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PHOSPHATE-MOBILISING PROPERTIES OF FUNGI OF THE GENUS *PENICILLIUM* ISOLATED FROM SOYBEAN HISTOSPHERE

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Objective. *To research the ability of fungi of the genus Penicillium, isolated from the histosphere of soybean plants, release phosphorus from mineral and organic phosphates, study their effect on the general phosphorus content in plant shoots.* ***Methods.*** *Microbiological (cultivation of the tested fungi on Pikovska's medium and its modifications, Czapek-Dox agar with tricalcium phosphate or phenolphthalein phosphate, wort agar), vegetation experiment (content determination of general phosphorus in the aboveground mass of soybean plants), statistical.* ***Results.*** *The use of three insoluble phosphates in Pikovska medium showed that the tested fungi dissolve to varying degrees* $Ca_3(PO_4)_2$ *and are unable to dissolve* $AlPO_4$ *and* $FePO_4$*. On the seventh day of cultivation, clearly visible zones of enlightenment were formed around the colonies of P. funiculosum 20312 and P. variabile 20173, with phosphate dissolution indexes of 1.17 and 1.18, respectively. When cultivating fungi on Pikovska medium with the addition of bromophenol blue dye in P. funiculosum 20312 and P. variabile 20173, the medium quickly changed colour from green to yellow, indicating the diffusion of organic acids produced by the fungi into the agar. Starting from the twelfth day of the experiment, the environment around the colonies of fungi P. glauco-lanosum 20401 also acquired a rich yellow colour and the halo zones formation was observed. The presence of phosphatase activity was demonstrated for all the tested fungi. The tested strains of fungi had a positive effect on the general phosphorus content in the dry matter of soybean shoots, this indicator increased notably in the variant with the use of P. funiculosum 20312 — 0.751 % against 0.643 % in the control variant.* ***Conclusions.*** *The tested fungi of the genus Penicillium, isolated from surface-sterilised roots of soybean plants, are capable of releasing phosphorus by dissolving inorganic and mineralising organic phosphates, and have a positive effect on the content of general phosphorus in soybean shoots.*

Key words: *endophytic fungi of soybean, PSF (phosphate solubilising fungi), inorganic phosphate dissolution, organic phosphate mineralisation, phosphatase.*

Introduction. Plants require about 16 macro- and microelements for optimal growth, with phosphorus being the most limiting nutrient for crops productivity after nitrogen [1; 2]. It plays an important role in virtually all major metabolic processes in plants, including photosynthesis, respiration, energy metabolism, macromolecular biosynthesis [3] and biological nitrogen fixation in legumes [4]. Adequate phosphorus supply in the early stages of plant development is essential for the establishment of the plants reproductive organs germs. Phosphorus also has a significant impact on the formation of the root system and its branching. Phosphorus accounts from 0.05 % to 0.5 % [5], and according to other sources, from 0.2 % to 0.8 % of the plant's dry matter [6]. This element is found in plants either in the form of a free inorganic orthophosphate group (Pi) or in the form of organophosphate compounds [7]. The total amount of Pi in plant cells is divided into two physiologically distinct pools. The first one is located in the cytoplasm and constitutes the metabolically active Pi pool, and the second one, which is a specific phosphorus reserve, is stored in vacuoles [7]. With a sufficient supply of phosphorus, vacuoles contain 85–95 % of cellular phosphorus, while the cytoplasmic pool is 5–15 % [8].

Organophosphorus compounds in living organisms are predominantly organic phosphate esters, in which phosphate groups are linked to organic units via a C-O-P bond. The main pools for esterified phosphorus are nucleic acids (DNA and RNA), phosphoproteins, phospholipids, sugar phosphates, and energy-rich phosphate compounds (in particular, adenosine triphosphate) [9].

Phospholipids are the class of lipids based on a glycerol backbone to which two long chains of acyl groups of fatty acids and orthophosphate acid residues are attached. These substances are not only the most important building blocks of cell membranes, but also participate in membrane transport, cytoskeleton organisation, and signal transduction [10]. Phospholipid metabolism plays an important role in seed germination, proper pollen formation, cotyledon vascularity, stress reactions, and the transduction of light and sugar signals [11].

