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ARTICLE

Antifungal Potential of *Beauveria bassiana* on *Solanum lycopersicum* L. Infected with *Fusarium oxysporum* f. sp. *lycopersici*

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ABSTRACT

The objective of this work was to evaluate the effect of *Beauveria bassiana* (*Bb* 1205) on controlling *Fusarium oxysporum* f. sp. *lycopersici* (*Fol* 17108) in tomato plants in greenhouse conditions. Inoculation of Bb 1205 was the most promising among the agronomic variables and expression of the activity of the enzymes β-1,3-glucanases and chitinases. Inoculation of *Bb* 1205 occurred at a concentration of 1×10^8 conidia·mL^{-1}, which was administered onto the leaves, directly into the soil and via injection. Infection with *Fol* 17108 occurred with 1×10^6 spores·mL^{-1}, which were added directly to the soil. Spectrophotometry was used for measuring agronomic parameters, namely activity of chitinases and β-1,3-glucanases in foliage and roots. When *Bb* 1205 was added to the soil, the chlorophyll index and aerial part length showed significant differences. In addition, it was determined that root length, fresh weight of foliage, flower, and fruit count increased 82 days after inoculation (dai). Chitinase activity induced by *Bb* 1205 in leaves and roots of tomato plants infected with *Fol* 17108 was observed when injected into the stem at 32 dai (41.8 and 11.6-fold, respectively). Inoculation on the foliage showed a 10-fold increase of β-1,3-glucanases in the roots after 82 dpi. As for leaves, a 3.8-fold increase was found when the stem was inoculated. In the different *in vivo* applications, *Bb* 1205 activated its defenses by expressing the chitinase enzymes and β-1,3-glucanase, thus reducing the damage caused by *Fol* 17108, demonstrating increase plant growth thereafter.

KEYWORDS

Mycoparasitism; agronomic parameters; chitinases; β-1,3-glucanases

1 Introduction

The excessive use of chemical pesticides for pathogen control has led to pesticide-resistant weeds. The bioaccumulation of pesticides in plant tissues causes potential risks to human health [1]. Therefore, biopesticides focus on having an effect on the target pathogen ecologically and sustainably for the environment. In this way, they are an alternative for more sustainable management in the phytosanitary field [2].

Entomopathogenic fungi (EF) are highly whidespread geographically and are highly capable of colonizing soil, which has led to their use as biological control agents worldwide. One of these EF is *Beauveria bassiana* fungus, which is an ascomycete that belongs to the Cordycipitaceae family of the Hypocreales order, capable of infecting more than 700 species of invertebrates through the cuticle via its conidia [3,4]. Furthermore, this order has great incidence as an asymptomatic endophyte in tissues of different plant species (*Zea mays*, *Theobroma cacao*, *Phoenix dactylifera*, *Coffea* L., *Musa paradisiaca* L., *Pinus radiata*, *Vicia faba*, *Papaver somniferum*, *Gossypium*, *Manihot esculenta*, *Phaseolus vulgaris*, and *Solanum lycopersicum* L.). Also, EF in this order can significantly modify the host plant while significantly modifying the presence of insect pests and diseases in the host plant [5–7].

Based on the needs for more environmentally friendly crop production and a more efficient use of resources, the management of some EF has been attempted in order to aid plants, and it has been shown that they can provide benefits by competing over the rhizosphere, phylosphere or intracellularly. They actively dispute the sources of carbon, nitrogen, and various microelements with pathogens [8]. *B. bassiana* can achieve these functions by producing secondary metabolites and extracellular enzymes with biological activity. Chitinase and glucanase enzymes (among others) are considered to be the most important metabolites produced by this EF [9,10]. Even when used only in minimal applications, they can help establish long-term protection to plants. Because of the smaller amounts used, they can benefit farmers by offering cost reductions as compared to the use of synthetic pesticides and can also reduce health risks for consumers [11].

The culture of *S. lycopersicum* L. L. is very important due to worldwide demand for bioactive compounds (lycopene, ascorbic acid, phenolic compounds, tocopherol, β-carotene, flavonoids, folates, fiber, and others). In addition, it has high economic value due to its consumption as fresh or processed product [12,13]. The production of *S. lycopersicum* L. has continued increasing because the producer has observed a cost-benefit relationship; for each peso invested, he acquires between 1.04 and 2.16 pesos of profit (this will depend on the system in place). However, in his total production costs, he invests 4.93% ($79,049.99) in inputs for pest and disease control, 38.08% ($609,500) in labor, including activities for the application of such inputs, as well as preventive or corrective management [14].

Known species of *Fusarium* cause a wide range of diseases in an extraordinary variety of plants. This soil-borne, cosmopolitan filamentous fungi group is vital because many members are the causative agents of vascular root rot or wilt diseases in agricultural and ornamental crops worldwide [15]. The losses caused in the culture of *S. lycopersicum* L. by this genus are due to *Fusarium oxysporum* f. sp. *lycopersici* (Fol), which favor vascular wilting due to the colonization of vascular tissue (forming a dark brown color), after which chlorosis in the lower leaves extending to the apex through the vascular bundle (xylem and phloem) can be seen, causing wilting, collapse, and plant death. This disease is on the rise due to the combination of mycotoxin production, tyloses production, mycelial accumulation, and the inactivation of host defenses [16].

A possible solution to these phytosanitary problems is the implementation of strategies such as the mycoparasitism of phytopathogenic fungi (PF), where EF present a good chemotropic growth of the mycelium towards the pathogenic fungus through recognition. With the help of appressoria, fungi can adhere effectively, facilitating the secretion of various hydrolytic enzymes. These will finally degrade the cell wall and membrane [2]. To date, the process of mycoparasitism of entomopathogenic fungi (for example, *Lecanicillium* spp. and *Trichoderma* spp.) has been thoroughly described *in vitro* in laboratory conditions but remains undemonstrated in the plant [17]. Some studies that have been carried out for the control of *Fol* in greenhouses with *B. bassiana* strain B2 have demonstrated the reduction of the pathogen, an increase in the number of branches, petioles, and a rise in fruit yields up to by 54%, 59%, 17%, and 36%, respectively. In addition, the expression of defense enzymes such as peroxidase, polyphenol oxidase, and lipoxygenase has been reported [18].

Similarly, endophytic colonization could be observed by inoculating seeds of *Triticum aestivum* L. with *B. bassiana*, obtaining a decrease in the incidence and severity of *F. culmorum* at 24 days after inoculation with 50% and 47% colonization in seeds, respectively [19]. *In vitro* and *in vivo* tests of *B. bassiana* allowed an observational study of the colonization of *S. lycopersicum* L. plants via the leaves with an effectiveness of 48%, reducing *Botrytis cinerea* infection to 36% [20]. The ability to antagonize *B. bassiana* on *Fol* race 3 in the laboratory showed an inhibition of 72% in the colonization of seeds, as well as an increase in chitinase enzyme production of up to 21% [10]. Aside from these findings, little evidence has demonstrated the antagonism of *B. bassiana* to plant-pathogenic fungi in the greenhouse.

Thus, the present study focused on controlling the pathogen *F. oxysporum* f. sp *lycopersici* (strain 17108) *in vivo* in *S. lycopersicum* L. plants with the *B. bassiana* strain 1205 with the objective of observing a promising application in agronomic variables and expression of enzymatic activity (β-1,3-glucanases and chitinases).

2 Materials and Methods

2.1 Plant Material

Seeds were provided by Eterno S. A. de C. V. and packaged in Guadalajara, Jalisco, Mexico. Seedlings of a *Fusarium*-susceptible Saladette supreme variety tomato (*Solanum lycopersicum* L.) were grown in 200 cavity trays from surface-sterilized seeds. This was done in accordance to the modified protocol established by [21]. 30 days after germination, they were transplanted into pots with sterilized peat moss (a substrate manufactured in Canada, endorsed by Premier Horticulture L TÉE1, Quebec, Canada GSR), and placed in a greenhouse. To keep plants in good conditions during the experiment, they were fertilized with different nutrient solution percentages, depending on the crop's different phenological phases according to [22].

The study was carried out in the Biotechnology and greenhouse soil laboratory of the Tecnológico Nacional de México Campus Tuxtla Gutiérrez (latitud of 16.758311°N, longitude-93.172347 W). The experiments used for evaluation were treatments without inoculation, with entomopathogen inoculum, treatments with interactions, and treatments that were inoculated only with the pathogen. Treatments without inoculation were control plant + foliar application of distilled water (PCf), control plant + injected application of distilled water (PCi), and control plant + application in the soil of distilled water (PCs). As for treatments with entomopathogen inoculum, these were plant + foliar application of *B. bassiana* (PBf), plant + injected application of *B. bassiana* (PBi), and plant + soil application of *B. bassiana* (PBs). The interaction treatments were plant + Fol + foliar application of *B. bassiana* (PFBf), plant + Fol + injected application of *B. bassiana* (PFBi), and plant + Fol + application in the soil of *B. bassiana* (PFBs). Lastly, treatments including only the pathogen were plant + Fol + foliar application of distilled water (PFf), plant + Fol + injected application of distilled water (PFi), and plant + Fol + application in the soil of distilled water (PFs). The distribution of the experiment was carried out in a completely randomized design with 12 treatments and nine repetitions per treatment, whereby the experimental unit was a pot with a plant.

