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ANTIBACTERIAL ACTIVITY OF DIFFERENT STRAINS OF THE GENUS *TRICHODERMA*

The main pathogens causing plant diseases are bacteria, viruses, and fungi. A number of strategies are usually used for plant protection and control of pathogenic microorganisms. The main interest of researchers is focused on the development of alternative synthetic chemicals to control bacterial diseases of plants. Among such approaches, biological control of bacterial diseases using agents such as antagonistic fungi and some other microorganisms is considered to be one of the most effective strategies. Species of the genus Trichoderma are known for their antagonistic activity against plant pathogenic fungi and bacteria and can be an effective safety strategy to control them. An important peculiarity of fungi of this genus is their ability to inhibit target pathogenic organisms without harming non-target (beneficial) microorganisms. The study of the antagonistic activity of fungi of the genus Trichoderma was conducted mainly against pathogenic fungi of agricultural plants. At the same time, the study of the antibacterial activity of fungi of this genus has attracted much less attention. Therefore, ***the aim*** *of our work was to determine the antibacterial activity of microscopic fungi of the genus Trichoderma against test cultures of bacteria causing pathogenesis of agricultural plants.* ***Methods.*** *The objects of research were 100 fungal strains of the genus Trichoderma and six economically important plant pathogenic bacteria such as Pseudomonas syringae UCM B-1027^{T}, Pseudomonas fluorescens 8573, Pectobacterium carotovorum UCM B-1095^{T}, Xanthomonas campestris pv. campestris UCM B-1049, Clavibacter michiganensis subsp. michiganensis 10$_{2}$, and Agrobacterium tumefaciens UCM B-1000. Cultures of the studied fungi were grown on potato-dextrose agar. The antagonistic activity of fungi of the genus Trichoderma against plant pathogenic bacteria was studied using the conventional method of diffusion in agar and method of dual culture. The antibacterial activity of culture filtrates of Trichoderma strains was evaluated via the zone of growth inhibition of plant pathogenic bacteria. The percentages of growth inhibition of plant pathogenic bacteria were calculated, and the antagonistic activity of strains was concluded on the basis of the obtained values.* ***Results.*** *In general, the studied Trichoderma strains had the antagonistic activity against plant pathogenic bacteria. Using method of diffusion in agar, it was shown that among the 100 studied Tricho-*

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derma strains, 12 had the effect of growth inhibition (bacteriostatic effect) of all six studied species of pathogenic bacteria; 20 strains inhibited the growth of five ones, 36 — four, 12 — three, and 7 — of two strains. The strains with a wide spectrum of antibacterial activity were studied by the double culture method. This made it possible to demonstrate the high selectivity of the antagonistic effect of Trichoderma strains on individual test cultures of phytopathogenic bacteria. For example, strain No7A inhibited the growth of C. michiganensis subsp. michiganensis 102 by 47% and the growth of P. syringae UCM B-1027^T by 30%, while the zones of growth inhibition of these test cultures, determined by the method of diffusion in agar, were 5 and 6 mm, respectively. ***Conclusions.*** *The obtained results indicated the potential and overall ability of Trichoderma strains to biologically control bacterial pathogens. The most promising for the use of plant pathogenic bacteria as agents for biocontrol were strains F-60, 1515, and 320, which were active against all studied bacteria. Such strains may have the potential as a preventive biocontrol agent of plant pathogens with a wide range of action. On the other hand, Trichoderma strains with high activity against certain pathogens may have the potential to be used as a control agent against a specific target pathogen.*

Keywords: *Trichoderma strains,* antagonism, *plant pathogenic bacteria, biocontrol.*

The plant pathogenic microorganisms such as fungi, bacteria, and viruses cause the pathogenesis of plants. Different strategies have been used to prevent and control plant diseases. Today, the main strategy for the control of agricultural plant pathogens is the use of chemical substances. Excessive use of agrochemicals in agriculture has led to pollution of the environment and ecosystem, which requires significant changes in the use of pesticides. Currently, in the world, strict rules for the use of chemical pesticides are being developed, and special programs are used for removing the most dangerous chemicals from the market. Due to the constant and excessive use of chemical preparations for plant protection, the process of adaptation and development of new resistant races of plant pathogenic microorganisms is observed [1].

Therefore, the main aim of the researchers is to study and develop new methods to control plant diseases. Antagonistic fungi (AF) and some other microorganisms are considered to be most effective strategies to control bacterial diseases. AF includes various species of fungi that effectively counteract plant diseases of fungal and bacterial etiology. In addition, they can play the important role of regulators of various physiological pathways of plants and their interaction with microorganisms in general [2].

Species of the genus *Trichoderma* are known for their antagonistic activity against plant pathogenic microorganisms [3]. The effective use of fungi of this genus against bacterial pathogens can be a safe strategy to address global food security issues. On the other hand, there is a steady trend in the world for the development of organic farming. Ukraine is among the top five countries in terms of the pace of development of organic agriculture which is the most export-oriented branch of agriculture and therefore needs to find new effective agents of biological control of plant pathogens [4].

Notably, many studies (up to 90%) related to the use of AF for the treatment of plant diseases have been conducted using different strains of microscopic fungi of the genus *Trichoderma*. The successful use of *Trichoderma* species as biocontrol agents is due to their ability to survive in various adverse conditions, high reproductive capacity (high growth rate, intensity of sporulation), efficient use of nutrient sources, ability to positively affect the composition of the rhizosphere, and strong antagonism against pathogenic fungi and bacteria. An important peculiarity of fungi of this genus is their ability to inhibit target pathogenic organisms without harming non-target (beneficial) microorganisms [5].

