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Ya.I. SAVCHUK*, O.M. YURIEVA, S.O. SYRCHIN, L.T. NAKONECHNA, T.I. TUHAI, A.V. TUHAI, K.S. TSYHANENKO, A.K. PAVLYCHENKO, I.M. KURCHENKO

D.K. Zabolotny Institute of Microbiology and Virology, NAS of Ukraine,
154 Akademika Zabolotnoho Str., Kyiv, 03143, Ukraine

* Author for correspondence; e-mail: majka42@ukr.net

TRICHODERMA STRAINS — ANTAGONISTS OF PLANT PATHOGENIC MICROMYCETES

Species of the genus Trichoderma are known as producers of many biologically active substances, in particular, enzymes that have found their practical application in many industries. In addition, active Trichoderma strains are used as biological control agents for plant pathogenic micromycetes. Trichoderma strains are able to exhibit antagonistic properties against plant pathogens very effectively due to their peculiarities: high growth rate; synthesis of chitinolytic enzymes and secondary metabolites with antifungal activity. Thus, highly active Trichoderma strains hasve been successfully used to control plant pathogenic isolates of Fusarium, Alternaria, Botrytis, Sclerotinia, Verticillium, Pythium, and other genera. The ***aim*** *of the study was to evaluate the antagonistic activity of 100 Trichoderma strains against eight test cultures of plant pathogenic micromycetes of different species and to select the most active strains for further studies of their physiological properties.* ***Methods****. Cultures of the studied fungi were grown on potato-dextrose agar. The antagonistic activity of fungi of the genus Trichoderma against fungal plant pathogens was established using the conventional method of dual culture. The percentages of growth inhibition of plant pathogens were calculated, and on the basis of those values, the antagonistic activity of strains was concluded. Microsoft Excel and Origin 8.0 (OriginLab) packages were used for statistical data processing.* ***Results****. According to the results for the antagonistic activity of Trichoderma strains against plant pathogenic micromycetes in general, it was shown that the strains have a high level of antifungal activity. Thus, the most numerous group (38%) of the total studied Trichoderma strains were "highly active" ones that inhibited the growth of plant pathogens from 70 to 80%. Second largest group (27%) included "moderately active" strains with 60—70% inhibition of plant pathogenic test cultures. The smallest (6%) but the most active group consisted of the "most active" strains with an average value of inhibition of more than 80%. Thus, almost three quarters (71%) of the studied Trichoderma strains showed a high level of antagonistic activity against plant pathogens with the inhibition of more than 60%. In addition, only 17% of Trichoderma strains were "inactive" and 12% of them showed insufficient activity with a growth inhibition of plant pathogens of less than 50%. Notably, 35% of Trichoderma strains were active against all eight test*

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cultures of plant pathogenic micromycetes. ***Conclusions****. The studied Trichoderma strains have significant antagonistic potential both for individual strains of plant pathogenic micromycetes and for all studied plant pathogens. The involvement of a wide range of test cultures of plant pathogens, as well as a significant number (100) of Trichoderma strains, allowed a more objective and systematic assessment of the antagonistic potential of fungi of this genus. Thus, our study of the action of the wide range of Trichoderma strains against test cultures of different species showed that the fungi of the genus Trichoderma were effective antagonists of plant pathogenic fungi. The 38% of Trichoderma strains showed a high level of antifungal action and inhibited the growth of plant pathogens by 70% and more. Only 12% of strains showed less than 50% activity. In addition, 35% of Trichoderma strains were active against all eight tested plant pathogen cultures. The significant number of studied Trichoderma strains was highly active, and thus they can be used as a basis for further research to obtain effective biological control agents of plant pathogenic micromycetes.*

Keywords: *Trichoderma strains, antagonism, plant pathogenic micromycetes, mycoparasitism, biocontrol.*

Plant pathogenic microorganisms cause large losses in the cultivation of crops, fruits, and ornamental plants. Of the various groups of plant pathogens, the most harmful are microscopic fungi, which, unlike plant pathogenic bacteria or viruses, are able to infect many more species and varieties of plants and are more resistant to pesticides [1]. Along with this, infection of plants with plant pathogenic micromycetes opens the "door" for bacterial and viral infections. Therefore, the control of plant pathogenic fungi is one of the priority areas of current science for the development of effective plant protection methods [2]. Usually, to control plant pathogens, chemical fungicides are used, which are highly effective but not environmentally friendly. There is growing interest in the use of methods and strategies for biological control of plant pathogens, in particular, the interest of agricultural producers in the use of environmentally friendly methods of biological control of plant pathogenic microorganisms using *Trichoderma* strains. For this, highly active agents of biological control of plant pathogens — antagonistic strains based on their biological activity — are increasingly used [3]. The consumer demand for organic farming products that are grown without pesticides of chemical origin is also growing. Thus, scientific and commercial interest in the study and implementation of new highly active strains for biological control of plant pathogenic micromycetes is a vanguard in strategies to protect and increase the yield of agricultural plants.

