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ENDOPHYTIC FUNGI OF SPHAGNUM BOG PLANTS OF UKRAINIAN POLISSYA

Endophytic fungi exist asymptotically within living tissues of host plants. The formation and coexistence of endophytic micromycete associations with mosses, ericoid, herbaceous and woody plants of Ukrainian Polissya sphagnum bogs were investigated along with the physiological properties of endophytes, plant pathogenic and soil isolates. The existence of endophytic micromycetes in plants of this ecosystem is a common phenomenon that integrates mosses, herbaceous and woody plants into the common trophic chain. The studied endophytic micromycetes belong to the Class 2 and 3 endophytes (NC-endophytes) in accordance with their spread in different plants and their organs, i.e. those that are present in all organs of bog plants and characterized by considerable diversity. Based on detection of endophytic species in different organs of certain plants and certain plant species, this classification is supplemented by new data on significant biodiversity of Class 2 endophytic micromycetes in plants.

It was established for the first time that the endophytic way of existence of micromycetes is determined by ecological and physiological peculiarities of this group: fast extensional colonization of different species of bog plants, ability to transform the more toxic base T-2 toxin to its less toxic derivatives, a required presence of polygalacturonase activity and its higher level than for the isolates from other econiches.

K e y w o r d s: endophytic micromycetes, species diversity, mutualism, growth characteristics, hydrolytic activity, trichothecene mycotoxins, vitamins of B group.

Association of endophytic fungi with plants can be defined as a currently asymptomatic existence within living tissues of host plants [3, 21]. The coexistence of plants with endophytic and mycorrhizal fungi comprises more than 400 million years when plants had just begun to colonize land [12, 28]. Endophytic fungi vary in symbiotic and ecological functions, they were found in plants of all terrestrial biomes. This group of fungi significantly affects plant communities and facilitates their adaptation to abiotic and biotic environmental factors [27, 31]. At the level of individual plants in this symbiosis, the fungus obtains organic nutrients from the host and transports mineral nutrients to it, especially in oligotrophic ecosystems [34]. Endophytic micromycetes can be latent pathogens of plants and antagonists of plant pathogenic fungi, bacteria and viruses [5, 6, 35, 36].

Despite a more than 100-year period of study of endophytic fungi, their ecological significance and physiological features are still poorly understood. Almost nothing is known about the complexes of endophytic micromycetes and their role in ecosystems with adverse and extreme conditions. The species composition of endophytic micromycetes of the wetland ecosystems of Ukrainian Polissya, contaminated with radionuclides after the Chornobyl disaster, is not investigated. Sphagnum bogs in Zhytomyr and Rivne regions are characterized by poor mineral nutrition; accumulation of the main mineral

elements in the inaccessible to plants forms; formation of peat with low degree of decomposition (10–15 %); phytocenoses composed of 5–10 plant species; presence of a powerful moss layer, that is dominated by sphagnum mosses [26].

Biologically active metabolites of the endophytic fungi are insufficiently studied, and only those that have a therapeutic effect or are a promising means of plant protection against pathogens and pests have been well investigated [27]. Trophic and biosynthetic peculiarities of endophytic micromycetes (the synthesis of toxins, vitamins, and hydrolytic enzyme complexes) are also largely unexplored. In particular, nothing is known about the growth characteristics of endophytes. Research of various aspects of ‘microorganism-plant’ interaction is relevant, since the complex of physiological and biochemical properties of micromycetes affects the processes of change in their trophic states. Characterization of micromycetes with different nutrient types within the same species requires a study of ecological and physiological properties of endophytic micromycete isolates in comparison with plant pathogens and soil saprophytes. Notably, species composition of endophytic micromycetes of sphagnum bog plants is still not investigated, including individual plants and their organs. The processes of endophytic degradation of plant polymers, their synthesis of toxins and vitamins; the growth characteristics of endophytes under different culture conditions and utilization peculiarities of the different carbon sources remain almost not studied. Therefore, a study of the species composition and physiological characteristics of endophytic micromycetes of sphagnum bog plants of Ukrainian Polissya is highly appropriate and relevant today.

The aim of our study was to establish the species composition of endophytic microscopic fungi and the peculiarities of their localization in plants of sphagnum bogs of Ukrainian Polissya, to perform a comparative analysis of physiological characteristics (growth parameters, enzymatic activity, production of trichothecene mycotoxins and some B vitamins) of endophytes, plant pathogenic and soil isolates and to provide a scientific-theoretical evidence of the ecological role of endophytic micromycetes.

