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ADAPTATION OF MICROFUNGI TO CHRONIC IONIZING RADIATION. NEW FACTS AND HYPOTHESES

Analysis of modern data on ecological, physiological and biochemical adaptation of microfungi for living under exposure to chronic radiation is presented in this review. Special attention has been paid to the analysis of adaptive responses of microfungi exposed to high doses (150Gy and 800 Gy), and the formation in such conditions of new radioadaptive properties: radiotropism and radiostimulation. Literature data concerning the possible biochemical mechanisms of microfungi adaptation to the radiation was summarized. A hypothesis was suggested for the first time providing the basis for microfungi realization of positive reactions to high doses of radiation, such as radiotropism and radiostimulation. One of the ways underlying the positive radiotropism of fungi is their growth in the direction of low (micro and Nano molar) concentrations of hydrogen peroxide, which is locally formed under the influence of radiation. The hypothesis is supported by the evidence that such low concentrations of hydrogen peroxide created electric field causing electrochemical changes in the membranes of fungal apexes. This determined their directional movement towards hydrogen peroxide, which was produced by the action of radiation, thus, played a role of attractant and served as a source of additional energy for them. It was shown for the first time that the antioxidant capacity of melanin in the strains with radioadaptive properties, Cladosporium cladosporioides and Aspergillus versicolor, is 5 to 8 times higher than such in the control strains of these species respectively. It was suggested that the substantial (5.0–8.0-fold) increase in the antioxidant capacity of melanin in the strains with radioadaptive properties compared to the control cultures is one of the main mechanisms of implementation of their ability not only to adapt to significant (150 Gy, 800 Gy) doses of radiation, but also to positively respond to them. The potential contribution of fungi to determining the fate of radionuclides in the environment and the potential and actual roles of fungi in decomposition of "hot particles" and in site remediation was discussed.

K e y w o r d s: microfungi; chronic radiation, radiotropism, radioadaptive properties; antioxidant system, melanin.

The accident in the 4th reactor block of the Chernobyl Nuclear Power Plant (ChNPP) has resulted in radioactive contamination of millions of acres, but the major fallout is in the remnants of the reactor premises and surrounding areas. Thus, large areas have been subjected to the long-term influence of chronic irradiation, although of varied intensity. The peculiarity of Chernobyl disaster is that a significant portion of radionuclides included so-called radioactive "hot particles" of highly specific activity [39]. The aftermath of the nuclear reactor accident in Chernobyl in 1986, heightened our awareness of the potential fate of radionuclides in the environment. Recent works demonstrate that some of microfungi isolated from around the ChNPP are capable of growing in the presence and decomposing the "hot particles", carbon based radioactive graphite from the reactor [36, 37].

Thus, the influence of ionizing radiation on fungi has become a topic of interest in the scientific community [5, 6, 7, 15, 16, 18, 19, 20].

Despite a considerable amount of these studies, a lot of questions have not been answered yet: which adaptive processes take place in microfungi under conditions of chronic radiation exposure and what are the possible mechanisms of their implementation; in direction of which components (the "hot particles", or contaminants (trace elements, organic compounds, etc.), or actually the ionizing radiation itself) does the directional growth of microscopic fungi occur? It is yet unknown how this feature manifests itself in microfungi, if it is a characteristic of certain species, or it is formed as an adaptive property in various taxa that have been for a long time exposed to chronic irradiation.

Observations that fungi are capable of growing in the presence of radioactive "hot particles" and decomposing the latter [36, 37], assumed that they may sense radiation as well as the chemical signals from the resource. This was suggested to be a radiotropic response to ionizing radiation [6, 7, 19, 24].

To study in depth the behavioral adaptations of microfungi formed under chronic ionizing radiation exposure and the possible mechanisms of their realization, a model systems was created imitating the influence of "hot particles" [19, 24, 38].