According to the literature, the most effective antagonists of plant pathogenic micromycetes are species of the genus *Trichoderma* [4]. Strains of this genus are widely spread in various econiches. Biologically active *Trichoderma* strains are known as producers of many active metabolites against plant pathogens [5]. High antifungal activity of *Trichoderma* fungi is associated with their ability to synthesize a complex of hydrolytic enzymes, in particular, chitinases, which destroy the cell walls of plant pathogenic fungi and create conditions for mycoparasitism. Along with this, the researchers provide data on the synthesis by Trichoderma strains secondary metabolites of low molecular mass, primarily non-ribosomally synthesized peptides — peptaibols that exhibit antifungal and antibacterial activities [6]. Due to the complex action of metabolites synthesized by *Trichoderma* strains, they are highly effective antagonists of plant pathogenic micromycetes. The biological activity of different strains of the genus *Trichoderma* can vary greatly, so scientists focus on the study of individual strains [7]. At the same time, there are very few works devoted to the extensive screening of antifungal activity of the *Trichoderma* species. In view of this, studies of the antifungal activity of strains of this genus isolated from different econiches may be promising for screening highly active plant pathogen antagonists. Notably, the large-scale screening of *Trichoderma* strains with the involvement of a significant number of test cultures of plant

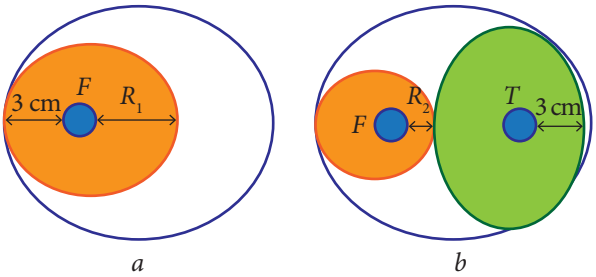

Fig. 1. Scheme of study of antagonistic activity of *Trichoderma* strains by the method of dual culture: *a* — control Petri dish; *b* — the dish with a dual culture

pathogenic fungi will provide an opportunity to expand the understanding of the potential of antifungal activity of different strains of this genus.

The **aim** of the present study was to assess the antagonistic activity of 100 strains of the genus *Trichoderma* against eight test cultures of plant pathogenic micromycetes and selection of the most active strains for further studies of their physiological properties.

Materials and methods. The objects of the research were 100 fungal strains of the genus *Trichoderma* and eight test cultures of plant pathogenic fungi from the Culture collection of microscopic fungi of the Department of Physiology and Taxonomy of Micromycetes of D.K. Zabolotny Institute of Microbiology and Virology of the NAS of Ukraine (Table 1).

The method of dual culture. Cultures of the studied fungi were preliminarily grown on potato-dextrose agar (PDA) in Petri dishes and incubated at a temperature of 26 ± 2°C for 10—14 days.

The conventional method of dual culture [8] was used to determine the antagonistic activity of fungi of the genus *Trichoderma* against plant pathogenic fungi (Fig. 1). An inoculum (5×5 mm) from the edge of the colony of each isolate (*Trichoderma* strains and plant pathogenic test cultures) was used to inoculate standard size Petri dishes (9 cm diameter) with Czapek's agar medium (20 mL/dish).

The inoculum of the phytopathogenic test strain was placed at a distance of 3 cm from the dish edge. On the other side, this dish was inoculated with the studied *Trichoderma* strain at a distance of 3 cm from the edge. The distance between the sites inoculated with the plant pathogenic strain and *Trichoderma* ones was 3 cm. In control Petri dishes, appropriate test cultures of plant pathogenic micromycetes were cultured without an antagonistic strain of the genus *Trichoderma*.

Incubation of the studied fungi was carried out at a temperature of 26 ± 2°C for 2—7 days. The percentage of growth inhibition of plant pathogenic fungi by the antagonistic *Trichoderma* strains was evaluated according to the formula [9]:

$$I\ (\%) = \frac{R_1 - R_2}{R_1} \cdot 100,$$

where R_1 is the radius of the colony of the plant pathogenic strain under control; R_2 is the ra-

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

No	Strain	Source	Region of isolation, year
1	15966 *Nigrospora oryzae*	Wheat grain	Mykolaiv oblast, 1986
2	50718 *Fusarium solani*	Ash branch	Kyiv oblast, 2014
3	3043 *Alternaria alternata*	Onion seeds	Kherson oblast, 2016
4	3041 *Nectria inventa*	Corn grain	Kyiv oblast, 2003
5	16884 *Botrytis cinerea*	Cherry stalk	Kyiv oblast, 2019
6	16868 *Bipolaris sorokiniana*	Wheat grain	Poltava oblast, 1998
7	16883 *Sclerotinia sclerotiorum*	Tomatoes	Kyiv oblast, 1999
8	16036 *Rhizoctonia solani*	Wheat grain	Kyiv oblast, 1998

dius of the colony of the plant pathogen with a *Trichoderma* strain.

All experiments were performed in triplicate. The percentage of growth inhibition of plant pathogens was calculated. It was concluded about the antagonistic activity of *Trichoderma* strains against plant pathogens.

Microsoft Excel and Origin 8.0 (OriginLab) packages were used for statistical data processing.

Results. It was found that the antifungal potential of the studied *Trichoderma* strains is high, and the most active strains are promising for further studies to obtain on their basis biological control agents for plant pathogenic micromycetes (Table 2). Figure 2 shows the antagonistic interaction of fungi of the *Trichoderma* genus with test cultures of plant pathogenic fungi.

Thus, almost all studied *Trichoderma* strains showed inhibitory activity against plant pathogenic test cultures (Fig. 2). Only one in one hundred strains 1302 did not show significant antifungal activity against any of the test plant

Table 2. **Growth inhibitiaon (%) of plant pathogens under the action of the fungi of *Trichoderma* genus**