Biodiversity of endophytic fungi of sphagnum bog plants. The species number and the distribution of endophytic fungi in 36 species of mosses and vascular plants from sphagnum bogs of Ukrainian Polissya were studied. Over 3000 strains of endophytic microscopic fungi were isolated from 220 plant samples from sphagnum bogs [15]. They belong to 118 species of 58 genera of Zygomycota and Ascomycota divisions. From 1 to 16 species of endophytic micromycetes were identified in each plant. The number of common species of endophytic micromycetes for all plant organs varied in different plant species and reached 50–100 %. This fact is consistent with scientific data provided by other researchers [4, 21, 27, 31]. The studied endophytic micromycetes from different plant organs belonged to the same species in more than 80 % of cases [15]. Each plant species is characterized by its own complex of fungal endophytes in different plant organs, where 3–4 of them are detected in all cases, while 1–10 (and more) appear rarely.

Endophytic micromycetes were isolated from different organs of sphagnum bog plants; in particular, this was typical of endophytes with a high frequency of occurrence. The complex of endophytic micromycetes in all plant organs

in more than 60 % cases was identical. Thus, they can be classified as Class 2 of NC-endophytes. At the same time, Rodriguez et al. [31] consider that this class is characterized by low biodiversity in plants. We obtained data about the existence of up to 16 species of endophytic fungi in each individual plant and up to 60 – in plants of the same species. Thus, we assume that the classification of endophytes should be used as supplemental information about significant biodiversity of Class 2 endophytes in plants. Because the endophytic complex of stems and leaves in 19.4 % of cases was similar, we assume that the studied endophytes belong to Class 3 endophytes. The endophyte classification of Rodriguez et al. [31] was complemented by our data on significant biodiversity in bog plants of Class 2 endophytes. Thus, endophytic micromycetes represent a permanent component of the sphagnum bog ecosystem of Ukrainian Polissya that associates mosses, grasses, ericoid plants and trees into a common biogeochemical cycle [15].

Growth characteristics of micromycetes isolated from different ecological niches. Physiological and biochemical features of endophytic micromycetes, including their growth characteristics, determine largely the biological activity of fungi and are very important in symbiotic interactions of endophytes with plants.

Soil micromycetes (saprophytes) were characterized by the lowest average of radial growth rate and significantly differed from biotrophs (plant pathogenic and endophytic strains). High growth rate of endophytic and plant pathogenic strains of *Fusarium poae*, *Alternaria alternata* and *Ceratocystis* sp. promotes rapid colonization of their host plants [20].

Endophytic *A. alternata* was characterized by higher specific growth rate than the plant pathogens. Endophytic *F. poae*, *Penicillium funiculosum*, *Ceratocystis* sp. and *A. alternata* had higher biomass concentration compared with the strains of these species from other niches. Endophytic strains generally had higher economic coefficients and biomass concentration. Thus, the studied strains of micromycetes *F. poae*, *A. alternata*, *P. funiculosum* and *Ceratocystis* sp. were characterized by peculiarities of growth parameters that were determined by the biotrophic way of existence in plants as well as by the saprotrophic existence in soil [17].

Enzymatic activity of endophytic, plant pathogenic and soil micromycetes. Endophytic fungi – mycosymbionts of ericoid and other sphagnum bog plants are able to transform plant polymers using a wide range of hydrolases – cellulases, hemicellulases, ligninases, polyphenoloxidases, polygalacturonases, phosphatases [4, 30]. Fungi synthesize enzyme complex acting as an invasive agent and facilitating the pathogen penetration into the host plant tissues and their assimilation, thus, significantly disrupting the metabolism of plants. Saprophytic fungi also need the hydrolase complex for the transformation of plant residues.

Polyphenoloxidase activity of endophytic fungi *A. alternata*, *P. funiculosum* and *Mycelia sterilia* was higher in the strains isolated from plant roots and decreased in the ones from leaves [18]. Hydrolytic activity of *Fusarium* spp., *A. alternata*, *Ceratocystis* sp. and *P. funiculosum* strains of different trophic groups and endophytic *Mycelia sterilia* increased in the following order: amylolytic → cellulolytic → polygalacturonase → xylanase [39]. β-D-glucosidase activity of endophytic fungi depended on the plant organ, which

they were isolated from, and didn't depend on the host plant species [18].

