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ANTIBACTERIAL, ANTIFUNGAL, PHYTOTOXIC AND ANTIVIRAL ACTIVITY OF ENDOPHYTIC AND SAPROTROPHIC *PENICILLIUM FUNICULOSUM* THOM STRAINS

*Olena M. Yurieva, Anhelina M. Kyrychenko, Kateryna S. Tsyhanenko, Anna K. Pavlychenko, Serhii O. Syrchin, Yaroslav I. Savchuk**

Address(es): Dr. Yaroslav I. Savchuk,
Zabolotny Institute of Microbiology and Virology of National Academy of Science of Ukraine, Department of physiology and systematics of micromycetes, 154 Akad. Zabolotny Str., Kyiv, 03143, Ukraine, +380445261179.

*Corresponding author: majka42@ukr.net

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ABSTRACT

Fungi of the genus *Penicillium* provide an almost inexhaustible source of biologically active metabolites with a wide range of activities due to their physiological and biochemical features. *Penicillium funiculosum* Thom can adopt various lifestyles, ranging from soil saprotrophs and endophytic mutualists. *P. funiculosum* represent a resource for the discovery of new biologically active molecules and biocatalysts. **The aim** of the research was to investigate the antibacterial, antifungal, antiviral, and phytotoxic activities of endophytic and saprotrophic *P. funiculosum* strains. **Methods.** The antibacterial and antifungal activities of *P. funiculosum* strains were determined using the agar well diffusion method. Antiviral activity was tested *in vitro* using the tobacco mosaic virus (TMV, strain U1) model. Phytotoxic effects were assessed using corn seedlings test and the bioassay method for *Chlorella*. **Results.** Saprotrophic *P. funiculosum* strains demonstrated a high level of antibacterial activity against plant pathogenic bacteria, the growth inhibition zones were 15 to 45 mm. Endophytes had selective antibacterial activity against these test cultures. The absence antifungal activity of all investigated *P. funiculosum* strains was shown. Saprotrophic strains inhibiting the growth of corn roots and sprouts by 4–61%, while endophytic strains proved to be non-phytotoxic. Endophytic and saprotrophic strains expressed the anti-viral activity against TMV. **Conclusion.** The biological activities of endophytic and saprotrophic *P. funiculosum* strains indicate significant differences between these two ecological-trophic groups. The differences in certain physiological and biochemical characteristics of these two groups of strains and suggest that these traits may serve as markers for their differentiation.

Keywords: *Penicillium funiculosum*, saprotrophs, endophytes, biological activity, biologically active metabolites

INTRODUCTION

It is widely recognized that micromycetes, due to their physiological and biochemical properties as well as their species diversity, serve as an almost inexhaustible source of biologically active metabolites with a wide range of activities. Among this group of organisms, microscopic endophytic fungi have recently attracted significant attention from researchers as an important source of broad-spectrum metabolites, including compounds with notable antibiotic effects (**Kusari *et al.*, 2012, 2013; Leitão and Enguita, 2016; Martinez-Klimova *et al.*, 2017; Wani *et al.*, 2015, 2016**). Metabolites with antagonistic properties belong to various chemical classes and are of interest for potential applications in agriculture and the pharmaceutical industry.

Endophytic fungi represent a dominant group within the plant microbiome and, similarly to saprotrophic fungi, are a vast and underexplored resource for the discovery of new diverse natural compounds. In this context, the potential of endophytic fungi has recently received increased attention. For example, between 2017 and 2019, 449 new compounds, primarily terpenoids, ketones, steroids, and other classes of compounds, were isolated and identified (**Zheng *et al.*, 2021**). Among the most well-known compounds derived from endophytes are antiviral agents such as podophyllotoxin, isoindolone, talaromyolid, cytonic acid, and antibacterial agents such as altersolanol, cryptocandin, and rutin (**Nisa *et al.*, 2015; Strobel *et al.*, 2004**). Notably, phytotoxic eremophilane sesquiterpenes, which inhibit *Amaranthus hypochondriacus* and *Echinochloa crus-galli*, were isolated from the microscopic fungus *Penicillium* sp. G1-a14 (**Valle *et al.*, 2015**). Moreover, **Bezerra *et al.* (2015**), using the disk diffusion method, identified the antibiotic activity of the endophytic isolates *Penicillium commune*, *P. glabrum*, *Gibberella baccata*, *Aspergillus ochraceus*, and *Khuskia oryzae*, obtained from *Bauhinia forficata* in Brazil.

Species of the genus *Penicillium* are also active producers of various classes of biologically active metabolites. These species exhibit diverse lifestyles, ranging from soil saprotrophs and endophytic mutualists to plant and warm-blooded animal pathogens, making them important subjects of research in fields such as biotechnology, medicine, plant pathology, food preservation, etc. (**Leitão and Enguita, 2016; Martinez-Klimova *et al.*, 2017; Cho *et al.*, 2005**). Since the discovery of penicillin from *P. chrysogenum* (later reclassified as *P. rubens*), extensive research has been conducted on thousands of *Penicillium* isolates for their capacity to produce biologically active metabolites. To this day, new compounds continue to be identified from these fungi (**Houbraken *et al.*, 2011**). Although significant progress has been made in identifying biologically active metabolites from *Penicillium* species, particularly in the context of antibacterial and antiviral agents for human use (**Li *et al.*, 2008; Tenguria *et al.*, 2011; Yu *et al.*, 2020; Shope, 1953**), the impact of endophytic organisms on plant viruses remains largely unexplored.