To differentiate the influence of substrate chemistry from the effect of ionizing radiation, a series of experiments were set up to investigate hyphal growth in the presence of pure ionizing radiation by exposing fungal hyphae to collimated beams of ionizing radioactive emissions from ^{32}P (beta emissions) and ^{109}Cd (gamma emissions) at approximately 2×10^8 Bq. In this study, the directional growth has been shown to originate in response to pure beta and gamma emissions (Fig. 1) [6, 7, 19, 20, 23].

These studies suggest that the presence of ionizing radiation and long-term effects of exposure to radiation can alter the growth response of fungi. The fact that fungi can withstand high levels of radiation makes them candidates for regulating radionuclide movement in highly contaminated areas [1, 5, 18]. Saprotrophic microfungi isolated from contaminated areas seem to possess an attribute of being attracted to and grow more rapidly to sources of ionizing radiation, which they are able to decompose [6, 7, 18, 19, 20, 25, 30].

In regard to forest soil, it is likely that these organisms play an important role in both mineralization of bound (inorganically or organically) radionuclides allowing these to be available for immobilization by plants, leaching down the soil profile, or to be immobilized again by fungi and retained in the upper soil horizons [1, 6, 7, 18].

The underlying mechanisms of enhanced hyphal growth and directed growth of hyphae towards the source of ionizing radiation are yet not fully understood. For the first time we suggest a hypothesis generated from our data: one of the mechanisms, through which positive radiotropism is realized by fungi, is local formation of low (micro and Nano molar) concentrations of hydrogen peroxide under the influence of irradiation.

Support of this hypothesis comes from the evidence that such low concentrations of hydrogen peroxide create an electric field [2, 8, 12], which causes electrochemical changes in membranes of fungal apexes. This determines their directional movement towards hydrogen peroxide formed by the action of radiation and, thus, playing a role of an attractant and an additional

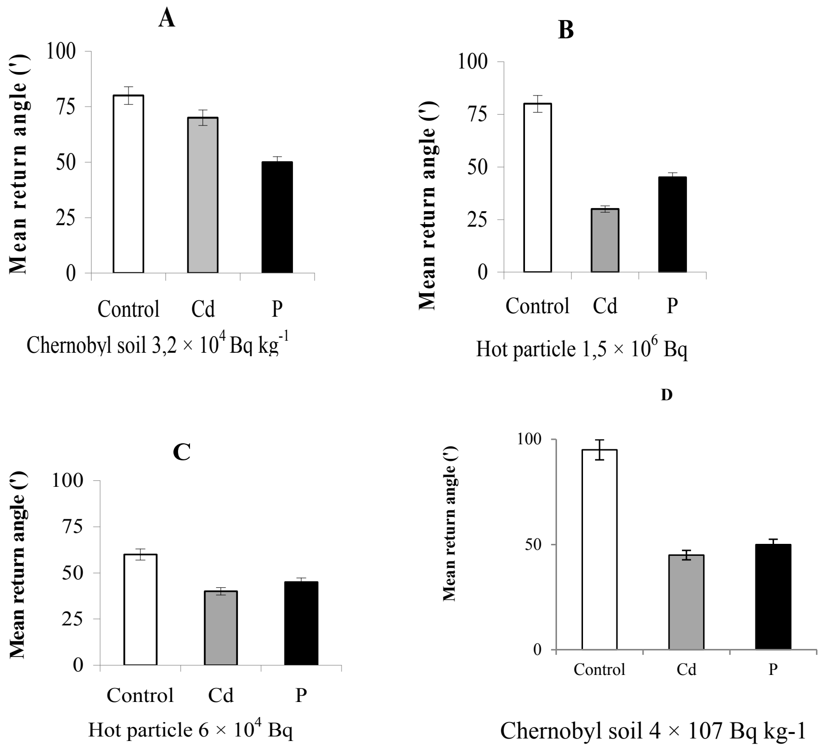

Fig. 1. Mean “return angle” of hyphal extension from spores of *Penicillium*, *Paecilomyces* and *Cladosporium* (*P. lilacinus 1941* (A), *P.hirsutum 3* (B), *P. hirsutum 1* (C), *C. cladosporioides 4* (D)) isolated from sites of contrasting radioactive pollution – small “return angle” represents hyphae growing towards the source of ionizing radiation