Trichoderma species are opportunistic plant colonizers that trigger host-induced systemic resistance and can also trigger systemic acquired resistance. Root and leaf colonization by *Trichoderma* can pre-activate (prime) plant defense, enabling robust plant responses to subsequent

pathogen challenges. Priming accelerates the plant's immune system via activating the defenses to best cope with a wide range of biotic and abiotic stresses [6].

Such physiological features determine the ability of *Trichoderma* strains to exist in a variety of econiches. Among the representatives of the genus *Trichoderma* species of *T. asperellum*, *T. viride*, *T. harzianum*, *T. virens*, and *T. hamatum* are characterized by high antagonistic activity against plant pathogens. Based on the ability of these fungi to control the development of pathogenic microorganisms, a large number of commercial preparations based on different species of *Trichoderma* have been developed. Among them, the most used biocontrol agents against plant pathogens are *T. parareesei* T6, *T. asperellum* T25 and T34, and *T. harzianum* T22. However, these strains are not able to demonstrate a high level of effectiveness in controlling pathogenic bacteria. Therefore, the search for new strains with antibacterial activity is of considerable scientific and practical interest [7].

The study of antagonistic activity of fungi of the genus *Trichoderma* was conducted mainly against pathogenic fungi of agricultural plants. At the same time, the study of antibacterial activity of fungi of this genus has received much less attention. Therefore, **the aim** of our work was to determine the antibacterial activity of microscopic fungi of the genus *Trichoderma* against test cultures of bacteria causing pathogenesis of agricultural plants.

Materials and methods. The objects of research were 100 strains of the genus *Trichoderma* fungi that were obtained from the culture collection of microscopic fungi of the Department of Physiology and Taxonomy of Micromycetes of Zabolotnyi Institute of Microbiology and Virology of NAS of Ukraine (IMV NASU). Test strains of phytopathogenic bacteria were obtained from the Ukrainian Collection of Microorganisms (UCM) and the culture collection of plant pathogenic bacteria of the Department of Phytopathogenic Bacteria of the IMV NASU (Table 1).

The antagonistic activity of fungi of the genus *Trichoderma* against plant pathogenic bacteria was determined using the conventional agar well diffusion and dual culture methods [8, 9].

Method of diffusion in agar. The antibacterial activity of culture filtrates (CF) of *Trichoderma* strains was determined by the method of diffusion in agar [8]. Microscopic fungi of the genus *Trichoderma* were preliminarily grown on potato-dextrose agar (PDA) in Petri dishes at a temperature of 26 ± 2 °C for 10—14 days. A standard suspension (1×10^6 conidia/mL) was then prepared and added to the Czapek liquid medium that con-

Table 1. **The studied cultures of plant pathogenic bacteria**

No	Test organism	Strain	Plant pathogenic properties
1	*Pseudomonas syringae*	UCM B-1027^T	Spotting a wide range of agricultural and flowering plants
2	*Pseudomonas fluorescens*	8573	Spots and soft rot
3	*Pectobacterium carotovorum*	UCM B-1095^T	Rot of many species of agricultural and flowering plants
4	*Xanthomonas campestris* pv. *campestris*	UCM B-1049	Vascular bacteriosis of a wide range of agricultural plants
5	*Clavibacter michiganensis* subsp. *michiganensis*	10_2	Bacterial cancer of tomatoes and other nightshades (Solanaceae), brown spot of pepper
6	*Agrobacterium tumefaciens*	UCM B-1000	Tumours and necrosis of crops

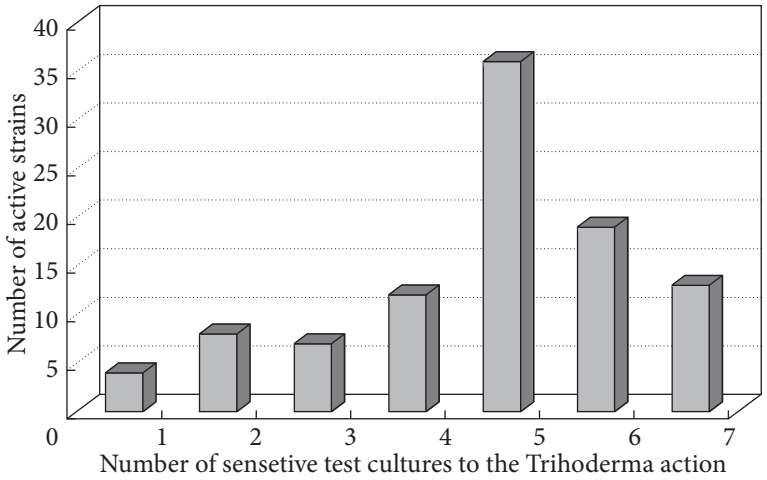

Fig. 1. Quantitative distribution of strains of microscopic fungi of the genus *Trichoderma* by the activity against the studied bacterial pathogens

tained 20 g/L of glucose [8]. Micromycetes were grown in 750 mL Erlenmeyer flasks under static conditions at 26 ± 2 °C for 21 days. After cultivation, the fungal mycelium was separated by filtration through ashless paper filters (blue tape).

Test bacteria were cultured on potato agar (PA) at a temperature of 26 ± 2°C for 24 hours. After that, a bacterial suspension ($1 \cdot 10^6$ cells/mL) was prepared according to the turbidity standard. 20 mL of PA was added to Petri dishes, cooled,and 1 mL of bacterial suspension was spread on top of agar (bacterial lawn technique). A sterile cork borer was used to cut holes with a diameter of 8 mm in agar, where 100 μL of CF of *Trichoderma* strains was added. Sterile distilled water was used as a control. Petri dishes were incubated at a temperature of 26 ± 2°C for 2—5 days.

