https://doi.org/10.1016/j.mimet.2015.09.021.

Pobożniak, M., and E. H. Koschier. 2013. "Effect of Pea (*Pisum sativum* L.) Cultivars on *Thrips tabaci* Londeman Preference and Performance." *Journal of Agricultural Science* 152, no. 6: 885–893. https://doi.org/10.1017/S0021859613000518.

Pobożniak, M., M. Olczyk, T. Wójtowicz, et al. 2021. "Anatomical and Biochemical Traits Associated With Field Resistance of Onion Cultivars

to Onion Thrips and the Effect of Mechanical Injury on the Level of Biochemical Compounds in Onion Leaves." *Agronomy* 12, no. 1: 147. https://doi.org/10.3390/agronomy12010147.

Powell, W. A., W. E. Klingeman, B. H. Ownley, and K. Gwinn. 2009. "Evidence of Endophytic *Beauveria bassiana* in Seed-Treated Tomato Plants Acting as a Systemic Entomopathogen to Larval *Helicoverpa zea* (Lepidoptera: Noctuidae)." *Journal of Entomological Science* 44, no. 4: 391–396. https://doi.org/10.18474/0749-8004-44.4.391.

Pozzer, L., I. C. Bezerra, R. Kormelink, et al. 1999. "Characterization of a Tospovirus Isolate of Iris Yellow Spot Virus Associated With a Disease in Onion Fields in Brazil." *Plant Disease* 83, no. 4: 345–350. https://doi.org/10.1094/PDIS.1999.83.4.345.

R Core Team. 2023. "R: A Language and Environment for Statistical Computing (Version 4.2.3) (Computer software)," R Foundation for Statistical Computing. http://www.R-project.org.

Rasool, S., N. H. Vidkjaer, K. Hooshmand, B. Jensen, I. S. Fomsgaard, and N. V. Meyling. 2021. "Seed Inoculations With Entomopathogenic Fungi Affect Aphid Populations Coinciding With Modulation of Plant Secondary Metabolite Profiles Across Plant Families." *New Phytologist* 229, no. 3: 1715–1727. https://doi.org/10.1111/nph.16979.

Rodriguez, R. J., J. F. White Jr., A. E. Arnold, and R. S. Redman. 2009. "Fungal Endophytes: Diversity and Functional Roles." *New Phytologist* 182: 314–330. https://doi.org/10.1111/j.1469-8137.2009.02773.x.

Rozenberg, T., L. Shaltiel-Harpaz, and M. Coll. 2015. "Visualizing Eggs of *Nesidiocoris tenuis* (Heteroptera: Miridae) Embedded in Tomato Plant Tissues." *Entomological Science* 18: 400–402. https://doi.org/10.1111/ens.12125.

Russo, M. L., A. C. Scorsetti, M. F. Vianna, et al. 2018. "Effects of Endophytic *Beauveria bassiana* (Ascomycota: Hypocreales) on Biological, Reproductive Parameters and Food Preference of the Soybean Pest *Helicoverpa gelotopoeon*." *Journal of King Saud University, Science* 31: 1077–1082. https://doi.org/10.1016/j.jksus.2018.11.009.

Saikkonen, K., P. E. Gundel, and M. Helander. 2013. "Chemical Ecology Mediated by Fungal Endophytes in Grasses." *Journal of Chemical Ecology* 39: 962–968. https://doi.org/10.1007/s10886-013-0310-3.

Saini, S., K. Raj, A. K. Saini, et al. 2024. "Unravelling the Synergistic Interaction of *Thrips tabaci* and Newly Recorded, *Thrips parvispinus* With *Alternaria porri* (Ellis.) Cif., Inciting Onion Purple Blotch." *Frontiers in Microbiology* 15: 1321921. https://doi.org/10.3389/fmicb.2024.1321921.

Salas, J. 1994. "Biology and Life Habits of the Onion Thrips (*Thrips tabaci* Lindeman)." *Acta Horticulturae* 358: 383–387.

Schulz, B., and C. Boyle. 2006. "What Are Endophytes?" *Microbial Root Endophytes* 9: 1–13.

Shelton, A. M., J. Z. Zhao, B. A. Nault, J. Plate, F. Musser, and E. Larentzaki. 2006. "Patterns of Insecticide Resistance in Onion Thrips (Thysanoptera: Thripidae) in Onion Fields in New York." *Journal of Economic Entomology* 99, no. 5: 1798–1804. https://doi.org/10.1603/0022-0493-99.5.1798.