Note: Cd – ^{109}Cd, P – ^{32}P.

source of energy for them. In the created model system, it is almost impossible to calculate the exact amount of active forms of oxygen formed in the cells due to the instability of time of reactive oxygen species (ROS) formation. However, based on theoretical calculations and the data known, from 4 to 10 electronic pairs are formed at 100 EV from the interaction of electrons with the substance. According to the results of direct physical-chemical studies on model installations at an irradiation of water sources γ-beams with low linear energy transfer (LET), one can with some probability assume that the concentration of the ROS in terms of hydrogen peroxide is 10^{-6}-10^{-9} M depending on the type of radiation source used [5, 6]. It is known that hydrogen peroxide at the concentration of 0.1–50.0 μm activates K channels on the outer membrane surface, the membrane potential back-changes in the direction of hyper-depolarization depending on cell type, causes the rise of intracellular Ca^{2+}, increases the conductivity of Ca-channels [2, 11, 17, 21]. Based on the fact that in the directed growth of fungal hyphae a significant role is played by the cell-connecting electrical currents, gradients, H, K, and the increase of Ca2+ in the region of hyphal tops [11, 17], namely the electric gradients in fungi hyphae apexes may be at least a part of the control system, which carries out the control and regulation of apical growth, including its supply. The ability of hydrogen peroxide itself to cause chemotaxis of mouse neutrophils is well-known [11]. In addition, in accordance with the redox theory, which was developed in the 1980-s, hydrogen peroxide was viewed as an energetically valuable molecule [2, 11].

While examining the radiotropism we found another unknown radioadaptive reaction of microfungi – radiostimulation under exposure to high doses of radiation of 150Gy and 800 Gy [6, 7, 23, 24, 31, 32].

The study of the frequency of radioadaptive properties in microfungi and the possible mechanisms of their realization was carried out on a model system in comparative aspect using two artificial sources of radiation, which energy essentially differed [6, 7, 19, 24]. The total absorbed doze when using ^{121}Sn was 150 Gy, and for ^{137}Cs it was 800 Gy. Strains of 10 species of microscopic fungi were used in the research. They were conditionally referred to 4 groups, depending on the exposition dozes at the places of their isolation: first (I) – the control including fungi from the ecotops with a background radioactivity level; second (II) – from 0,5 up to 100 mR/hours (3,6 10^{-11}- 7,17 10^{-9} A/kg); third (III) – from 100 up to 500 mR/hours (7,17 10^{-9} - 3,59 10^{-8} A/kg); fourth (IV) – from 500 mR/hours and higher.

Among the strains demonstrating positive radiotropism, some at the same time showed stimulation of growth of emerging hyphae. To characterize the

