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ENDOPHYTIC FUNGUS *BEAUVERIA BASSIANA* INDUCES ANTIOXIDANT ENZYME ACTIVITIES AND ENHANCES THE GROWTH OF *RHIZOCTONIA SOLANI*-INFECTED POTATO PLANTS

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The physiological and biochemical changes in potato plants colonized by the endophytic form of the entomopathogenic fungus *Beauveria bassiana* (Ascomycota: Hypocreales) were analyzed under biotic stress caused by infection with the phytopathogen *Rhizoctonia solani* (Basidiomycetes: Ceratobasidiales). A high level of plant colonization by entomopathogenic endophyte was observed, and infection with *R. solani* did not have a significant effect on the degree of plant colonization. The colonization of potatoes by *B. bassiana* compensated for the growth retardation of *Rhizoctonia*-infected plants, especially the roots, and significantly reduced *Rhizoctonia* damage to stems and developing stolons. Inoculation of plants with both fungi resulted in an increase in antioxidant activity, with *B. bassiana* contributing to this effect. There were significant increases in the activity of the following antioxidant enzymes: peroxidases, superoxide dismutases, polyphenol oxidases and phenylalanine-ammonia-lyase. *B. bassiana* triggered the host plant's defense system, namely a complex of antioxidant enzymes, to overcome biotic stress caused by *R. solani*. Therefore, *B. bassiana* is a promising modulator of plant defense metabolism against phytopathogens.

Keywords: entomopathogenic fungus, fungal phytopathogen, oxidative stress, antioxidant enzymes, induced resistance, plant protection

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Introduction

Entomopathogenic fungi of the genus *Beauveria* are cosmopolitan and widespread throughout the world. They traditionally attract attention due to their ability to cause mycoses in arthropods from various taxonomic groups (Zimmerman, 2007). Many commercial mycoinsecticides have been developed using *Beauveria bassiana* s.l. to control different types of arthropods in agriculture, forestry and veterinary settings (Mascarin, Jaronski, 2016). In addition to their insecticidal properties, researchers are interested in the endophytic ability of fungi of this genus, i.e. their ability to colonize plant tissues asymptotically. Unlike other endophytic entomopathogenic fungi, which are mainly associated with the rhizosphere and roots, *Beauveria* can colonize plants systemically and is often isolated from the roots, stems, and leaves (Behie et al., 2015). A lot of experimental data demonstrates the ability of *Beauveria* spp. to endophytically colonize more than a hundred plant species from various families (Poaceae, Fabaceae, Solanaceae, Brassicaceae, Cucurbitaceae, Rosaceae, Amaryllidaceae, etc.), including economically important ones (reviewed by McKinnon et al., 2016; Vega, 2018; Bamisile et al., 2018), one of which is the potato (Tomilova et al., 2021; Tyurin et al., 2021). It has been noted that plants associated with *Beauveria* grow more actively and tolerate abiotic and biotic stresses more easily. Artificial inoculation with *B. bassiana* has a positive effect on the growth of various crops, including cotton (Lopez, Sword, 2015), beans (Jaber, Enkerli, 2016), corn (Tall, Meyling, 2018; Liu et al., 2022), garlic (Espinoza et al., 2019),

cucumber (Shalan et al., 2021), grapevine (Mantzoukas et al., 2021) and wheat (Gonzalez-Guzman et al., 2021). The growth-stimulating effect of the endophyte *B. bassiana* has also been observed in plants of the Solanaceae family. It has been found that inoculation with *B. bassiana* increases the growth of hot and sweet peppers (Saragih et al., 2019; Tomilova et al., 2022; Wilberts et al., 2023), tomatoes (Wei et al., 2020; Sui et al., 2023), and potatoes (Tomilova et al., 2023).

Increased drought tolerance as a result of endophytic colonization by *B. bassiana* has been demonstrated on cabbage (Dara et al., 2017), corn (Kuzhuppillymyal-Prabhakarankuttu et al., 2020), onions (Gana et al., 2022), as well as seedlings of oak (Ferus et al., 2019) and tomato (Guo et al., 2024). The mitigation of the negative effects of salt stress during endophytic colonization by *B. bassiana* was established in rice plants (Akter et al., 2023). Previously, we studied the effects of *B. bassiana* (strain Sar-31) inoculation on potato growth and physiological parameters under conditions of chloride-associated salinity. Our results showed that the fungal association reduced the effects of salt stress on potato tissues by increasing the activity of antioxidant enzymes and promoting the accumulation of free proline (Tomilova et al., 2023).

Plants colonized by the endophytic fungus *B. bassiana* cope better with biotic stresses. It has been reported that the endophytic relationship between plants and *B. bassiana* has an adverse effect on crop pests, both directly and indirectly (reviewed by Vidal, Jaber, 2015; and Mantzoukas, Eliopoulos,

2020). For instance, Pourtaghi et al. (2020) observed a significant increase in mortality among the nymphs and adults of the greenhouse whitefly *Trialeurodes vaporariorum* which developed on tomato plants, containing *B. bassiana* as an endophyte. Conversely, tomato leaves which were not inoculated with *B. bassiana* were preferred by the whitefly *Bemisia tabaci* compared to the inoculated ones (Wei et al., 2020). Probably, this was due to the ability of *B. bassiana* to modulate the production of secondary metabolites (e.g., alkaloids and flavonoids) in tomatoes, which suppress the survival and fertility of *B. tabaci*, as was demonstrated by Wang et al. in their 2023 study. Moreover, feeding on leaves colonized by *B. bassiana* has a negative effect on the growth, development, and survival of *Helicoverpa armigera* (Toffa et al., 2021), *Tuta absoluta* (Allegrucci et al., 2017; Silva et al., 2020; Geremew et al., 2024), and *Phthorimaea operculella* (Zhang et al., 2023).

A number of studies demonstrate the ability of various species of endophytic entomopathogenic fungi to suppress the development of phytopathogens and reduce the severity of plant diseases (reviewed by Bamisile et al., 2018; Jaber, Ownley, 2018; Vega, 2018). In particular, it has been demonstrated that the colonization of plants by *Beauveria* fungi inhibits the development of necrotrophic pathogens, including *Pythium myriotylum* and *Rhizoctonia solani* (Ownley et al. 2008), *Fusarium* spp. (Jaber, Alananbeh, 2018), *Verticillium dahliae* (Miranda-Fuentes et al., 2020), *Sclerotinia sclerotiorum* (Raad et al., 2019), *Botrytis cinerea* (Barra-Bucarei et al., 2020; Gupta et al., 2022; Sui et al., 2023; Proietti et al., 2023). Our previous studies showed that treating potato planting material with *B. bassiana* reduces its infection by *R. solani* (Tomilova et al., 2020). It also protects feed beans against root rot and leaf

spot caused by a complex of phytopathogenic species from the genera *Fusarium* and *Alternaria* (Ashmarina et al., 2021).