2.2 Inoculation of Fusarium oxysporum f. sp. lycopersici

The *Fol* strain (17108) (Not registred) was provided by the Plant Breeding Department of the University Autonomous Agrarian Antonio Narro, based in Saltillo, Coahuila, Mexico. To guarantee infection, plants were inoculated with a stock solution with a concentration of 1×10^6 spores·mL^{-1} was used according to descriptions by [23] with modifications. Consecutively, 10 mL of the *Fol* 17108 spore suspension were used to infect the substrate directly for the PFf, PFi, PFs, PFBf, PFBi, and PFBs treatments. In addition, 10 mL of sterilized distilled water were applied to the control plants and to those treated with *B. bassiana*, and 10 mL of sterilized distilled water plus the Bb spores were also applied. This application happened only once and occurred five days after transplanting (dat).

2.3 Inoculation of Beauveria bassiana (Bb)

The entomopathogenic fungus *Bb* 1205 (accession number in the Genbank KX232465.1) was donated by the Technological Institute of Tlajomulco, located in Tlajomulco de Zúñiga, Jalisco, México. The inoculum preparation followed the description provided by [24], where a solution of 1×10^8 conidia·mL^{-1} was obtained. Ten mL of the inoculum were taken and applied directly on the substrate for PBs and PFBs treatments, and 10 mL were used for spraying foliage for PBf and PFBf treatments. For the corresponding PBi and PFBi treatments, 0.5 mL of the conidia suspension were taken out with the help of a hypodermic needle and injected at the base of the stem, at a height of 1 cm above the substrate. Sterile distilled water was used as the control and PFf, PFi, and PFs treatments (foliar, injected, and soil application). Subsequent applications of *Bb* 1205 occurred in the same manner as described above and were applied every eight days, until reaching 90 days.

2.4 The Effect of Fusarium oxysporum f. sp. lycopersici and Beauveria bassiana on the Chlorophyll Index and Agronomic Variables

Six evaluations were carried out at 8, 16, 24, 32, 58, and 82 days after inoculation (dai). Three measurements were done for each plant in order to report the chlorophyll index, for which a Minolta SPAD 502 plus chlorophyll meter was used by directly measuring the intensity of chlorophyll in the leaf according to [25]. In addition, the length of the aerial parts of *S. lycopersicum* L. plants was measured with a fluxmeter. Measurements were taken from the base of the plant to the axil of the youngest leaf. Stem diameter was measured at the base of the stem at a height of 1 cm above the substrate with the help of a vernier caliper. Chlorophyll measurements were performed in triplicate, for which three measurements were done in three different leaves per plant following the methodology of [26]. For all the variables mentioned above, readings were taken every eight days after inoculation day (dai) with *Bb* 1205. Additional agronomic data obtained included the 82 dai root length with a measuring tape, fresh plant weight (foliage and root) in grams with the help of an analytical balance (Ohaus) according to [27], number of flowers, and number of fruits by visual count as described by [28].

2.5 Enzyme Assay of S. lycopersicum L. Plants Inoculated with Beauveria bassiana and Infected with Fusarium oxysporum f. sp. lycopersici

Total protein extraction was performed from leaves and roots of tomato plants as described by [10]. Samples were collected at eight dai with *Bb* 1205 and then evaluated 6 times (8, 16, 24, 32, 58, 58, and 82 dai), which were frozen in liquid nitrogen and preserved at −70°C until processing. Total protein concentration was determined with the Bio-Rad kit (Bio-Rad Laboratories, USA), which is based on the Bradford method [29], where three replicates for each treatment were performed.

For the identification of chitinases in leaves and roots, the discontinuous colorimetric method described by [30] and modified by [10] was implemented, for which colloidal chitin made from reagent-grade chitin was used (Sigma-Aldrich). Absorbance readings were carried out at 585 nm in a spectrophotometer. For the enzymatic activity of ß-1,3-glucanases in leaves and roots, the discontinuous and colorimetric method modified by [10] was carried out, where laminarin (Sigma-Aldrich) is used as a substrate. The generated sugars were quantified with a spectrophotometer by the Nelson-Somogyi method [31] at an absorbance of 660 nm. In addition, the specific activity of each enzyme was converted and reported in microkatals (μKat) and picokatals (pKat) per milligram of total protein (pKat/mg protein).

2.6 Statistical Analyses

The data obtained from the chlorophyll index, agronomic variables, quality, specific activity of chitinases and ß-1,3-glucanases, was analyzed with analysis of variance (ANOVA). Obtained data was compared with a test of means by Tukey's method ($p \leq 0.05$) with the help of the Statgraphics Centurion XVI.I. computer package.

3 Results

Plants in the control treatment with *Fusarium oxysporum* began to show signs of wilting 60 days after the transfer. At the end of the study, it was observed that 60% of the control plants that were contaminated with *F. oxysporum* were dead, which helped in verifying the severity of the damage of this pathogen. As for the other treatments in which *F. oxysporum* was also ammended, all plants survived.

3.1 Effect of the Application of B. bassiana (1205) on S. lycopersicum L. Plants Infected with Fusarium oxysporum f. sp. lycopersici (17108) in Agronomic Variables and Chlorophyll Index

The application of *Bb* 1205 on *Fol* 17108-infected plants as a potential biological control method could prove to be a suitable method of biological control. Results in Table 1 show the chlorophyll content value found in the greenhouse trial, showing a decrease in chlorophyll content after 24 dai for all treatments where only *Fol* 17108 appeared, as well as the death of plants in the same treatments after 58 dai. A more significant loss was observed due to the PFs treatment as compared to other forms of infection (PFf and PFi). In general, it was shown that *Bb* 1205 preserves 53.6% (at 24 dai) of SPAD levels in *S. lycopersicum* L. plants infected with *Fol* 17108. The effect demonstrated by *Bb* 1205 on SPAD values in *S. lycopersicum* L. L. showed a statistically significant difference in the PFBi treatments at 32 dai and PFBs at 16 and 24 dai, with an increase of 36%, 50%, and 23%, respectively.

Table 1: Foliar chlorophyll content in *S. lycopersicum* L. plants, when *B. bassiana* 1205 is applied to control the *F. oxysporum* f. sp. *lycopersici* 17108 pathogen

Treatments	Days after inoculation (dai) of *B. bassiana* 1205					
	8	16	24	32	58	82
	SPAD index					
PCf	$28.9^{ab} \pm 4.9$	$25.6^{cd} \pm 2.5$	$40.7^{ab} \pm 2.8$	$44.3^{ab} \pm 4$	$49.7^{b} \pm 2.8$	**$52.7^{a} \pm 8.9$**
PCi	**$30.5^{a} \pm 3.6$**	$25.3^{cd} \pm 2.7$	$36.2^{b} \pm 4.8$	$36.0^{c} \pm 3.6$	$45.4^{bcd} \pm 2.4$	$50.1^{ab} \pm 2.4$
PCs	**$30.3^{a} \pm 3.5$**	$25.0^{cd} \pm 2.6$	$36.6^{b} \pm 6.2$	$38.1^{bc} \pm 6.7$	$42.0^{cd} \pm 9.4$	$48.1^{ab} \pm 2.1$
PBf	$27.8^{b} \pm 5.1$	$26.9^{bc} \pm 3$	$35.3^{b} \pm 5.5$	$42.2^{abc} \pm 5$	$48.6^{bc} \pm 5.2$	$49.7^{ab} \pm 6.7$
PBi	$27.7^{b} \pm 4.6$	$26.5^{bc} \pm 3.7$	$39.0^{ab} \pm 2.7$	$44.2^{ab} \pm 1.9$	**$57.5^{a} \pm 7.8$**	**$52.8^{a} \pm 4.1$**
PBs	$28.4^{ab} \pm 4.9$	$28.6^{b} \pm 4.4$	$36.5^{b} \pm 6.4$	$43.9^{ab} \pm 3.5$	$45.1^{bcd} \pm 3$	**$53.4^{a} \pm 7.6$**
PFBf	$24.9^{c} \pm 2.6$	**$36.5^{a} \pm 0.2$**	**$45.5^{a} \pm 4.7$**	**$49.3^{a} \pm 5.8$**	$48.4^{bc} \pm 4.1$	$44.1^{abc} \pm 9.4$
PFBi	$24.8^{c} \pm 3.3$	**$36.9^{a} \pm 4.6$**	**$43.5^{a} \pm 6.7$**	**$49.3^{a} \pm 3.7$**	$40.9^{d} \pm 7$	$41.3^{bc} \pm 3.^{9}$
PFBs	$24.9^{c} \pm 2.9$	**$37.6^{a} \pm 4.1$**	**$45.1^{a} \pm 5.7$**	**$46.2^{a} \pm 3.5$**	$41.7^{d} \pm 2.8$	$33.8^{c} \pm 9.8$
PFf	$28.7^{ab} \pm 4.1$	$25.7^{cd} \pm 4.7$	$9.7^{c} \pm 16.6$	$7.5^{d} \pm 17$	$0.0^{e} \pm 0.0$	$0.0^{d} \pm 0.0$
Pfi	$28.7^{ab} \pm 5.0$	$23.6^{d} \pm 3.8$	$11.6^{c} \pm 18.5$	$10.9^{d} \pm 19.3$	$0.0^{e} \pm 0.0$	$0.0^{d} \pm 0.0$
PFs	$28.8^{ab} \pm 5.3$	$25.8^{cd} \pm 5.3$	$0.0^{d} \pm 0.0$	$0.0^{e} \pm 0.0$	$0.0^{e} \pm 0.0$	$0.0^{d} \pm 0.0$
HSD	2.5	2.4	6.9	7.9	6.7	11.12

Note: Values with different letters are significantly different between treatments ($p \leq 0.05$); each value represents the mean of three repetitions ± the standard deviation according to the Tukey test; HSD: least significant difference.