Phosphate derivatives of sugars are essential metabolic intermediates and some of them, such as phytic acid (Ins P6), are also a reservoir of phosphorus in plants. In seeds, phytic acid is contained in the form of the mixed salt of potassium, magnesium, calcium, manganese, iron and zinc cations and accumulates in membrane-bound inclusions called globules [12]. Depending on the type of plant, the phosphorus content of phytate has been found to be between 30 % and 60 % of the general phosphorus in seeds. In addition to phosphorus storage, the functions of Ins P6 include mRNA export, chromatin remodelling and DNA double-strand break repair. The ability of phytic acid to complex with iron ions Fe^{2+} helps to reduce the formation of active oxygen forms during the lipid peroxidation reaction [13].

There are various forms of phosphate derivatives of nucleotides containing up to three esterified phosphate residues linked to ribose or deoxyribose links. A large group of phosphoesters nucleoside derivatives (e. g. ATP, ADP, UDP) is a specific primary energy reservoir distributed in phosphorylation and dephosphorylation reactions of other chemical compounds. The role of ATP as an energy source is well known, and extracellular ATP (eATP) in plants is also a specific signalling agent that generates an increase in cytosolic Ca^{2+}, promoting plants development and defence reactions [14].

Analysis of recent researches and publications. Although the total amount of phosphorus in the soil (50–3000 mg/kg) is considered sufficient, the fraction available to plants is less than 1 % of its total amount [15; 16]. Suboptimal levels of phosphorus nutrition can reduce crop yields by up to 15 % [17]. The effectiveness of chemical phosphate fertilisers is usually less than 30 % due to its fixation either in the form of iron and aluminium phosphates in acidic soils [18] or calcium phosphate in neutral and alkaline soils [19].

Phosphorus in soil is found in inorganic and organic forms and is divided into three pools that are in equilibrium with each other. The first pool is called the fixed or unstable fraction and cannot be used by plants. It includes primary minerals (insoluble inorganic phosphates apatite, strangite and variscite), sorbed phosphorus (clays, iron and aluminium oxides, carbonates) and organic phosphorus compounds. The second pool contains secondary phosphate minerals (calcium, iron and aluminium phosphates) and is known as the active (labile) fraction of phosphorus because it is slowly released for plants absorption. The third pool is the soluble fraction of phosphorus, i. e. inorganic phosphorus dissolved in water or soil solution and available to plants (in the form of $H_2PO_4^-$ and HPO_4^{2-} anions) [20].

The main processes in the soil phosphorus cycle that affect its soluble fraction are: 1) dissolution-precipitation (mineral equilibrium); 2) sorption-desorption (interaction between phosphorus in soil solution and on the solid surface of soil aggregates); 3) mineralisation-immobilisation (biologically mediated transformation of phosphorus between inorganic and organic forms) [6; 21].

Microorganisms mobilise insoluble and fixed forms of phosphorus in the soil through dissolution and mineralisation.

According to Kucey [22], the number of fungi capable of releasing phosphorus from insoluble compounds is about 0.1–0.5 % of their total population. Soil fungi capable of converting phosphorus into a form accessible to plants have a number of advantages over bacteria: firstly, micromycetes tend to produce more acids than bacteria [23]; secondly, they usually do not lose their ability to dissolve insoluble phosphorus compounds after repeated subcultivation in the laboratory, as it can happen with bacteria; thirdly, fungi in soils can travel long distances more easily, which is important for crops [22].

PSF (phosphate-solubilising fungi) or fungi that dissolve different types of phosphates are representatives of different genera. The best-described PSF in the scientific literature today are micromycetes of the genera *Penicillium*, *Aspergillus*, *Alternaria*, *Helminthosporium*, *Arthrobotrys*, *Rhizopus*, *Fusarium*, *Trichoderma* та *Sclerotium* [24; 25].