Penicillium species, isolated from various ecological niches, have demonstrated the ability to synthesize both well-known and novel physiologically active compounds with diverse biochemical properties. Some species are capable of producing mycotoxins or causing damage to agricultural crops during storage (**Ropars *et al.*, 2016**), while others serve as producers of hydrolytic enzymes (**Visagie *et al.*, 2014**). *Penicillium* species are also recognized for their production of a wide range of bioactive secondary metabolites, including antibacterial (**Rancic *et al.*, 2006; Lucas *et al.*, 2007**) and antifungal agents (**Nicoletti *et al.*, 2007**), as well as immunosuppressants and cholesterol-lowering compounds (**Kwon *et al.*, 2002**). Ongoing research continues to underscore the significance of *Penicillium* as a valuable source of novel bioactive compounds with promising applications in the pharmaceutical industry. For instance, the endophyte *Talaromyces funiculosus* (teleomorph of *P. funiculosum*), isolated from *Salicornia bigelovii* Torr., exhibited a broad spectrum of antibacterial activity against pathogenic bacteria such as *Staphylococcus aureus*, *Micrococcus tetragenus*, *Mycobacterium phlei*, *M. smegmatis*, and *Escherichia coli*. Novel bioactive compounds, chrodrimanin A and chrodrimanin B, with antibacterial and insecticidal properties, were isolated from *T. funiculosus* (**Guo *et al.*, 2016**).

Thus, endophytic fungi, along with saprotrophs, are promising producers of biologically active metabolites. They represent a vast resource for the discovery of new bioactive molecules and biocatalysts for use in medicine, agriculture, and industry. Their ability to synthesize bioactive compounds may be related to their approximately 400 million years of co-evolution with plants, during which endophytes developed symbiotic relationships with their host plants while simultaneously competing with other species. The exploration of endophytes' biological activities holds great potential for the discovery of novel bioactive compounds and the development of biopreparations for agricultural applications. Endophytic fungi from the genus *Penicillium* are known to produce bioactive substances with antagonistic properties against various organisms, including

filamentous fungi, yeast-like fungi, and bacteria (**Alvin *et al.*, 2014, 2016**). On that basis, investigating the antagonistic activity of both endophytic and saprotrophic strains of *P. funiculosum* against a broad spectrum of phytopathogenic fungi is a critical research objective.

In view of this, **the objective** of this study is to assess the antibacterial, antifungal, antiviral, and phytotoxic activities of endophytic and saprotrophic strains of *P. funiculosum*, to determine how these activities vary based on the ecological niche of the strains, and to identify the most active strains for further detailed research into their biological properties.

MATERIAL AND METHODS

In this study, we used 20 strains of *Penicillium funiculosum* Thom from the collection of fungi at the Department of physiology and systematics of micromycetes, Zabolotny Institute of Microbiology and Virology, National Academy of Sciences of Ukraine (IMV, NASU). This included 10 saprotrophic strains isolated from various soil types and 10 endophytic strains isolated from different plant organs of bog cranberry (*Oxycoccus palustris* Pres.), hare's-tail cottongrass (*Eriophorum vaginatum* L.), purple marshlocks (*Comarum palustre* L.), and St. John's wort (*Hypericum perforatum* L.).

The fungi were cultured for 14 days on potato glucose agar (PGA) at 26±2°C. Afterward, a standard suspension (1×10^6 conidia/ml) was prepared and inoculated into a liquid medium to obtain the inoculum. The inoculum was grown in a liquid potato glucose medium in 750 ml Erlenmeyer flasks under submerged conditions, stirred at 210–230 rpm, and maintained at 26±2°C for 48 hours (Bilai, 1983). To assess antibacterial, antifungal, phytotoxic, and antiviral activities, the micromycetes were cultivated under the same conditions for 6 days in Czapek's liquid nutrient medium containing 20 g/L glucose.

Antibacterial activity

The antibacterial activity of the culture filtrates (CF) from *P. funiculosum* strains was determined using the well-diffusion method (**Balouiri *et al.*, 2016**). A total of 26 microbial strains from Ukrainian Collection of Microorganisms (UCM) were used in this trial to assess antibacterial activity: gram-negative bacteria *Escherichia coli* B-906, B-916, *Proteus vulgaris* B-905, *Pseudomonas aeruginosa* B-900, B-907, *Salmonella enterica* subsp. *enterica* B-921, *Agrobacterium tumefaciens* B-1000, B-8471, B-8464, B-8465, B-8470, *Pectobacterium carotovorum* B-1095, B-8907, and plant pathogens *P. fluorescens* B-8573, *P. syringae* B-1027, *P. syringae* pv. *atrofaciens* B-8281, B-9900, *P. syringae* pv. *coronafaciens* B-9030, *Xanthomonas campestris* pv. *campestris* B-1049; gram-positive bacteria *Bacillus subtilis* B-901, B-902, *Staphylococcus aureus* B-904, B-909, *Micrococcus varians* Ac-613, Ac-634, and plant pathogen *Clavibacter michiganensis* subsp. *michiganensis* B-102.

The bacterial test organisms were cultured on agar media for 24 hours. *A. tumefaciens*, *P. carotovorum*, species of the genera *Pseudomonas*, *Xanthomonas*, *Bacillus*, *Micrococcus*, and *Clavibacterium*, were grown on potato glucose agar. Meat-peptone agar was used to grow strains of *E. coli*, *P. vulgaris*, *P. aeruginosa*, *S. enterica* subsp. *enterica*, and *S. aureus*. The bacterial test cultures of *E. coli*, *P. vulgaris*, *P. aeruginosa*, *S. enterica* subsp. *enterica*, *S. aureus*, *B. subtilis*, and *M. varians* were incubated at 37±2°C, while all other bacteria were grown at 26±2°C.

Antifungal activity

The antifungal activity of the CFs from *P. funiculosum* strains was determined using the well-diffusion method (**Balouiri *et al.*, 2016**). Three strains of yeast-like fungi *Candida albicans* F-690, *Atelosaccharomyces pseudotropicalis* F-899, and *Trichosporon cutaneum* F-1502 along with eight strains of mycelial fungi *Alternaria alternata* F-16819, *Bipolaris sorokiniana* F-16868, *Fusarium culmorum* F-50716, *F. lactis* F-50719, *F. oxysporum* F-54201, *F. poae* F-50704, *F. solani* F-50715, and *F. verticillioides* F-50463 were used for the study of this one. The test organisms of these fungi were cultured on Czapek's agar medium at 26±2°C.