The antibacterial activity of CF of *Trichoderma* strains was evaluated by the zone of growth inhibition of plant pathogenic bacteria [10].

The method of dual culture. According to the results of the method of diffusion in agar, the most active antagonistic strains of *Trichoderma* were preliminarily grown on PDA as described earlier.

The conventional method of dual culture [11] was used to determine the antagonistic activity of fungi of the genus *Trichoderma* against plant pathogenic bacteria. An inoculum (5 × 5 mm) from the edge of the colony of each *Trichoderma* strain was used to inoculate standard Petri dishes (9 cm diameter) with Czapek agar medium (20 mL/dish).

The inoculum (3×3 mm) of a test strain of phytopathogenic bacteria was placed at a distance of 3 cm from the edge of the Petri dish. The studied *Trichoderma* strain was inoculated at a distance of 3 cm from the edge of the opposite side of this Petri dish. The distance between the sites inoculated with the plant pathogenic bacteria and *Trichoderma* strains was 3 cm apart. In control Petri dishes, appropriate test strains of plant pathogenic bacteria were cultured without an antagonistic *Trichoderma* strain.

Incubation of the studied fungi and bacteria was carried out at a temperature of 26 ± 2 °C for 2—7 days. The percentage of growth inhibition of plant pathogenic bacteria by the antagonistic *Trichoderma* strains was evaluated [12].

All assays were performed in three independent experiments. The obtained data were processed statistically using Microsoft Excel and Origin 8.0 (OriginLab). Differences in averages were considered significant at a level of $P<0.05$. Data on inhibition level were analyzed for normality with the analytical methods Shapiro-Wilk and Kolmogorov-Smirnov using trial version Prism (GraphPad Software).

Results. The results of our study indicated that different *Trichoderma* strains had the potential to inhibit the growth of six economically important

plant pathogenic bacteria: *Pseudomonas syringae* UCM B-1027^T, *Pseudomonas fluorescens* 8573, *Pectobacterium carotovorum* UCM B-1095^T, *Xanthomonas campestris* pv. *campestris* UCM B-1049, *Clavibacter michiganensis* subsp. *michiganensis* $10_{2,}$ and *Agrobacterium tumefaciens* UCM B-1000.

Among the 100 studied *Trichoderma* strains, 12 showed the effect of growth inhibition (bacteriostatic effect) of all six studied species of pathogenic bacteria; 20 strains inhibited the growth of five ones, 36 — four, 12 — three, and 7 — of two strains (Table 2, Fig. 1).

Table 2. **Antibacterial activity of fungi of the genus *Trichoderma***

No	*Trichoderma* strains	Zone of growth inhibition (mm)					
		1	2	3	4	5	6
1	3089	7.0 ± 0.5	0	2.0 ± 0.2	17.0 ± 0.9	18.0 ± 1.0	3.0 ± 0.2
2	3077	4.0 ± 0.3	2.0 ± 0.3	0	5.0 ± 0.2	0	0
3	3083	1 ± 0.2	0	0	5.0 ± 0.3	10.0 ± 1.0	0
4	3074	0	0	0	7.0 ± 0.3	6.0 ± 0.7	0
5	3067	0	0	2.0 ± 0.3	9.0 ± 0.7	7.0 ± 0.6	0
6	3064	5.0 ± 0.4	3.0 ± 0.3	0	3.0 ± 0.2	3.0 ± 0.4	0
7	3062	8.0 ± 0.5	14.0 ± 0.6	5.0 ± 0.4	16.0 ± 0.8	18.0 ± 0.9	4.0 ± 0.4
8	3082	4.0 ± 0.3	0	0	0	5.0 ± 0.4	0
9	3072	2.0 ± 0.2	0	0	7.0 ± 0.6	2.0 ± 0.2	0
10	3087	2.0 ± 0.1	0	0	6.0 ± 0.5	0	0
11	3066	3.0 ± 0.5	0	3.0 ± 0.4	13.0 ± 0.8	18.0 ± 0.8	4.0 ± 0.3
12	3057	10.0 ± 0.8	6.0 ± 0.4	2.0 ± 0.2	16.0 ± 1.0	9.0 ± 0.7	0
13	3059	2.0 ± 0.2	3.0 ± 0.3	4.0 ± 0.3	11.0 ± 1.0	12.0 ± 0.9	1.0 ± 0.2
14	3070	2.0 ± 0.1	0	0	4.0 ± 0.3	6.0 ± 0.4	0
15	344	9.0 ± 0.8	0	7.0 ± 0.6	3.0 ± 0.4	5.0 ± 0.3	0
16	3102	8.0 ± 0.7	2.0 ± 0.3	6.0 ± 0.5	4.0 ± 0.3	5.0 ± 0.5	8.0 ± 0.6
17	3100	6.0 ± 0.7	0	4.0 ± 0.3	3.0 ± 0.4	5.0 ± 0.5	0
18	3099	7.0 ± 0.8	0	6.0 ± 0.5	5.0 ± 0.6	6.0 ± 0.6	0
19	3091	5.0 ± 0.6	0	0	7.0 ± 0.6	0	0
20	2925	6.0 ± 0.7	11.0 ± 0.9	4.0 ± 0.3	17.0 ± 1.0	14.0 ± 0.8	3.0 ± 0.4
21	3093	9.0 ± 0.8	0	8.0 ± 0.7	7.0 ± 0.6	10.0 ± 1.0	0
22	3104	9.0 ± 1.0	0	7.0 ± 0.9	6.0 ± 0.4	7.0 ± 0.7	0
23	2928	3.0 ± 0.4	0	4.0 ± 0.5	5.0 ± 0.3	19.0 ± 1.1	2.0 ± 0.1
24	3101	8.0 ± 0.6	0	7.0 ± 0.6	6.0 ± 0.5	7.0 ± 0.4	0
25	3103	7.0 ± 0.8	0	4.0 ± 0.3	5.0 ± 0.4	4.0 ± 0.3	0
26	2932	5.0 ± 0.3	10 ± 0.8	6.0 ± 0.4	11.0 ± 1.0	16.0 ± 1.0	2.0 ± 0.2
27	3107	7.0 ± 0.5	0	3.0 ± 0.2	5.0 ± 0.4	5.0 ± 0.3	0
28	2916	15.0 ± 1.1	7.0 ± 0.6	4.0 ± 0.3	16.0 ± 0.9	20.0 ± 1.5	0
29	3096	8.0 ± 0.6	0	2.0 ± 0.1	4.0 ± 0.6	3.0 ± 0.1	0
30	3105	4.0 ± 0.2	0	5.0 ± 0.3	3.0 ± 0.2	6.0 ± 0.4	0
31	1602	2.0 ± 0.2	0	0	4.0 ± 0.3	8.0 ± 0.7	0
32	3094	4.0 ± 0.4	0	6.0 ± 0.4	4.0 ± 0.2	4.0 ± 0.3	0
33	2768	7.0 ± 0.6	0	6.0 ± 0.6	6.0 ± 0.5	7.0 ± 0.5	0
34	1242	9.0 ± 0.8	5.0 ± 0.2	1.0 ± 0.2	14.0 ± 1.0	7.0 ± 0.6	0