The ability to dissolve mineral phosphates *in vitro* has been demonstrated for a number of species of the genus *Penicillium*: *P. oxalicum* [26–29], *P. albidum* [30], *P. thomii* [30], *P. restrictum* [30], *P. frequentans* [30], *P. aurantiogriseum* [31], *P. radicum* [32], *P. rugulosum* [33], *P. citrinum* [34], *P. expansum* [35; 36], *P. funiculosum* [37], *P. variabile* [38–41], *P. italicum* [42], *P. soli, P. austrosinense* [43], *P. olsonii* [44], *P. bilaiae* [45], *P. guanacastense* [46]. In addition, there are studies showing the phosphate-mobilising properties of penicilli that have not been identified to species [47–49]. Phosphorus release occurs through the organic acids production (as a result of oxidative respiration or fermentation of organic carbon sources), which can either directly dissolve mineral phosphates as a result of anion exchange or chelate cations Fe^{3+}, Al^{3+} і Ca^{2+} [50]. High-performance liquid chromatography method has shown that PSF-penicilli of different species secrete glucuronic [26; 32; 33; 39], oxalic [26; 31], citric [26; 33], malic [26], tartaric [23; 26] and lactic [23] acids.

The mineralisation of soil organic phosphates plays an important role in the phosphorus cycle in the agricultural system. Phosphorus in organic compounds can account for 4–90 % of the total soil phosphorus [51]. The mineralisation of organophosphates occurs with the help of the enzymes phosphomonoesterases, phytases, phosphonatases and C-P lyases. Phosphomonoesterases (often simply referred to as phosphatases), which are the most common and best studied [52], dephosphorylate phosphoesters or phosphoanhydride bonds of organic matter. Phytases specifically cause the release of phosphorus through the decomposition of phytates. Microorganisms are a key factor in regulating phytate mineralisation in the soil, and their presence in the rhizosphere compensates for the inability of plants to obtain phosphorus directly from phytate [53]. C-P lyases split the C-P bond of organophosphates [54].

Despite the large number of researches on the ability of penicilli to mobilise phosphorus from organic and inorganic compounds, only few reports on this activity of soybean endophytic fungi are available in the literature. Thus, in the article by Khan et al. [37] there is a mention that the soybean endophyte *P. funiculosum* LHL06 dissolves tricalcium phosphate.

The effect of phosphate-mobilising Penicillium strains on soybean plants is also insufficiently covered in the literature. Noteworthy is the work of El-Azouni [42], whose objects of study were fungi *Aspergillus niger* and *Penicillium italicum*. Both micromycetes showed the ability to dissolve insoluble phosphate in agar plates, and in Pikovska liquid medium *P. italicum* released 275 µg P/ml, while *A. niger* released 490 µg P/ml after seven days of incubation. The author found that the simultaneous use of both fungi in the vegetation experiment significantly increased the dry matter weight and phosphorus content in soybean plants versus the control indicators.

Taking into consideration the above mentioned, **the aim** of our work was to research the ability of soybean endophytes of the genus *Penicillium* to release phosphorus from mineral and organic phosphates, to study their effect on the content of total phosphorus in plant shoots.

Materials and methods.

Fungal strains involved in the researches (*Penicillium funiculosum* 20312, *P. variabile* 20173, *P. glauco-lanosum* 20401), isolated from surface-sterilised roots of soybean plants of the Legend variety grown on sod-medium podzolic dusty sandy loam soil and identified by morphological and cultural characteristics [56].

The ability of the tested fungal strains to dissolve mineral phosphates was studied by the method of agar plates on Pikovska medium [57] with the addition of $Ca_3(PO_4)_2$, $AlPO_4$, $FePO_4$ in various variants as the only source of phosphorus. When microorganisms characterised by this ability are cultivated, transparent zones of light are formed around the colonies. Additionally, modifications of Pikovska medium [58; 59] and Czapek-Dox agar with the addition of 5 g/l $Ca_3(PO_4)_2$ were used. The sizes of fungal colonies and light zones were measured on the seventh day of cultivation. The phosphate solubility index (PSI) was calculated as the quotient of the diameter of the zone of enlightenment divided by the diameter of the colony [60].