No	*Trichoderma* strain	Test culture of plant pathogenic fungi							
		Nigrospora oryzae	*Fusarium solani*	*Alternaria alternata*	*Nectria inventa*	*Botrytis cinerea*	*Bipolaris sorokiniana*	*Sclerotinia sclerotiorum*	*Rhizoctonia solani*
1	3076	69	40	60	44	58	43	48	59
2	3089	63	64	54	44	40	57	61	58
3	3077	60	52	68	50	65	55	68	64
4	3083	72	48	72	63	45	62	64	58
5	3069	75	60	58	56	48	52	57	70
6	3074	71	38	60	50	60	57	70	65
7	3075	66	29	54	50	35	48	68	63
8	3067	78	52	58	44	55	55	57	69
9	3064	69	48	68	63	53	52	59	55
10	3062	74	36	52	50	60	45	61	64
11	3060	54	24	24	50	3	52	9	74
12	3082	60	29	46	44	35	48	50	60
13	3072	80	48	64	81	90	69	82	83
14	3087	94	62	82	81	95	81	95	96
15	3066	86	62	64	88	95	74	93	90
16	3068	76	38	62	81	95	76	75	69
17	3057	86	52	60	88	90	74	77	85
18	3061	73	48	62	81	90	71	89	72
19	3059	88	57	72	81	88	62	91	85
20	3070	70	38	58	81	95	60	93	78
21	344	81	36	60	63	90	76	82	79
22	3102	84	57	72	63	88	60	86	96
23	3100	78	10	64	38	60	52	80	66
24	3099	97	19	58	56	95	52	73	96
25	3091	78	2	48	75	90	50	91	48
26	2925	84	43	52	69	63	76	84	55

Continuation of table 3

No	*Trichoderma* strain	Test culture of plant pathogenic fungi							
		Nigrospora oryzae	*Fusarium solani*	*Alternaria alternata*	*Nectria inventa*	*Botrytis cinerea*	*Bipolaris sorokiniana*	*Sclerotinia sclerotiorum*	*Rhizoctonia solani*
27	3093	95	48	58	63	90	64	91	73
28	3104	85	36	66	44	88	74	89	95
29	2928	85	33	60	56	88	67	89	73
30	2933	83	12	46	44	45	40	77	74
31	1244	78	57	62	50	68	64	70	74
32	3095	69	55	58	56	30	57	52	78
33	3101	79	64	72	69	90	76	91	82
34	3103	86	67	72	75	63	74	57	75
35	3349	73	55	54	63	83	67	70	83
36	2932	97	79	62	69	90	71	77	84
37	3107	79	71	76	75	73	74	80	92
38	2916	73	55	50	44	60	64	68	78
39	3096	66	57	50	38	83	67	77	74
40	3105	70	62	56	63	83	62	48	67
41	1602	78	26	62	56	70	60	73	72
42	3094	85	38	66	56	55	67	68	91
43	2768	86	29	80	25	48	64	77	85
44	1242	87	57	66	75	78	81	57	95
45	1662	84	60	76	50	85	60	61	72
46	368	89	57	68	75	55	62	68	73
47	843	90	62	64	50	78	74	77	88
48	2930	69	48	52	63	70	57	59	82
49	1299	67	29	60	50	50	62	45	78
50	904	72	52	68	88	50	67	73	89
51	3121	89	10	38	50	63	48	43	63
52	3126	93	64	64	50	88	57	66	77
53	3124	72	24	46	50	45	50	75	77
54	3120	66	2	56	63	48	60	73	68
55	3122	75	24	68	88	70	64	70	95
56	3127	81	24	72	81	85	69	68	88
57	3128	72	62	74	69	85	64	59	87
58	3123	87	48	76	75	83	69	80	84
59	3125	80	19	54	50	35	50	50	92
60	3097	79	48	58	88	88	64	75	87
61	2924	86	64	84	75	80	71	91	79
62	2455	71	40	48	25	55	50	80	63
63	1243	69	67	70	75	75	55	73	76
64	No1	90	71	80	81	85	71	91	77

Continuation of table 3

No	*Trichoderma* strain	Test culture of plant pathogenic fungi							
		Nigrospora oryzae	*Fusarium solani*	*Alternaria alternata*	*Nectria inventa*	*Botrytis cinerea*	*Bipolaris sorokiniana*	*Sclerotinia sclerotiorum*	*Rhizoctonia solani*
65	No2	93	60	72	75	85	67	84	83
66	No3	80	60	72	75	80	71	77	86
67	No4	84	57	82	75	85	50	77	80
68	No5	81	45	72	44	73	67	89	87
69	No6	86	57	64	75	80	81	84	71
70	No7A	82	79	78	88	80	86	77	91
71	3112	72	71	72	75	85	71	86	73
72	3117	83	48	60	63	75	76	91	69
73	3108	93	62	80	75	85	76	95	75
74	3109	98	76	76	88	95	81	95	91
75	3115	91	52	40	63	35	43	77	78
76	16p	83	62	60	75	75	71	77	78
77	3118	72	67	76	75	50	57	95	91
78	3113	83	67	68	75	85	76	86	82
79	3111	86	62	72	75	90	71	86	78
80	3116	79	52	76	88	95	57	91	82
81	3058	63	7	38	36	30	16	43	37
82	3063	65	14	27	42	40	25	58	37
83	3065	66	24	36	57	56	41	87	41
84	3071	66	7	19	71	38	20	64	39
85	3073	67	17	20	71	47	33	62	32
86	3081	64	7	19	16	18	15	58	33
87	3084	75	21	39	64	36	25	85	39
88	3085	80	29	41	51	47	29	75	42
89	3088	66	11	33	40	42	33	76	43
90	906	81	14	30	43	47	33	45	40
91	3010	66	44	35	100	100	37	75	47
92	3078	74	41	67	100	100	50	58	44
93	3079	54	41	52	100	100	58	90	45
94	F-60	73	35	57	100	100	50	87	53
95	1515	74	50	57	100	100	58	100	51
96	2989	63	36	45	100	100	36	100	48
97	320	82	50	52	100	100	62	100	70
98	2554	65	47	47	100	100	58	78	48
99	1302	38	20	29	43	15	10	30	29
100	2550	60	40	40	100	100	50	78	47

Note: All assays were performed in three independent experiments. Differences in averages were considered significant at a level of $P<0.05$.

pathogenic fungi. The degree of growth inhibition of plant pathogens by this strain did not exceed 43%, which is lower than 50% proposed by our chosen method as a sufficient level of activity. Along with this, the more active *Trichoderma* strains showed antifungal activity against several test cultures. In particular, 906 and 3058 strains inhibited only one test culture *N. oryzae* with a percentage of inhibition of 84 and 63%, respectively. More active 3082, 2933, 3071, 3073, 3084, and 3085 strains had an inhibitory effect on three test cultures of plant pathogenic micromycetes.