Moreover, inoculation of plants with *B. bassiana* reduces damage caused by hemibiotrophic and biotrophic pathogens, including *Plasmopara viticola* (Jaber, 2015), *Phytophthora infestans* (Maksimov et al., 2015), *Oidium neolycopersici* and *Leveillula taurica* (Gupta et al., 2022), *Podosphaera xanthii* (Iida et al., 2023), *Zucchini yellow mosaic virus* (Jaber, Salem, 2014), and *Cucumber mosaic virus* (Shaalán et al., 2022).

Researchers associate the decreased disease rate in plants colonized by endophytes with direct effects, such as competition, antibiosis, and mycoparasitism, as well as indirect effects, such as the induction of plant immune responses. Nevertheless, most of the mechanisms associated with the resistance of plants colonized by endophytic fungi to phytopathogens are not well understood. Since both endophytes and phytopathogens can be fungal, many questions arise about how plants recognize them and how plants develop resistance to phytopathogens.

Previously, we carried out a series of laboratory and field experiments to study the interactions between the endophytic fungus *B. bassiana* and potato plants. This study continued the investigation of this experimental model, focusing on how potatoes respond to colonization by fungal endophytes and/or phytopathogens. We selected *R. solani*, the pathogen that causes black scab in potatoes, as the phytopathogen, since this disease is widespread and dangerous in regions where potatoes are grown (Shaldyayeva, 1990; Tomilova et al., 2020). The aim of this work was to evaluate the impact of the endophytic fungus *B. bassiana* on the growth, oxidative stress, and antioxidant activity of enzymes in potato plants infected with the black scurf pathogen *R. solani*.

Materials and Methods

The experiment used “Red Scarlet” potato tubers (elite reproduction) obtained from “Priobskoe” ZAO in the Novosibirsk region. Before sowing, the potato tubers were washed and dried, the healthy ones (without mechanical damage or signs of disease) were selected and sorted by size (diameter $\approx$ 3 cm). After the sprouts appeared (3–5 mm), the tubers were planted one by one in an isolated 1-litre pot and considered as an independent replication (20 plants per variant). Potato plants were grown at a temperature of 20–22 °C with a long photoperiod (LD 16:8), in the universal unsterilized soil substrate “Terra Vita”. The soil substrate was preliminarily analyzed for the absence of conidia of entomopathogenic fungi and *R. solani* propagules by sowing an aqueous suspension on artificial nutrient media with the addition of a mixture of antibiotics (Tomilova et al., 2020). Watering was carried out twice a week using settled tap water. The experiment included 4 variants: 1) control – without soil inoculation with fungi; 2) soil inoculation with a suspension of *B. bassiana* conidia; 3) soil inoculation with *R. solani* sclerotia; 4) combined soil inoculation with *B. bassiana* and *R. solani*. The duration of the experiment was 30 days post inoculation with fungi (dpi). The experiment was conducted twice.

A strain of the entomopathogenic fungus *B. bassiana* (Sar-31) from the collection of microorganisms at the Institute of Systematics and Ecology of Animals (the Siberian Branch of the Russian Academy of Sciences) was used for inoculation of plants. The species was identified on the basis of a partial

sequence of translation elongation factor (EF-1 α), GenBank accession number MZ564259. This strain has high insecticidal activity (Kryukov et al., 2017), is capable of actively colonizing potatoes (Tomilova et al., 2023), and also shows antagonistic properties towards several phytopathogens (Ashmarina et al., 2021). The fungal culture was incubated at 26 °C for 10 days in the dark on Sabouraud dextrose agar with the addition of 0.25 % yeast extract. A Tween 80 (0.03 %) aqueous solution was used to prepare the conidial suspension, and the concentration of conidia was counted using a haemocytometer. The plants were inoculated by applying the conidial suspension to the root growth area, three days after planting (titration of 5×10^7 spores/ml, volume – 10 ml/plant).

The phytopathogen used for infection was strain *R. solani* AG-3 (anastomotic group 3), originally isolated from potato tubers infected with sclerotia (the strain was kindly provided for research by professor E.M. Shaldyayeva from the collection of microorganisms of the Department of Plant Protection of Novosibirsk State Agrarian University). An artificial infectious background was created using an original method (Shaldyayeva, 1990) with a background density three times higher than the biological threshold of harmfulness. To prepare the inoculum, the *R. solani* strain was cultivated in Petri dishes for 7 days on potato dextrose agar (PDA) with the addition of streptomycin (to suppress bacterial microbiota). Then, 100 g of millet and 10 ml of water were placed in a 0.5-litre flask and autoclaved at 1 atmosphere for one hour. The

inoculation of the millet was carried out using agar discs of the *R. solani* culture (incubation – for 18 days at a temperature of 24°C). To ensure the even distribution of the fungal mass, the millet in the flasks was periodically shaken. The inoculated millet was transferred to sterile paper filter bags and dried at room temperature. The dried sclerotia of *R. solani* (2 sclerotia/container) were introduced into the root zone simultaneously with the inoculation of *B. bassiana*.

The load and method of inoculation with fungi were experimentally selected based on preliminary experiments, allowing for a high proportion of *B. bassiana* colonization of plants and the development of rhizoctonia symptoms.

At the end of the experiment, an evaluation of the growth parameters of the plants (height, fresh and dry weight of above-ground and below-ground parts) was carried out, as well as the colonization of potato plants by *B. bassiana* and *R. solani*, and the incidence of Rhizoctonia disease in stems and stolons. All indicators, except for dry weight, were recorded from each plant (20 replications per variant). The dry weight was determined after drying at 70°C to a constant weight (pooled sample from 5 plants, 4 replications per variant).

The colonization of plants by fungi was evaluated by plant explants plating onto artificial nutrient media with the addition of a mixture of antibiotics (Tomilova et al., 2020). From each plant (underground part – stem, root) 6 explants were selected. Sterilisation of plant fragments was carried out according to the method described by Posada et al. (2007). If growth of the studied fungi was recorded in one or more fragments, it was considered colonized. Identification of fungal colonies grown on plant explants was carried out based on light microscopy. Quality control of surface sterilisation was performed using the imprint method (McKinnon et al., 2016). Samples that showed fungal growth in their imprints were excluded from the analysis.