The ability of the tested penicilli to synthesise the enzyme phosphatase was determined on Czapek-Dox medium, which did not contain a source of available phosphorus-potassium hydrophosphate. Instead, sodium phenolphthalein phosphate (10 % solution in ammonia buffer) was sterilely added to the molten medium cooled to 40 °C before inoculation of the fungi in an amount of 1 ml/l. On the fifth day of micromycetes cultivation, Petri dishes with fungal colonies were kept for 10 min in ammonia vapour (5 drops of 25 % ammonia solution were added to the lids of the Petri dishes). The presence of phosphatase was determined by the appearance of crimson colour under and around the fungal colonies (phenolphthalein, which was formed as a result of dephosphorylation of sodium phenolphthalein phosphate with the participation of phosphatase, turns crimson in alkaline medium) [61].

The vegetation experiment was conducted in a vegetation house on soddy-medium podzolic dusty sandy loam soil characterised by the following agrochemical parameters: humus content was 1.02 %; nitrogen (according to Kornfield) — 54.9 mg/kg; mobile forms of phosphorus (according to Kirsanov) — 110–120 mg P_2O_5; exchangeable potassium (according to Kirsanov) — 120–130 mg K_2O per 1 kg of soil; $pH_{sol.}$ — 5,2; pH_{water} 6.0. Soybean seeds of the Arnica variety were used. Soil moisture was maintained at 60 % of the total moisture capacity. The experiment was repeated five times. The phosphorus content in the aboveground mass was determined on the 35th day.

In order to obtain micromycete spores for pre-sowing handling of soybean seeds, the studied fungi of the genus *Penicillium* were grown on wort agar for 10 days. The inoculation load was 1×10^5 spores per seed.

Scheme of the vegetation experiment:

1. Control (wetting the seeds with sterile tap water at the rate of 1.5 % by weight of seeds).
2. Soybean seed handling with fungal spores *P. funiculosum* 20312.
3. Soybean seed handling with fungal spores *P. variabile* 20173.
4. Soybean seed handling with fungal spores *P. glauco-lanosum* 20401.

The phosphorus content in the aboveground mass of plants and in soybean grain was determined by the Denige method in the modification of Bouvaitier [61]. Wet ashing of plant material was carried out by the method of V. T. Kurkaiev [61].

The results and their discussion. Taking into consideration that phosphorus is fixed in soils not only in the form of calcium phosphate, but also in the form of iron and aluminium phosphates, which depends on soil acidity, Bashan et al. [55] it is recommend to use several sources of insoluble phosphate when studying the phosphate-mobilising properties of microorganisms. We evaluated the ability of endophytic fungi of the genus *Penicillium* associated with soybean roots, to dissolve $Ca_3(PO_4)_2$, $AlPO_4$ or $FePO_4$ salts in Pikovska medium (PVK) (Table 1).

According to the results obtained, the studied strains formed colonies with a diameter of 36.7–42.3 mm on the medium with $Ca_3(PO_4)_2$, 24,7–38,0 mm on the medium with $AlPO_4$ and 26,3–40,0 mm on the medium with $FePO_4$

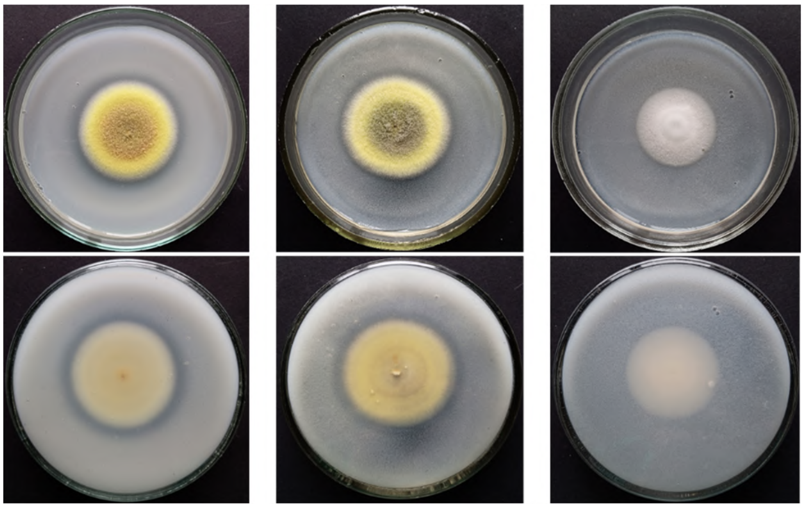
Table 1. ***Phosphate dissolution during cultivation of soybean-associated endophytic fungi of the genus Penicillium on Pikovska medium*** *(the 7th day)*