Continuation of Table 2.

No	*Trichoderma* strains	Zone of growth inhibition (mm)					
		1	2	3	4	5	6
35	1662	11.0 ± 1.0	8.0 ± 0.5	8.0 ± 0.6	12.0 ± 0.9	12.0 ± 0.9	0
36	368	0	0	0	7.0 ± 0.8	2.0 ± 0.1	0
37	843	5.0 ± 0.4	6.0 ± 0.4	3.0 ± 0.4	12.0 ± 0.8	14.0 ± 1.1	1.0 ± 0.2
38	2930	5.0 ± 0.5	0	1.0 ± 0.2	7.0 ± 0.6	0	0
39	1299	2.0 ± 0.2	0	3.0 ± 0.2	10.0 ± 1.0	16.0 ± 1.1	0
40	904	4.0 ± 0.3	0	3.0 ± 0.4	8.0 ± 0.7	0	0
41	3121	4.0 ± 0.2	0	6.0 ± 0.6	5.0 ± 0.4	6.0 ± 0.8	0
42	3126	6.0 ± 0.5	0	9.0 ± 0.8	5.0 ± 0.5	7.0 ± 0.6	0
43	3124	6.0 ± 0.4	0	7.0 ± 0.6	4.0 ± 0.2	7.0 ± 0.7	0
44	3120	0	0	4.0 ± 0.5	4.0 ± 0.3	3.0 ± 0.2	0
45	3122	8.0 ± 0.6	0	5.0 ± 0.4	7.0 ± 0.5	6.0 ± 0.5	0
46	3127	3.0 ± 0.4	0	8.0 ± 0.6	9.0 ± 0.8	5.0 ± 0.6	0
47	3128	6.0 ± 0.3	0	9.0 ± 0.8	6.0 ± 0.7	4.0 ± 0.2	0
48	3123	9.0 ± 0.9	0	7.0 ± 0.7	5.0 ± 0.6	9.0 ± 0.8	0
49	3125	4.0 ± 0.3	0	4.0 ± 0.3	4.0 ± 0.2	6.0 ± 0.5	0
50	3097	3.0 ± 0.4	0	2.0 ± 0.2	3.0 ± 0.2	4.0 ± 0.2	0
51	2924	7.0 ± 0.5	0	9.0 ± 0.9	5.0 ± 0.4	6.0 ± 0.7	0
52	2455	8.0 ± 0.7	0	6.0 ± 0.6	2.0 ± 0.1	9.0 ± 1.0	0
53	1243	8.0 ± 0.6	0	9.0 ± 0.9	2.0 ± 0.2	7.0 ± 0.8	0
54	No1	8.0 ± 0.7	7.0 ± 0.5	2.0 ± 0.1	5.0 ± 0.4	7.0 ± 0.7	1.0 ± 0.2
55	No3	4.0 ± 0.2	0	5.0 ± 0.4	8.0 ± 0.6	2.0 ± 0.1	0
56	No5	6.0 ± 0.3	0	4.0 ± 0.2	4.0 ± 0.5	5.0 ± 0.3	0
57	No6	8.0 ± 0.5	0	7.0 ± 0.8	8.0 ± 0.6	9.0 ± 0.5	0
58	No7A	6.0 ± 0.5	0	4.0 ± 0.3	5.0 ± 0.4	6.0 ± 0.4	0
59	3112	8.0 ± 0.7	0	6.0 ± 0.4	5.0 ± 0.6	9.0 ± 0.8	0
60	3117	4.0 ± 0.3	3.0 ± 0.3	2.0 ± 0.1	2.0 ± 0.3	4.0 ± 0.5	0
61	3108	9.0 ± 0.8	0	3.0 ± 0.3	4.0 ± 0.3	7.0 ± 0.7	0
62	3109	9.0 ± 1.0	0	8.0 ± 0.9	7.0 ± 0.5	8.0 ± 0.6	0
63	3115	2.0 ± 0.2	6.0 ± 0.5	4.0 ± 0.2	3.0 ± 0.4	3.0 ± 0.4	0
64	16p	3.0 ± 0.4	4.0 ± 0.3	1.0 ± 0.1	1.0 ± 0.2	3.0 ± 0.3	0
65	3118	9.0 ± 0.8	8.0 ± 0.9	7.0 ± 0.6	4.0 ± 0.3	8.0 ± 0.7	0
66	3113	9.0 ± 1.0	7.0 ± 0.6	5.0 ± 0.5	4.0 ± 0.2	8.0 ± 0.8	0
67	3111	8.0 ± 1.0	0	5.0 ± 0.2	4.0 ± 0.4	9.0 ± 0.8	0
68	3116	10.0 ± 0.8	4.0 ± 0.2	3.0 ± 0.2	4.0 ± 0.3	6.0 ± 0.4	0
69	3058	5.0 ± 0.4	3.0 ± 0.1	1.0 ± 0.1	6.0 ± 0.6	9.0 ± 0.8	0
70	3065	1.0 ± 0.2	0	2.0 ± 0.2	11.0 ± 1.0	13.0 ± 0.9	2.0 ± 0.1
71	3071	7.0 ± 0.5	0	0	16.0 ± 1.1	14.0 ± 1.0	0
72	3073	2.0 ± 0.1	0	2.0 ± 0.2	11.0 ± 0.8	0	0
73	3081	0	0	0	3.0 ± 0.4	1.0 ± 0.1	0
74	3084	4.0 ± 0.2	2.0 ± 0.1	3.0 ± 0.5	8.0 ± 0.6	13.0 ± 1.0	0
75	3085	1.0 ± 0.2	8.0 ± 0.6	5.0 ± 0.4	6.0 ± 0.5	17.0 ± 1.3	5.0 ± 0.4
76	3088	5.0 ± 0.4	0	0	8.0 ± 0.7	4.0 ± 0.2	0