Phytotoxic activity

To evaluate the phytotoxic activity of the CFs of *P. funiculosum* strains, a growth bioassay was conducted according to the Berestetskiy method (**Berestetsky and Sinitsky, 1973**). In this method, the phytotoxicity of the strain is determined based on its ability to cause 30% or more inhibition of both sprout and root growth of common corn (*Zea mays* L.) seedlings. Additionally, the CFs were subjected to the bioassay method for *Chlorella* (**Bilai, 1983**) using unicellular freshwater green algae as test organisms. For this assay, three strains of *Chlorella vulgaris* Al-190, Al-191, Al-192 and three strains of *C. kessleri* Al-200, Al-201, Al-205 were employed to assess potential algal growth inhibition.

Antiviral activity

The antiviral activity of *P. funiculosum* was evaluated against tobacco mosaic virus (TMV, U1 strain) using the half-leaf method on *Datura stramonium* L. plants. For this assay, equal volumes of the virus suspension and CF of *P. funiculosum* were mixed (1:1, v). After 20 minutes of incubation, the solution was applied to the left half of the *Datura* leaves. As a control, the right half of the leaves was inoculated with a solution containing TMV and buffer mixed in the same ratio.

The antiviral effect was assessed by calculating the inhibition rate (I) based on a local lesion assay, using the formula: $I=(1–E/C)\times100\%$, where I (%) represents the percentage of inhibition, E is the number of local lesions on the treated ("experiment") half of the leaf, and C is the number of lesions on the control leaf half.

TMV was extracted from systemically infected *Nicotiana tabacum* var. *immune* 580 (Revertant) plants following the protocol described (**Gooding and Hebert, 1967**). The assay was performed in triplicate under greenhouse conditions, with daily average temperatures ranging from 25 to 28°C.

RESULTS AND DISCUSSION

Antibacterial activity

To assess the antibacterial activity of *P. funiculosum* strains, their biological effects were screened against 26 test microbial strains. Our findings revealed that the CFs of both endophytic and saprotrophic *P. funiculosum* strains exhibited no inhibitory effect on the growth of several gram-negative bacteria, including *A. tumefaciens* 1000, *E. coli* 906, 916, *P. carotovorum* 1095, 8907, *P. vulgaris* 905, *P. aeruginosa* 900, 907, *P. fluorescens* 8573, *S. enterica* subsp. *enterica* 921, and *X. campestris* pv. *campestris* 1049. Similarly, no activity was observed against gram-positive strains such as *B. subtilis* 901, 902, *S. aureus* 904, 909, *M. varians* 613, 634, and *C. michiganensis* subsp. *michiganensis* 102. Due to the lack of observed activity, these results were excluded from Table 1. However, the CFs of endophytic and saprotrophic *P. funiculosum* strains exhibited notable antibacterial activity against four strains of gram-negative *A. tumefaciens* 1000, 8471, 8464, 8465 and strains of *P. syringae* 1027 and *P. syringae* pv. *atrofaciens* 8281, 9900. Specifically, CFs from endophytic *P. funiculosum* strains showed significant antibacterial activity against the four strains of *A. tumefaciens*, with inhibition zones ranging from 13 to 35 mm. The highest level of antibacterial activity was exhibited by endophytic strains 16784 and 16787 against *A. tumefaciens* 8464, with inhibition zones of 35 mm. In contrast, CFs from strains 16786 and 16788 demonstrated no antibacterial activity against any of the tested bacterial cultures. Seven CFs from endophytic strains showed antibacterial effects against *P. syringae* 1027, with inhibition zones ranging from 13 to 25 mm. However, three strains 16786, 16788, 16795 were found to be inactive against this pathogen.

Table 1 The antibacterial activity of *Penicillium funiculosum* strains

No. s/n	Penicillium funiculosum strains	Diameter of the growth inhibition zone of test bacteria, mm							
		Agrobacterium tumefaciens strains				Pseudomonas syringae strain	Pseudomonas syringae pv. atrofaciens strains		Pseudomonas syringae pv. coronafaciens strain
		1000	8464	8465	8471	1027	8281	9900	9030
Endophytes									
1	16784	19±0,9	25±1,5	35±2,4	20±1,2	16±0,6	20±1,4	20±1,2	0
2	16785	13±0,7	0	20±1,3	0	13±0,5	0	0	0
3	16786	0	0	0	0	0	0	0	0

4	16787	19±1,0	20±1,2	35±2,3	20±1,1	15±0,5	17±0,7	17±0,6	0
5	16788	0	0	0	0	0	0	0	0
6	16795	13±0,6	0	0	0	0	15±0,1	13±0,5	0
7	16879	20±1,1	0	0	0	17±0,6	0	0	0
8	16880	18±1,2	25±1,6	0	0	15±0,5	15±0,5	18±0,7	0
9	16881	20±1,0	20±1,2	0	0	17±0,5	0	0	0
10	16882	20±1,3	0	0	0	25±1,3	0	0	0
Saprotrophs									
11	16783	19±1,1	25±1,7	30±1,5	15±0,6	13±0,8	15±0,7	15±0,6	15±0,8
12	16789	23±1,5	30±1,9	35±2,5	25±1,2	18±0,9	18±1,0	15±0,7	15±0,5
13	16790	20±1,0	30±2,2	40±2,4	22±1,1	20±0,9	18±0,9	25±1,3	17±0,7
14	16791	16±0,8	25±1,5	30±1,7	15±0,7	15±0,5	15±0,6	20±1,1	18±0,8
15	16792	19±0,8	25±1,7	25±1,1	17±1,1	15±0,7	18±0,9	18±0,7	20±1,2
16	16793	17±0,9	20±1,1	25±1,3	18±0,8	15±0,6	20±0,9	15±0,6	20±0,9
17	16794	13±0,7	0	0	20±1,2	0	15±0,7	0	0
18	16825	22±1,4	25±1,8	40±2,2	22±1,4	20±1,2	20±0,8	17±0,9	20±1,0
19	16826	20±1,1	30±2,1	45±2,6	30±1,6	20±1,0	20±1,1	20±0,9	15±0,8
20	16874	18±0,7	20±1,0	30±1,8	24±1,4	17±1,0	20±1,1	20±1,3	20±1,0