Variants	Insoluble phosphates in the medium					
	$Ca_3(PO_4)_2$		$AlPO_4$		$FePO_4$	
	colony diameter, mm	PSI	colony diameter, mm	PSI	colony diameter, mm	PSI
P. funiculosum 20312	42,3 ± 0,3	1,17 ± 0,01	38,0 ± 0,6	–	40,0 ± 0,6	–
P. variabile 20173	42,7 ± 0,3	1,18 ± 0,01	30,3 ± 0,3	–	30,3 ± 0,3	–
P. glauco-lanosum 20401	36,7 ± 0,3	–	24,7 ± 0,3	–	26,3 ± 0,3	–

(Table 1). However, clearly visible zones of enlightenment were formed only around the colonies of *P. funiculosum* 20312 and *P. variabile* 20173 mm on the medium with $Ca_3(PO_4)_2$, the phosphate dissolution indices (PSI) determined on the seventh day of observation were 1.17 and 1.18, respectively (Table 1, Fig. 1 a, b).

In order to clarify the ability of *P. glauco-lanosum* 20401 to produce organic acids, the fungus was additionally cultured on modifications of Pikovska medium and Czapek-Dox agar with $Ca_3(PO_4)_2$ as the only source of phosphate (Table 2). Phosphate-mobilising microorganisms differ significantly in the amount and quality of organic acids they produce. Organic acids have different diffusion rates in the agarified medium. To eliminate the cases when isolates, capable of dissolving mineral phosphates, do not form visible zones of enlightenment on agar plates, Gupta et al. [58] proposed to modify Pikovska agar by adding bromophenol blue dye, which reacts to changes in the pH of the medium. When all the studied strains were cultivated on this medium, we observed a change from green (in the control) to yellow of varying intensity, which is associated with the diffusion of organic acids produced by fungi into the agar (Fig. 2). On the seventh day of observation, clearly visible zones of enlightenment were formed only around the colonies *P. funiculosum* 20312 and *P. variabile* 20173 (Fig. 2 b, c), the phosphate dissolution index was 1.13 for both fungi (Table 2). On the twelfth day of cultivation, halo zones were also formed around the colonies of *P. glauco-lanosum* 20401 (Fig. 2 e).

The medium proposed by Nautiyal (National Botanical Research Institute) for phosphate-dissolving microorganisms (NBRIP) [59] was created as a result of studying the effect of the concentrations of individual components of the



a **b** **c**

Fig. 1. Colonies of soybean-associated endophytic fungi of the genus Penicillium on Pikovska medium with $Ca_3(PO_4)_2$ (the 7th day): a) P. funiculosum 20312, b) P. variabile 20173, c) P. glauco-lanosum 20401.

Table 2. ***Dissolution of tricalcium phosphate during cultivation of soybean endophytic fungi of the genus Penicillium on modified variants of Pikovska agar and Czapek-Dox medium*** *(the 7th day)*

Variants	Medium with $Ca_3(PO_4)_2$					
	PVK with bromothymol addition		NBRIP		Czapek-Dox	
	colony diameter, mm	PSI	colony diameter, mm	PSI	colony diameter, mm	PSI
P. funiculosum 20312	39,3 ± 0,3	1,13 ± 0,02	32,7 ± 0,3	1,12 ± 0,02	34,0 ± 0,6	1,12 ± 0,00
P. variabile 20173	38,7 ± 0,9	1,13 ± 0,01	35,3 ± 0,3	1,08 ± 0,01	44,3 ± 0,3	1,11 ± 0,01
P. glauco-lanosum 20401	30,0 ± 0,6	–	23,7 ± 0,3	–	31,0 ± 0,6	–