Only three of the studied *Trichoderma* strains (3081, 3063, and 3088) showed antifungal activity against two plant pathogenic test cultures *N. oryzae* and *S. sclerotiorum*, with the percentage of growth inhibition of test fungi being in the range from 58 to 76%. A histogram of the distribution of antifungal activity of the studied *Trichoderma* strains is shown in Fig. 3.

Another group includes 3076, 3060, 3121, 3065, 3010, and 2989 *Trichoderma* strains which were active against four plant pathogens. The most sensitive to the action of these strains were test cultures of *N. oryzae* and *S. sclerotiorum*.

The eight *Trichoderma* strains 3075, 3091, 2768, 3124, 2455, 3115, 2554, and 2550 showed inhibitory activity against five test fungi. In this group, strain 3115 was highly active against *N. oryzae*, *S. sclerotiorum,* and *R. solani* with a percentage of growth inhibition of plant pathogens 91, 77, and 78%, respectively. Another strain 3091 had high activity against *B. cinerea* and *S. sclerotiorum* with growth inhibition of these plant pathogens over 90%.

The most numerous and the most active group of *Trichoderma* strains were 3089, 3083, 3062, 3104, 3100, 2916, 3096, 1299, 3120, 3125, No5, 3078, and 3079 inhibited the growth of six plant pathogens. Among them, strain 3104 had high inhibitory activity against *N. oryzae, B. cinerea, S. sclerotiorum,* and *R. solani* with a percentage of inhibition over 80%.

The largest group of *Trichoderma* strains consists of 26 strains that showed antifungal activity against seven test cultures of plant pathogenic fungi. The most active of the studied *Trichoderma* strains were 35 ones that showed antifungal activity against all plant pathogens. From two the most active groups, promising strains for further research were selected. Six strains, namely 3087, 3066, No1, No7A, 3108, and 3109 with an average value of growth inhibition of plant pathogens over 80%, were the most active of them.

The data on the average value of the growth inhibition of test cultures of plant pathogenic micromycetes were obtained and analyzed (Fig. 4).

Thus, the majority of strains (38%) were classified as "highly active". That is, the average values of growth inhibition of plant pathogens under the action of *Trichoderma* strains of this group were not less than 70%. The smallest *Trichoderma* group of strains was classified as "most active" (6%). These strains are promising for further research because they are able to inhibit the growth of plant pathogens by 80% and more. However, we do not rule out the fact that among the most numerous groups of "highly active strains" there are no less competitive isolates. Notably, the second largest group included strains that were classified by us as "moderately active" (27%), which indicates a very high antagonistic potential of the studied *Trichoderma* strains against plant pathogenic fungi. The growth inhibition of plant pathogens under the action of these strains was in the range of 60—69%. It should be noted that among the classified as "inactive" strains there are some ones that may also deserve the attention of researchers as capable to selectively act on individual plant pathogens. Thus, strains 3085 and 906 with average values of growth inhibition of plant pathogens 49 and 42%, respectively, are able to inhibit the growth of *N. oryzae* by more than 80%.

Based on the results ~~of~~ for the resistance of plant pathogenic fungi to *Trichoderma* strains, the following conclusions can be drawn. The most sensitive to the antagonistic action of *Trichoderma* strains was the *Nigrospora oryzae*

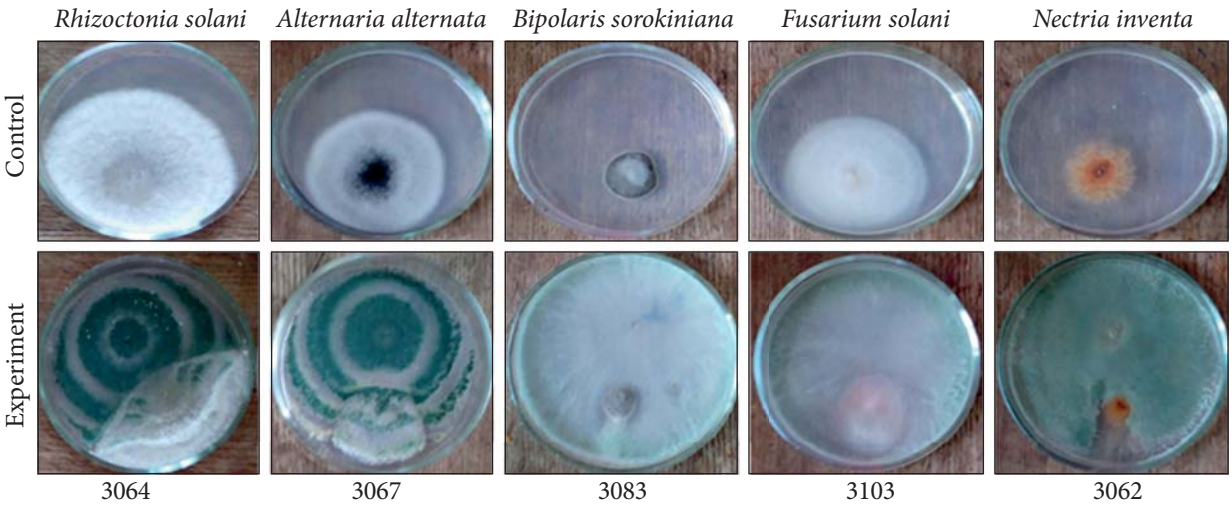

Fig. 2. Antifungal activity of *Trichoderma* strains against plant pathogenic micromycetes