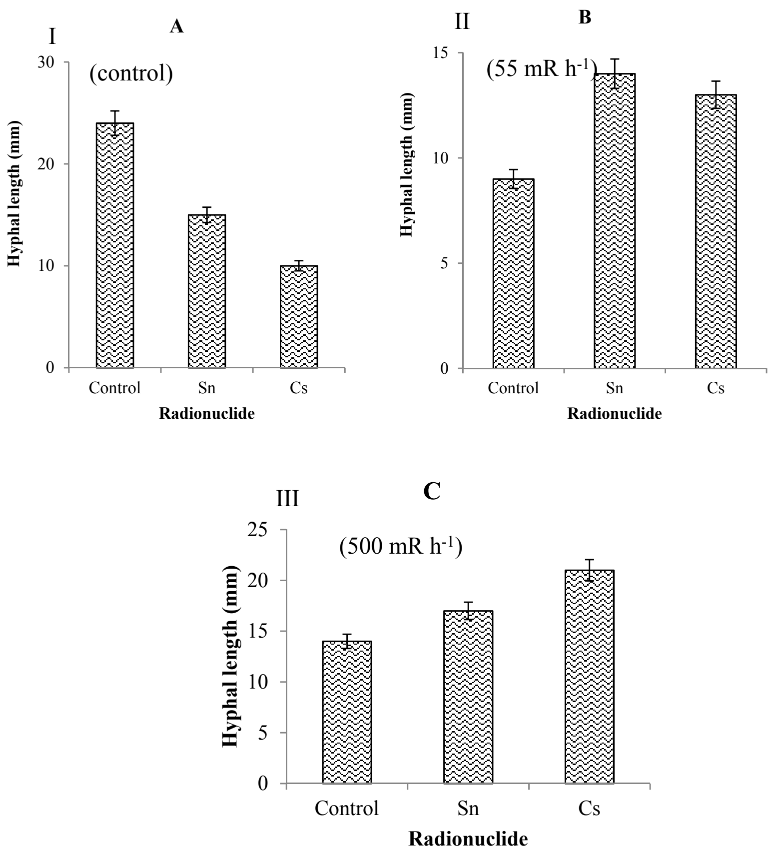

Fig. 2. Hyphal extension of three isolates of *Aspergillus versicolor* (*A. versicolor 432* (A), *A. versicolor 43* (B), *A. versicolor* 57 (C)) cultured from contrasting radiation exposure when grown in the presence of γ-ionizing radiation

Note: Sn – ^{121}Sn, Cs – ^{137}Cs.

degree and frequency of this process we measured hyphae length. The influence of two types of radiation sources – ^{121}Sn as the source of gamma radiation, and ^{137}Cs for mixed beta and gamma radiation – on the percent of conidia germination and the length of the emerging hyphae were investigated (Fig. 2).

T.I. Tugay with co-authors [6, 7, 19, 24] have examined the changes in fungal growth patterns when fungi that have previously been exposed to elevated levels of radiation are exposed to radiation again. When grown under the influence of ionizing radiation, 69 % of fungi isolated from sites of low and high levels of radioactive pollution, showed an increase in spore germination in the presence of ionizing radiation from ^{137}Cs and 46 %, when exposed to ^{121}Sn.

About a half of these fungal strains showed enhanced conidial germination under the exposure to mixed $\gamma + \beta$ radiation, and a half demonstrated activation under either γ or β radiation alone. In contrast, fungi isolated from radioactively clean locations did not show radiostimulation of conidial germination. Similarly, when exposed to ionizing radiation, hyphal extension rates were increased in fungi isolated from radioactively contaminated areas [19, 24].

The influence of both sources of radiation on hyphal length correlates with radioactivity in the areas from which the strains were isolated (Fig. 3).

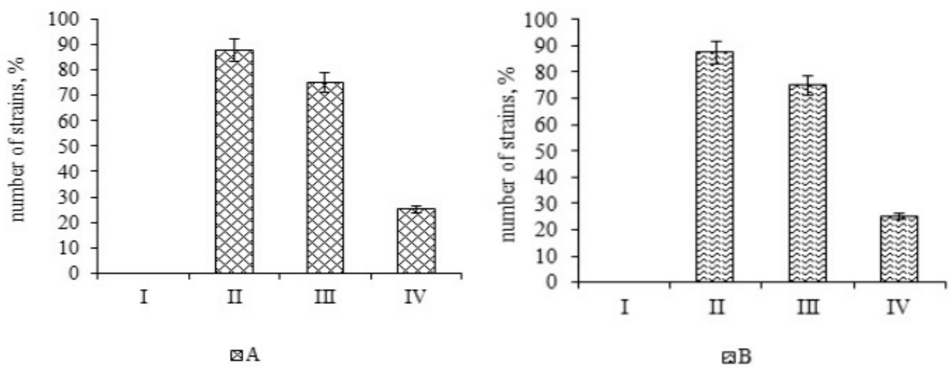

Fig. 3 Frequency of the revealed increase in the length of the microscopic fungi germinating hyphae depending on the exposition doze capacity in the places of their isolation under the action of ^{121}Sn (150 Gy) and ^{137}Cs (800 Gy) as radiation sources

Note: A – ^{121}Sn; B – ^{137}Cs; * – Statistically authentic differences in relation to the control ($p < 0,05$), M±m, n=30 – 40.