Continuation of Table 2.

No	*Trichoderma* strains	Zone of growth inhibition (mm)					
		1	2	3	4	5	6
77	906	5.0 ± 0.5	3.0 ± 0.4	2.0 ± 0.2	10.0 ± 0.9	9.0 ± 0.8	0
78	3010	5.0 ± 0.3	5.0 ± 0.4	2.0 ± 0.2	15.0 ± 1.2	9.0 ± 0.7	0
79	3078	0	0	0	8.0 ± 0.7	5.0 ± 0.2	0
80	3079	2.0 ± 0.1	0	2.0 ± 0.1	12.0 ± 1.0	0	0
81	F-60	6.0 ± 0.3	12.0 ± 0.8	10.0 ± 0.8	15.0 ± 1.2	18.0 ± 1.1	6.0 ± 0.3
82	1515	7.0 ± 0.6	14.0 ± 1.0	9.0 ± 0.7	12.0 ± 0.8	16.0 ± 0.9	5.0 ± 0.2
83	2989	4.0 ± 0.2	4.0 ± 0.4	1.0 ± 0.2	16.0 ± 1.0	9.0 ± 0.6	0
84	320	10.0 ± 1.0	2.0 ± 0.2	4.0 ± 0.3	12.0 ± 0.7	20.0 ± 1.4	3.0 ± 0.1
85	2554	2.0 ± 0.2	0	2.0 ± 0.2	12.0 ± 0.9	12.0 ± 1.1	1.0 ± 0.2
86	1302	10.0 ± 0.8	0	2.0 ± 0.2	12.0 ± 1.0	10.0 ± 0.8	0
87	2550	4.0 ± 0.3	1.0 ± 0.1	3.0 ± 0.4	13.0 ± 1.1	16.0 ± 1.0	2.0 ± 0.2

Note: 1—6 — Test cultures of phytopathogenic bacteria: 1 — *Pseudomonas syringae* UCM B-1027^T; 2 — *Pseudomonas fluorescens* 8573; 3 — *Pectobacterium carotovorum* UCM B-1095^T; 4 — *Xanthomonas campestris* pv. *campestris* UCM B-1049; 5 — *Clavibacter michiganensis* subsp. *michiganensis* 10_2 ; 6 — *Agrobacterium tumefaciens* UCM B-1000.

Table 2 contains data on the activity of *Trichoderma* strains against two and more test strains of bacteria. Four strains (1244, 3349, No4, and 3063) of the genus *Trichoderma* did not show any biological activity against the studied test cultures of plant pathogenic bacteria. Nine *Trichoderma* strains demonstrated activity against only one test culture. So, the antagonistic activity against *P. syringae* UCM B-1027^T was observed for *Trichoderma* strains 3060, 3068, and 3095 with growth inhibition zones of 3 mm; against *P. fluorescens* 8573 — for fungal strain 3076 (inhibition zone 7 mm); against *X. campestris* pv. *campestris* UCM B-1049 — for fungal strains 3069, 3075, 2933, and No2 — with growth inhibition zones of 10, 2, 2, and 6 mm respectively; against *C. michiganensis* subsp. *michiganensis* 10_2 — for *Trichoderma* strain 3061 (2 mm).

The highest activity was observed against the gram-positive bacterium *C. michiganensis* subsp. *michiganensis* 10_2; the most active were *Trichoderma* strains 320, 2916, 2928, 2915, 3066, 3062, and 3089 (Table 2).

The highest activity against gram-negative bacteria was showed for fungal strains: 3089, 2925, 3062, 2989, 3071, 2916, and 3057 against *X. campestris* UCM B-1049; 2916, and 1662 against *P. syringae* UCM B-1027^T; 3062 and 1515 against *P. fluorescens*8573. At the same time, all studied strains showed low antibacterial activity against *A. tumefaciens* UCM B-1000 (Table 2).