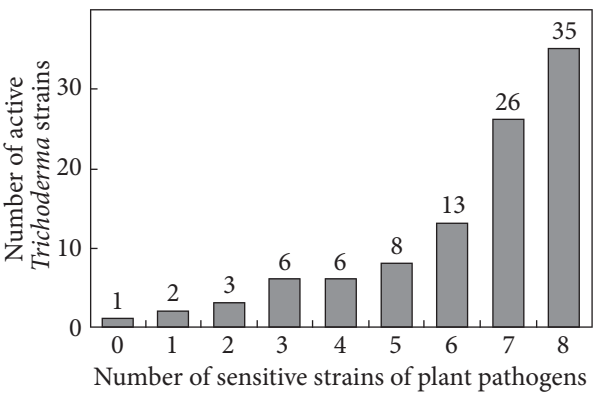

Fig. 3. Distribution of antifungal activity of *Trichoderma* strains

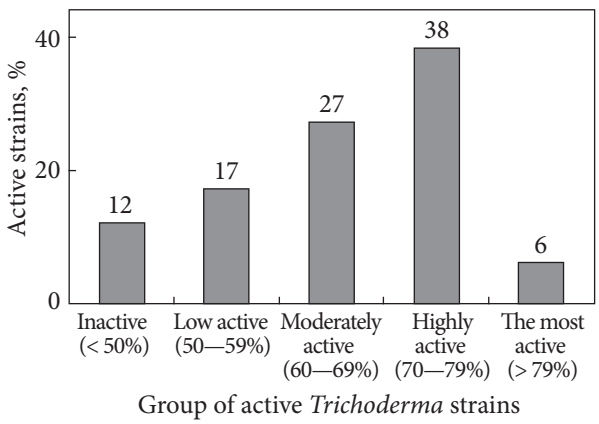

Fig. 4. Antifungal activity of *Trichoderma* strains by the average value of growth inhibition of plant pathogens

strain, because only one (1302) of one hundred *Trichoderma* strains did not show the proper level of activity. On the other hand, the most resistant was *Fusarium solani*: 55 *Trichoderma* strains did not show sufficient antagonistic activity against it. In addition, a relatively sensitive was plant pathogen *Sclerotinia sclerotiorum*, to which only eight *Trichoderma* strains were not active.

Thus, the studied *Trichoderma* strains have significant antagonistic potential both for individual strains of plant pathogenic micromycetes and for all plant pathogens studied.

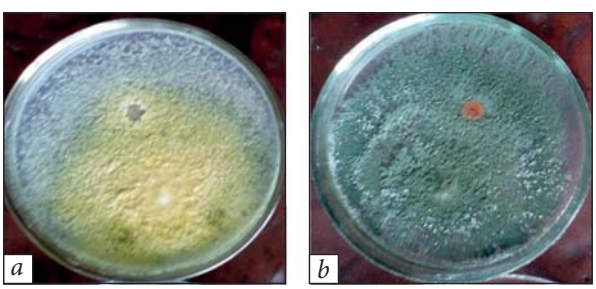

Fig. 5. Antifungal activity of *Trichoderma* 2932 (*a*) and 344 (*b*) strains against *Nectria inventa*

Discussion. *Trichoderma* species are quite common in natural econiches (soil, plant residues) as saprotrophs and endophytes [10, 11]. Thanks to the fruitful work of scientists, *Trichoderma* strains are used not only in industry for the synthesis of important enzyme preparations but also occupy a leading position in the market of preparations for biological control of plant pathogenic microorganisms [4]. Plant pathogens cause significant and sometimes catastrophic crop losses. Despite significant success in the use of chemical pesticides, technologies for obtaining resistant plants and advanced methods of agricultural science, the problem of biological control of plant pathogens is relevant. Among plant pathogenic microorganisms, micromycetes cause the greatest damage. The use of fungicides is a common practice in the world to control phytopathogenic fungi, but this strategy has some disadvantages that significantly limit their use [12]. Among agents of biological control of plant pathogenic micromycetes, the most effective are preparations created on the basis *Trichoderma* strains with high antagonistic activity [13]. These preparations are widely represented on the market, in particular, in Ukraine.

The data on the antifungal activity of the studied *Trichoderma* strains suggest that their antagonistic potential against plant pathogenic micromycetes is significant. According to the results of research, promising antagonistic strains can be selected. Thus, the most active were six *Trichoderma* strains, which almost completely inhibited the growth of plant pathogens with growth inhibition values of more than 80%. In addition, the group with high antagonistic activity was the largest (38 strains) among the studied *Trichoderma* strains (Fig. 4). In general, according to the average values of growth inhibition of plant pathogens, 88% of the studied *Trichoderma* strains can be considered active, which significantly indicates the high antifungal potential of these micromycetes.

Although researchers have not definitively concluded the main mechanism of antifungal activity of *Trichoderma* species, they point to two possible factors: the synthesis of a complex chitinolytic enzymes and the synthesis of secondary metabolites with antifungal activity [14]. In our opinion, researchers often do not pay due attention to the third factor — the growth rate of *Trichoderma* fungi, which also affects the antagonistic activity. It is known that the genus *Trichoderma* belongs to the micromycetes that grow rapidly. Due to this ability, *Trichoderma* strains quickly colonize the substrates, depriving the competitor fungus of living space and nutrient sources consequently. We have repeatedly observed this factor of antagonism in this study. Thus, the antagonistic interaction of *Trichoderma* 2932 and 344 strains with plant pathogen *Nectria inventa*, which has significantly lower growth rate, is shown in Fig. 5. Due to the high growth rate, strains 2932 and 344 almost completely colonize the substrate, thus significantly limiting the growth of the plant pathogen.