When analyzing the effect of *Bb* 1205 for the length variable of *S. lycopersicum* L. (Table 2) infected with *Fol* 17108, it was shown that the PFBs treatment presented a statistically significant difference in three stages of the experiment (16, 24, and 32 dai), as compared to other treatments, with 26.6%, 27.8%, and 20.3%, respectively.

Table 2: Plant length of *S. lycopersicum* L., when applying *B. bassiana* 1205 to control the *F. oxysporum* f. sp. *lycopersici* 17108 pathogen

Treatments	Days after inoculation (dai) of *B. bassiana* 1205					
	8	16	24	32	58	82
	Plant length (cm)					
PCf	$13.5^{abc} \pm 1.3$	$17.4^{c} \pm 2.6$	$7.7^{c} \pm 13.9$	$8.6^{e} \pm 19.7$	$68.8^{bc} \pm 6.0$	$74.8^{ab} \pm 7.5$
PCi	$13.3^{abc} \pm 1.2$	$19.3^{bc} \pm 2.7$	$29.4^{ab} \pm 6.6$	$42.4^{abc} \pm 11.3$	**$84.6^{a} \pm 3.4$**	**$88.7^{a} \pm 4.1$**
PCs	$13.5^{abc} \pm 1.4$	$19.9^{bc} \pm 2.3$	$28.0^{b} \pm 6.1$	$41.4^{abc} \pm 5.1$	$69.8^{bc} \pm 6.0$	$70.8^{ab} \pm 7.5$
PBf	$12.8^{bc} \pm 1.3$	$20.7^{b} \pm 5.5$	$30.4^{ab} \pm 7.9$	$46.4^{ab} \pm 7.8$	$51.7^{d} \pm 4.6$	$55.3^{b} \pm 4.9$
PBi	$13.0^{bc} \pm 1.2$	$19.2^{bc} \pm 6.2$	$29.2^{ab} \pm 7.9$	$36.6^{cd} \pm 7.4$	$68.0^{bc} \pm 5.1$	$62.1^{b} \pm 2.1$
PBs	$13.1^{abc} \pm 1.3$	$18.2^{bc} \pm 2.1$	$26.5^{b} \pm 4.5$	$39.0^{abcd} \pm 7.6$	$79.1^{ab} \pm 4.7$	**$87.2^{a} \pm 1.3$**
PFBf	$11.8^{d} \pm 1.5$	$18.8^{bc} \pm 2.5$	$26.3^{b} \pm 5.3$	$31.2^{cd} \pm 7.4$	$61.7^{cd} \pm 3.5$	$69.7^{ab} \pm 2.6$
PFBi	$13.2^{abc} \pm 1.0$	$19.3^{bc} \pm 2.8$	$29.9^{ab} \pm 6.3$	$44.^{ab} 1 \pm 5.9$	$60.6^{cd} \pm 7.6$	**$87.2^{a} \pm 7.6$**
PFBs	$12.6^{cd} \pm 1.7$	**$25.2^{a} \pm 6.5$**	**$35.8^{a} \pm 8.9$**	**$49.8^{a} \pm 8.8$**	$73.0^{b} \pm 8.4$	$76.5^{ab} \pm 10.6$
PFf	$13.4^{abc} \pm 1.6$	$18.9^{bc} \pm 2.4$	$26.2^{b} \pm 5.0$	$30.1^{d} \pm 3.1$	$0.0^{e} \pm 0.0$	$0.0^{d} \pm 0.0$
PFi	**$14.0^{a} \pm 1.2$**	$17.6^{c} \pm 1.3$	$6.8^{c} \pm 11.9$	$13.7^{e} \pm 20.5$	$0.0^{e} \pm 0.0$	$0.0^{d} \pm 0.0$
PFs	$13.5^{ab} \pm 1.1$	$17.5^{c} \pm 1.5$	$0.0^{c} \pm 0.0$	$0.0^{f} \pm 0.0$	$0.0^{e} \pm 0.0$	$0.0^{d} \pm 0.0$
HSD	1	2.8	7.2	11.2	11.2	22.5

Note: Values with different letters are significantly different between treatments ($p \leq 0.05$); each value represents the mean of three repetitions ± the standard deviation according to the Tukey test; HSD: Least significant difference.

In regard to the stem diameter parameter of *S. lycopersicum* L. (Table 3), it is evident that the PFBf treatment was the one that best induced an increase as of 16 dai, which continued at 24, 32, and 82 dai. At 58 dai, it was shown that, when inoculating *S. lycopersicum* L. plants foliarly with *Bb* 1205, an increase of 17.4% was observed, whereby a statistically significant difference associated to all other treatments was evident.

Table 3: Diameter of the stem of *S. lycopersicum* L. with different types of application of *B. bassiana* 1205 for the control of *F. oxysporum* f. sp. *lycopersici* 17108

Treatments	Days after inoculation (dai) of *B. bassiana* 1205					
	8	16	24	32	58	82
	Diameter (mm)					
PCf	$2.0^{a} \pm 0.1$	$2.5^{cdef} \pm 0.4$	$3.8^{ab} \pm 0.9$	$4.3^{abc} \pm 0.7$	$6.3^{ab} \pm 1.2$	**$7.5^{a} \pm 0.8$**
PCi	$2.0^{a} \pm 0.1$	$2.3^{f} \pm 0.4$	$3.6^{b} \pm 0.7$	$3.4^{c} \pm 0.4$	$5.0^{c} \pm 0.1$	**$5.6^{a} \pm 0.1$**
PCs	$1.9^{a} \pm 0.1$	$2.5^{def} \pm 0.4$	$3.6^{b} \pm 0.6$	$3.5^{c} \pm 0.7$	$6.2^{abc} \pm 0.3$	**$7.1^{a} \pm 0.6$**
PBf	$2.0^{a} \pm 0.1$	$2.6^{cdef} \pm 0.4$	$4.0^{ab} \pm 0.8$	$3.9^{bc} \pm 0.7$	**$7.4^{a} \pm 0.7$**	**$6.8^{a} \pm 0.3$**
PBi	$2.0^{a} \pm 0.1$	$2.7^{bcd} \pm 0.4$	$4.2^{ab} \pm 0.7$	$4.7^{ab} \pm 1.2$	$6.3^{abc} \pm 0.2$	**$6.8^{a} \pm 0.4$**
PBs	$1.9^{a} \pm 0.1$	$2.7^{bcde} \pm 0.4$	$4.6^{ab} \pm 1.2$	$4.5^{abc} \pm 0.6$	$6.7^{ab} \pm 0.5$	**$6.5^{a} \pm 0.6$**
PFBf	$1.9^{a} \pm 0.1$	**$3.4^{a} \pm 0.6$**	**$4.7^{a} \pm 0.7$**	**$5.0^{a} \pm 0.7$**	$6.7^{ab} \pm 0.4$	**$7.1^{a} \pm 0.3$**
PFBi	$1.9^{a} \pm 0.1$	$3.0^{b} \pm 0.6$	$4.0^{ab} \pm 0.8$	**$5.3^{a} \pm 1.1$**	$6.4^{ab} \pm 0.2$	**$7.6^{a} \pm 1.4$**

(Continued)

Table 3 (continued)

Treatments	Days after inoculation (dai) of *B. bassiana* 1205					
	8	16	24	32	58	82
	Diameter (mm)					
PFBs	$2.0^{a} \pm 0.1$	$2.8^{bc} \pm 0.6$	$3.8^{ab} \pm 0.7$	$4.4^{abc} \pm 0.8$	$6.0^{bc} \pm 0.4$	$5.3^{ab} \pm 0.4$
PFf	$2.0^{a} \pm 0.1$	$2.3^{ef} \pm 0.2$	$1.0^{c} \pm 1.8$	$0.9^{d} \pm 2.0$	$0.0^{d} \pm 0.0$	$0.0^{c} \pm 0.0$
PFi	$2.0^{a} \pm 0.1$	$2.4^{def} \pm 0.2$	$1.1^{c} \pm 1.9$	$1.0^{d} \pm 1.7$	$0.0^{d} \pm 0.0$	$0.0^{c} \pm 0.0$
PFs	$2.0^{a} \pm 0.1$	$2.3^{ef} \pm 0.2$	$0.0^{d} \pm 0.0$	$0.0^{e} \pm 0.0$	$0.0^{d} \pm 0.0$	$0.0^{c} \pm 0.0$
HSD	0.07	0.3	1	1.1	1.3	2.7

Note: Values with different letters are significantly different between treatments ($p \leq 0.05$); each value represents the mean of three repetitions ± the standard deviation according to the Tukey test; HSD: Least significant difference.