Note**:** Effect of *P. funiculosum* strains on the diameter of inhibition zone of bacterial growth ± the standard error (± SE) of triplicates

The CFs of endophytic *P. funiculosum* strains 16784, 16787, 16795 and 16880 exhibited antimicrobial activity against the tested *P. syringae* pv. *atrofaciens* strains 8281 and 9900. However, none of the studied endophytic CFs demonstrated antimicrobial effects against *P. syringae* pv. *coronafaciens* strain 9030.

In comparison, the CFs of saprotrophic *P. funiculosum* strains demonstrated stronger antimicrobial activity against all tested organisms. The inhibition zones for gram-positive bacteria, including *A. tumefaciens* 1000, 8471, 8464, 8465, *P. syringae* 1027, *P. syringae* pv. *atrofaciens* 8281, 9900, and *P. syringae* pv. *coronafaciens* 9030, ranged from 13 mm to 45 mm.

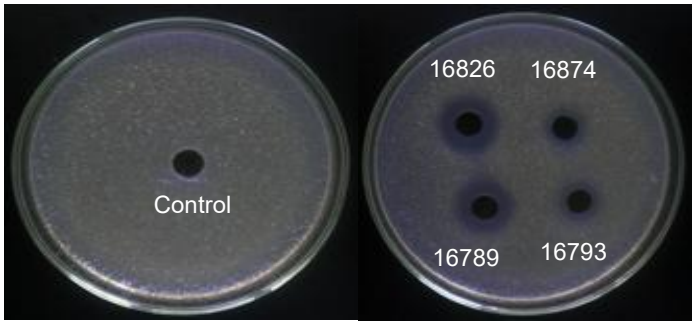


Figure 1 Antimicrobial activity of saprotrophic *Penicillium funiculosum* 16826, 16789, 16874 and 16793 strains against *Agrobacterium tumefaciens* 8464

In the agar diffusion test, *A. tumefaciens* 8465 was inhibited strongly by saprotrophic *P. funiculosum* strains. The size inhibition zones varied as follows: 45 mm for strain 16826, 40 mm for strains 16790 and 16825, 35 mm for strain 16789, 30 mm for strains 16783, 16791, 16874, and 25 mm for strains 16792 and 16793. It should be noted that saprotrophic strain 16794 did not show antibacterial activity against several microorganisms, including *A. tumefaciens* 8464. *A. tumefaciens* 8471, *P. syringae* 1027, *P. syringae* pv. *atrofaciens* 9900, and *P. syringae* pv. *coronafaciens* 9030.

The studied saprotroph strain 16794 exhibited antibacterial activity only in relation to three phytopathogenic bacteria: *A. tumefaciens* 1000 (inhibition zone of 13 mm), 8465 (inhibition zone of 20 mm), and *P. syringae* pv. *atrofaciens* 8281 (inhibition zone of 15 mm).

The data obtained indicate that not all *P. funiculosum* strains from different ecological niches exhibited antibacterial activity. It is essential to highlight the distinct properties of the CFs from both endophytic and saprotrophic *P. funiculosum* strains, as they demonstrate notable differences in antimicrobial activity. Thus, the endophytic strains exhibited relatively lower antibacterial activity, with inhibition zones ranging from 13 mm to 35 mm, and were active against only seven of the 26 test cultures. It's noteworthy that all tested saprotrophic strains *P. funiculosum* demonstrated notable antibacterial effects, particularly against *A. tumefaciens* 1000, 8471, 8464, 8465, *P. syringae* strains 1027, and *P. syringae* pv. *atrofaciens* 8281, 9900, with growth inhibition zones of 13-45 mm. The highest antimicrobial activity was observed in saprotrophic strain 16826, which produced a 45 mm inhibition zone against *A. tumefaciens* 8464, highlighting its potent bioactivity.

Antifungal activity

The antifungal activity of CFs from *P. funiculosum* strains isolated from different ecological niches was tested against three strains of yeast-like fungi as well as against 8 mycelial fungi. The results have revealed that none of the *P. funiculosum* strains exhibited detectable antifungal activity, showing no inhibitory effects against any of the 11 tested strains of fungi.

Phytotoxic activity

The evaluation of phytotoxic activity of *P. funiculosum* strains revealed that the endophytic strains have no inhibitory effects on the growth of corn (*Zea mays* L.) sprouts and roots and therefore can be considered as nontoxic. Thus, the greatest increase in corn sprout length, 20% relative to the control, was observed under the exposure with the endophytic strain 16784, while the increase in root length was only 3%. The increase in root length under the influence of the CFs of *P. funiculosum* strains 16785, 16786, 16788, 16795, 16789, and 16882 ranged from 10% to 18%, while sprout length increased by 3% to 12%. A slight increase in the length of corn sprouts and roots, less than 10%, was demonstrated by endophytic strains 16787, 16880, and 16881 (Fig. 2).