Polygalacturonase presence in endophytic fungi is of particular importance for oligotrophic sphagnum bogs [23, 29], especially for the exchange and migration of K^+ and $^{137}Cs^+$ in oligotrophic bog ecosystems [23, 26]. The majority of the studied species strains showed medium polygalacturonase activity [14]. Endophytic *P. funiculosum*, *F. poae* and some *A. alternata* strains were characterized by high endopolygalacturonase activity (EPGA). So, polygalacturonase and high EPGA activities of endophytic fungal species of sphagnum bog plants of Ukrainian Polissya indicate that endophytic microscopic fungi hydrolyze pectin substances in plant tissues and might play an important role in the migration of monovalent cations in sphagnum bog ecosystems.

Thus, the endophytes were characterized by the lowest hydrolytic activity and the plant pathogens – by the highest one. Plant pathogenic and endophytic isolates can be differentiated by ANOVA based on their polygalacturonase and xylanase activities. Plant pathogens and soil strains were characterized by high xylanase and low polygalacturonase activities. Endophytes demonstrated medium polygalacturonase and lower xylanase activities.

Trichothecene mycotoxin complex of *Fusarium poae*. The soil *Fusarium poae* strains had the highest content of T-2, HT-2 and T-2 tetraol toxins, while the plant pathogens actively synthesized T-2 triol [19]. Soil *F. poae* strains were characterized by a higher toxicity level compared with endophytes. Thus, the results on *F. poae* endophytes indicated the potential ability of the strains of this group to synthesize trichothecene mycotoxins in lesser quantities and of a significantly limited quality compared with the soil and plant pathogenic isolates. Representatives of the biotrophic group are able to rapidly transform the T-2 toxin into less toxic derivatives. This physiological peculiarity of endophytes is one of the factors of mutualistic coexistence of endophytic micromycetes with host plants [27, 33, 35, 36]. This fact is consistent with our results, and indicates the high activity of enzymes that metabolize T-2 toxin into less toxic derivatives, and may be regarded as a defence mechanism of the producing strains against their own toxic metabolites [37].

It was shown that the content of the studied trichothecene toxins, except for T-2 triol, was higher in the soil strains than in the plant pathogens and endophytes. This fact can be explained by the biological peculiarities of fungi of *Fusarium* genus, which are not obligate biotrophs and often inhabit soil as saprophytes or facultative parasites. In particular, *F. poae* species exists in different soil types and it is a part of the species complex causing *Fusarium* head blight. Therefore, apparently, weak pathogens prefer biologically not to “kill” the host plant immediately using highly active enzymes and toxins, but to secure a long continued existence in the living plant, using, for example, the mechanism of transformation of more toxic T-2 toxin into less toxic derivatives. Decomposition and disintegration of plants and other residues are the functions of such soil isolates. In this case, the competition for nutrient sources with other microscopic saprotrophs increases promoting the production of toxic metabolite spectrum by the fungus [25].

Riboflavin and nicotinic acid production by endophytic fungi. In the formation of associative symbiotic interaction with plants endophytic fungi can produce a large spectrum of vitamins, including riboflavin and nicotinic acid [9]. Our data showed that the studied endophytes are not the sources of B

group vitamins for sphagnum bog plants [16].

Discussion. The endophytes with neutral or positive influence on a host plant are called “classic” endophytes and the endophytes that have a negative influence are referred to as “pathogens” since the existence of endophytes in plants can be transformed from mutualism to antagonism for almost any type of plant-microbe interactions. These two concepts are regarded as the opposite result of the ‘microorganism-plant’ interaction [3, 21, 27, 31, 38, 40]. A group of biotrophs combines mutualistic symbiosis (endophytism) and plant pathogenic lifestyles. At the same time, a group of saprotrophs that transform dead plant tissues is present in soil. Such species of microscopic fungi as *Fusarium* are well adapted for living in different conditions (soil, plant substrates, technical materials etc.). Therefore, a study of the species diversity and the ecological and physiological properties of endophytic micromycetes in comparison with saprophytic and plant pathogenic ones of the same species is important.

We found that endophytic micromycetes of plants present a constant component of sphagnum bogs of Ukrainian Polissya. The existence of endophytic micromycetes in plants of this ecosystem is a common phenomenon that integrates the mosses, herbaceous and woody plants into a common trophic chain [15, 39]. The studied endophytic micromycetes belong to the Class 2 and 3 endophytes (NC-endophytes) in relation to their spread in different plants and their organs, i.e. those that are present in all organs of bog plants and are characterized by considerable diversity. On the basis of detection of endophytic species in different organs of certain plants and certain plant species, this classification is supplemented by new data on significant biodiversity of endophytic micromycetes of Class 2 in plants.