In order to evaluate the effect of *Bb* 1205 on *S. lycopersicum* L. at the end of the experiment, other morphometric and harvest variables also were considered (Table 4). It was shown that at 82 dai, the interaction of *Bb* 1205 and *Fol* 17108 did not generate significant statistical differences in total plant length, foliage length, fresh root weight, and whole plant. However, an average increase of 30% in total height, 54% in root length and up to 20.7% in canopy length was found.

Table 4: Morphometric variables at 82 dai of *S. lycopersicum* L. with different types of application *B. bassiana* 1205 for the control of *F. oxysporum* f. sp. *lycopersici* 17108

Treatments	L Total (cm)	L Foliage (cm)	L Root (cm)	PF Total (g)	P Foliage (g)	P Root (g)	N° Flowers	N° Fruit
PCf	**$125.2^{a} \pm 2.8$**	**$92.3^{a} \pm 2.3$**	$32.8^{bc} \pm 2.0$	**$207.0^{a} \pm 1.7$**	**$163.3^{a} \pm 1.2$**	**$43.7^{a} \pm 0.6$**	**$39.3^{a} \pm 2.9$**	$8.7^{ab} \pm 0.6$
PCi	**$114.7^{a} \pm 1.2$**	**$71.7^{a} \pm 1.5$**	$43.0^{ab} \pm 1.0$	$107.0^{c} \pm 0.0$	$84.0^{bc} \pm 0.0$	$23.0^{bc} \pm 0.0$	$16.0^{bcd} \pm 0.0$	$0.0^{d} \pm 0.0$
PCs	**$113.7^{a} \pm 1.5$**	**$78.3^{a} \pm 3.1$**	$35.3^{b} \pm 1.5$	$181.3^{ab} \pm 21.9$	$150.7^{ab} \pm 26.6$	$30.7^{ab} \pm 4.6$	$37.0^{ab} \pm 1.7$	$2.7^{cd} \pm 1.2$
PBf	**$135.2^{a} \pm 8.5$**	**$78.2^{a} \pm 2.3$**	**$57.0^{a} \pm 7.0$**	**$199.0^{a} \pm 11.5$**	**$176.3^{a} \pm 9.0$**	$22.7^{bc} \pm 2.9$	$28.3^{abc} \pm 9.2$	**$13.0^{a} \pm 2.0$**
PBi	**$136.7^{a} \pm 0.6$**	**$88.3^{a} \pm 1.2$**	$48.3^{ab} \pm 1.5$	**$199.0^{a} \pm 7.2$**	**$176.0^{a} \pm 4.6$**	$23.0^{bc} \pm 2.6$	$37.0^{ab} \pm 1.7$	**$13^{a} \pm 1.7$**
PBs	**$142.0^{a} \pm 7.9$**	**$94.8^{a} \pm 8.8$**	$47.2^{ab} \pm 1.3$	$172^{ab} \pm 5.0$	$143.0^{ab} \pm 2.0$	$29.0^{ab} \pm 3.0$	**$41.3^{a} \pm 1.5$**	$6.0^{bc} \pm 1.0$
PFBf	**$151.0^{a} \pm 6.7$**	**$99.5^{a} \pm 3.3$**	$51.5^{ab} \pm 3.9$	**$193.7^{a} \pm 4.5$**	**$170.3^{a} \pm 2.5$**	$23.3^{bc} \pm 2.1$	**$43.3^{a} \pm 20.6$**	**$13.3^{a} \pm 1.5$**
PFBi	**$156.0^{a} \pm 3.0$**	**$95.3^{a} \pm 3.1$**	**$60.7^{a} \pm 0.06$**	**$198.3^{a} \pm 3.1$**	**$174.7^{a} \pm 1.5$**	$23.7^{bc} \pm 1.5$	$27.7^{abc} \pm 8.1$	**$12.0^{a} \pm 1.2$**
PFBs	**$153.2^{a} \pm 1.5$**	**$95.2^{a} \pm 2.5$**	**$58.0^{a} \pm 1.0$**	$191^{ab} \pm 2.0$	**$166.0^{a} \pm 1.0$**	$25.0^{bc} \pm 1.0$	**$48.0^{a} \pm 1.7$**	**$13.0^{a} \pm 1.0$**
PFf	$0.0^{b} \pm 0.0$	$0.0^{b} \pm 0.0$	$0.0^{d} \pm 0.0$	$0.0^{d} \pm 0.0$	$0.0^{d} \pm 0.0$	$0.0^{d} \pm 0.0$	$0.0^{d} \pm 0.0^{d}$	$0.0^{d} \pm 0.0$
Pfi	$0.0^{b} \pm 0.0$	$0.0^{b} \pm 0.0$	$0.0^{d} \pm 0.0$	$0.0^{d} \pm 0.0$	$0.0^{d} \pm 0.0$	$0.0^{d} \pm 0.0$	$0.0^{d} \pm 0.0^{d}$	$0.0^{d} \pm 0.0$
PFs	$0.0^{b} \pm 0.0$	$0.0^{b} \pm 0.0$	$0.0^{d} \pm 0.0$	$0.0^{d} \pm 0.0$	$0.0^{d} \pm 0.0$	$0.0^{d} \pm 0.0$	$0.0^{d} \pm 0.0$	$0.0^{d} \pm 0.0$
HSD	55.6	36.6	20.3	86.1	71.1	17.4	22.6	5.6

Note: Values with different letters are significantly different between treatments ($p \leq 0.05$); each value represents the mean of three repetitions ± the standard deviation according to the Tukey test; HSD: least significant difference; L Total: total length of the plant; L Foliage: length of foliage; L Root: length of the root; P F Total: total fresh weight of the plant; P Foliage: fresh weight of the foliage; P Root: fresh weight of the root; N° Flowers: number of flowers; N° Fruits: number of fruits.

3.2 Enzymatic Assay of Solanum lycopersicum Plants Inoculated with Beauveria bassiana and Infected with Fusarium oxysporum f. sp. lycopersici

The chitinase enzyme activity in the root of *S. lycopersicum* L. inoculated with *Bb* 1205 appears in Table 5. Before *S. lycopersicum* L. plants were attacked by *Fol* 17108, they showed low activity since the beginning of the experiment until 32 dai, where all treatments resulted in death. The PFBi treatment presented specific activity with a statistically significant difference in regard to the control on days 8, 32,

and 82 dai (1.9, 41.8, and 9.5 times more in the enzyme activity, respectively). Thus, they are inducing a decrement in the intensity of the attack by the phytopathogenic fungus.

Table 5: The activity of the chitinase enzyme in roots of *S. lycopersicum* L. inoculated with *B. bassiana* 1205 for controlling *F. oxysporum* f. sp. *lycopersici* 17108

	Days after inoculation (dai) of *B. bassiana* 1205					
Treatments	8	16	24	32	58	82
PCf	$1290.0^{g} \pm 10$	$36.6^{i} \pm 1.3$	**$6298.4^{a} \pm 1.5$**	$18947.0^{f} \pm 17.5$	$482.3^{i} \pm 2.8$	$760.9^{i} \pm 2.8$
PCi	$2968.0^{d} \pm 50.8$	$410.2^{g} \pm 23.3$	$4715.8^{b} \pm 2.4$	$3943.0^{i} \pm 20.8$	$1597.5^{g} \pm 2.6$	$1724.9^{g} \pm 3.3$
PCs	$1953.6^{e} \pm 29.4$	$2934.2^{d} \pm 82.8$	$1683.6^{f} \pm 2.3$	$1690.8^{k} \pm 8.7$	$1072.5^{h} \pm 7.0$	$1479.8^{h} \pm 6.1$
PBf	$553.4^{i} \pm 1.0$	$582.8^{f} \pm 2.0$	$543.3^{k} \pm 3.5$	$26379.0^{e} \pm 5.0$	$4052.7^{e} \pm 3.2$	$4345.0^{f} \pm 4.5$
PBi	$1086.0^{h} \pm 1.0$	$248.4^{h} \pm 10.0$	$812.0^{j} \pm 5.1$	$33790.1^{d} \pm 2.1$	**$7613.2^{a} \pm 3.9$**	$5275.8^{e} \pm 5.5$
PBs	$317.0^{j} \pm 1.6$	$3170.6^{b} \pm 26.5$	$1134.5^{i} \pm 2.1$	$7791.9^{g} \pm 6.4$	$3031.3^{f} \pm 2.6$	$6564.6^{d} \pm 1.8$
PFBf	$5691.1^{b} \pm 37.4$	$3061.9^{c} \pm 4.4$	$3379.8^{e} \pm 3.2$	$82474.7^{c} \pm 4.1$	$4467.1^{d} \pm 4.4$	$10039.2^{c} \pm 4.2$
PFBi	**$5823.2^{a} \pm 12.0$**	$1880.5^{e} \pm 21.8$	$3612.3^{d} \pm 4.4$	**$164940.0^{a} \pm 1.3$**	$5889.0^{b} \pm 6.6$	**$16394.5^{a} \pm 1.3$**
PFBs	$4474.9^{c} \pm 95.7$	$190.7^{hi} \pm 4.0$	$4189.6^{c} \pm 2.1$	$92379.5^{b} \pm 2.6$	$5424.9^{c} \pm 5.0$	$11463.5^{b} \pm 2.5$
PFf	$1186.6^{gh} \pm 17.7$	**$5142.6^{a} \pm 53.7$**	$1144.4^{h} \pm 2.0$	$3325.2^{j} \pm 3.6$	$0.0^{j} \pm 0.0$	$0.0^{j} \pm 0.0$
Pfi	$1686.9^{f} \pm 11.3$	$112.1^{ij} \pm 9.3$	$1413.5^{g} \pm 81$	$5383.8^{h} \pm 2.2$	$0.0^{j} \pm 0.0$	$0.0^{j} \pm 0.0$
PFs	$346.0^{j} \pm 20.3$	$161.2^{hi} \pm 2.1$	$0.0^{i} \pm 0.0$	$0.0^{j} \pm 0.0$	$0.0^{j} \pm 0.0$	$0.0^{j} \pm 0.0$
HSD	104.4	91.9	8.3	25.9	11.5	9.9