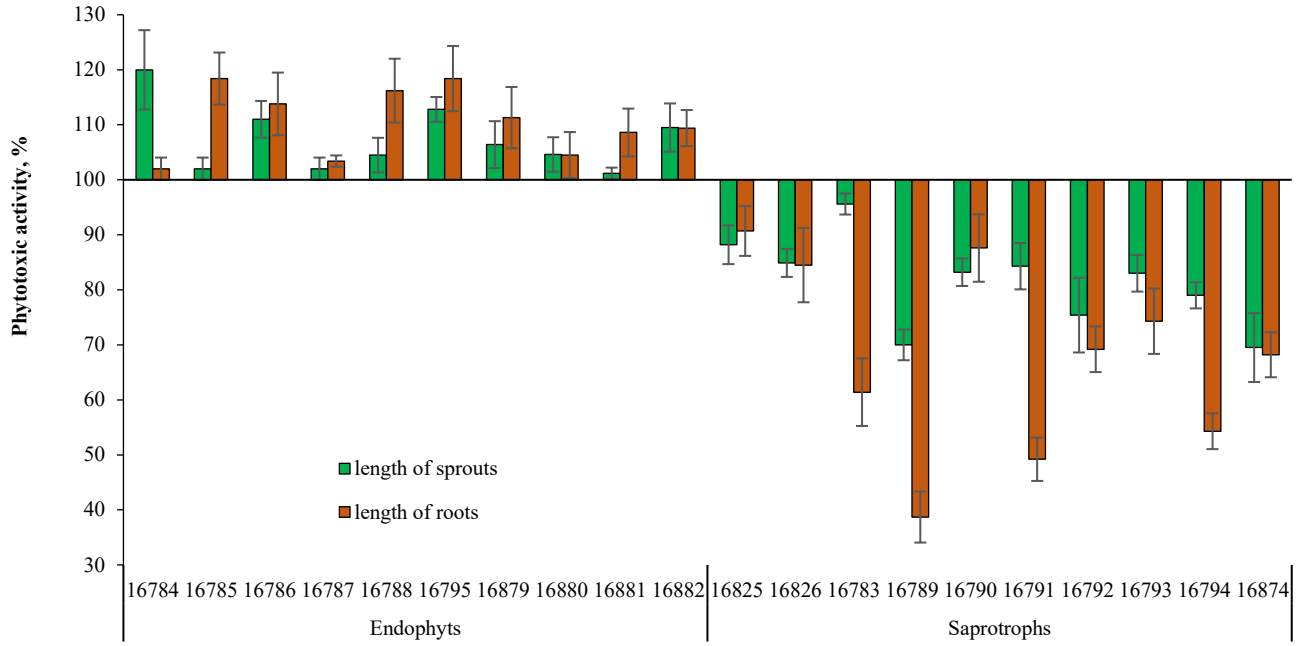


Figure 2 Phytotoxic activity of *Penicillium funiculosum* strains by the length of corn sprouts and roots

According to the data obtained, no phytotoxic effects were observed among the endophytic strains regarding absolute dry biomass (ADB) of sprouts and roots. The endophytic strain 16795 exhibited the highest increase in root ADB at 17%, while the increase in sprout ADB was 9%.

Other endophytic *P. funiculosum* strains 16788, 16879, 16880, 16881, and 16882 demonstrated increases in sprout ADB ranging from 2% to 15% and in root ADB from 8% to 12% compared to the control. No statistically significant differences in sprout or root ADB were observed among strains 16784, 16785, 16786, and 16787 (Fig. 3).

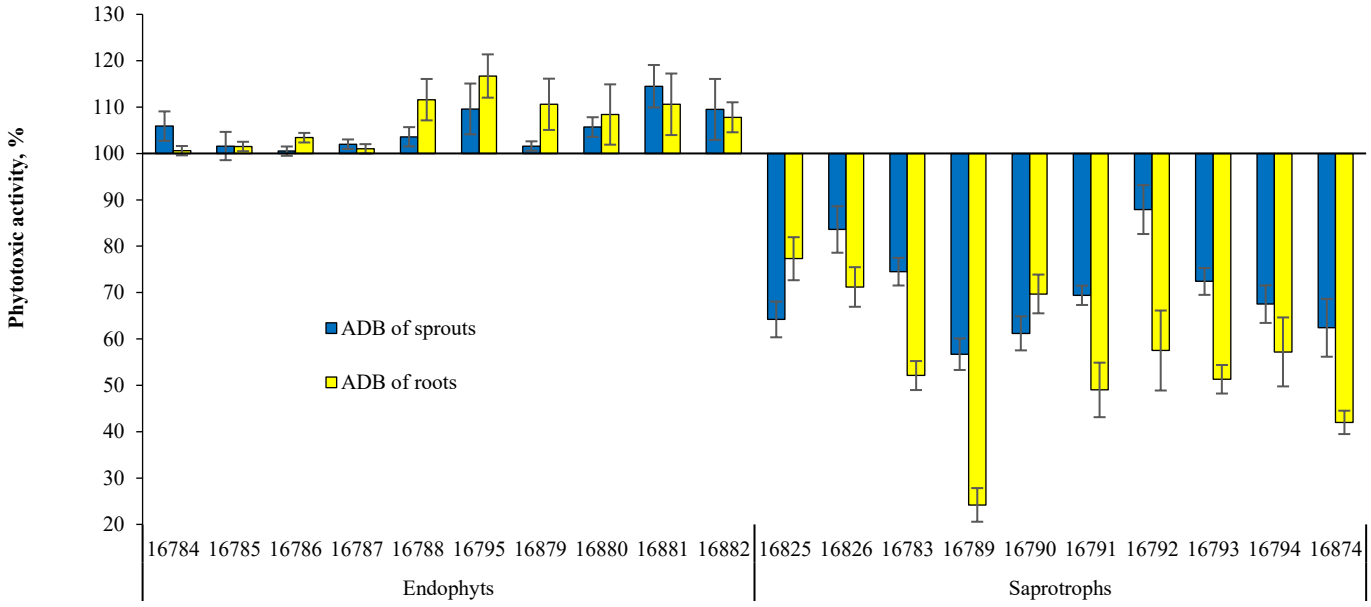


Figure 3 Phytotoxic activity of *Penicillium funiculosum* strains by the absolutely dry biomass (ADB) of corn sprouts and roots

In contrast, all saprotrophic *P. funiculosum* strains inhibited the growth of corn sprouts and roots. The saprotrophic *P. funiculosum* strains 16785, 16789, 16791, 16792, 16794, and 16874 exhibited phytotoxicity, reducing corn root length by more than 60%, while the phytotoxic effect observed in strains 16825, 16826, 16790, and 16793 ranged from 9% to 26%. Additionally, all saprotrophic *P. funiculosum* isolates demonstrated phytotoxicity, with reductions in the ADB of corn sprouts and roots ranging from 30% to 75%.