The development of Rhizoctonia disease symptoms was estimated using the widely accepted methodology based on the 5-point scale of Frank (Frank et al., 1976). The methodology is detailed in our paper (Tomilova et al., 2020).

The biochemical parameters of plants: pigment composition, the amount of malondialdehyde (MDA), as well as the activity of antioxidant enzymes in potato leaves were estimated using spectrophotometric methods (with 20 replications per variant). At the end of the experiment (30 dpi) the pigment composition

was measured spectrophotometrically in ethyl alcohol extracts using the Lichtenthaler method (1987). Optical density of a leaf ethanol extract was measured at wavelengths of 470, 664, 648, and 720 nm. The amount of MDA was estimated spectrophotometrically at a wavelength of 532 and 600 nm using a modified method by Buege and Aust (1978), with the 2-thiobarbituric acid as the substrate. Thiobarbituric acid reactive substances were quantified in 100 mg of the plant material. The assessments were carried out in two stages after 14 and 30 days.

The activity of antioxidant enzymes such as: peroxidases (POX), polyphenol oxidases (PPO), superoxide dismutases (SOD), and L-phenylalanine ammonia lyase (PAL) was estimated in potato leaves as indicators of the plant immune response. Assessments were also carried out in two stages, at 14 and 30 dpi. Samples were prepared according to the method by Wang et al. (2008). Enzyme activity was estimated spectrophotometrically. The total activity of peroxidases was measured using the method of Nicell and Wright (1997) with modifications at a wavelength of 510 nm, with the 4-aminoantipyrine as the substrate. The activity of superoxide dismutases was determined at a wavelength of 560 nm by the rate of reduction of nitro blue tetrazolium (Beauchamp, Fridovich, 1971). The activity of polyphenol oxidases was assessed at a wavelength of 490 nm according the method of Holzapfel et al. (2010) with the 4 mM L-DOPA as the substrate. The activity of L-phenylalanine ammonia-lyase was measured at a wavelength of 290 nm based on the formation of trans-cinnamic acid, using 0.02 M L-phenylalanine as the substrate (Assis et al., 2001). Enzyme activity in the incubation mixture was estimated in units of absorption density (ΔA) per minute, per 1 mg of protein in the sample. The protein concentration in plant tissues was determined by the method of Bradford (1976), for the plotting of a calibration curve used bovine serum albumin.

Data analysis was performed using Statistica 8 (Stat Soft, Inc., USA). The normality of the data distribution was checked by the Shapiro-Wilk W test. Normally distributed data of the growth and biochemical parameters were analyzed by two-way ANOVA followed by Fisher's post hoc LSD test. Student's *t*-test was used to evaluate Rhizoctonia lesions on stems and stolons. Fisher's exact test was used to assess differences in plant colonization by fungi.

Results

The colonization of plants by endophyte and phytopathogen (30 dpi) reached high values, with separate inoculation resulting in 85% for *B. bassiana* and 95% for *R. solani*. However, when the fungi were applied together, a decrease in fungal colonization was detected (1.3 times for *B. bassiana* and 2.4 times for *R. solani* compared to mono-inoculation), with the level of colonization by the phytopathogen decreasing at a statistically significant level (Fisher's exact test, $p = 0.0002$; Fig. 1).

The artificially created infection by *R. solani* over a 30-day period resulted in the development of clear symptoms of damage to the underground parts of potato plants (Fig. 2). No signs of disease were detected in the control variant or when inoculated with *B. bassiana* in its pure form. Using *R. solani* and *B. bassiana* together resulted in a significant reduction in Rhizoctonia damage to stems (Student's *t*-test, $p = 0.038$) and

developing stolons ($p = 0.016$) compared to mono-infection (Fig. 3).

When assessing potato growth parameters (30 dpi), a significant reduction in root length was observed in both variants where *R. solani* infection was present (Fisher's LSD test, $p \leq 0.030$ compared with the control and *B. bassiana* treatment only; Fig. 4A). The fresh weight of the plant roots grown in the presence of *R. solani* also decreased significantly compared to all other experimental variants ($p \leq 0.017$; Fig. 4B). Compared to the control, the *R. solani* variant and the combined fungi variant, the inoculation of *B. bassiana* resulted in a significant increase in total plant length ($p \leq 0.047$). Dry weight measurements further demonstrated the significant impact of fungal treatment on plant growth. Both total dry biomass and root dry weight in *B. bassiana*-inoculated plants

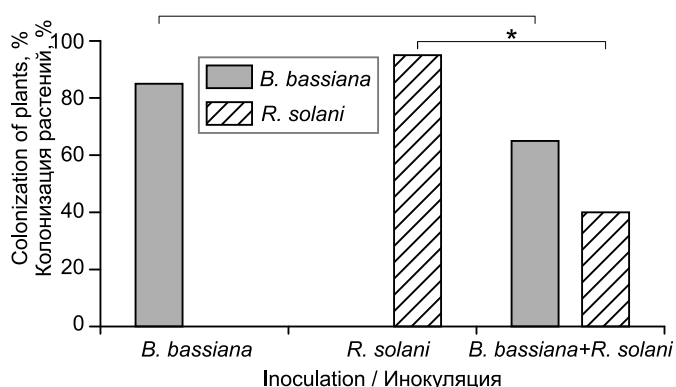


Figure 1. The proportion of plants colonized by fungi (30 dpi). Asterisks indicate significant differences in the level of colonization by one species under mono- and co-inoculation (Fisher's exact test, $p < 0.05$)

Рисунок 1. Доля колонизированных грибами растений на 30 сут после инокуляции. Звездочки указывают наличие существенных различий в уровне колонизации одним видом при моно- и совместном внесении (Точный тест Фишера, $p < 0.05$)