Efficacy testing of candidate antagonists is an essential part of each screening program. For the selection of potential agents for the biocontrol of phytopathogens, the method of primary selection is important; for this purpose, agar well-diffusion and dual culture methods are generally accepted.

Microbial biological control agents (BCAs) protect crops from damage by diseases via different modes of action. BCAs may interact directly with the pathogen in two ways, by mycoparasitism or antibiosis [13]. If mycoparasitism plays a major role in the antifungal activity, then the production of antimicrobial secondary metabolites with inhibiting effects is the main mode of action on phytopathogenic bacteria. Therefore, we used the method of diffusion in agar to determine the antibacterial activity of *Trichoderma* strains. Such a testing in dual cultures of patho-

gen and candidate antagonist will result in the selection of those candidates that produce toxins secreted into the medium and cause growth inhibition of the pathogen. If the method of diffusion in agar makes it possible to evaluate antibacterial activity mainly by the inhibitory effect of exometabolites, then the use of the dual culture method allows us to take into account more complex interactions including competition for nutrients sources and living space [14].

The dual culture method was used in the study of *Trichoderma* strains, which had both a broad and selective effect on the test strains of phytopathogenic bacteria. Table 3 shows the most active *Trichoderma* strains against phytopathogenic bacteria determined by the dual culture method (Table 3).

In general, the results obtained by the two methods were comparable. This made it possible to demonstrate the high selectivity of the antagonistic effect of *Trichoderma* strains on individual test cultures of phytopathogenic bacteria (Fig. 3). For example, the *Trichoderma* strain No7A inhibited the growth of *C. michiganensis* subsp. *michiganensis* 10_2 by 47% and the growth of *P. syringae* UCM B-1027^T by 30%, while the zones of growth inhibition of these test bacteria, determined by the method of diffusion in agar, were 5 and 6 mm, respectively (Table 2).

Discussion. The results of our study indicated that *Trichoderma* strains had the potential to inhibit the growth of six economically important plant pathogenic bacteria: *P. syringae* UCM B-1027^T, *P. fluorescens* 8573, *P. carotovorum* UCM B-1095^T, *X. campestris* pv. *campestris* UCM B-1049, *C. michiganensis* subsp. *michiganensis* 10_2, and *A. tumefaciens* UCM B-1000. Notably, different *Trichoderma* species have also been reported previously for the suppression of phytopathogenic bacteria [15].

Earlier, in the studies of *Trichoderma* activity, a number of authors concluded that gram-negative bacteria were more sensitive to the antibacterial action of *Trichoderma* species than Gram-positive ones [16, 17]. As for our data, this conclusion is not confirmed because most of the studied fungal strains showed antibacterial activity against *C. michiganensis* subsp. *michiganensis* 10_2. Vizcaino et al. (2005), Sadykova et al. (2015), and Leylaie et al. (2018) obtained similar results for the activity against *C. michiganensis* subsp. *michiganensis* 10_2 and other Gram-positive bacteria [15, 18, 19].

Table 3. **Inhibition of the growth (%) of phytopathogenic bacteria under the action of fungi of the genus *Trichoderma***

No	*Trichoderma* strain	Test culture of phytopathogenic bacteria					
		1	2	3	4	5	6
1	2550	0	12.5	17	0	0	10
2	906	0	25	17	47	22	40
3	320	0	25	0	20	0	20
4	No1	0	12.5	0	33	0	10
5	1515	0	25	17	33	11	10
6	F-60	0	12.5	0	20	0	23
7	3093	0	12.5	25	20	11	20
8	No7A	30	25	15	47	0	0

Note: 1—6 — Test cultures of phytopathogenic bacteria: 1 — *Pseudomonas syringae* UCM B-1027^T; 2 — *Pseudomonas fluorescens* 8573; 3 — *Pectobacterium carotovorum* UCM B-1095^T; 4 — *Xanthomonas campestris* pv. *campestris* UCM B-1049; 5 — *Clavibacter michiganensis* subsp. *michiganensis* 10_2; 6 — *Agrobacterium tumefaciens* UCM B-1000.

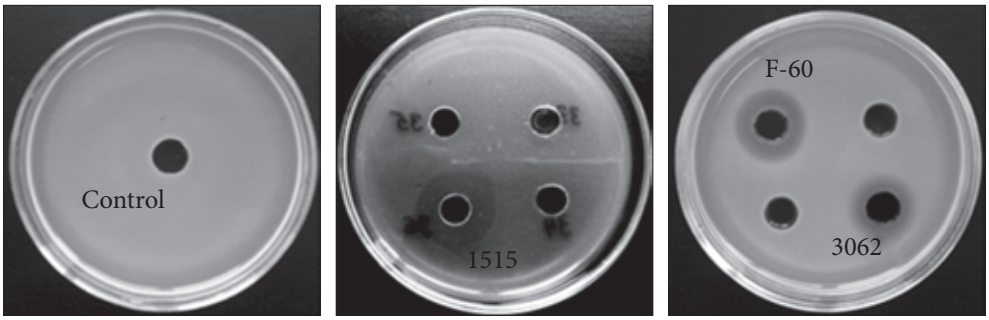

Fig. 2. Determination of the antibacterial activity of *Trichoderma* strains (1 — 1515, 2 — F-60 and 3062) by the method of diffusion in agar using *Pseudomonas fluorescens* 8573: Control — growth of bacteria with sterile distilled water