The endophytic strains exhibited no phytotoxic activity against *C. vulgaris* or *C. kessleri.* In contrast, the saprotrophic strains 16825 and 16794 demonstrated significant phytotoxicity, inhibiting the growth of all six *Chlorella* strains. Inhibition zones ranged from 16 to 20 mm for *C. vulgaris* and from 15 to 26 mm for *C. kessleri* (Fig. 4, 5).

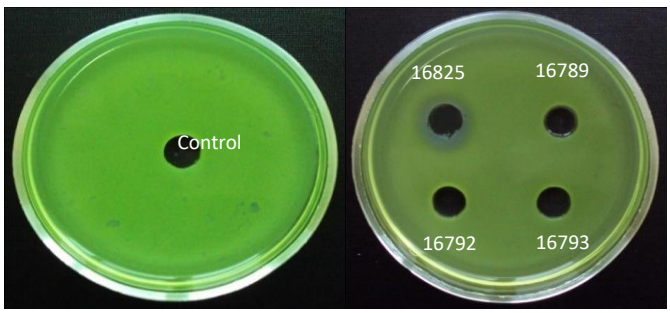


Figure 4 Phytotoxic activity of saprotrophic *Penicillium funiculosum* 16825 strain against *Chlorella vulgaris* 190

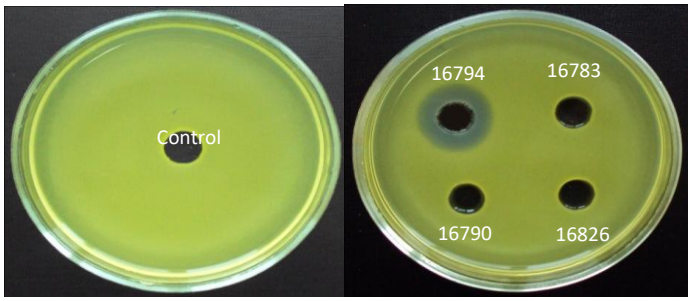


Figure 5 Phytotoxic activity of saprotrophic *Penicillium funiculosum* 16794 strain against *Chlorella kessleri* 200

Therefore, our study confirmed the absence of phytotoxicity in endophytic *P. funiculosum* strains using two different methodologies. Conversely, saprotrophic strains exhibited phytotoxic activity, affecting corn sprout and root length as well as ABD. Notably, saprotrophic strains 16825 and 16794 inhibited the growth of all tested strains of green algae.

Antiviral activity

The antiviral activity assays of *P. funiculosum* strains demonstrated significant inhibition of tobacco mosaic virus, with reductions in the number of localized lesions on *D. stramonium* leaves ranging between 50–70% (Tab. 2, Fig. 6). Both endophytic and saprotrophic strains exhibited antiviral potential, with five strains from each group inhibiting TMV by more than 50%. At the same time, endophytic strains 16784, 16786, and 16879, while effective, displayed slightly lower activity, reducing TMV by 39%, 39%, and 47%, respectively. A second group of saprotrophic *P. funiculosum* displayed moderate antiviral activity, ranging between 30–50%. Only strain 16826 showed minimal inhibition, reducing necrosis formation by strains just 29%. Among the saprotrophic strains, strain 16789 showed the highest antiviral potential, inhibiting lesion formation by 85% after 30-minute incubation with the virus. In the group of endophytes, strain 16882 was the most effective, reducing local lesions by 65%.

These findings highlight that *P. funiculosum* strains, especially saprotrophic ones, demonstrate excellent antiviral activity against TMV *in vitro*. Saprotrophic strains appear to be generally more potent in reducing viral lesions.

Table 2 Antiviral activity of *Penicillium funiculosum* strains obtained from different ecological niches

No. s/n	Strain number	E/C, %	I, %	No. s/n	Strain number	E/C, %	I, %
Endophytes				Saprotrophs			
1	16784	61±4	39	1	16825	30±1	70
2	16786	61±1	39	2	16826	71±2	29
3	16785	40±2	60	3	16783	51±3	49
4	16788	40±1	60	4	16789	15±2	85
5	16795	71±5	29	5	16790	30±8	70
6	16787	42±8	58	6	16791	51±6	49
7	16879	53±3	47	7	16792	60±7	40
8	16880	67±3	23	8	16793	34±1	66
9	16881	48±2	52	9	16794	55±2	45
10	16882	35±3	65	10	16874	62±5	38

Note: values are presented as the mean±SE; $^{++}$–indicate significant difference at $p<0.01$, $^{+}$–at $p<0.05$ level.