Endophytic species of micromycetes that could potentially be plant pathogens (*Fusarium*, *Alternaria*, *Botrytis*, *Colletotrichum*, *Ceratocystis*, *Acremonium*, *Sarocladium* and *Leptographium*) were identified in sphagnum bog plants of Ukrainian Polissya. A great part of endophytes which asymptotically exist in plants belongs to the potential plant pathogens [2, 8]. The disease process in plants depends on their general resistance, aggressiveness of the pathogens and environmental factors. However, the majority of biotrophic pathogens induce systemic resistance of host plants to other infectious agents [7, 27]. So, the resistance of sphagnum bog plants to high virulent or aggressive plant pathogens is possible due to the influence of latent pathogens in particular of endophytic micromycetes.

Endophytes synthesize enzymes that transform cellulose and hemicellulose and such a property is associated with the mutualistic relationships between endophytes and plants. There is not enough information about physiological nature of this interaction. An important aspect of hydrolase activity investigation is an involvement of endophytic fungi in the hydrolysis of plant polymers. So far, the endophytic symbionts present in dead plant tissues can initiate the hydrolysis of the afore mentioned saprophytic species. Therefore, we can conclude that the synthesis of hydrolytic enzymes by endophytic species may be important for the nutrition of a fungus not only at the endophytic stage, but also at the saprophytic stage and it is consistent with data of other authors [30]. It was shown that endophytic fungi from the leaves of mangrove plants of different age produced hydrolytic enzymes and were more common after defoliation rather than in live leaves [13]. This fact indicates the participation

of endophytes in the transformation of plant residues.

The quantity of substrates that could be transformed by endophytic microorganisms is an important sign of their enzymatic activity. Our research showed that endophytes are capable to synthesize enzymes and metabolize many plant polymers *in vitro*, that coincides with the literature [22, 33]. Evaluation of endophytic fungi ability to convert a wide spectrum of natural polymers will become the base of their use in biotechnology as efficient transformers of plant biomass.

At the present time, the researchers of endophytic fungi are focused on a generalization of physiological characteristics and a description of their trophic peculiarities for establishing consistent patterns of their interaction with host plants. Thus, Kusari et al. proposed the scheme that explains the ability of endophytes to synthesize the same biologically active substances as their host plants [21]. However, this scheme has not established why some species (or strains of certain species) exist in plants as endophytes and the other ones – as disease agents, and why endophytes are ahead of pathogens in the colonization of host plants. The type of trophic relations in the ‘microorganism-plant’ association is a transition between three key trophic states – pathogenicity, mutualism, and parasitism [24]. Microorganisms are capable of transformation between trophic states of pathogenicity and symbiosis and/or between mutualism and parasitism during their life cycles; symbiotic relationship varies from mutualistic (plants and microorganisms get mutual benefits) to parasitic (a microorganism benefits from a plant). Such transformations from one state to another are induced by triggers, the role of which in trophic changes of a microorganism remains unclear.

The researchers conclude that the associations contributing to the survival of all organisms in the interaction of microsymbionts with plants are an ecological norm, and their pathogenic condition is ecologically unstable. Thus, pathogenesis is a functional stage of the microorganism’s life cycle then its spread in host plant becomes a priority for a microsymbiont. This scheme [24] explains the transformation from biotrophy to hemibiotrophy but doesn’t include microorganisms with a saprotrophic stage of existence in soil in their life cycle, which is connected with their transformation of dead plant tissues and with the competition for nutrition sources.

Based on our experimental data, we suggest a new conceptual model of possible transition of microscopic fungi from saprotrophic to biotrophic stages and provide a characteristic of their ecological and physiological peculiarities (Fig. 1). Endophytic and plant pathogenic organisms have a saprotrophic stage in their life cycle: they continue to exist in the host plants even after their death hydrolyzing dead plant tissues. Endophytes are already located in the colonized plant substrate and synthesize the toxic substances; it improves their position in the struggle for nutrients. So, micromycetes at this stage of their life cycle exist in fact in soil as saprotrophs in an active state or in a form of chlamydospores. When micromycetes get an opportunity to colonize a plant (in the case of overcoming the competition for the substrate with other microorganisms and host plant protection systems), they realize it by the transformation to the biotrophic way of life as asymptomatic symbionts (endophytes) or plant pathogens.

Fig. 1 – The conceptual model of interaction of trophic groups of micromycetes and their physiological properties

According to many authors, C-endophytes in stressful conditions benefit from the survival of host plants. The disruption of balance by environmental factors can change the state of micromycetes from latent to parasitic and cause plant diseases. For the NC-endophytes such data is not available.