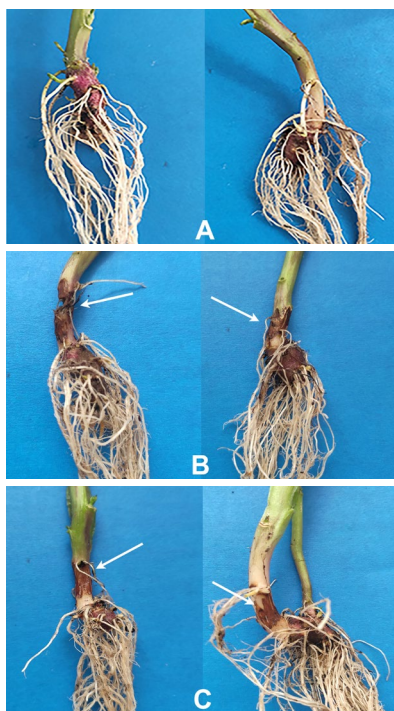


Figure 2. Development of Rhizoctonia disease symptoms on the underground part of potato shoots (30 dpi): healthy plants obtained in the Control and *Beauveria bassiana* variants (A); plants affected by 2–5 points, obtained in the *Rhizoctonia solani* variant (B); plants affected by 1–2 points, obtained in the *B. bassiana* + *R. solani* variant (C). The arrows indicate the areas of stem rhizoctonia damage

Рисунок 2. Развитие симптомов ризиктониоза на подземной части побегов картофеля на 30 сут после грибной инокуляции: здоровые растения, полученные в вариантах Контроль и *Beauveria bassiana* (A); пораженные растения на 2–5 баллов, полученные в варианте *Rhizoctonia solani* (B); пораженные растения на 1–2 балла, полученные в варианте *B. bassiana* + *R. solani* (C). Стрелки указывают на участки поражения стеблей ризиктониозом

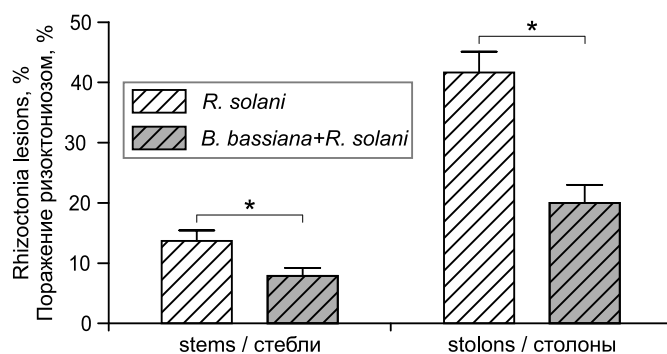


Figure 3. The effect of endophytic colonization by *Beauveria bassiana* on the level of Rhizoctonia damage to potato stems and stolons (30 dpi). The asterisks indicate significant differences between the variants; comparisons were made by organs (Student's t -test, $p < 0.05$)

Рисунок 3. Влияние эндофитной колонизации *Beauveria bassiana* на уровень поражения ризиктониозом стеблей и столонов картофеля, через 30 сут после инокуляции грибами. Звездочки указывают на существенные различия между вариантами, сравнение по органам (t -критерий Стьюдента, $p < 0.05$)

were substantially higher than in control plants ($p \leq 0.002$) and in *R. solani*-infected plants ($p < 0.001$; Fig. 4C).

A statistically significant influence of the *R. solani* factor was established for shoot length, root length, root wet weight and root dry mass (two-factor ANOVA, $F_{1,74} \geq 6.091$, $p \leq 0.016$; $F_{1,74} = 9.486$, $p = 0.003$; $F_{1,12} = 18.744$, $p = 0.001$, respectively). A significant influence of the *B. bassiana* factor was established for total plant length ($F_{1,74} = 5.738$, $p = 0.019$), root wet weight and whole plant wet weight ($F_{1,74} \geq 5.992$, $p \leq 0.017$), as well as root dry weight and total dry weight ($F_{1,12} \geq 20.643$, $p \leq 0.0007$). Thus, introducing fungi significantly affected growth parameters, particularly root growth. The development of plants was inhibited by infection with *R. solani*, while active growth of potatoes was promoted by inoculation with *B. bassiana*, largely compensating for the negative effects of *R. solani* when the fungi were applied together.

A downward trend in the total content of photosynthetic pigments (chlorophyll a, chlorophyll b, and carotenoids) as well as a decrease in total chlorophyll content, was observed in potato plants infected with *R. solani* compared to the control and *B. bassiana* variants (Fisher's LSD test, $p \geq 0.080$; Fig. 5A). The chlorophyll a/b ratio decreased significantly in *R. solani*-infected plants relative to those treated solely with *B. bassiana* ($p = 0.035$). Similarly, the chlorophyll/carotenoids ratio was significantly lower than in plants treated with *B. bassiana* alone or in combination with *R. solani* ($p = 0.045$; Fig. 5B). Therefore, the *R. solani* factor was found to have a statistically significant effect on the ratio of chlorophyll a/b (two-factor ANOVA, $F_{1,74} = 7.820$, $p = 0.007$).

At the initial stage of plant colonization with *B. bassiana* (14 dpi), a significant increase in MDA level was observed compared to the other variants (Fisher's LSD test, $p \leq 0.016$). However, by the end of the experiment (30 dpi), this parameter had decreased to reach the level of the control ($p \leq 0.028$; Fig. 6). On day 30, a significant decrease in MDA level was also observed with the combined inoculation of both fungi ($p = 0.014$ compared to inoculation of *B. bassiana* alone), being marginally significant ($p = 0.052$) compared to control. Both factors had a statistically significant effect on the MDA

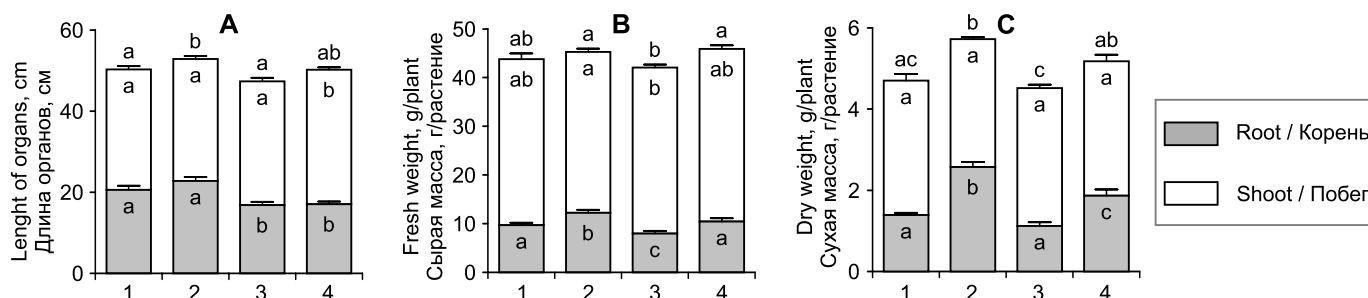


Figure 4. Effect of endophytic colonization by *Beauveria bassiana* and infection with of *Rhizoctonia solani* on the length of potato axial organs (A), wet biomass (B), and dry biomass (C) (30 dpi): 1 – Control; 2 – *B. bassiana*; 3 – *R. solani*; 4 – *B. bassiana* + *R. solani*. Different letters indicate significant differences between variants (Fisher's LSD test, $p < 0.05$).