However, only the growth rate of the fungus is not enough to detect a high degree of antagonism. As mentioned above, there are two key factors in the high antifungal activity of the genus *Trichoderma:* synthesis of enzymes and secondary metabolites. Today there is a large array of data on the synthesis of enzyme complexes and the role of chitinolytic enzymes in the detection process of antifungal activity of these fungi [15—18]. Since chitin is the major component of fungal cell walls, a primary role has been attributed to chitinases in the biocontrol activity of *Trichoderma*. The *Trichoderma* strains are able to synthesize complexes of chitinases, β-glucanases, and proteases. These enzymes are induced by contact of *Trichoderma* hyphae with ones of plant pathogenic micromycetes. The enzyme system responsible for the chitinolytic activity of *Trichoderma* consists of at least six enzymes: two N-acetylglucosaminidases and four endochitinases [16]. The enzymatic activity of this complex is induced by chitin, cell walls of other fungi, or lack of carbohydrate nutrition, while the inhibition of the activity of these enzymes occurs in the presence of glucose. Genes encoding enzymes of chitinase

complex were isolated from *Trichoderma* strains and were named *chit42* and *chit33* [19, 20]. The study of the structure and properties of genes encoding the chitinolytic complex of enzymes will provide a better understanding of the relationship between the diversity of enzymes and their effect on the processes of antagonistic activity against plant pathogenic micromycetes. Thus, it has been reported [17] that *T. harzianum* strains under growing in a liquid nutrient medium containing inducers (laminarin, chitin, and remnants of the cell wall of fungi) are able to synthesize high levels of endogluconases and chitinases. According to the authors, this fact is the cause of mycoparasitic activity of the studied *Trichoderma* strains against fungi of the genus *Fusarium*. Mycoparasitism is a direct attack of one fungus (mycoparasite) on another (victim) in order to use prey as a source of nutrients. Key stages of the process include the recognition of prey, positive chemotropic growth to it, and chemical-physical attacks (combination of both usually leads to the death of the hyphae of the victim and the absorption of nutrients). The pre-contact chemical attack includes the induced production of cell wall degrading enzymes; on the other hand, physical attack acts during the contact phase and is accompanied by significant morphological changes: intense branching, hyphal coiling or the formation of appressorium-like structures on hyphal tips [21, 22].

Another, no less effective, mechanism of antifungal activity of *Trichoderma* fungi is the synthesis of low molecular mass metabolites with antifungal activity. More than ten active fractions exhibiting antifungal activity were isolated from the extract obtained from the endophyte *T. longibrachiatum* T6 [14]. The two most active compounds MEPH and DIBP showed a significant level of activity against *Valsa mail* and other plant pathogens. The researchers concluded that the *T. longibrachiatum* T6 may be an effective antagonist of *V. mail*, and the mechanism of this activity is the synthesis of highly active secondary metabolites by this strain.

T. atroviride and *T. asperellum* strains showed a high level of antibacterial activity against both gram-positive and gram-negative bacteria, as well as antifungal activity against five isolates of plant pathogenic fungi [23]. Extracts of *T. brevicompactum* showed activity against plant pathogens: *S. rolfsii*, *Colletotrichum gloesporioides*, *V. dahliae*, *F. oxysporum*, and *Cylindrocladium* sp. [24]. The *Trichoderma* strains can be a source of many biologically active metabolites with wide practical use [25].

There is a wide range of data on the biological activity of different groups of secondary metabolites produced by *Trichoderma* species. A group of compounds belonging to the class of epipolithiodioxypiperazines shows significant antifungal activity, and the most active among them is the antibiotic gliotoxin [26]. This metabolite is able to inhibit the growth of a wide range of plant pathogens such as *Rhizoctonia* spp., *Macrophomina* spp., *Pythium* spp., *Sclerotium* spp., etc. Metabolites belonging to peptaibols, in particular trichoconins isolated from *T. koningii*, show a high level of activity against plant pathogens *Rhizoctonia solani*, *F. oxysporum*, *V. dahlia*, and *B. cinerea* [27]. Isolated from *T. koningii* and *T. harzianum* secondary metabolites of the pyrones class inhibit the growth of plant pathogens *F. oxysporum* and *R. solani* at a concentration of 0.3 mg/mL [28, 29]. The compounds belonging to the group of butenolides, in particular two metabolites isolated from *T. harzianum*, garzanolide and butenolide, exhibit antifungal activity against plant pathogens *P. ultimum*, *R. solani,* and *B. cinerea* [30]. Isolated from the active *T. harzianum* strain garzianopyridone, belonging to the group of pyridones, has an antifungal effect against *P. ultimum*, *G. graminis* var. *tritici*, *R. solani,* and *B. cinerea* [31].

Therefore, basing on these data, we can conclude that the synthesis of secondary metabolites with the antifungal action of fungi of the genus *Trichoderma* is one of the effective mechanisms of their high antagonistic activity against plant pathogenic micromycetes. It should be noted that

such a high antagonistic potential of *Trichoderma* fungi is achieved not only due to the antifungal activity of individual metabolites but also due to the synthesis of a range of such metabolites of different chemical structures. It is obvious that such complexes of metabolites were formed during the long coevolution of *Trichoderma* fungi and the plant pathogens, with which they competed for living space. As a result of this evolutionary progress, *Trichoderma* species have gained the ability to compete with plant pathogens in the most effective way, which is an undeniable advantage of using biological products based on these fungi over using chemical pesticides.