Note: The values with different letters are significantly different between treatments ($p \leq 0.05$) according to the Tukey test; Days after inoculation (dai); HSD: least significant difference.

Chitinase activity in *S. lycopersicum* L. leaves (Table 6) showed that the enzyme activity decreased in the first two evaluations of the experiment. For 24 and 32 dai, statistically significant values were obtained in the PFBi treatment with 2.3 and 11.6 times more than the control. PFBf also showed activity at 58 dai with 4.3 times greater activity. Finally, PFBs treatment showed 5.8 times greater activity at 82 dai.

Table 6: The activity of the chitinase enzyme in leaves of *S. lycopersicum* L. inoculated with *B. bassiana* 1205 for controlling *F. oxysporum* f. sp. *lycopersici* 17108

	Days after inoculation (dai) of *B. bassiana* 1205					
Treatments	8	16	24	32	58	82
	Pkat/mg protein					
PCf	$147.2^{hi} \pm 2.4$	$287.5^{i} \pm 43.1$	$432.1^{i} \pm 1.8$	$322.6^{h} \pm 3.1$	$272.7^{h} \pm 3.8$	$875.6^{f} \pm 2.5$
PCi	$97.6^{i} \pm 7.5$	$225.1^{j} \pm 9.1$	$938.1^{f} \pm 1.4$	$298.9^{i} \pm 2.7$	$558.2^{g} \pm 2.2$	$564.5^{i} \pm 0.9$
PCs	$136.0^{i} \pm 5.1$	$298.4^{i} \pm 10.9$	$829.3^{g} \pm 2.0$	$107.9^{k} \pm 1.7$	$969.6^{d} \pm 1.5$	$659.2^{g} \pm 3.6$
PBf	$691.8^{g} \pm 6.4$	$1202.8^{f} \pm 5.4$	$1567.5^{c} \pm 0.9$	$1807.5^{e} \pm 0.8$	$1095.8^{c} \pm 2.2$	$945.8^{e} \pm 1.3$
PBi	$197.0^{h} \pm 5.0$	$2801.4^{b} \pm 5.9$	$1438.8^{d} \pm 1.4$	$1895.3^{d} \pm 5.0$	$1140.8^{b} \pm 2.6$	$599.3^{h} \pm 4.4$
PBs	$146.1^{hi} \pm 5.1$	**$3273.7^{a} \pm 13.3$**	$1135.3^{e} \pm 3.0$	$702.5^{g} \pm 3.5$	$964.6^{d} \pm 2.0$	$1106.6^{d} \pm 2.2$
PFBf	$1615.5^{d} \pm 8.3$	$1721.8^{e} \pm 7.9$	$579.6^{h} \pm 0.8$	$2347.6^{c} \pm 1.9$	**$1198.8^{a} \pm 4.7$**	$1398.0^{c} \pm 2.2$
PFBi	$2470.3^{b} \pm 28.8$	$241.1^{j} \pm 2.2$	**$2247.3^{a} \pm 0.8$**	**$3479.3^{a} \pm 4.2$**	$747.7^{e} \pm 1.2$	$2939.2^{b} \pm 1.7$

(Continued)

Table 6 (continued)

Treatments	Days after inoculation (dai) of *B. bassiana* 1205					
	8	16	24	32	58	82
	Pkat/mg protein					
PFBs	$2302.6^{c} \pm 19.4$	$848.7^{g} \pm 6.1$	$1650.2^{b} \pm 3.8$	$2417.4^{b} \pm 0.8$	$658.0^{f} \pm 2.0$	**$3838.2^{a} \pm 2.7$**
PFf	**$4896.6^{a} \pm 25.2$**	$1785.7^{d} \pm 14.1$	$45.0^{k} \pm 3.1$	$257.8^{j} \pm 1.8$	$0.0^{i} \pm 0.0$	$0.0^{j} \pm 0.0$
Pfi	$1110.7^{e} \pm 27.0$	$532.9^{h} \pm 10.3$	$75.1^{j} \pm 3.2$	$1405.0^{f} \pm 1.3$	$0.0^{i} \pm 0.0$	$0.0^{j} \pm 0.0$
PFs	$819.7^{f} \pm 29.8$	$2056.3^{c} \pm 9.7$	$0.0^{l} \pm 0.0$	$0.0^{j} \pm 0.0$	$0.0^{i} \pm 0.0$	$0.0^{j} \pm 0.0$
HSD	51.8	45	6.4	7.8	6.8	6.6

Note: The values with different letters are significantly different between treatments ($p \leq 0.05$) according to the Tukey test; Days after inoculation (dai); HSD: least significant difference.

The enzymatic activity of β-1,3-glucanase in *S. lycopersicum* L. roots inoculated with *Bb* 1205 and infected with *Fol* 17108 can be seen in Table 7. The results indicate that the expression of the enzyme remained basal in the first three evaluations. Subsequently, they presented statistically significant differences compared with the control in PFBf treatment at 32 and 82 dai, as the enzmatic activity increased by 3.2 and 10 times, respectively. On the other hand, PFBs treatment generated only increased activity after 58 dai, showing a 35.7-fold rise.

Table 7: Activity of the enzyme β-1,3-glucanase in roots of *S. lycopersicum* L., inoculated with *B. bassiana* 1205 for the control of *F. oxysporum* f. sp. *lycopersici* 17108

Treatments	Days after inoculation (dai) of *B. bassiana* 1205					
	8	16	24	32	58	82
	μkat/mg protein					
PCf	$1.0^{e} \pm 0.09$	$0.2^{h} \pm 0.02$	**$3.4^{a} \pm 0.06$**	$49.8^{c} \pm 1.0$	$1.0^{f} \pm 0.07$	$1.4^{e} \pm 0.06$
PCi	$0.9^{ef} \pm 0.03$	**$2.9^{a} \pm 0.06$**	$0.5^{e} \pm 0.05$	$3.6^{g} \pm 0.1$	$0.5^{g} \pm 0.05$	$0.3^{gh} \pm 0.05$
PCs	**$16.2^{a} \pm 0.10$**	$0.6^{e} \pm 0.04$	$0.8^{d} \pm 0.22$	$22.7^{e} \pm 1.2$	$1.7^{d} \pm 0.09$	$0.5^{g} \pm 0.11$
PBf	$2.3^{c} \pm 0.02$	$1.0^{d} \pm 0.02$	$0.23^{fg} \pm 0.02$	$21.3^{e} \pm 0.15$	$2.7^{c} \pm 0.1$	$0.9^{f} \pm 0.11$
PBi	$0.9^{fg} \pm 0.02$	$1.1^{c} \pm 0.03$	$0.2^{fg} \pm 0.01$	$16.8^{e} \pm 1.0$	$15.5^{b} \pm 0.1$	$1.8^{e} \pm 0.05$
PBs	$0.1^{j} \pm 0.02$	$2.1^{b} \pm 0.02$	$0.4^{g} \pm 0.01$	$12.5^{f} \pm 1.0$	$0.39^{g} \pm 0.06$	$2.4^{d} \pm 0.22$
PFBf	$0.7^{h} \pm 0.04$	$0.5^{f} \pm 0.05$	$1.4^{b} \pm 0.15$	**$162.1^{a} \pm 3.9$**	$1.4^{e} \pm 0.03$	**$14.02^{a} \pm 0.2$**
PFBi	$1.7^{d} \pm 0.02$	$2.2^{b} \pm 0.06$	$0.7^{de} \pm 0.09$	$127.1^{b} \pm 0.8$	$2.8^{c} \pm 0.1$	$4.4^{c} \pm 0.04$
PFBs	$0.8^{gh} \pm 0.04$	$0.1^{j} \pm 0.03$	$1.1^{c} \pm 0.11$	$32.1^{d} \pm 0.8$	**$60.7^{a} \pm 0.04$**	$10.5^{b} \pm 0.13$
PFf	$0.3^{i} \pm 0.09$	$1.2^{c} \pm 0.05$	$0.06^{g} \pm 0.01$	$1.5^{g} \pm 0.1$	$0.0^{h} \pm 0.0$	$0.0^{i} \pm 0.0$
Pfi	$4.4^{b} \pm 0.11$	$0.1^{i} \pm 0.02$	$0.1^{g} \pm 0.05$	$3.4^{g} \pm 0.1$	$0.0^{h} \pm 0.0$	$0.0^{i} \pm 0.0$
PFs	$1.8^{d} \pm 0.04$	$0.3^{g} \pm 0.02$	$0.0^{g} \pm 0.0$	$0.0^{g} \pm 0.0$	$0.0^{h} \pm 0.0$	$0.0^{i} \pm 0.0$
HSD	0.1	0.1	0.18	3.8	0.2	0.3

Note: The values with different letters are significantly different between treatments ($p \leq 0.05$) according to the Tukey test; Days after inoculation (dai); HSD: least significant difference.