Letters on a grey background indicate differences in roots, on a white background indicate differences in shoots and above columns indicate differences in the estimated indicators in the plant as a whole

Рисунок 4. Влияние эндофитной колонизации *Beauveria bassiana* и инфицирования *Rhizoctonia solani* на длину осевых органов (A), биомассу сырую (B) и сухую (C) картофеля (30 сут после инокуляции грибами): 1 – Контроль; 2 – *B. bassiana*; 3 – *R. solani*; 4 – *B. bassiana* + *R. solani*. Различные буквы указывают на существенные различия между вариантами (НСР Фишера, $p < 0.05$). Буквы в столбцах на сером фоне указывают на различия в оцениваемых показателях по корням, на белом фоне – по побегам, над столбцами – по растению в целом

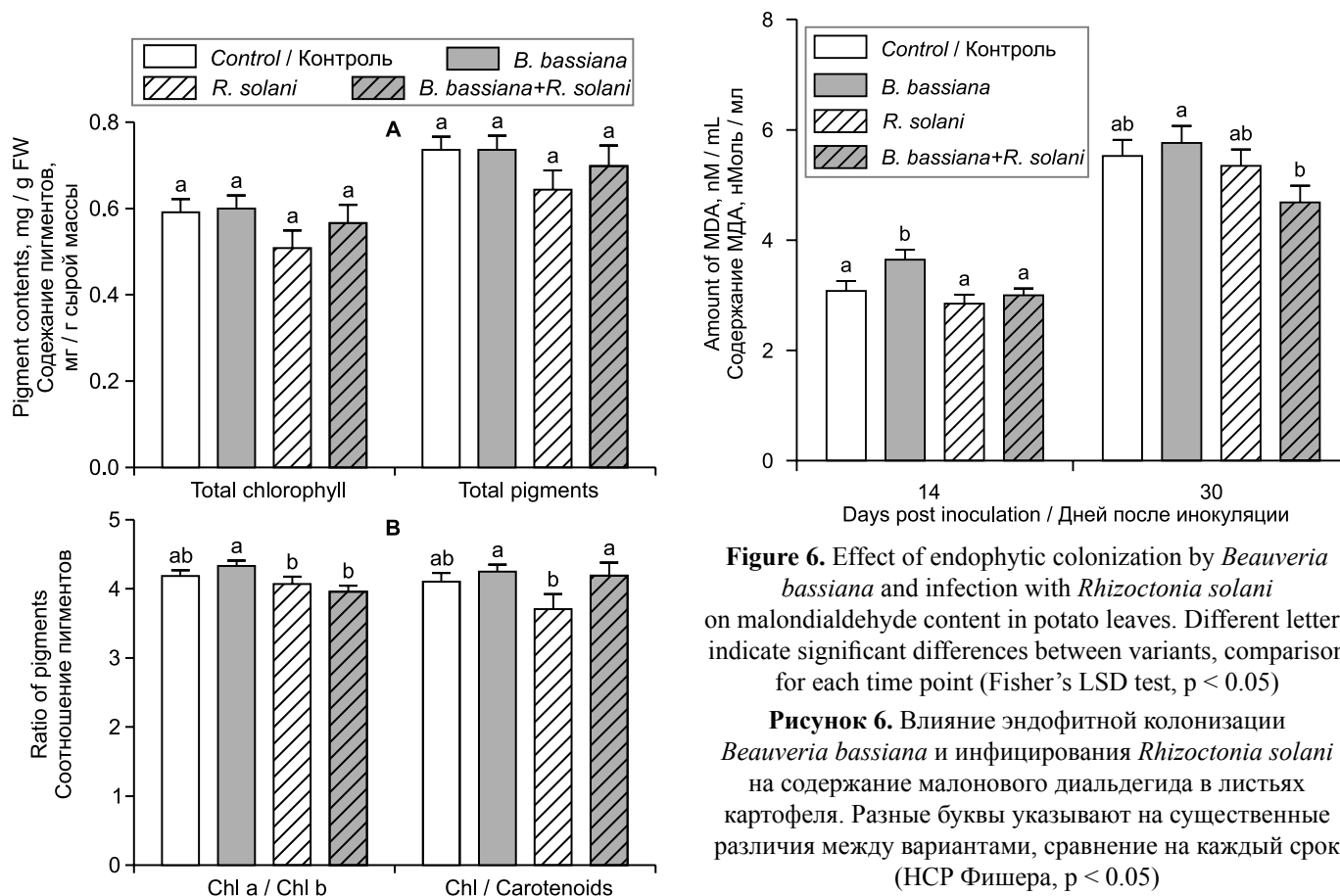


Figure 5. Effect of endophytic colonization by *Beauveria bassiana* and infection with *Rhizoctonia solani* on the content of photosynthetic pigments in potato plants (A) and their ratio (B) (30 dpi). Different letters indicate significant differences between variants (Fisher's LSD test, $p < 0.05$)

Рисунок 5. Влияние эндофитной колонизации *Beauveria bassiana* и инфицирования *Rhizoctonia solani* на содержание фотосинтетических пигментов растений картофеля (A) и их соотношение (B) (30 сут после инокуляции грибами). Различные буквы указывают на существенные различия между вариантами (НСР Фишера, $p < 0.05$)

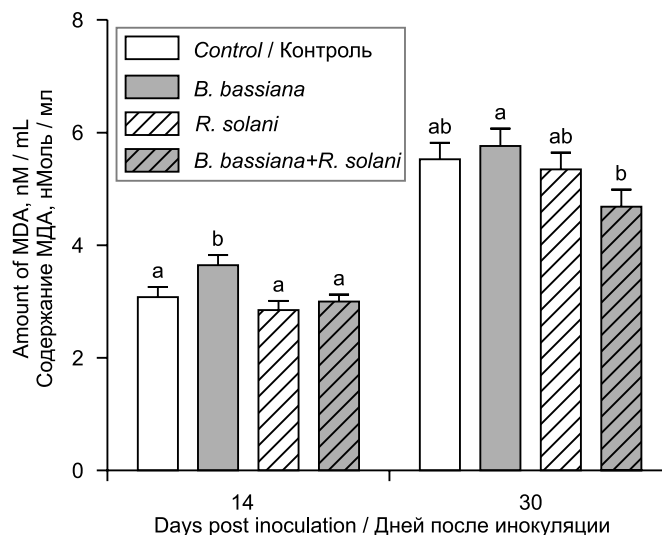


Figure 6. Effect of endophytic colonization by *Beauveria bassiana* and infection with *Rhizoctonia solani* on malondialdehyde content in potato leaves. Different letters indicate significant differences between variants, comparison for each time point (Fisher's LSD test, $p < 0.05$)