Thus, it was established that one of the ecologically significant factors that determines the frequency of manifestation of the fungi radioadaptive properties is the level of radioactivity of the places of their isolation. It was established that soils with radioactivity levels of up to 500 mR/h are the main areas where about 70–80 % of isolated fungi shown radioadaptive properties [19, 24].

The ecophysiological interaction between low-level ionizing radiation, behavior, and the functioning of fungal communities is largely unknown. Unraveling these complex interactions may be important in allowing us to understand the potential role of fungi in determining the fate of radionuclide pollutants in the environment, and the potential and actual roles of fungi in site remediation [1, 5, 6, 7, 18, 19, 22, 24].

It was shown for the first time that one of the mechanisms of microfungi adaptation to the action of relatively large doses of radiation is the trophic change that is implemented in raising their oligocarbotolerance, formed under exposure to ionizing radiation [26, 27]. It was established that in oligocarbotrophic conditions microfungi radioadaptive properties correlate with the high efficiency of substrate utilization (2.0–3.5 times higher than that of the control strains) [26, 27]. The high efficiency utilization of substrate in olìgocarbotrophic conditions is not a unique phenomenon inherent to strains of one species, but rather a widespread physiological property of microfungi with radioadaptive properties formed in the conditions of chronic exposure.

The mechanism of oligocarbotolerance in microfungi with radioadaptive properties is unknown. We suggest a hypothesis that a possible mechanism of high efficiency substrate assimilation under the growth of strains with radio-adaptive properties in oligocarbotrophic conditions is in the restructuring their energy metabolism [26, 27]. A support of this hypothesis came from the evidence suggesting that in some microorganisms the main way of restructuring their energy metabolism lies in the increase of an alternative oxidase activity level, which is economically profitable for a cell metabolism, in comparison with the cytochrome oxidase way as the final electron acceptor [13]. Mirocha and de Vay showed that, subject to strict oligocarbotrophic conditions, $^{14}C0_2$ included in the metabolic processes of *Fusarium sp*. and ^{14}C were detected in hyphae of the fungi [14]. Autotrophic CO_2 fixation, however, is extremely energy intensive process, which is usually not associated with fungi [9]. The authors suggest that hydrogen oxidation may be this source of energy for autotrophic growth and provide evidence that *Fusarium sp.* required a hydrogenase for this process [10, 14]. Wainwright found that fungi use energy derived from oxidation of thiosulfate, which allows them to grow as oligotrophs [34]. It was shown that *F. oxysporum* was able to oxidize 13 % of thiosulfate, which was added when grown in oligotrophic conditions. It was sufficient, according to the authors, for 25 % of energy biomass accumulation by this fungus [10, 34, 35].

Thus, the obtained data testify that long-time growth in the territories with an elevated radiation background leads to the formation of new adaptive reactions of microfungi. Microfungi species isolated from clean territories do not reveal this property [6, 7, 19, 24, 26, 27].

At the present time the research of physiological and biochemical characteristics of microscopic fungi is highly relevant, in particular, in the direction of analysis of the antioxidant system functioning in strains that show such properties as compared with the control. The question of whether there are universal mechanisms of adaptation in microfungi or whether they are individual in each species also requires a study.

It is shown that under the exposure to chronic radiation each of the investigated species or strains of microfungi was characterized by unique changes in the profile of their antioxidant enzymes activity, which provide their adaptation to ionizing radiation [28, 29, 30, 33].