Regarding the specific activity of the β-1,3 enzyme-glucanase, results were obtained from leaf samples of *S. lycopersicum* L. infected with *Fol* 17108, which were subsequently treated with *Bb* 1205 via foliar and soil applications, as well as by injections (Table 8). It was demonstrated that the enzyme activity had a statistically significant difference in the PFBi treatment at 24 and 82 dai, expressing 1.1 and 3.8 times more activity of β-1,3-glucanase, respectively. Also, the PFBf treatment showed an increase of 1.1 and 1.6 times after 32 and 82 dai, correspondingly.

Table 8: The activity of the enzyme β-1,3-glucanase in leaves of *S. lycopersicum* L. inoculated with *B. bassiana* 1205 for the control of *F. oxysporum* f. sp. *lycopersici* 17108

Treatments	Days after inoculation (dai) of *B. bassiana* 1205					
	8	16	24	32	58	82
	Pkat/mg protein					
PCf	$10.1^{j} \pm 0.03$	$35.9^{e} \pm 0.04$	$37.5^{ab} \pm 0.0$	$57.8^{c} \pm 0.02$	$42.8^{bc} \pm 0.5$	$24.2^{e} \pm 2.1$
PCi	$30.7^{d} \pm 0.02$	$4.3^{l} \pm 0.04$	$34.9^{b} \pm 1.0$	$59.5^{bc} \pm 0.1$	$36.4^{d} \pm 1.2$	$10.0^{f} \pm 0.0$
PCs	$36.2^{c} \pm 0.02$	$41.2^{c} \pm 0.019$	$24.6^{e} \pm 0.4$	$42.8^{f} \pm 0.3$	$42.0^{c} \pm 2.4$	$23.8^{e} \pm 0.9$
PBf	$15.2^{i} \pm 0.02$	$7.6^{j} \pm 0.017$	$27.5^{d} \pm 0.03$	$61.2^{b} \pm 0.1$	$35.1^{d} \pm 0.2$	$26.8^{de} \pm 1.1$
PBi	$7.5^{k} \pm 0.01$	$42.0^{b} \pm 0.02$	$9.1^{g} \pm 0.0$	$51.7^{e} \pm 0.04$	$44.7^{abc} \pm 1.2$	$31.9^{c} \pm 0.4$
PBs	$25.5^{f} \pm 0.02$	$32.5^{g} \pm 0.02$	$19.0^{f} \pm 0.02$	$44.6^{ef} \pm 0.03$	**$46.4^{a} \pm 0.3$**	$28.4^{d} \pm 2.8$
PFBf	$27.6^{e} \pm 0.02$	$26.6^{h} \pm 0.03$	$37.3^{ab} \pm 2.2$	**$63.2^{a} \pm 1.0$**	$45.1^{ab} \pm 1.1$	**$39.8^{a} \pm 0.9$**
PFBi	$21.4^{h} \pm 0.02$	$5.1^{k} \pm 0.03$	**$38.1^{a} \pm 1.7$**	$58.0^{c} \pm 1.6$	$31.5^{e} \pm 1.2$	**$38.7^{ab} \pm 0.4$**
PFBs	$25.2^{g} \pm 0.02$	$39.1^{d} \pm 0.06$	$31.3^{c} \pm 0.1$	$46.2^{e} \pm 0.2$	$37.0^{d} \pm 0.0$	$36.1^{b} \pm 0.6$
PFf	$45.3^{b} \pm 0.02$	$33.9^{f} \pm 0.10$	$20.6^{f} \pm 1.5$	$36.2^{g} \pm 0.7$	$0.0^{f} \pm 0.0$	$0.0^{g} \pm 0.0$
Pfi	**$52.0^{a} \pm 0.05$**	**$48.4^{a} \pm 0.04$**	$24.9^{de} \pm 0.0$	$35.2^{g} \pm 0.8$	$0.0^{f} \pm 0.0$	$0.0^{g} \pm 0.0$
PFs	$30.7^{d} \pm 0.35$	$25.7^{i} \pm 0.02$	$0.0^{h} \pm 0.0$	$0.0^{h} \pm 0.0$	$0.0^{f} \pm 0.0$	$0.0^{g} \pm 0.0$
HSD	0.2	0.09	2.9	1.9	3	3.4

Note: The values with different letters are significantly different between treatments ($p \leq 0.05$) according to the Tukey test; Days after inoculation (dai); HSD: least significant difference.

4 Discussion

4.1 Effect on Agronomic Variables and Chlorophyll Index after Application of B. bassiana (1205) on S. lycopersicum L. Plants Infected with Fusarium oxysporum f. sp. lycopersici (17108)

Our study demonstrated the ability of *Bb* 1205 in the PFBs treatment in doubling the chlorophyll index (Table 1), as compared to the data published by [32], where they obtained an increase in total chlorophyll (22.5%) from *S. lycopersicum* L. plants inoculated with *T. asperellum* in leaves infected with *F. oxysporum*. However, at the end of the experimentation, the PBi (58 and 82 dai) and PBs (82 dai) treatments presented statistically significant differences, increasing SPAD values in the plants of 26.6%, 5.4%, and 11%, respectively. Our results at 58 dai show that *Bb* 1205 behaves as an agent in the control of Fol and also increases the chlorophyll content, relating to the data obtained by [33] in *S. lycopersicum* L. plants inoculated with *T. asperellum* and infected with Fol at 60 dat, showing that the total chlorophyll content also increased by 15.5%. It was possible to determine that *B. bassiana* is a mutualistic fungus and it is likely that there was plant tissue colonization without generating an apparent negative effect (i.e., absence of phytopathogenic activity). On the contrary, it has been described as contributing towards the acquisition of nutrients (such as iron) for the development of the host, towards improving photosynthetic

productivity and concentration of total chlorophyll, and towards promoting tolerance to salinity in the plant [34–36]. Also relating to this, Quesada et al. [37] reported evidence of the endophytic and mutualistic colonization of *B. bassiana* on *Papaver somniferum* L. and its capacity to be transmitted vertically throughout a period of 120 dai. Positive development in *S. lycopersicum* L. plants by *B. bassiana* has been shown to occur when applied as a solid on the substrate, or by foliar spray, root dipping, and stem injection [38–40]. Recently, *Nicotiana benthamiana* inoculated with *B. bassiana* showed significant increases in chlorophyll a and b at 40 dai, from 37% to 46% and 33% to 40%, respectively [41]. Our results show low chlorophyll contents in treatments where *Bb* 1205 occurred, coinciding with those reported in *Manihot esculenta* plants with *B. bassiana*, where nutrient allocation occurs on the stem and root growth and tiny leaves [6]. Because of this, it is possible that lower leaf area and less adequate chlorophyll production occurred in *S. lycopersicum* L. It has also become apparent that the host plant determines the level of photosynthetic pigments when subjected to stress caused by a fungus or insect. Environmental factors can also influence chlorophyll synthesis and the adaptive process of the plant [42].

The results in Table 2 coincide with reports for *S. lycopersicum* L., where it is likely that the colonization of *B. bassiana* is limited to the inoculation region. It enters the mesophyll when applied in the substrate at concentrations of 1×10^8 conidia·mL^{-1}, and it is localized mainly in the stem or roots, and a colonization efficiency of 100% will be reached at 14 dai [43,44] achieved greater plant heights, reporting an increase of 12.5% after 30 dai in *S. lycopersicum* L. plants inoculated at the root with *B. bassiana*. An increase of 19.2% was also described for *Vitis vinifera* at 53 dai [45].

Parsa et al. [24] reported that *Beauveria bassiana* is capable of colonizing *Phaseolus vulgaris* cv. Calima regardless of the inoculation technique, when a solution is sprayed at a concentration of 1×10^8 conidia/mL on leaves, is capable of colonizing 30% of the plants; when applied to the soil it reaches a colonization index of 25% in roots and colonizes stems by 10% when sprayed and when placed in soil it reaches a colonization of 15%.