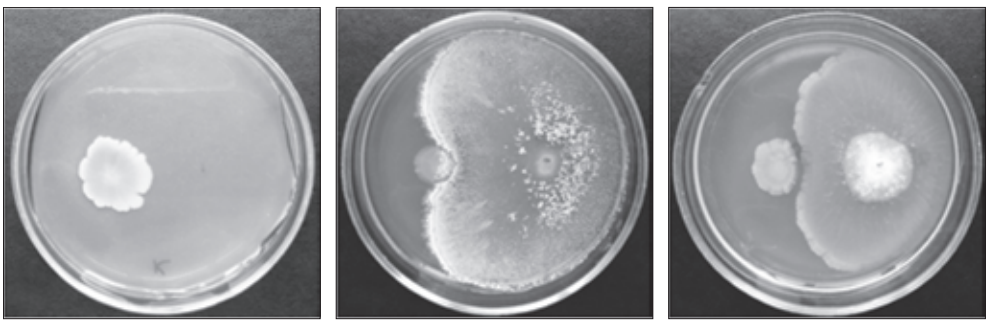

Fig. 3. Determination of the antibacterial activity of *Trichoderma* strains (1 — No7A and 2 — 320) using the dual culture method against *Pseudomonas syringae* UCM B-1027^{T}. Control — growth of bacterial pathogen without *Trichoderma*

In contrast to the antifungal activity of *Trichoderma*, where the main mechanism is mycoparasitism that is primarily due to the action of hydrolytic enzymes such as chitinases, glucanases, and proteases, the antibacterial effect is mainly due to secondary metabolites [20]. However, Khethr, et al. (2008) concluded that the antibacterial effect of *Trichoderma hamatum* metabolites against bacteria of the genus *Ruminococcus* was most likely due to two factors — inhibition of bacterial growth and synthesis of cellulolytic enzymes [17].

Bioactive compounds of *Trichoderma* damage bacterial cells by various mechanisms. Thus, alkaloids are able to inhibit important metabolic enzymes or act as DNA intercalating agents. Some flavonoids coagulate soluble proteins of bacterial cells, including important enzymes, via forming complexes with them. Other compounds disrupt the structure of the bacterial cell membrane or inhibit the synthesis of the cell wall and nucleic acids [21—23].

It is known that *Trichoderma* strains are able to synthesize more than 200 secondary metabolites, among which diterpene compounds showed high antibacterial activity [24, 25].

It should also be noted that most studies of the antibacterial action of fungi of the genus *Trichoderma* were conducted with extracts obtained using polar organic solvents such as methanol, butanol, and ethyl acetate [15]. In this case, the concentrations of active metabolites significantly exceed the concentrations of these compounds

in culture filtrates. Usually, the extracts are used for purification, isolation, and identification of active compounds that cause antagonistic activity. On the other hand, *in vivo* fungi synthesize complexes of secondary metabolites of concentrations close to those on a solid medium, and therefore the use of the method of diffusion in agar allows for obtaining results that will be more correlated with the biocontrol indicators under natural conditions.

The butanol and ethyl acetate extracts of such the most common *Trichoderma* species as *T. asperellum*, *T. viride*, *T. hamatum*, *T. koningii*, *T. atroviride*, *T. harzianum*, *T. citrinoviride*, and *T. longibrachiatum* were reported to demonstrate antibacterial activity against both gram-positive bacteria *Bacillus subtilis*, *B. mycoides*, *Micrococcus luteus*, including methicillin-resistant *Staphylococlaus aureus,* and gram-negative bacteria *Escherichia coli* and *Comamonas terrigena* [15]. The authors of this study pointed to the lack of antibacterial activity of *T. atroviride, T. longibrachiatum,* and *T. hamatum*.

However, recent studies have refuted the conclusions about the lack of antibacterial activity of these species. So, Leylaie et al. (2019) showed that methanol and ethyl acetate extracts of species such as *T. asperellum, T. brevicompactum, T. koningiopsis,* and *T. longibrachiatum* had high antibacterial activity against Gram-positive pathogenic bacteria *Staphylococcus aureus*, Gram-negative *Escherichia coli* and plant pathogens, Gram-negative *Ralstonia solanacearum* and Gram-positive *C. michiganensis* [19].

As mentioned earlier, the main mechanism of antifungal activity of *Trichoderma* is mycoparasitism, which is mainly due to the ability to synthesize a complex of hydrolytic enzymes. In the case of antibacterial activity, the main factor is the ability to synthesize secondary metabolites of various classes with antibiotic activity. It is believed that the main antibiotics produced by fungi of the genus *Trichoderma* are peptaibols, which have both antifungal and antibacterial actions. Until today, more than 1,000 of these fungal, non-ribosomal peptides have been described in the literature [26]. Peptaibols are naturally produced as a mixture of peptides that differ in some amino acid positions. The most studied and commercially available peptaibol is alamethicin — an antibiotic peptide belonging to the class of membrane-active peptides isolated from the fungus *T. viride*. The extracts of peptaibols (atroviridins) from *T. atroviride* O1 were found to have an inhibitory activity against Gram-positive bacteria, namely methicillin-resistant *S. aureus* [27].

It was shown that *T. asperellum* and *T. longibrachiatum* contain peptaibols and other antimicrobial peptides, which, in addition to antifungal, have also antibacterial activity against *M. luteus*. Similar results were obtained for *Bacillus subtilis* in the study of peptaibols from *T. pseudokoningii* [28, 29]. Species of the genus *Trichoderma* synthesized also specific peptaibols, such as Trichoconin VI, VII, and AVIII, with antibacterial activity [30].

In addition to peptaibols, *Trichoderma* species produce a number of other secondary metabolites with antibacterial activity. For example, *T. harzianum* T23 is able to produce viridiofungin A (VFA) that inhibits the growth of *Erwinia amylovora* and *C. michiganensis in vitro* [30, 31]. Chen et al. (2019) reported that diterpenes koninginols extracted from *T. koningiopsis* showed high antibacterial activity against *B. subtilis* and *S. aureus* [32]. *T. atroviride* synthesizes diterpene and sesquiterpene compounds with high antibacterial activity against *S. aureus, B. subtilis* and *M. luteus*; among them Harzianol I showed the highest activity [33].