Рисунок 6. Влияние эндофитной колонизации *Beauveria bassiana* и инфицирования *Rhizoctonia solani* на содержание малонового диальдегида в листьях картофеля. Разные буквы указывают на существенные различия между вариантами, сравнение на каждый срок (НСР Фишера, $p < 0.05$)

level at the first measurement (14 dpi): *B. bassiana* (two-factor ANOVA, $F_{1,74} = 4.138$, $p = 0.046$) and *R. solani* ($F_{1,74} = 9.323$, $p = 0.003$). By the end of the experiment, the influence of the *R. solani* factor was significant ($F_{1,74} = 9.063$, $p = 0.006$).

A significant change in enzymatic activity was detected in potato leaves in both the first and second measurements (Fig. 7A–D). The maximum increase in antioxidant enzyme activity was observed as a result of the combined application of fungi. However, while a significant increase in activity for the three enzymes studied (POX, SOD and PPO) was noted in the first period (14 dpi), with increases of 1.5–1.6 times compared to the control (Fisher's LSD test, $p \leq 0.004$). In

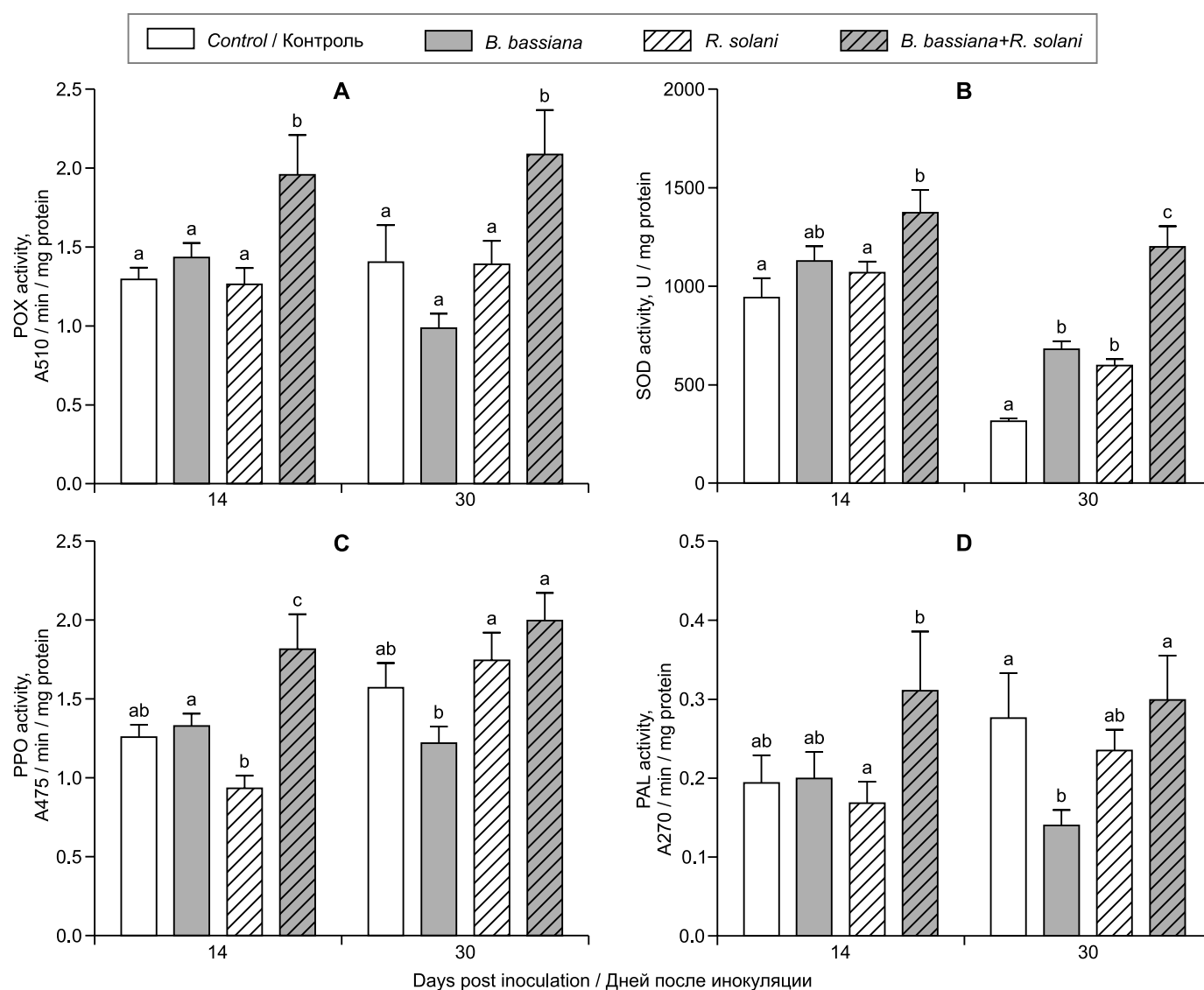


Figure 7. The impact of endophytic colonization by *Beauveria bassiana* and infection with *Rhizoctonia solani* on enzyme activity in potato leaves: peroxidase, POX (A); superoxide dismutase, SOD (B); polyphenol oxidase, PPO (C) and L-phenylalanine-ammonium-lyase, PAL (D). Different letters indicate significant differences between the variants compared at each time point (Fisher's LSD test, $p < 0.05$)

Рисунок 7. Влияние эндофитной колонизации *Beauveria bassiana* и инфицирования *Rhizoctonia solani* на ферментативную активность в листьях картофеля: пероксидаз, POX (A); супероксиддисмутаза, SOD (B); полифенолоксидаз, PPO (C) и L-фенилаланин-аммоний-лиазы, PAL (D). Разные буквы указывают на существенные различия между вариантами, сравниваемыми на каждый срок (НСР Фишера, $p < 0.05$)

the second period (30 dpi), this was only observed for POX and SOD, with an increase of 1.5–3.8 times compared to the control ($p \leq 0.036$). The mono-inoculation of fungi alone led to a significant increase in SOD activity after 30 dpi, with growth observed when the endophyte and phytopathogen were both present. It should also be noted that the introduction of *B. bassiana* was accompanied by a slight increase in enzyme activity at the first measurement and a decrease at the second one (with the exception of SOD).