At 82 dai, it was found that the best treatment was when *Bb* 1205 was injected into the stem of the *S. lycopersicum* L. plant and infection with *Fol* 17108 occurred (Table 2), where its ability to provide a protective effect in a complete production cycle was demonstrated. Our results were very comparable to those obtained for *Triticum durum* cv. Carpio with the application of *B. bassiana* in the soil, where an increase of 9.5% in the length of the plant at 31 dai was achieved [46]. The colonization of *B. bassiana* in *S. lycopersicum* L. plants has been reported as needing as much of 30 dai of EF, whereby proper colonization throughout the plant and a reduction in the survival of pests such as *Tuta absoluta* was observed, regardless of application type [44]. The studies carried out for *Gossypium hirsutum* L. used treatments with *B. bassiana* (1×10^7 conidia·mL^{-1}). At 28 dai, the pathogens *Rhizoctonia solani, Xanthomonas axonopodis* pv. *Malvacearum* were controlled. Also, an increase in the height of up to 33% was achieved and a 10% decrease in the severity was observed in plants infected by the pathogens *Rhizoctonia solani*, *Xanthomonas axonopodis* pv. *Malvacearum*, respectively. There was also evidence of possible mycoparasitism of EF on these fungi phytopathogens [47]. Similarly, it showed that *Trichoderma spirale* had been used for the control of *F. oxysporum* on *S. lycopersicum* L. cherry type in a greenhouse, presenting an increase in plant length of up to 20% after 60 dat [48]. In comparison with our results, it appeared that *Bb* 1205 shortened the expression time needed for increasing length in *S. lycopersicum* L. plants.

It could be observed that Bb 1205 impacted solely on increased enzymatic activity of chitinases and β-1,3-glucanase (II). As noted in the *in vitro* assays with *Arabidopsis thaliana* with different applications of *B. bassiana* against *Sclerotinia sclerotium* attack, a significant reduction in the lesion area of the phytopathogen was positively regulating up to 142 differentially expressed genes, which were related to jasmonic acid, salicylic acid, and ethylene. Also, the induction of 31 genes was observed, all of which are involved in cell organization, division, and transport in the plant, cell wall formation (10 genes). One of these genes is also related to the photosynthesis process [49]. Salicylic acid was expressed (9.34% at flowering), as well as jasmonic acid (shoot development by 18.9%) when *B. bassiana* was available in the

substrate. This was similar to what was reported by [46], where *Triticum durum* plants showed an increased expression of abscisic acid (10.34% at the flowering stage). Similarly, Pieterse et al. [50] mentioned that EF can be plant growth promoters (PGPF) by inducing salicylic acid, lipopolysaccharides, and iron regulatory metabolites such as pyoverdine.

Steiner [22] identified 180 *B. bassiana* metabolites that induce virulence factors (purine metabolic pathway activation), reactive oxygen and nitrogen responses; antioxidant compounds (acting on methionine and cysteine metabolic pathways), AMP-activated protein kinase expression, Janus-kinase family signaling pathways, and activators of transcription (JAK/STAT, which increase enzyme activity). They act to regulate the cell cycle, vegetative growth and strengthen the plant's immune system against pathogen infections. In addition, it shows that it can influence abiotic stress (thermotolerance), conidia quality and antioxidant activity in plants through genes such as cat2 and cat5.

In regard to the stem diameter parameter of *S. lycopersicum* L. (Table 3), a study carried out on plants of *Cucumis melo* var. *reticulatus* inoculated foliarly with *B. bassiana* showed via histological studies that a penetration and colonization capacity of EF in intercellular spaces and on the surface of the leaves of up to 40% of colonization can occur in as little as 96 h after inoculation. Endophytes and the production of secondary metabolites were reported, which prevented the spread of *Bemisia tabaci* throughout the plant [51]. Our results show similar timeframes to those of [44], where the colonization of *B. bassiana* in *S. lycopersicum* L. leaves was achieved at 14 dai with an increase in 53% in stem thickness at 25 and 30 dai. The ability of *B. bassiana* to induce positive effects on agronomic variables in plants could also be observed in the *V. vinifera* trial, where a stem growth by 6.8% was observed at 53 dai. These variations in stem increment could be due to the physiological circumstances of EF, such as a relationship between level of tissue specificity and the response of the host plant system [45]. The greenhouse experiment with *T. harzianum* applied on roots of *S. lycopersicum* L. with *F. oxysporum* showed a four-fold increase in stem diameter at 45 dat as compared to the control and to plants infected only with the pathogen, suggesting antifungal activity [52]. This is highly likely because of the support induced by the fungus, whereby the ability to absorb nitrogen and phosphorus is enhanced, likely improving the development of the plant. Thus, the host provides a carbon source to EF [53].

This behavior is observed in our results, the content of chlorophyll, diameter of the stem as well as in some morphometric variables are higher when the plants are co-inoculated, probably the development of the plant improves due to the solubilization of phosphorus and nitrogen caused by both microorganisms. It has been reported that *B. bassiana* in crop development can promote shoot and root biomass when the status of macronutrients such as nitrogen, carbon and essential microelements in plant nutrition are high [8]. On the other hand, the production of hydroxamate-type siderophores and the solubilization of phosphate by *B. bassiana* promote the development of biomass, height, and photosynthetic activity [20].

The effect of *Bb* 1205 on *S. lycopersicum* L. at the end of the experiment is shown in Table 4. These results are very similar to those obtained by [54] when inoculating seeds of *P. vulgaris* L. with *B. bassiana*, where after 14 dai an increase in the fresh weight of the root and the length of the foliage was observed (27.3% and 47.3%, respectively). Also, by applying *B. bassiana* in the soil, Culebro et al. [10] generated an increase of 13.7% in foliage length in *S. lycopersicum* L. plants infected with *Fol* race 3, as well as an increase in root length of 33.3% by the end of the experiment (25 dai). Compared with our results of the PFBs treatment, these parameters had increased by 21.6% and 64.3%, respectively. In experiments with *Capsicum annuum* L. seeds inoculated with *B. bassiana*, a 33% increase in root length was achieved at 121 dai [35] and for *P. vulgaris* L. a 12.5% increase was observed when applied to the ground [55]. The average increase in fresh root weight of the PFBf, PFBi, and PFBs treatments was as high as 41%, despite the attack by the phytopathogen. As for quality parameters, in spite of not finding any statistically significant differences, it was possible to generate an increase the quantity of flowers by 37.6% than in the control, out of which 52.8% became fruit. Sánchez et al. [56] demonstrated for the first

time that *B. bassiana* promotes the assimilation of phosphorus, potassium, iron, and zinc in *S. lycopersicum* L. plants, causing a significant increase in the biomass of the plant, in the length of its different organs, and in the possibility to decrease the pH of alkaline soils, which would imply an increase in production. In *Sorghum bicolor* L., it showed that there is also an increase in the number of leaves and in iron uptake for plant growth [36]. In *Brassica oleracea* var. *capitata* L., the ability to absorb nitrogen, tolerance to water stress, and plant health rose to 25% [57]. From the reported results, the decrease in the attack of *Fol* 17108 could be replicated on the fields when using strain *Bb* 1205. An increased production of *S. lycopersicum* L. may be related to the ability of another EF (*T. asperellum*) in reducing the incidence of the disease caused by *Fol* as much as 70.6% at 60 dat in *S. lycopersicum* L. plants [33].

4.2 Enzymatic Assay of Solanum lycopersicum Plants Inoculated with Beauveria bassiana and Infected by Fusarium oxysporum f. sp. lycopersici

Based on the results in Table 5, chitinase enzyme activity in the plant that is induced by *Bb* 1205 inoculation throughout the crop cycle is confirmed. One of the two organic and renewable polysaccharides that are abundant in the ecosystem is chitin (poly-β-1,4-N-acetylglucosamine), which is present in marine organisms, insect exoskeletons, and fungal cell walls [58]. In filamentous fungi, the wall essentially consists of 10% to 20% chitin, as well as β-1,3-and β-1,6-glucans. Also, it is part of the fungal defense against chemical compounds and physical environmental conditions [59,60]. In *Fol*, it is found as an outer layer [61]. Plants detecting and triggering defenses against fungi take advantage of pathogen-associated molecular pattern receptors (MAMPs), which are pattern recognition receptors (PRRs) and pathogenesis-related protein (PR) synthesis [62]. Despite having these defense mechanisms, the pathogenic fungus protects its chitin fibrils against detection and hydrolysis with effectors (for example, AVR and LysM), and with expression of deaminases to change chitin to chitosan [59]. Also, the exudation of proteins retains MAMPs, interrupting the downstream responses of the plant [63].