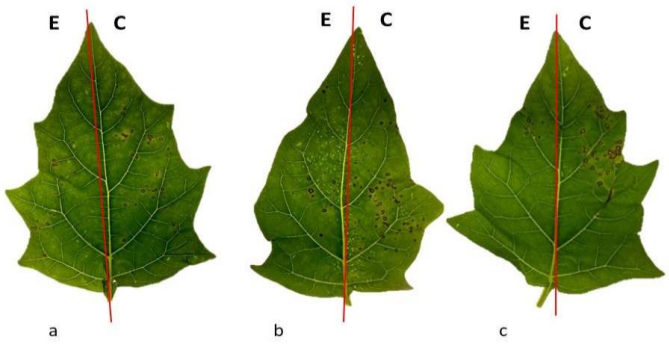


Figure 6 Antiviral activity of selected *Penicillium funiculosum* strains against TMV on half-leaves of *Datura stramonium.* Each leaf is divided into experimental (E, left half) and control (C, right half) sides: a) endophytic strain 16882; b) saprotrophic strain 16793; c) saprotrophic strain 16789.

It is known that *P. funiculosum* strains are highly versatile and can thrive in various ecosystems, including as endophytes in numerous plant species and as part of the plant-endophytic fungal communities in the sphagnum bogs of the Polissya region in Ukraine (**Kurchenko *et al.*, 2023**). That is why broad adaptive abilities of *P. funiculosum* strains are reflected in their wide biological activity and capacity to synthesize numerous biologically active compounds. In particular, strains of *P. funiculosum* synthesize a whole range of phytohormone-stimulating compounds, such as gibberellins (GA3, GA4, GA8, GA9) (**Martinez-Klimova *et al.*, 2017; Miller *et al.*, 2012; Yurieva *et al.*, 2018**), indole-3-acetic acid, and abscisic acid, which play an essential role in their symbiotic relationships with plants. In addition, *P. funiculosum* strains are characterized by the synthesis of enzyme complexes, particularly cellulolytic enzymes with high β-glucosidase activity. Thus, it has been demonstrated these enzyme complexes enable to effectively biodegrade a range of plant-derived substrates and it may be useful for biotechnology application (**Yurieva *et al.*, 2017**).

In addition, there are data showing that *P. funiculosum* fungi can synthesize secondary metabolites with a range of biological activities, including antitumor, insecticidal, interferon-stimulating, and anti-inflammatory effects (**Amer *et al.*, 2024; Cole and Schweikert, 2003; De Clercq, 2024; Santamarina *et al.*, 1987**). For example, an endophytic *P. funiculosum* strain isolated from the *Persicaria salicifolia* (Brouss. ex Willd.) Assenov seeds was found to produce compounds with antitumor properties (**Amer *et al.*, 2024**). This supports the idea that endophytic fungi are a valuable source of bioactive metabolites with potential applications in medicine and other fields.

However, there is limited data regarding the antibiotic activity of *P. funiculosum*, particularly in terms of antibacterial, antifungal, phytotoxic, and antiviral effects. It was reported on the antibacterial and antifungal activity of an extract from a *P. funiculosum* strain (**Santamarina *et al.*, 1987**), where the test organisms included various bacteria such as *B. megaterium*, *B. subtilis*, *Erwinia amylovora*, *E. coli*, *M. luteus*, *P. aeruginosa*, *S. aureus*, and several fungal strains, including *Armillariella mellea*, *Aspergillus parasiticus*, *Trichothecium roseum*, *P. italicum*, *F. culmorum*, and *Botrytis cinerea*. Our study found that the *P. funiculosum* extract did not display any antibiotic activity against these test organisms.

Similarly, our studies have shown that *P. funiculosum* strains exhibit no antifungal activity against either yeast or mycelial fungi, nor any antibacterial activity against *B. subtilis*, *E. coli*, *P. aeruginosa*, and *S. aureus*, which were also used as test organisms in the studies mentioned above (**Santamarina *et al.*, 1987**).

Another study highlighted the antibacterial activity of *P. funiculosum* strain extracts against various test cultures (**Amer *et al.*, 2024**). Specifically, these extracts exhibited activity against *B. subtilis* and *E. coli*. However, they did not demonstrate antifungal activity in the experiments with *C. albicans* and *A. fumigatus* as test cultures. Additionally, the extracts lacked activity against the bacterial strains *S. aureus* and *P. vulgaris*. Obviously, this suggests that the *P. funiculosum* strain studied by the authors likely synthesizes several specific

metabolites with antibacterial activity. In contrast to this, our study observed antibacterial activity against only four strains of phytopathogenic bacteria.

According to other researchers (**Brian *et al.*, 1957**), certain strains can produce the antibiotic wortmannin. This substance is noted for its potent antifungal activity against several micromycetes, including *B. allii*, *B. cinerea*, *B. fabae*, *Cladosporium herbarum*, and *R. stolonifer*. Moreover, the researchers have expanded the range of susceptible organisms and have demonstrated high antifungal efficacy of wortmannin against yeasts and micromycetes such as *Cryptococcus terreus*, *Trichophyton rubrum*, *Rhizoctonia oryzae*, *A. versicolor*, *A. fumigatus*, *Aureobasidium pullulans*, *F. moniliforme*, and *Saccharomyces cerevisiae* (**Singh *et al.*, 2015**). Importantly, the antifungal activity of wortmannin against these test organisms was reported to be superior to that of commonly used antifungal drugs, such as amphotericin B and fluconazole, which were used as a positive control.

The isolation of the funiculosin compound from *P. funiculosum*, which exhibits a broad spectrum of antifungal activity, has been previously documented (**Wang *et al.*, 2023**). Funiculosin has demonstrated effectiveness against several pathogenic fungi, including *C. albicans*, *C. utilis*, *C. neoformans*, *S. cerevisiae*, *T. mentagrophytes*, *T. rubrum*, *M. gypseum*, *Blastomyces dermatitidis*, and *Hormodendrum pedrosoi*. Another study (**Ando *et al.*, 1960**) also reported weak antibacterial activity of funiculosin against *B. subtilis* and *E. coli*. However, the concentration required for antibacterial activity is much higher compared to the concentration at which its antifungal properties are observed.