To date, the most studied strains-agents of biocontrol of fungal pathogens have been *T. parareesei* T6, *T. asperellum* T25, and *T. harzianum* T34. However, these strains were not able to demonstrate a high level of effectiveness in controlling pathogenic bacteria [7]. Therefore, further studies of selected strains with antibacterial activity are of considerable scientific and practical interest.

Notably, the antibacterial activity of *Trichoderma* strains as biocontrol agents can be improved by optimizing the composition of the nutrient medium. Optimally selected composition of the nutrient medium can lead to the synthesis of higher concentrations of compounds with antibacterial action. On the other hand, it is important to conduct experiments *in vivo* to enhance the effects of biological control due to the ability of secondary metabolites of fungi of the genus *Trichoderma* to induce systemic plant resistance to pathogens [2, 34, 35].

Conclusions. The obtained results indicated the potential and overall ability of *Trichoderma* strains to biologically control bacterial pathogens. The most promising for use as agents of biocontrol of plant pathogenic bacteria were strains F-60, 1515, and 320, which were active against all studied bacteria. Such strains may have the potential as preventive biocontrol agents of plant pathogens with a wide range of action. On the other hand, *Trichoderma* strains with high activity against certain pathogens may have the potential to be used for the biocontrol of a specific target pathogen.

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АНТИБАКТЕРІАЛЬНА АКТИВНІСТЬ РІЗНИХ ШТАМІВ РОДУ *TRICHODERMA*

Основними збудниками хвороб рослин є бактерії, віруси та гриби. Для захисту рослин і контролю патогенних мікроорганізмів зазвичай використовують низку стратегій. Основний інтерес дослідників зосереджено на розробці методів, що є альтернативою синтетичним хімічним речовинам для контролю бактеріальних хвороб рослин. Серед таких підходів однією з найефективніших стратегій вважають біологічний контроль бактеріальних хвороб за допомогою таких агентів як гриби-антагоністи, так і деякі інші мікроорганізми. Види роду *Trichoderma* відомі своєю антагоністичною активністю проти фітопатогенних грибів і бактерій та можуть бути ефективною безпечною стратегією їхнього контролю. Важливою особливістю грибів цього роду є їхня здатність пригнічувати ріст патогенних організмів-мішеней, не завдаючи шкоди нецільовим (корисним) мікроорганізмам. Вивчення антагоністичної активності грибів роду *Trichoderma* проводилося переважно проти патогенних грибів сільськогосподарських рослин. У той же час дослідженню антибактеріальної активності грибів цього роду приділено значно менше уваги. Тому **метою** нашої роботи було визначити антибактеріальну активність мікроскопічних грибів роду *Trichoderma* щодо тест-культур бактерій-збудників хвороб сільськогосподарських рослин. **Методи.** Об'єктами дослідження були 100 штамів грибів роду *Trichoderma* та шість економічно важливих фітопатогенних бактерій: *Pseudomonas syringae* УКМ В-1027^{T}, *Pseudomonas fluorescens* 8573, *Pectobacterium carotovorum* УКМ В-1095^{T}, *Xanthomonas campestris* pv. *campestris* УКМ В-1049, *Clavibacter michiganensis* subsp. *michiganensis* 10_2 і *Agrobacterium tumefaciens* УКМ В-1000. Культури досліджених грибів вирощували на картопляно-глюкозному агарі. Антагоністичну активність грибів роду *Trichoderma* проти фітопатогенних бактерій визначали традиційними методом дифузії в агар і методом дуальної культури. Антибактеріальну активність культуральних фільтратів штамів *Trichoderma* оцінювали за величиною зон пригнічення росту патогенних бактерій рослин. Розраховували відсотки пригнічення росту патогенних бактерій рослин, на основі котрих робили висновок про антагоністичну активність штамів. **Результати.** Загалом досліджені штами *Trichoderma* проявили антагоністичну активність проти фітопатогенних бактерій. Методом дифузії в агар показано, що 12 зі 100 досліджених штамів *Trichoderma* пригнічували ріст (бактеріостатичний ефект) усіх шести досліджених видів патогенних бактерій; 20 штамів пригнічували ріст п'яти штамів, 36 — чотирьох, 12 — трьох і 7 — двох штамів. Методом дуальної культури досліджено штами з широким спектром антибактеріальної активності. Це дозволило продемонструвати високу селективність антагоністичної дії штамів *Trichoderma* щодо окремих тест-культур фітопатогенних бактерій. Наприклад, штам No7A пригнічував ріст *C. michiganensis* subsp. *michiganensis* 102 на 47% і *P. syringae* УКМ В-1027^{T} —на 30%, а зони інгібування росту цих тест-культур, визначені методом дифузії в агар, становили відповідно 5 і 6 мм. **Висновки.** Отримані результати свідчать про здатність штамів *Trichoderma* до біологічного контролю бактеріальних патогенів. Найбільш перспективними для використання як засобів біоконтролю фітопатогенних бактерій були штами F-60, 1515, 320, які проявляли активність проти усіх досліджених бактерій. Такі штами можуть мати потенціал як агенти біоконтролю фітопатогенів з широким спектром дії. З іншого боку, штами *Trichoderma* з високою селективною активністю проти певних патогенів є перспективними для використання як агентів біоконтролю цільового патогена.

Ключові слова: *штами Trichoderma, антагонізм, фітопатогенні бактерії, біоконтроль.*