Therefore, the high level of antifungal activity of the studied *Trichoderma* strains can be explained by the presence of three mechanisms: high growth rate, synthesis of enzyme complexes, and secondary metabolites. Notably, these factors act effectively only in a complex. For example, the studied plant pathogenic strain of *N. oryzae* is not inferior to *Trichoderma* in growth rate but it is the least resistant to the antifungal action of *Trichoderma* strains. On the other hand, the used in our studies *F. solani* has also a fairly high growth rate, as well as *N. oryzae*, but *F. solani* strain is the most resistant to *Trichoderma* fungi among all studied plant pathogens. Thus, it can be assumed that along with the high growth rate, the resistance of *F. solani* is determined by other factors. In our opinion, among such factors may be the ability of *Fusarium* species to synthesize secondary metabolites from the group of trichothecene mycotoxins [32]. Trichothecenes, along with a significant level of cytotoxic and dermatocidal activity against warm-blooded animals, are able to show a high antifungal effect. Thus, due to the high growth rate and synthesis of trichothecenes, *F. solani* is resistant to the antagonistic effects of some *Trichoderma* strains. In particular, our data indicate that 55 strains of *Trichoderma* show inhibitory activity against *F. solani* at levels below 50%.

In general, the literature provides data on the use of *Trichoderma* strains against phytopathogenic *Fusarium* species. The problem of *Fusarium* wilt is quite acute, because *Fusarium* wilt can lead to yield losses in some crops up to 95% [33]. Two strains, namely *T. harzianum* and *T. longibrachiatum,* were effective in the control of *F. solani*. In addition, another strain of *T. harzianum* Ths97 showed a high level of antagonism against *F. solani* isolates, which parasitize on the roots of olive trees [34]. Only four of the 21 *Trichoderma* strains were selected as antagonists of pathogenic isolates of *F. solani* and *F. oxysporum,* which affected *Cicer arietinum* crops [35]. Our study has shown that 45 of 100 strains of *Trichoderma* exhibit antifungal activity against *F. solani*. In addition, more than half of them (26) inhibit the growth of *F. solani* by 60% and above. Six strains were highly active against this plant pathogen and inhibited the growth of *F. solani* by more than 70%.

The high activity of the studied by us *Trichoderma* strains may be a prerequisite for further research to obtain highly effective preparations for biological control of plant pathogens of the genus *Fusarium*.

It should be noted that the chosen by us method (dual culture method) for studying the antagonistic activity of *Trichoderma* fungi is widely used by scientists and allows complete assessing their antifungal potential against plant pathogenic isolates. In particular, the literature provides data obtained by this method on the antifungal activity of *Trichoderma* strains [36—39]. In particular, the results of the antagonistic action of *T. atroviride* and *T. asperellum* strains against phytopathogenic fungi were obtained using the dual culture method [24]. It was found that the highest values of growth inhibition of plant pathogens were 76 and 81%, respectively. Other authors obtained data on the activity of *Trichoderma* strains against the plant pathogen *Ceratocystis paradoxa* causing soft rot disease of pineapples [37].

Based on the method of dual culture, it was shown that the most active strain was *T. harzianum* IMI-392432, which inhibited the growth of plant pathogen by 80.82%; the other strains

studied by the authors were less active. The antagonistic activity of four *Trichoderma* strains against plant pathogens *Sclerotium rolfsii*, *Sclerotionia sclerotiorum*, *Fusarium solani,* and *Rhizoctonia solani* was studied. The authors found [38] that the plant pathogen *Sclerotium rolfsii* was almost completely inhibited by all *Trichoderma* strains. In contrast to it, *Sclerotionia sclerotiorum* was resistant to *Trichoderma:* the range of the growth inhibition of this plant pathogen did not exceed 22%. The *Trichoderma* strains were somewhat more active against *Rhizoctonia solani* with growth inhibition of plant pathogen ranging from 29—66%. The most active strain TS 215 inhibited the growth of *F. solani* by only 63%; the other strains were less active. Comparing these data with our results, it should be concluded that the studied by us strains were more active. Thus, 26 strains of *Trichoderma* inhibited the growth of the plant pathogen *F. solani* by more than 60%. In particular, strains 2932, 3107, No1, No7A, 3112, and 3109 showed a high level of activity against this plant pathogen and delayed its growth by 70% and more. The most active strains were two strains 2932 and No7A, which delayed the growth of *F. solani* by 79%.

In addition, studied in our work *Trichoderma* strains were also active against the plant pathogen *Rhizoctonia solani*. In particular, 13 strains inhibited the growth of plant pathogen by 90% or more, the most active of them were strains 3087, 3102, and 3099, which inhibited the growth of *Rhizoctonia solani* by 96%. The *Trichoderma* strains were also active against *Sclerotionia sclerotiorum*. In particular, 18 strains of *Trichoderma* inhibited the growth of this plant pathogen by 90% and more. This indicates unequivocally a very high level of antagonistic activity of *Trichoderma* strains against *Sclerotionia sclerotiorum*.

Therefore, our results are consistent with the data of the other researchers on the high antifungal potential of the genus *Trichoderma*. At the same time, our study allows one to expand our understanding of the antagonistic potential of fungi of the genus *Trichoderma*. The involvement of a wide range of test cultures of plant pathogens of different species, as well as 100 strains of *Trichoderma* allowed a more objective and systematic assessment of the antagonistic potential of fungi of this genus. In particular, the comparison of our data with the results of other scientists [39] showed that the involvement of a small number of test fungi and *Trichoderma* strains (only four strains) can lead to some incorrect conclusions. Thus, the authors found that their studied *Trichoderma* strains were inactive against *Sclerotionia sclerotiorum*, *Rhizoctonia solani,* and *F. solani*. At the same time, our studies showed the high antifungal potential of *Trichoderma* strains against the above plant pathogens. A large number of studied by us *Trichoderma* strains showed a high antagonism level, but some strains were less active.