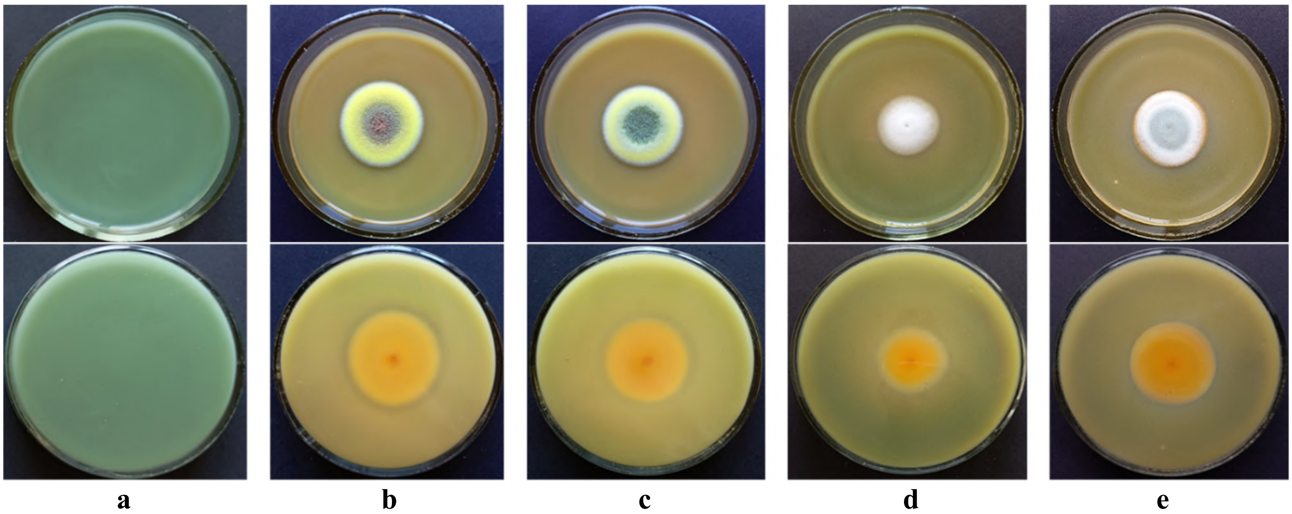


Fig. 2. Colonies of soybean-associated endophytic fungi of the genus Penicillium on Pikovska medium with bromophenol blue: a) control (medium without colonies), b) P. funiculosum 20312 (the 7th day), c) P. variabile 20173 (the 7th day), d) P. glauco-lanosum 20401 (the 7th day), e) P. glauco-lanosum 20401 (the 12th day).

Pikovska medium on the activity of phosphate dissolution by a number of microorganisms. The author showed a positive effect of the increased content of magnesium salts in the medium. We chose Czapek-Dox agar because the composition of this medium is optimal for growing fungi, in particular, representatives of the genus *Penicillium*, which are the objects of this research. The phosphate dissolution indexes determined using the modified media and Czapek-Dox agar were slightly inferior to the corresponding results obtained on Pikovska medium (Table 2).

In the studies on the selection of phosphate-mobilising fungi, the selected strains are usually characterised by phosphate dissolution indexes that are significantly higher than those obtained by us when cultivating the studied fungi in different mediums [47; 49; 62]. In our opinion, this is due to the adaptation of endophytic penicilli associated with soybean plants to the topological zone from which they were isolated, since excessive acid formation would disrupt the biochemical balance of the internal tissues of roots.

Thus, all the tested fungi are capable of producing organic acids and releasing phosphorus from $Ca_3(PO_4)_2$ to varying degrees. This ability is described in the literature for representatives of the species *P. funiculosum* and *P. variabile* [37; 40].

Since another important mechanism of phosphorus conversion into a form accessible to plants is the mineralisation of organic phosphates, the presence of the phosphatase enzyme in the tested penicillium strains was checked. This enzymatic activity was observed for all three fungi. The fungal phosphatases dephosphorylate sodium phenolphthalein phosphate added to the Czapek-Dox medium, and the released phenolphthalein is coloured bright crimson in ammonia vapour (Fig. 3).