As we can see from the literature data, *P. funiculosum* strains are capable of producing several biologically active metabolites that exhibit antifungal and antibacterial activity. Our study, in contrast, showed no antifungal activity in any of the 20 strains of *P. funiculosum* tested, and only limited antibacterial action against certain bacterial strains. This discrepancy may indicate that the strains we studied synthesized negligible amounts of metabolites such as funiculosin or wortmannin possessing antifungal and antibacterial properties.

Notably, our findings highlight that the *P. funiculosum* strains we studied did display strong antibacterial activity, particularly against certain strains (four strains) of phytopathogenic bacteria such as *A. tumefaciens*, with growth inhibition zones reaching up to 45 mm. This suggests that the strains we studied produce a compound (or a complex of compounds) with potent antibacterial activity against specific phytopathogenic species.

Importantly, saprotrophic strains exhibited significantly greater antibacterial activity compared to endophytic ones. Saprotrophic strains demonstrated a broader spectrum of activity and larger growth inhibition zones, which, in our opinion, could be attributed to higher levels of *P. funiculosum* metabolite synthesis. At the same time, it can be assumed that the spectrum of bioactive compounds synthesized by saprotrophic strains may be broader than that of endophytes, potentially explaining their enhanced antibacterial activity and saprotrophic *P. funiculosum* strains – more promising candidates for extraction bioactive metabolites.

There is limited information available in the literature regarding the phytotoxic activity of *P. funiculosum* strains. Thus, one study reported (**Catani-Catovic and Peterson, 1966**) the phytotoxic effects of the CF of a saprotrophic *P. funiculosum* strain isolated from the maple rhizosphere. It was found that the CF inhibited seed germination and restricted stem and root growth in tomato, radish, and eggplant. Additionally, the CF was shown to negatively affect vegetative plants, leading to their wilting and eventual death**.** The highest level of phytotoxic activity was observed on the 25th day of fungal cultivation, which suggests that the responsible toxins belong to the group of secondary metabolites.

At the same time, our studies on the effects of culture filtrates from both endophytic and saprotrophic *P. funiculosum* strains on corn root and sprouts length, as well as on accumulation of ADB, demonstrated that the endophytic strains did not exhibit any phytotoxic activity. In contrast, the saprotrophic isolates showed significant phytotoxic effects. This suggests that saprotrophic strains likely synthesize substances with phytotoxic activity, whereas endophytic *P. funiculosum* strains either do not produce these substances, or produce them in quantities too small to be effective. It should also be noted the correlation between higher levels of phytotoxic and antibacterial activity observed in our saprotrophic strains. This difference may point to an ecological and biochemical specialization in saprotrophic strains of *P. funiculosum*, which supports their saprotrophic lifestyle and mode of existence.

In terms of antiviral activity, it has been shown that *P. funiculosum* strains are capable of synthesizing compounds active against both DNA and RNA-containing viruses. For instance, funiculosin, which was previously mentioned in the context of its antibacterial and antifungal properties, has been reported to exhibit antiviral activity against viruses that infect animals (**Wang *et al.*, 2023; Ando *et al.*, 1960**). Additionally, another compound isolated from *P. funiculosum*, helenine (**Shope, 1966**), has been identified as having antiviral properties. Although the exact mechanism of helenine's antiviral activity remains unclear, it is hypothesized that it acts indirectly by inducing the host cells' defence mechanisms. Research by other scientists (**Sadovsky *et al.*, 1973**) also demonstrates the potential role of *P. funiculosum* mycoviruses in influencing viral infectivity (specifically, TMV) and host resistance. Furthermore, it is known that mycoviruses from *Penicillium* species can act as interferon inducers in animals, adding another layer to the antiviral potential of *P. funiculosum*.

In our studies, we have observed promising antiviral activity in culture filtrates from both endophytic and saprotrophic *P. funiculosum* strains against TMV. Notably, all strains displayed some level of activity, with several saprotrophic strains – such as 16825, 16790, and 16789 – showing particularly strong activity, preventing the formation of necrotic lesions on leaves by 70% or more. This points to a high antiviral potential, particularly in the saprotrophic *P. funiculosum* strains. It can be assumed that the strong antiviral activity observed in the strains can be attributed to the synthesis of low molecular weight secondary metabolites, such as funiculosin and helenine, mentioned above. However, as there is little to no data in the literature regarding the antiviral effects of *P. funiculosum* against plant viruses, further studies are necessary to verify this hypothesis.

Moreover, the higher antiviral activity observed in saprotrophic *P. funiculosum* strains appears to correlate with their stronger antibacterial and phytotoxic activities. In our opinion, this correlation may be explained by the ecological demands of saprotrophic strains. Being soil-dwelling organisms, saprotrophic strains must contend with numerous microorganisms, competing for resources and space and this competitive environment likely drives the need for these strains to produce a broad array of biologically active metabolites with antimicrobial and antiviral properties. In contrast, endophytic strains, which live inside host plants, have less need for such high levels of antagonistic activity. An overproduction of secondary metabolites by endophytes could be detrimental to the host plant, thus balancing their need to coexist within a more stable and less competitive environment. In contrast, endophytic strains, which live inside host plants, have less need for such high levels of antagonistic activity. An overproduction of secondary metabolites by endophytes could be detrimental to the host plant, thus determined by the balanced needs of plant-endophyte coexistence.

CONCLUSION

Analysis of our data on the biological activities of endophytic and saprotrophic *P. funiculosum* strains revealed significant differences between these two groups. Saprotrophic strains demonstrated significantly higher levels of antibacterial and antiviral activity compared to endophytic strains. Moreover, all saprotrophic strains exhibited phytotoxic activity, while none of the endophytes possessed this property. The data obtained indicate physiological and biochemical differences between the two groups, which can serve as markers for their differentiation.

The antiviral activity of *P. funiculosum* strains against plant viruses, using tobacco mosaic virus as a model, has been demonstrated for the first time. This finding opens up new avenues for exploring the antiviral potential of *P. funiculosum* strains in agricultural applications.

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