Our results show that the transformation of micromycetes in the plant from endophytic to pathogenic state should be held under rapid changes in their physiological properties (growth parameters, hydrolytic activity, and toxigenic potential).

Thus, the transformation of a plant pathogenic fungus to the endophytic state can be possible under certain conditions: the reduction of its toxicity and hydrolytic activity, the increase in the host plant resistance and the presence of favorable environmental factors.

Growth characteristics of endophytic micromycetes on solid and liquid nutrient media, their low values of hydrolytic activity and synthesis of trichothecene mycotoxins are the additional arguments in favor for that this group of fungi is better adapted to survival inside the host plant. They use less aggressive ways of plant colonization than plant pathogenic strains and therefore exist in more favorable conditions.

The presence of the common species of endophytic fungi (31 of 118) in mosses, ericoid, herbaceous and woody plants, established their ecological and physiological properties indirectly testify the legacy of our hypothesis about the existence of trophic connection between mosses and vascular plants, and participation of endophytic micromycetes in the transport of mineral elements including K^+ and $^{137}Cs^+$ from sphagnum mosses to vascular plants in sphagnum bogs, respectively. Our hypothesis is consistent with the literature data on the ability of ericoid mycorrhizal and endophytic fungi to synthesize hydrolytic enzymes transforming plant polymers [4, 27, 31].

At the present time, the fact that endophytic micromycetes in plants are a constant component of sphagnum bogs of Ukrainian Polissya that links mosses, ericoid, herbaceous and woody plants, peat and swamp water into one biogeochemical cycle is proved. Endophytism provides for the more favorable existence of fungi compared with plant pathogens and soil strains. This is confirmed by our experimental data: each species of plants is characterized by its own complex of fungal endophytes; in most cases (83.3 %) endophyte species composition is similar in different organs of plants and only in 11.1 % of cases the difference in species composition increases from the bottom to the top parts of a plant, 5.6 % recorded complete difference in endophyte complex in different organs; the presence of 31 common species of endophytic micromycetes in sphagnum bog plants; the similarity of species composition of endophytic micromycetes in vascular plants and mosses; high rate of spatial colonization of substrates by endophytes, more biomass and higher economic coefficients under cultivation in liquid media; low hydrolytic activity of endophytic micromycetes at medium polygalacturonase and absent amylase activities; the ability of *F. poae* endophytes to transform T-2 toxin in less toxic derivatives and neosolaniol absence.

It is known that endophytic bacteria can be potential human pathogens [11]. The literature available contains no information concerning NC-endophytic micromycete pathogenicity for animals and humans. At the same time, medical mycologists and veterinarians often isolate *A. alternata*, *P. funiculosus* and

F. poae species when a pathological process occurs in humans and animals [32]. Other representatives of these species can be plant endophytes.

Thus, the complex of differences between the isolates from different ecological niches is shown for the first time: the endophytes are characterized by higher economic coefficients and greater biomass in liquid media than the strains from other habitats; endophytes demonstrate higher polygalacturonase activity and plant pathogens and soil saprotrophs – the xylanase ones. The endophytic way of existence of micromycetes is determined by the ecological and physiological peculiarities of this group: simultaneous and rapid colonization rate of different species of bog plants; ability to transform the toxic T-2 toxin into its less toxic derivatives and higher polygalacturonase activity compared to the isolates from other habitats.

Conclusion. The coexistence principles of associations of endophytic micromycetes with mosses, ericoid, herbaceous and woody plants on the example of sphagnum bog ecosystem of Ukrainian Polissya were demonstrated. Species diversity, physiological and biochemical peculiarities of endophytes that determined their mutual coexistence with the host plants, and general regularities of plant colonization by endophytes were established. Thus, the complex of differences between the isolates from different ecological niches is shown for the first time: the endophytes are characterized by higher economic coefficients and greater biomass in liquid media than the strains from other habitats; endophytes demonstrate higher polygalacturonase activity and plant pathogens and soil saprotrophs – the xylanase ones. The endophytic way of existence of micromycetes is determined by the ecological and physiological peculiarities of this group: simultaneous and rapid colonization rate of different species of bog plants; ability to transform the toxic T-2 toxin into its less toxic derivatives and higher polygalacturonase activity compared to the isolates from other habitats.

The outlook study of endophytic fungi. Further studies of endophytic fungi obviously must be focused on a comprehensive study of plant endophytes – fungi, bacteria, viruses, etc. Endophytes metabolome, biologically active metabolites which determine the species composition of endophytic complexes able to penetrate into the host plants are an important area of modern studies.