According to Bashan et al. [55], a necessary step in the research of phosphate mobilising properties of a microorganism is to determine the direct contribution of phosphorus to inoculated plants. Taking this into consideration, we determined the content of general phosphorus (P_2O_5) in the aboveground mass of plants grown under the conditions of the vegetation experiment (Fig. 4). According to the data obtained, all the tested fungal strains had a positive effect on the content of general phosphorus in the dry matter of soybean shoots, but this indicator increased significantly in the variant with the use of *P. funiculosum* 20312 and was (0.751 ± ± 0.046) % against (0.643 ± 0.008) % in the control variant (Fig. 4).

Literature data shows that the ability of microorganisms to mobilise phosphorus does not necessarily correlate with the ability to stimulate plant growth [63]. However, our previous researches have shown a multidirectional effect of penicilliums on soybean plants. The tested strains produce phytohormonal substances, which in turn have a positive effect on both growth performance and the symbiotic apparatus of soybean plants [56].

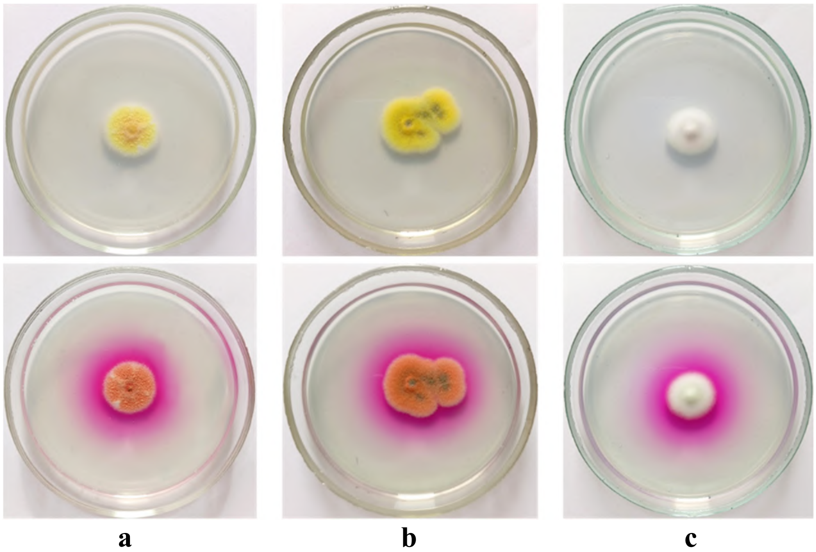


Fig. 3. Qualitative response to phosphatase during cultivation of Penicillium fungi on Czapek-Dox medium with sodium phenolphthalein phosphate (the 5th day): a) P. funiculosum 20312; b) P. variabile 20173; c) P. glauco-lanosum 20401; the top row of photos — fungal colonies before processing with ammonia vapour; the bottom row — fungal colonies after exposure to ammonia vapour.