The inoculation of plants with *B. bassiana* had a reliable

effect on the antioxidant enzyme system of potato plants, with the effect being maximal for POX, SOD and PPO at 14 dpi (two-factor ANOVA, $F_{1,74} \geq 6.702$, $p \leq 0.012$). The effect of *R. solani* infection (POX, SOD and PPO – $F_{1,74} \geq 6.702$, $p \leq 0.016$) and the interaction between the two factors (POX, SOD and PAL – $F_{1,74} \geq 4.500$, $p \leq 0.037$) were more pronounced after 30 dpi. Of the enzymes studied, SOD demonstrated the greatest reactivity, with its activity influenced by both factors, i.e. the introduction of *B. bassiana* and *R. solani*, resulting in a significant effect at both time points.

Discussion

In this study, we investigated the effect of endophytic colonization of *B. bassiana* on the plant growth promotion and development of resistance to the black scab pathogen *R. solani* in potatoes. It has been established that colonization by the entomopathogenic fungus *B. bassiana* stimulates

potato growth. A statistically significant increase in the length and mass of plants colonized by the endophyte has been demonstrated. These results align with those of previous studies on Solanaceae plants (Saragih et al., 2019; Tomilova et al., 2022; Wilberts et al., 2023). In particular, inoculation

with *B. bassiana* led to a significant increase in the root length of tomato seedlings and the height of potted plants (Sui et al., 2023), as well as growth stimulation chili pepper seedlings and plants (Saragih et al., 2019). In our previous work, we observed an increase in the height of inoculated plants and an earlier onset of the sweet pepper budding stage under the influence of *B. bassiana* (Tomilova et al., 2022), as well as a significant increase in the number of stolons in potatoes (Tomilova et al., 2023).

Inoculation with *B. bassiana* can compensate for growth retardation in plants that have been artificially infected with phytopathogens or grown in an environment with an artificial phytopathogenic load. For instance, a notable increase in tomato yield was observed in a field experiment in which tomatoes were treated with spores of *B. cinerea* and *B. bassiana* (Sui et al., 2023). In our experiment, plants infected with *R. solani* and treated with endophytes exhibited similar length and weight values compared to the control group. The development of rhizoctoniosis in the absence of the endophytes was accompanied by a significant growth delay and decreased photosynthetic pigment content of marginal significance. The combined application of the fungi led to an equalisation of chlorophyll levels, which further contributed to the activation of growth processes.

In earlier *in vitro* experiments on the co-cultivation of the entomopathogenic fungi *B. bassiana* and *Metarhizium robertsii* with *R. solani*, we demonstrated their antagonistic interactions (Tomilova et al., 2020). Both entomopathogenic fungi were found to be capable of enveloping and degrading aerial mycelium, as well as delaying the formation of *R. solani* sclerotia. Subsequently, Deb et al. (2023) established mycoparasitism of *B. bassiana*, accompanied by the deformation, plasmolysis, and death of *R. solani* cells. It was also noted that the formation of phytopathogenic sclerotia was either delayed or inhibited in the presence of volatile compounds released by *B. bassiana* mycelium during its growth (Deb et al., 2023). Based on these findings, we hypothesized that the fungal strains selected for our study would actively compete to establish trophic relationships with potato plants. This hypothesis was supported by colonization data, which revealed that while mono-inoculation resulted in high colonization rates, co-inoculation significantly reduced plant colonization – particularly by the phytopathogen (2.4-fold decrease). We observed a significant reduction of Rhizoctonia infection of potato stems and forming stolons through the combined application of fungal inoculants. These results align with existing literature on the growth suppression of *R. solani* by *B. bassiana* in laboratory and greenhouse conditions on various crops, including cotton, tomato, and cucumber (Griffin et al., 2005; Ownley et al., 2008; Azadi et al., 2016; Rhouma et al., 2024). Notably, a significant reduction in Rhizoctonia disease development on plants colonized by *B. bassiana* was also observed under field conditions. In particular, combined treatments of rice with *B. bassiana* (seed treatment, seedling root dipping, and foliar spraying) reduced the incidence and severity of the sheath blight disease caused by *R. solani* by 69% and 61%, respectively (Deb et al., 2023). Our previous studies showed that treatment of seed tubers with *B. bassiana* conidia prior to planting provides protection against Rhizoctonia disease, even at high infection levels. Specifically, this treatment reduced the development of disease on potato

plant stems by 3.61-fold and on stolons by 2.2-fold, and also decreasing the formation of *R. solani* sclerotia on the surface of new crop tubers (Tomilova et al., 2020).

However, most authors argue that the disease-reducing effect is due not only to antimicrobial properties of *B. bassiana* against *R. solani*, but also to its ability to activate the plant's defense mechanisms. We investigated the level of MDA, which indicates the presence of oxidative stress, as well as the activity of antioxidant enzymes in the leaves of plants colonized by the endophyte and the phytopathogen. It was interesting to compare the reaction of potato plants to the introduction of these fungi, both separately and jointly, into the tissue, and to observe the changes in the plants' immune status.

The presence of weak oxidative stress resulting from *B. bassiana* colonization was indicated by increased malondialdehyde levels, particularly in the initial stage (1.2 times higher than the control). Nevertheless, plant growth was enhanced in this variant. It is likely that the stress caused to the plants by endophytic colonization did not exceed the potatoes' adaptive capacity. The work of Nchu et al. (2022) shows stimulation of the growth of tomatoes inoculated with *B. bassiana* at higher ROS levels. Notably, the combined inoculation of fungi after 30 days resulted in a 1.2-fold decrease in MDA levels compared to the control and the inoculation of *B. bassiana* alone. Apparently, this decrease in the mixture may be due to the sharp increase in antioxidant enzyme activity.