The use of *B. bassiana* is based on evidence available regarding the ability to produce extracellular lytic enzymes, chitinases and ß-1,3 glucanases to degrade the cell wall of the phytopathogenic fungus through mechanisms of mycoparasitism, competition, or local accumulation at the infection site and the surrounding tissues [64,65]. From the *in vitro* assay in which *F. oxysporum* served as a carbon source for *B. bassiana*, it was possible to verify the production of the CHIT1 gene encoding chitinase with a 2.2-fold increase, degrading and taking advantage of the pathogen as a food source as of seven dai [66]. A somewhat similar phenomenon was demonstrated when *R. solani* was used as a substrate for *B. bassiana*, reaching peak enzymatic activity at four dai (1.1 $U \cdot mL^{-1}$ of catalytic activity). However, it also showed that the enzyme is slow in being expressed at three dai, and that its activity is reduced after the peak is reached (four dai) until the end of the assay at eight dai [67].

Similarly, chitinase inhibits *F. oxysporum* by cleaving the C1 and C4 bonds of the chitin in the cell wall, causing the release of elicitors, inducing a plant response in *Linum usitatissimum* L. plants. Once infected with *F. oxysporum*, there is a decrease in chitinase genes expression (CMT1 and CMT3) by up to 50% after six h post-infection, and there is also a decrease in the ROS1 gene by 20% at 36 h [68]. Something similar occurred in *Cucumis sativus* L. plants, which produce chitinases from the GH19 family (CsChi23) in a basal manner, which have more significant activity in setting up defense and activating a rapid immune response against *F. oxysporum* f. sp. *Cucumerinum* [69]. Our results are related to the expression of chitinases in the control treatments in roots (Table 5) and leaves (Table 6) of *S. lycopersicum* L. inoculated with *Bb* 1205. Data published by [70] demonstrated the ability of *B. bassiana* to produce an endochitinase (Bb chit1) to improve virulence and interact with proteases, thus hydrolyzing the cuticle of insects and possibly also the wall of filamentous fungi. The tests carried out by [10] showed that *B. bassiana* can induce chitinase activity at two dai in *S. lycopersicum* L. infected with *Fol* race 3. Consistent results with the PFBi treatment showed a 96% increase in chitinase production during the

early stages of our experiment. The expression of chitinases induced by EF has demonstrated the ability in plants to decrease cell death and in improving resistance to *F. oxysporum* [71]. When *T. erinaceum* was used on *S. lycopersicum* L. contaminated with *Fol*, the ability to increase chitinase expression up to 3-fold at two dai in plant roots was observed (as compared with control), as demonstrated by RT-PCR. This is in addition to the increased expression of the SlWRKY31 gene by 16.5% after 24 h, where these genes (WRKY) are responsible for inducing the defense reaction in the plant, resulting in induced systemic resistance (ISR) and in causing plant growth [72].

The stimulation of *B. bassiana* colonization in plants depends on its ability to express transcription factors (such as C2H2, BBA_00971), G protein-coupled receptors (such as Pth11, BBA_03214), and signal transduction kinases that translate amino acids into the cell. surface of the cuticle of the leaf, as well as mobilization of nitrogenous nutrients within the plant; this suggests a general strategy for the development of *B. bassiana* and the production of lytic enzymes such as chitinases to protect plants from vascular pathogens [73].

It was observed that enzyme activity is lower in leaves of *S. lycopersicum* L., compared to activity observed in roots. Results derived from the use of *Trichoderma* sp. in the soil of *Fol*-infected *S. lycopersicum* L. plants showed a 1.1-fold increase in chitinase gene expression at 128 dat compared to the control [74]. This activity is much higher in our PFBs treatment, confirming that *Bb* 1205 is a biological control agent of phytopathogenic fungi. It has been reported that *B. bassiana* is capable of producing up to 20 chitinases from the GH18 family due to the need to secrete them before host arrival [75]. This could explain why a more significant activity of the enzyme in roots and leaves of *S. lycopersicum* L. was observed, especially in the PFBi treatment. Our results were lower in chitinase yields than values reported by [72], which was up to 18-fold higher in leaves. It was also proven that SlWRKY37 gene transcription could be induced up to 14% for activating plant immunity against a *Fol* attack.

On the other hand, the enzymatic activity of β-1,3-glucanase in roots is shown in Table 7. It can be seen that our data are higher reduced activity to those obtained by [72], where they used *T. erinaceum* in the *Fol* control, from which enzyme production was up to 5 times higher than for control. Furthermore, our results demonstrated the ability to induce the expression of β-1,3-glucanases by *Bb* 1205 in a higher proportion in the greenhouse, compared to those presented by [10], where activity was much lower throughout the trial. The β-glucan polysaccharides are the most abundant in the fungal wall, comprising between 50% and 60% of the dry weight. These are synthesized at the tip of the hyphae during cell growth [59,76], but in Fol it is found as an internal layer [61]. The ability of *B. bassiana* to use *F. oxysporum* as a carbon source in the production of β-1,3-glucanases has been observed in the *in vitro* test carried out by [77], where expression of 60% more Exo-β-1,3-glucanase genes was reported as of 7 dai. The results found by [78] show that the β-1,3-glucanases produced by *Bacillus* sp., show a peak activity in the middle of experimentation (15.61 U $mL^{-1} \cdot min^{-1}$), which subsequently decrease. This is probably related to the activity of using *Fol* as a carbon source. In the same manner, the use of *Pseudomona fluorescens* in roots of *S. lycopersicum* L. displayed (13 dai) a 2.2-fold increase in enzymatic activity promoting an ISR in the plants at the end of the experiment, which resulted in a reduction of the severity of of disease and in the optimization of the other enzymes, which could be related to the phenylpropanoid pathway [79]. The PFBf treatment's effects at the end of the trial demonstrated a much more significant increase of up to 7.8-fold, according to the data mentioned above. The accumulation and expression of the enzyme are affected by the penetration site of *Fol*, which determines the release of oligosaccharides, and will be inducing responses for the synthesis of lignification and phytoalexins in the plant [80].

Results in Table 8 demonstrated that *Bb* 1205 is a fungus with a similar potential to that of *T. erinaceum* against *Fol* attack on tomato plants, as *T. erinaceum* exhibits a 4.5-fold increase in the induction of β-1,3-glucanases in leaves [72]. This is in close proximity to our results. In addition, *Cucumerinum*, β-1,3-glucanase activity was observed all along the experimentation (2.3, 3.5, 1.5, and 1.5 times more than the

control), similar to levels expressed in our experiment [71]. From the above, it was confirmed that β-1,3-glucanases can be found in chloroplasts before infection by a pathogen, after which they are transferred to the vacuole and finally to the wall, in order to control the infection. Therefore, the induction by some external agent is essential in triggering the active defense of the plant [81]. For this reason, amplification of the enzyme expression was probably achieved in the PFBf treatment (Table 8) in our *in vivo* assay. It has become evident that entomopathogenic fungi such as Trichoderma can induce the formation of phenolic compounds and reactive oxygen species in the plant, which improve the mechanical resistance in the wall, thus contributing in inhibiting the development of phytopathogenic fungi [82]. Also, the control of *Fol* by *Bacillus* spp. on tomato plants under greenhouse conditions generated siderophores, which decreased disease incidence (up to 55%), plant growth (44%), and β-1,3-glucanase activity by up to a factor of 1.4 [83]. Likewise, the production of jasmonic acid by *Bacillus* sp. SJ-5 with the antifungal activity of *F. oxysporum* in *Glycine max* L. Merrill of 99% has been reported [84].

Our results show that the activity of the enzymes chitinase (Tables 5 and 6) and glucanase (Tables 7 and 8) increase in tissues that were not inoculated (root). This increase could be occurring because *B. bassiana* is capable of colonizing and moving systemically to different tissues, regardless of the method of inoculation. as well as the tissue where it is inoculated, this behavior has been reported in other species such as *Helicoverpa armigera*, *Vitis vinifera*, *Arabidopsis thaliana* and *Phaseolus vulgaris* L. [40,45,49,55].

5 Conclusions

In this study, death was observed in 60% of the control plants that were contaminated with *Fusarium oxysporum*, with which the severity of the damage by this pathogen was confirmed. The entomopathogenic fungus *Beauveria bassiana* 1205 presented endophytism in roots and leaves of *Solanum lycopersicum* L. without affecting the development of the plant. The presence of *Beauveria bassiana* 1205 on *S. lycopersicum* L. infected with *Fusarium oxysporum* f. sp. *lycopersici* 17108 is responsible for increasing the greenness index and the height of the aerial part when applied to the soil. Application to the soil also caused improvements in the quality variables. Stem diameter proved to increase when application was done on the leaves. Regarding the production of chitinases in the root part and leaves of *S. lycopersicum* L. infected with *Fusarium oxysporum* f. sp. *lycopersici* 17108, the best treatment was when applied by injection into the stem (presenting higher specific activity of chitinases in roots). The specific activity of β-1,3-glucanase was higher in roots when used on the leaves, and enzyme activity in leaves occurred when injected into the stem. In short, *Beauveria bassiana* 1205 stimulated the biological control on *Fusarium oxysporum* f. sp. *lycopersici* 17108, inducing and enhancing an active defense of the plants and allowing maturity of the fruits to occur. Finally, the fungistatic potential of *Beauveria bassiana* 1205 in the expression of lytic enzymes for the control of *Fusarium oxysporum* f. sp. *lycopersici* and its possible incorporation into integrated disease management for sustainable agriculture was confirmed.

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