The bioactive metabolites originate from endophytes are of a particular importance in this context. They define the mutualistic co-existence of fungi and plants, while also producing a new generation of drugs to be used in green technologies for the induction of systemic plant resistance to stress and protection against plant pathogens.

Many endophytes have a potential to synthesize various bioactive metabolites that may directly or indirectly be used as therapeutic agents against numerous diseases [21]. Endophytes can produce host plant secondary metabolites with therapeutic effect, for example, paclitaxel (Taxol), podophyllotoxin (deoxypodophyllotoxin, camptothecin, hypericin, emodin, and azadirachtin). The production of bioactive compounds by endophytes is not only important from a physiological perspective but also from an ecological standpoint. Exciting possibilities exist for using endophytic fungi for the production of novel biologically active secondary metabolites.

In particular, it is already known that *P. funiculosum* endophytes have a high ability to produce plant hormones and cellulolytic active enzymes [1, 10,

30]. Further research is advisable to focus on a complex study of the species diversity of endophytic fungi, bacteria and other endophytes of plants from temperate latitudes, their physiological features compared to the strains of the same species from other habitats and the ones belonging to different trophic groups.

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ЕНДОФІТНІ ГРИБИ РОСЛИН СФАГНОВИХ БОЛІТ ПОЛІССЯ УКРАЇНИ

Резюме

Ендофітні гриби безсимптомно існують у живих тканинах рослин-хазяїнів. Вивчено формування і співіснування асоціацій ендофітних мікроміцетів з мохами, ерикоїдними, трав'янистими і деревними рослинами на прикладі сфагнових боліт Полісся України, а також здійснено порівняльне дослідження фізіологічних властивостей ендофітних, фітопатогенних і ґрунтових ізолятів.

Існування ендофітних мікроміцетів у рослинах цієї екосистеми є загальним явищем, що об'єднує мохи, трав'янисті і деревні рослини у спільний трофічний ланцюг. На основі розповсюдження в різних рослинах і їх органах досліджені ендофітні мікроміцети належать до класів 2 і 3 (NC-ендофітів), тобто вони присутні в усіх органах болотних рослин і характеризуються значною різноманітністю. На підставі виявлення ендофітних видів у різних органах певних рослин і певних видів рослин цю класифікацію доповнено новими даними щодо значного біорізноманіття ендофітних мікроміцетів класу 2 в рослинах.

Вперше встановлено, що ендофітний спосіб існування мікроміцетів визначається екологічними і фізіологічними особливостями цієї групи: швидкою колонізацією різних видів болотних рослин, здатністю трансформувати більш токсичний базовий Т-2 токсин у його менш токсичні похідні, наявністю полігалактуроноазної активності та її вищим рівнем, ніж у ізолятів з інших еконіш.

Ключові слова: ендофітні мікроміцети, видове різноманіття, мутуалізм, росто-ві характеристики, гідролітична активність, трихотеценові мікотоксини, вітаміни групи В.

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ЕНДОФИТНЫЕ ГРИБЫ РАСТЕНИЙ СФАГНОВЫХ БОЛОТ ПОЛЕСЬЯ УКРАИНЫ

Резюме

Эндофитные грибы бессимптомно существуют в живых тканях растений-хозяев. Исследовано формирование и сосуществование ассоциаций эндофитных микромицетов с мхами, эрикоидными, травянистыми и древесными растениями на примере сфагновых болот Полесья Украины, а также проведено сравнительное изучение физиологических свойств эндофитных, фитопатогенных и почвенных изолятов.

Существование эндофитных микромицетов в растениях этой экосистемы является общим явлением, объединяющим мхи, травянистые и древесные растения в общую трофическую цепь. На основе распространения в различных растениях и их органах исследованные эндофитные микромицеты относятся к классам 2 и 3 (NC-эндофитам), то есть они присутствуют во всех органах болотных растений и характеризуются значительным разнообразием. На основании выявления эндофитных видов в различных органах определенных растений и определенных видов растений эта классификация дополнена новыми данными о значительном биоразнообразии эндофитных микромицетов класса 2 в растениях.

Впервые установлено, что эндофитный способ существования микромицетов определяется экологическими и физиологическими особенностями этой группы: быстрой колонизацией различных видов болотных растений, способностью трансформировать более токсичный базовый Т-2 токсин в его менее токсичные производные, наличием полигалактуроназной активности и ее более высоким уровнем, чем у изолятов из других экосистем.

Ключевые слова: эндофитные микромицеты, видовое разнообразие, мутуализм, ростовые характеристики, гидролитическая активность, трихотеценовые микотоксины, витамины группы В.