Shikano, I., C. Rosa, C. Tan, and G. W. Felton. 2017. "Tritrophic Interactions: Microbe-Mediated Plant Effects on Insect Herbivores." *Annual Review of Phytopathology* 55: 313–331. https://doi.org/10.1146/annurev-phyto-080516035319.

Sieber, T. N., and C. R. Grünig. 2006. "Biodiversity of Fungal Root-Endophyte Communities and Populations, in Particular of the Dark Septate Endophyte *Phialocephala fortinii* s.I." *Soil Biology* 9: 107–132. https://doi.org/10.1007/3-540-33526-9_7.

Silva, V. C. P., M. M. Bettoni, C. Bona, and L. A. Foerster. 2015. "Morphological and Chemical Characteristics of Onion Plants (*Allium cepa* L.) Associated With Resistance to Onion Thrips." *Acta Scientiarum Agronomy* 37, no. 1: 85–92. https://doi.org/10.4025/actasciagron.v37i1.17436.

Srinivasan, R., S. Sundaraj, H. R. Pappu, S. Diffie, D. G. Riley, and R. D. Gitaitis. 2012. "Transmission of Iris Yellow Spot Virus by *Frankliniella fusca* and *Thrips tabaci* (Thysanoptera: Thripidae)." *Journal of Economic Entomology* 105, no. 1: 40–47. https://doi.org/10.1603/ec11094.

Szostek, S., and H. F. Schwartz. 2015. "Overwintering Sites of Iris Yellow Spot Virus and *Thrips tabaci* (Thysanoptera: Thripidae) in Colorado." *Southwestern Entomologist* 40, no. 2: 273–290. https://doi.org/10.3958/059.040.0204.

Van Hee, S., I. Stockmans, T. Alınç, A. Cusumano, H. Jacquemyn, and B. Lievens. 2023. "Effects of Plant-Beneficial Fungi on Plant Growth and Herbivore Resistance Under Contrasting Fertilizer Conditions." *Plant and Soil* 493: 157–172. https://doi.org/10.1007/s11104-023-06220-2.

Vega, F. E. 2018. "The Use of Fungal Entomopathogens as Endophytes in Biological Control: A Review." *Mycologia* 110, no. 1: 4–30. https://doi.org/10.1080/00275514.2017.1418578.

Vega, F. E., M. S. Goettel, M. S. A. Blackwell, et al. 2009. "Fungal Entomopathogens: New Insights on Their Ecology." *Fungal Ecology* 2: 149–159. https://doi.org/10.1016/j.funeco.2009.05.001.

Vega, F. E., F. Posada, M. C. Aime, M. Pava-Ripoll, F. Infante, and S. A. Rehner. 2008. "Entomopathogenic Fungal Endophytes." *Biological Control* 46, no. 1: 72–82. https://doi.org/10.1016/j.biocontrol.2008.01.008.

Vidal, S., and L. R. Jaber. 2015. "Entomopathogenic Fungi as Endophytes: Plant–Endophyte–Herbivore Interactions and Prospects for Use in Biological Control." *Current Science* 109, no. 1: 46–54.

Wilson, D. 1995. "Endophyte: The Evolution of a Term, and Clarification of Its Use and Definition." *Oikos* 73, no. 2: 274–276. https://doi.org/10.2307/3545919.

Yousef-yousef, M., F. García-Espinoza, M. J. G. del Rosal, and E. Quesada-Moraga. 2024. "Guardians Within: Entomopathogenic Fungi-Driven Antibiosis and Compensatory Growth Combines to Reduce the Damage of Herbivores to Melon Plants." *Journal of Pest Science* 98: 291–308. https://doi.org/10.1007/s10340-024-01812-y.

Zhang, D., Z. Xiao, B. Zeng, K. Li, and Y. Tang. 2019. "Insect Behavior and Physiological Adaptation Mechanisms Under Starvation Stress." *Frontiers in Physiology* 10: 163. https://doi.org/10.3389/fphys.2019.00163.

Zhang, Y., H. Wen, Q. Li, Y. Lu, Z. Zhang, and L. Sui. 2025. "From Function to Omics: Endophytic *Beauveria bassiana* Promotes Maize Growth by Activating Phytohormone Signaling Pathways Under Elevated Carbon Dioxide." *BMC Plant Biology* 25: 1759. https://doi.org/10.1186/s12870-025-07763-5.

Zhou, Y. M., D. Y. Ma, W. Xie, D. Y. Li, J. R. Zhi, and X. Zou. 2025. "*Lecanicillium* Enhances Kidney Bean Growth and Confers Resistance Against *Frankliniella occidentalis* (Thysanoptera: Thripidae) Infestation." *Biological Control* 211: 105921. https://doi.org/10.1016/j.biocontrol.2025.10592.