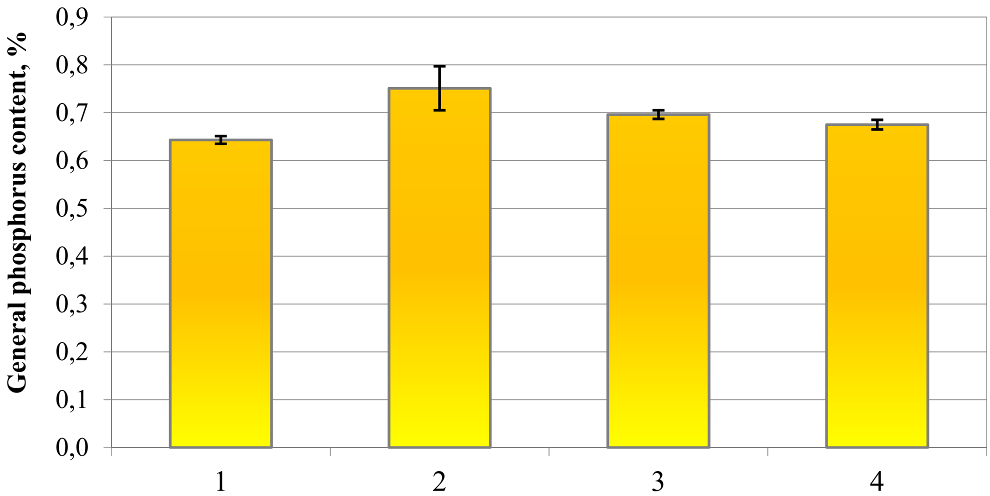


Fig. 4. Influence of endophytic fungi of the genus Penicillium on the content of general phosphorus in shoots of soybean plants of the Arnica variety (vegetation experiment, budding — beginning of blooming): 1 — control (water); 2 — P. funiculosum 20312; 3 — P. variabile 20173; 4 — P. glauco-lanosum 20401.

Conclusions. The tested fungi of the genus *Penicillium*, isolated from surface-sterilised roots of soybean plants, are capable of releasing phosphorus by dissolving inorganic and mineralising organic phosphates. There is a tendency to increase the content of general phosphorus in the aboveground mass of soybean plants after processing soybean seeds with *P. variabile* 20173 and *P. glauco-lanosum* 20401 spores and a significant increase from 0.643 % in the control to 0.751 % in the variant with the use of the fungus *P. funiculosum* 20312.

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ФОСФАТМОБІЛІЗУВАЛЬНІ ВЛАСТИВОСТІ ГРИБІВ РОДУ *PENICILLIUM,* ВИДІЛЕНИХ З ГІСТОСФЕРИ СОЇ

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Мета. *Дослідити здатність грибів роду Penicillium, ізольованих із гістосфери рослин сої, вивільняти фосфор із мінеральних та органічних фосфатів, вивчити їхній вплив на вміст загального фосфору в пагонах рослин.* ***Методи.*** *Мікробіологічні (культивування досліджуваних грибів на середовищі Піковської та його модифікаціях, агарі Чапека-Докса із додаванням трикальційфосфату або фенолфталеїнфосфату, сусловому агарі), вегетаційного досліду (визначення вмісту загального фосфору в надземній масі рослин сої), статистичні.* ***Результати****. Використання трьох нерозчинних фосфатів у складі середовища Піковської показало, що досліджувані гриби різною мірою розчиняють* $Ca_3(PO_4)_2$ *і не здатні розчиняти* $AlPO_4$ *та* $FePO_4$*. На сьому добу культивування навколо колоній P. funiculosum 20312 і P. variabile 20173 утворювалися добре помітні зони просвітлення, індекси розчинення фосфату становили 1,17 і 1,18 відповідно. За культивування грибів на середовищі Піковської з додаванням бромфенолового синього барвника у варіантах P. funiculosum 20312 і P. variabile 20173 середовище швидко змінювало колір з зеленого на жовтий, що свідчить про дифузію в агар органічних кислот, продукованих грибами. Починаючи з дванадцятої доби досліду, середовище навколо колоній гриба P. glauco-lanosum 20401 також набувало насиченого жовтого кольору і було відзначено появу гало-зон. Для всіх досліджуваних грибів показано наявність фосфатазної активності. Досліджувані штами грибів позитивно впливали на вміст загального фосфору в сухій речовині пагонів сої, достовірно цей показник підвищувався у варіанті із застосуванням P. funiculosum 20312 — 0,751 % проти 0,643 % у контрольному варіанті.* ***Висновки.*** *Досліджувані гриби роду Penicillium, ізольовані з поверхнево стерилізованих коренів рослин сої, здатні вивільняти фосфор за рахунок розчинення неорганічних і мінералізації органічних фосфатів, позитивно впливають на вміст загального фосфору в пагонах рослин сої.*

Ключові слова: *гриби-ендофіти сої, PSF (гриби, які розчиняють фосфати), розчинення неорганічних фосфатів, мінералізація органічних фосфатів, фосфатаза.*

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