It was empirically established that antagonistic activity of the studied strains increases with increasing spore formation levels. This pattern may have a significant prognostic effect at the level of pre-selection of potentially active antagonists among *Trichoderma* strains. We can assume that a higher level of sporulation of our studied *Trichoderma* strains is related to a higher level of antifungal activity.

Conclusions. Thus, our study of the action of the wide range of *Trichoderma* strains against test cultures of plant pathogens of different species showed that the fungi of the genus *Trichoderma* are effective antagonists of plant pathogenic fungi. The 38% of *Trichoderma* strains showed a high level of antifungal action and inhibited the growth of plant pathogens by 70% and more. Only 12% of strains showed less than 50% activity. In addition, 35% of *Trichoderma* strains were active against all eight tested plant pathogen test cultures. The significant number of studied *Trichoderma* strains was highly active, and thus they can be used as a basis for further research to obtain effective biological control agents for plant pathogenic micromycetes [40].

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Я.І. Савчук, О.М. Юр'єва, С.О. Сирчін, Л.Т. Наконечна,
Т.І. Тугай, А.В. Тугай, К.С. Циганенко, А.К. Павличенко, І.М. Курченко

Інститут мікробіології і вірусології ім. Д.К. Заболотного НАН України,
вул. Академіка Заболотного, *154,* Київ, *03143,* Україна

ШТАМИ *TRICHODERMA* — АНТАГОНІСТИ ФІТОПАТОГЕННИХ МІКРОМІЦЕТІВ

Види роду *Trichoderma* відомі як продуценти багатьох біологічно активних речовин, зокрема ферментів, що знайшли своє практичне застосування у багатьох галузях промисловості. Поряд з цим, активні штами роду *Trichoderma* застосовують як агенти біологічного контролю фітопатогенних мікроміцетів. Завдяки ряду особливостей (висока швидкість росту; синтез комплексу хітинолітичних ферментів; синтез вторинних метаболітів з антифунгальною активністю), штами *Trichoderma* здатні дуже ефективно проявляти антагоністичні властивості щодо фітопатогенів. Так, високоактивні штами р. *Trichoderma* успішно застосовують для контролю фітопатогенних ізолятів родів *Fusarium, Alternaria, Botrytis, Sclerotinia, Verticillium, Pythium* та ін. **Мета**. Оцінити антагоністичну активність 100 штамів роду *Trichoderma* щодо восьми тест-культур фітопатогенних мікроміцетів різних видів і відібрати найбільш активні штами для подальших досліджень їхніх фізіологічних властивостей. **Методи**. Культури досліджених грибів попередньо вирощували на картопляно-глюкозному агарі. Для визначення антагоністичної активності грибів роду *Trichoderma* щодо фітопатогенних грибів використовували загальноприйнятий метод дуальної культури. Обчислювали відсотки інгібування росту фітопатогенів і на основі цих значень робили висновок про активність щодо них штамів-антагоністів. Для статистичної обробки даних використовували пакети Microsoft Excel та Origin 8.0 (OriginLab). **Результати**. За результатами проведеного дослідження антагоністичної активності штамів *Trichoderma* проти фітопатогенних мікроміцетів, загалом було показано, що штами мають високий рівень антифунгальної активності. Так, найбільш чисельну групу (38 %) з усіх досліджених штамів *Trichoderma* складали «високоактивні» штами, які інгібували ріст фітопатогенів від 70 до 80 %. Другу за чисельністю групу (27 %) штамів складали «середньоактивні» штами з відсотком інгібування фітопатогенних тест-культур 60—70 %. Найменшу за чисельністю (6 %), але найбільш активну групу складали «найактивніші» штами із середнім значенням відсотка інгібування більше 80 %. Отже, майже три чверті (71 %) досліджених штамів *Trichoderma* проявляли високий рівень антагоністичної активності проти фітопатогенів з інгібуванням більше 60 %. Поряд з цим, лише 17 % штамів *Trichoderma* були «малоактивними» і 12 % штамів проявляли недостатній рівень активності щодо інгібування росту фітопатогенів — менше за 50 %. Також слід зазначити, що 35 % штамів *Trichoderma* проявляли активність щодо всіх восьми досліджених тест-культур фітопатогенних мікроміцетів. **Висновки**. Досліджені штами *Trichoderma* мають значний антагоністичний потенціал як проти окремих штамів фітопатогенних мікроміцетів, так і проти усіх досліджених фітопатогенів. Залучення широкого спектру тест-культур фітопатогенів різних видів, а також значної кількості (100) штамів роду *Trichoderma* дозволило більш об'єктивно і системно оцінити антагоністичний потенціал грибів цього роду. Отже, наше дослідження дії широкого спектру штамів *Trichoderma* на тест-культури різних видів показало, що гриби роду *Trichoderma* є ефективними антагоністами фітопатогенних грибів. 38 % штамів *Trichoderma* показали високий рівень антифунгальної активності і пригнічували ріст фітопатогенів на 70 % і більше. Лише 12 % штамів виявили нижчу за 50 % активність. Крім того, 35 % штамів *Trichoderma* були активні проти усіх восьми тест-культур фітопатогенів. Значна кількість досліджених штамів *Trichoderma* виявилася високоактивною, і вони можуть бути використані як основа для подальших досліджень з метою отримання ефективних засобів біологічного контролю фітопатогенних мікроміцетів.

Ключові слова: *штами Trichoderma, антагонізм, фітопатогенні мікроміцети, мікопаразитизм, біоконтроль.*