Activation of melanin synthesis and significant changes of enzymes activity, such as polyphenol oxidase and tyrosinase, which regulate melanin synthesis, were observed under the influence of small radiation doses in *Hormoconis resinae* strains, isolated from the fourth block of ChNPP [30]. A significant increase in the electron paramagnetic resonance (EPR) of melanin pigments and an activation of growth processes was also observed under the influence of ionizing radiation in melanin containing fungi [3, 4, 25, 29, 30].

Although high energy photons such as those in gamma rays are unlikely to be captured by organic pigments, these investigators showed that exposure of fungal melanin pigments to gamma radiation changed its electronic properties as measured by the changes in its stable free radical electron spin resonance [4, 5, 6, 7]. Hence, radiation passing through melanin could polarize melanin and change its electronic structures. Furthermore, gamma-irradiated melanin was able to promote oxidation-reduction reactions suggesting a potential mechanism for electromagnetic radiation to be converted into biologically useful energy.

It was found that the implementation of adaptation action of ionizing radiation in the melanin-containing fungi is the result of changes of physico-chemical characteristics of the melanin, which lead to the increased antioxidant capacity [6, 7, 20]. It was discovered that a significant (5 to 8 times) increase of the melanin pigments antioxidant capacity is one of the mechanisms for realization of radioadaptive properties in *Cladosporium cladosporioides* and *Aspergillus versicolor*.

In summary, fungi appear to be very resistant to radionuclides in the environment. The influence of ionizing radiation on cells is well known in terms of altered genetic structure and the induction of cellular reparation mechanisms. For fungi, however, this information has largely been garnered from yeast and there is much less information available for hyphal fungal forms. However, within these mycelial fungi it is apparent that melanin, and possibly other pigments, may be important. The increased frequency of melanized fungal species in the communities grown in the areas of high radionulide load suggests their potential protective role. It has been implicated in the growth response of the radiologically adapted fungal isolates [4, 18] and in the directional growth stimulation attracting fungi to the sources of radioactivity [26]. Although somewhat far-fetched, there is an idea that fungal biomass production can be induced on oligotrophic media for food being powered from the outer space by ionizing radiation [4]. The underlying biochemical mechanisms involved in these novel processes of radiologically adapted species need to be determined. Are we really looking at a new form of autotrophism?

Many aspects of the interaction between fungi and radionuclides need further investigation. The intriguing concept of behavioral adaptations of fungi to evolve radiotripism needs further study to identify the triggers and the physiological mechanisms of the response. In terms of ecosystem processes? The potential for immobilization of a range of radionuclides by fungal tissues as well as the usefulness of fungi for environmental remediation need to be evaluated. The abundance of fungal biomass in the upper soil horizons of forest ecosystem has been suggested as in important determinant of long-term accumulation of radionuclides [1, 5, 6, 7, 18]. Indeed, biomass figures of 2 t ha^{-1} of hyphae have been reported by Zvyaginsev [40, 41], such biomass forms diffuse but extensive surface of adsorbtion and absorbtion. Research along those lines should yield significant practical advances, because currently the use of fungi in phytoremediation is often disregarded.

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АДАПТАЦІЯ МІКРОМІЦЕТІВ ДО ХРОНІЧНОГО ІОНІЗУЮЧОГО ВИПРОМІНЮВАННЯ. НОВІ ФАКТИ І ГІПОТЕЗИ