1. Adejuwon AO, Oni AO, Ajayi AA, Olutiola PO. Cellulase activity in tomato fruits infected with *Penicillium funiculosum* Thom. Afr J Plant Sci. 2009; 3(5): 113–116.
2. Albrechtsen BR, Björkén L, Varad A, Hagner Å, Wedin M, Karlsson J, et al. Endophytic fungi in European aspen (*Populus tremula*) leaves – diversity, detection, and a suggested correlation with herbivory resistance. Fungal Diversity. 2010; 41(1): 17–28.
3. Bacon CW, White JFJ. Physiological adaptations in the evolution of endophytism in the Clavicipitaceae. In: Microbial endophytes. New York, USA: Marcel Dekker Inc., 2000. p. 237–63.
4. Cairney JW, Burke RM. Extracellular enzyme activities of the ericoid mycorrhizal endophyte *Hymenoscyphus ericae* (Read) Korf et Korman: their likely roles in decomposition of dead plant tissue in soil. Plant and Soil. 1998; 205(1): 181–92.
5. Carroll G. Fungal endophytes in stems and leaves: from latent pathogen to mutualistic symbionts. Ecology. 1988; 69(1): 2–9.
6. Clay K. Clavicipitaceous fungal endophytes of grasses: their potential as biocontrol agents. Mycol Res. 1989; 92(1): 1–12.
7. Gao FK, Dai CC, Liu XZ. Mechanisms of fungal endophytes in plant protection against pathogens. Afr J Microbiol Res. 2010; 4(13): 1346–51.
8. Gazis R, Chaverri P. Diversity of fungal endophytes in leaves and stems of wild rubber trees (*Hevea brasiliensis*) in Peru. Fungal Ecology. 2010; 3(3): 240–54.
9. Geltser FYu. [The symbiosis with microorganisms is the basis of the life of plants]. Moscow: Publishing house of the MAA, 1990. Russian.
10. Khan AL, Lee I-J. Endophytic *Penicillium funiculosum* LHL06 secretes gibberellins that reprograms *Glycine max* L. growth during copper stress. BMC Plant Biology. 2013; 13:86. <http://www.biomedcentral.com/1471-2229/13/86>.
11. Kozyrovska N. Endophyty.ua. Kyiv: LAT&K, 2011. Ukrainian.
12. Krings M, Taylor TN, Hass H, Kerp H, Dotzler N, Hermsen EJ. Fungal endophytes in a 400-million-yr-old land plant: infection pathways, spatial distribution, and host