In the first assessment (after 14 dpi), a significant increase in the activity of antioxidant enzymes was observed (by 45–60% in potato leaves when the fungi were applied together). SOD showed the greatest increase under the influence of the fungal mixture on the 30th day of the experiment (278%). Similar induction of POX and PAL enzyme activity, as well as an increase in the concentration of phenolic compounds, in tomato plants, was reported by Azadi et al. in 2016 as a result of treatment with *B. bassiana*. The authors demonstrated that colonized plants can successfully control tomato blight caused by *R. solani* by stimulating induced systemic resistance.

It is known that a number of antioxidant enzymes are actively involved in the biosynthesis of polyphenolic protective compounds in plants (e.g., POX, PPO, and PAL). Recently, we also studied the content of phenolic compounds in potato leaves inoculated with *B. bassiana*. Peak values of flavonoid content and antioxidant activity were observed in the phase of plant colonization by the fungus, which probably enhanced resistance to biotic stress (Tomilova et al., unpublished data). We have previously demonstrated an increase in the levels of stigmasterol, minor sterols and certain hydroxy fatty acids in potato leaves colonized by *B. bassiana*. Elevated levels of hydroxycinnamic acids, especially chlorogenic acid, were observed in roots after inoculation with *B. bassiana*. We believe that these changes could also have been caused by oxidative reactions (Tyurin et al., 2023).

Changes in the activity of plant defense enzymes are often recorded based on the level of expression of genes related to disease resistance. A significant increase in the relative expression levels of three disease resistance-associated genes (oxalate oxidase, chitinase and ATP synthase) was observed in tomato plants inoculated with *B. bassiana* and *B. cinerea*, compared to mono-inoculation with *B. cinerea* and the control treatment (Sui et al., 2023). Consequently, the incidence,

lesion diameter and disease index of grey mould (*B. cinerea*) were significantly lower in tomato plants inoculated with *B. bassiana* than in untreated plants, in both pot experiments and field conditions. Maximov et al. (2015) demonstrated that, under sterile conditions, *B. bassiana* can colonize potato plants *in vitro* and increase the transcriptional activity of genes responsible for synthesising anion peroxidase and proteinase inhibitors. According to the authors, this led to a reduction in the development of late blight (Maksimov et al., 2015). Raad et al. (2019) presented data showing that *Arabidopsis* colonized by *B. bassiana*, exhibits induced resistance to *Sclerotinia sclerotiorum* based on increased regulation of pathogenesis-related proteins, as well as activation of reactive oxygen species (ROS) scavengers, camalexin, phytohormones, and other defense-related genes.

It is interesting to note that, in our experiments, mono-infection with *R. solani* did not lead to an increase in MDA or the activation of antioxidant enzymes, with the exception

of SOD at 30 days. Similar effects were observed Nchu et al. (2022) in tomatoes infected with the fusarium wilt pathogen *Fusarium oxysporum* f. sp. *lycopersici*: low levels of superoxide and hydroxyl radicals, and low antioxidant enzyme activity. In contrast, colonization of tomatoes by *B. bassiana* caused an increase in ROS and antioxidant activity (Nchu et al., 2022). The authors suggested that the pathogenic fungus may have employed a hiding strategy to evade the host's immune response, in contrast to the endophyte.

Probably in response to endophytic colonization by *B. bassiana*, accompanied by oxidative stress and activation of a complex of antioxidant enzymes, various physiological systems of the host-plant are involved, which are aimed at inducing systemic plant resistance, stimulating the production of secondary metabolites and plant growth hormones (Jaber, Ownley, 2017; González-Guzmán et al., 2022), finally leading to the growth-stimulating and protective effect of *B. bassiana* on plants.

Conclusion

Thus, colonization of potato plants by the endophytic entomopathogenic fungus *B. bassiana* under biotic stress (*R. solani* infection) induced changes in multiple physiological parameters and key plant immunity markers, ultimately enhancing stress resistance. Under experimental conditions, both *B. bassiana* colonization and *R. solani* infection significantly influenced most of the measured parameters. Treatment with *B. bassiana* reduced Rhizoctonia-induced damage and mitigated the negative effects of infection on plant growth, particularly root development. Stress resistance in plants appears to be closely associated with their capacity to

counteract oxidative stress. The primary antioxidants involved are protective enzymes, which are synthesized in response to fungal invasion. A significant increase in antioxidant activity was observed following *B. bassiana* colonization, as well as in the combined treatment with both fungi. Mono-inoculation with *B. bassiana* triggered an earlier antioxidant response (14 dpi), whereas the maximum increase in antioxidant levels under co-inoculation coincided with the onset of disease symptoms (30 dpi). These results demonstrate the potential of *B. bassiana* to stimulate potato growth and mitigate the impact of black scurf disease.

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Полнотекстовая статья

ЭНДОФИТНЫЙ ГРИБ *BEAUVERIA BASSIANA* ИНДУЦИРУЕТ АКТИВНОСТЬ АНТИОКСИДАНТНЫХ ФЕРМЕНТОВ И УСИЛИВАЕТ РОСТ РАСТЕНИЙ КАРТОФЕЛЯ, ИНФИЦИРОВАННОГО *RHIZOCTONIA SOLANI*

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Проведен анализ физиологических и биохимических изменений растений картофеля, колонизированных эндофитной формой энтомопатогенного гриба *Beauveria bassiana* (Ascomycota: Hypocreales) на фоне биотического стресса, обусловленного внесением инфекционной нагрузки фитопатогена *Rhizoctonia solani* (Basidiomycetes: Ceratobasidiales). Установлена высокая доля колонизации растений энтомопатогенным эндофитом, причем на степень колонизации растений инфицирование *R. solani* не оказало существенного влияния. Колонизация картофеля *B. bassiana* компенсировала отставание в росте зараженных *R. solani* растений (особенно корней) и обеспечила существенное снижение поражения ризоктониозом стеблей и формирующихся столонов. Инокуляция *B. bassiana* усилила антиоксидантную активность в растениях, инокулированных обоими грибами. Установлено значительное повышение активности антиоксидантных ферментов (пероксидаз, супероксиддисмутаз, полифенолоксидаз и фенилаланин-аммоний-лиазы). На основании проведенных экспериментов можно утверждать, что в преодолении биотического стресса, вызванного инфицированием *R. solani*, *B. bassiana* запускает активизацию защитной системы растения-хозяина, а именно комплекса антиоксидантных ферментов. Таким образом, *B. bassiana* может выступать в качестве перспективного модулятора защитного метаболизма растений по отношению к фитопатогенам.

Ключевые слова: энтомопатогенный гриб, грибной фитопатоген, окислительный стресс, антиоксидантные ферменты, индуцированная устойчивость, защита растений

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