Резюме

В огляді наведено аналіз сучасних даних щодо адаптації мікроміцетів до хронічного опромінення на екологічному, фізіологічному та біохімічному рівнях. Особливу увагу було приділено аналізу адаптивних реакцій мікроміцетів, що зазнали впливу високих доз (150 Гр і 800 Гр) опромінення, і формуванню у них нових радіоадаптивних властивостей: радіотропізму та радіостимуляції. Проаналізовані літературні дані, що стосуються можливих біохімічних механізмів адаптації мікроміцетів до іонізуючого опромінення. Вперше сформульована гіпотеза, яка пояснює механізм реалізації позитивних реакцій мікроміцетів, таких як радіотропізм і радіостимуляція, на дію високих доз іонізуючого опромінення. Одним із механізмів, що лежать в основі позитивного радіотропізму грибів, є їх ріст у напрямку низьких (мікро- і наномолярних) концентрацій перекису водню, які локально формуються під впливом радіації. Гіпотеза базується на даних, які свідчать, що такі низькі концентрації перекису водню створили електричне поле, яке викликає електрохімічні зміни в мембранах грибних апексів, що призводить до їх спрямованого руху до утвореного за дією іонізуючого опромінення перекису водню, який відіграє роль атрактанту і слугує джерелом додаткової енергії для них. Уперше показано, що антиоксидантна активність меланіну у досліджених штамів з радіоадаптивними властивостями *Cladosporium cladosporioides* і *Aspergillus versicolor* від 5 до 8 разів вища, ніж у контрольних штамів цих видів. Виявлений факт свідчить про те, що збільшення антиоксидантної активності меланіну є одним з основних механізмів реалізації їх здатності не тільки адаптуватися до значних (150 Гр, 800 Гр) доз радіації, але й позитивно реагувати на них. Обговорюється потенційний внесок грибів у регуляцію переміщення радіонуклідів у навколишньому середовищі, а також потенційна та фактична роль грибів у трансформації «гарячих частинок», а також їх можливе використання в біотехнологіях по ремедіації радіоактивно забруднених територій.

Ключові слова: мікроскопічні гриби, хронічне випромінювання, радіотропізм, радіоадаптивні властивості, антиоксидантна система, меланін.

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АДАПТАЦИЯ МИКРОМИЦЕТОВ К ХРОНИЧЕСКОМУ ИОНИЗИРУЮЩЕМУ ИЗЛУЧЕНИЮ. НОВЫЕ ФАКТЫ И ГИПОТЕЗЫ

Резюме

В данном обзоре представлен анализ современных данных относительно адаптации микромицетов к хроническому облучению на экологическом, физиологическом и биохимическом уровнях. Особое внимание было уделено анализу адаптивных реакций микромицетов, подвергшихся воздействию высоких доз радиации (150 Гр и

800 Гр), и формированию у них новых радиоадаптивных свойств: радиотропизма и радиостимуляции. Проанализированы литературные данные, касающиеся возможных биохимических механизмов адаптации микромицетов к ионизирующему излучению. Впервые была предложена гипотеза, объясняющая механизм реализации положительных реакций микромицетов, таких как радиотропизм и радиостимуляция, на действие высоких доз радиации. Одним из механизмов, лежащих в основе положительного радиотропизма грибов, является их рост в направлении низких (микро- и наномолярных) концентраций перекиси водорода, которые локально формируются под воздействием радиации. Эта гипотеза базируется на данных, свидетельствующих о том, что такие низкие концентрации перекиси водорода создают электрическое поле, вызывающее электрохимические изменения в мембранах грибных апексов, что вызывает их направленное движение к образующейся под действием излучения перекиси водорода, которая играет роль аттрактанта и может служить в качестве источника дополнительной энергии для них. Впервые показано, что антиоксидантная активность меланина у исследованных штаммов с радиоадаптивными свойствами *Cladosporium cladosporioides* и *Aspergillus versicolor* от 5 до 8 раз выше, чем таковая у контрольных штаммов этих видов. Выявленный факт свидетельствует о том, что увеличение антиоксидантной активности меланина является одним из основных механизмов реализации способности микромицетов не только адаптироваться к значительным (150 Гр, 800 Гр) дозам радиации, но и положительно реагировать на них. Обсуждается потенциальный вклад грибов в регуляцию перемещения радионуклидов в окружающей среде, а также потенциальная и фактическая роль грибов в трансформации «горячих частиц», и их возможное использование в биотехнологиях по ремедиации радиоактивно загрязненных территорий.

Ключевые слова: микроскопические грибы, хроническое излучение, радиотропизм, радиоадаптивные свойства, антиоксидантная система, меланин.

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