- responses. *New Phytol.* 2007; 174(3): 648–57.
13. Kumaresan V, Suryanarayanan TS. Endophyte assemblages in young, mature and senescent of *Rhizophora apiculata*: evidence for the role of endophytes in mangrove litter degradation. *Fungal Diversity*. 2002; 9: 81–91.
 14. Kurchenko IN. [Polygalacturonase activity of microscopic fungi of different trophic groups]. *Mikrobiol Z.* 2013; 75(2): 57–66. Russian.
 15. Kurchenko IM. [Distribution of endophytic mycobiota in sphagnum bog plants of Ukrainian Polissya]. *Scientific Reports of NULES of Ukraine*. 2015; 6(55). nd.nubip.edu.ua/ 2015_6/2.pdf. Ukrainian.
 16. Kurchenko IM, Kharkevych OS, Yurieva OM, Pavlychenko AK, Suprun SM. [Riboflavin and nicotinic acid production by microscopic fungi of different trophic groups]. *Vynohrads'kyj Society of Microbiologists of Ukraine: Proceedings of the XIII Congress*; 2013 Oct 1–6; Yalta, Ukraine. Yalta; 2013. p. 104.
 17. Kurchenko IN, Pavlychenko AK, Yurieva EM. [Growth characteristics of *Fusarium poae* (Peck) Wollenw. and *Penicillium funiculosum* Thom strains]. *Mikrobiol Z.* 2013; 75(5): 40–4. Russian.
 18. Kurchenko IN, Sokolova EV, Zhdanova NN, Orlov AA. [Some enzyme activity of endophytic fungi from vascular plants of Ukrainian Polessye sphagnum peat bogs]. *Bulletin of the Odessa National University. Series Biology*. 2005; 10(7): 255–61. Ukrainian.
 19. Kurchenko IM, Tsyganenko KS. [Comparative characteristic of trichothecene mycotoxin complex of *Fusarium poae* (Peck) Wollenw. the strains from different trophic groups]. *Microbiol Biotechnol.* 2013; 3(23): 40–9. Russian.
 20. Kurchenko IM, Yurieva OM, Voychuk SI. [Growth of micromycetes from different ecological niches on agar nutrient media]. *Mikrobiol Z.* 2015; 77(5): 37–46. Ukrainian.
 21. Kusari S, Hertweck C, Spiteller M. Chemical ecology of endophytic fungi: origins of secondary metabolites. *Chemistry & Biology*. 2012; 19(7): 792–8.
 22. Lumyong S, Lumyong P, McKenzie EH, Hyde KD. Enzymatic activity of endophytic fungi of six native seedling species from Doi Suthep-Pui National Park, Thailand. *Can J Microbiol.* 2002; 48(12): 1109–12.
 23. Malmer N. Mineral nutrients in vegetation and surface layers of *Sphagnum* dominated peat-forming systems. *Advances in Bryology. Vol. 5: Biology of Sphagnum*. Berlin-Stuttgart: J. Kramer, 1993. p. 223–48.
 24. Newton AC, Fitt BDL, Atkins SD, Walters DR, Daniell TJ. Pathogenesis, parasitism and mutualism in the trophic space of microbe-plant interactions. *Trends Microbiol.* 2010; 18(8): 365–73.
 25. Odum Yu. [Fundamentals of ecology]: in 2 vol.; translation from English. Moscow: Mir; V. 1, 1986; V. 2, 1986. Russian.
 26. Orlov OO, Dolin VV. [Biogeochemistry of cesium-137 in the swamp forest ecosystems of Ukrainian Polissya]. Kyiv: Nauk. dumka, 2010. Ukrainian.
 27. Partida-Martínez LP, Heil M. The microbe-free plant: fact or artifact? *Front Plant Sci.* 2011; 100(2): 1–16.
 28. Redecker D, Kodner R, Graham LE. Glomalean fungi from the Ordovician. *Science*. 2000; 289(5486): 1920–1.
 29. Richter C, Dainty J. Ion behaviour in *Sphagnum* cell walls: IV. Selective cation binding by *Sphagnum russowii* cell walls. *Can J Bot.* 1990; 68(4): 773–81.
 30. Robl D, da Silva Delabona P, Mergel CM, Rojas JD, dos Santos Costa P, Chapaval

- Pimentel I, et al.* The capability of endophytic fungi for production of hemicellulases and related enzymes. *BMC Biotechnol.* 2013;13:94. doi:10.1186/1472-6750-13-94.
31. *Rodriguez RJ, White JF, Jr, Arnold AE, Redman RS.* Fungal endophytes: Diversity and functional roles. *New Phytol.* 2009; 182(2): 314–30.
 32. *Rudenko AV, Koval EZ, Ryzhko PP, Zaplavskaya EA.* [Onychomycosis. Diagnosis, etiology, epidemiology, treatment]. Kiev: [ChP VMB], 2007. Russian.
 33. *Schulz B, Boyle C.* The endophytic continuum. *Mycol Res.* 2005; 109(6): 661–86.
 34. *Schulz B, Römmert A-K, Dammann U, Aust H-J, Strack D.* The endophyte-host interaction: a balanced antagonism. *Mycol Res.* 1999; 103(10): 1275–83.
 35. *Sinclair JB.* Latent infection of soybean plants and seeds by fungi. *Plant Dis.* 1991; 75(3): 220–4.
 36. *Slippers B, Wingfield MJ.* Botryosphaeriaceae as endophytes and latent pathogens of woody plants: diversity, ecology and impact. *Fungal Biology Reviews.* 2007; 21(2–3): 90–106.
 37. *Smirnov VV, Zaichenko AM, Rubezhniak IG.* [Mycotoxins: fundamental and applied aspects]. *Modern Problems of Toxicology.* 2000; (1): 5–12.
 38. *Wilson D.* Endophyte – the evolution of a term, and clarification of its use and definition. *Oikos.* 1995; 73(2): 274–6.
 39. *Zhdanova NN, Zakharchenko VA, Vasilevskaya AI, Shkolny AT, Kuchma ND, Artyschkova LV, et al.* [Mycobiota of Ukrainian Polissya: the effects of the Chernobyl disaster]. Kyiv: Naukova dumka, 2013. Russian.
 40. *Zuccaro A, Lahrmann U, Güldener U, Langen G, Pfiffi S, Biedenkopf D, et al.* Endophytic life strategies decoded by genome and transcriptome analyses of the mutualistic root symbiont *Piriformospora indica*. *PLoS Pathog.* 2011;7(10):e1002290. doi: 10.1371/journal.ppat.1002290.

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