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EXPERIMENTAL ARTICLES

Stress Resistance Mechanisms in the Indicator Fungi from Highly Radioactive Chernobyl Zone Sites

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Abstract—Comparison of the levels of the protein carbonyl groups in response to peroxide stress revealed enhanced stress resistance in *Purpureocillium lilacinum* strains isolated from soils with high content of copper or radionuclides compared to the strains isolated from uncontaminated soils. While in background strains resistance to peroxide stress increased with glucose content in the medium increasing from 0.002 to 2%, the strains from radionuclides- or copper-contaminated soils did not exhibit this pattern. Respiratory activity and polyphosphate content were compared for radiation-resistant strain 1941 and strain SM from the area with background radioactivity. For the protoplasts of strain 1941 isolated from the Chernobyl zone, elevated respiratory activity was revealed on the media with low glucose content. Under the control conditions, the content of inorganic polyphosphates (polyP) in strains 1941 and SM was the same. Under conditions of peroxide stress, only the background strain SM grown on the medium with low glucose concentration exhibited decreased levels of inorganic polyphosphates. Independent of glucose concentration in the medium, in both *P. lilacinum* strains polyP content increased in the course of regeneration after peroxide stress.

Keywords: *Purpureocillium lilacinum,* resistance, oxidative stress, respiratory activity, polyphosphates

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Intensification of anthropogenic pressure on the environment contributes to development of the conditions that many microorganisms have not been exposed to previously. Micromycetes have a high survival potential under extreme conditions and are resistant to environmental pollution with heavy metals, radionuclides, petrochemicals, etc. [1]. Selection of the microorganisms resistant to increasing environmental pollution load is facilitated by such properties of some groups of extremophilic fungi as morphological variability and the absence of sexual process.

Important factors for survival under extreme conditions include the formation of stress protection systems and the ability to use energy resources efficiently when growing on nutrient sources that are not easily accessible.

The abilities of fungi to adsorb radionuclides, to transport radioactive elements into a cell, and to convert them into a soluble form are used in biotechnological processes [2]. Fungi are also promising models for understanding the evolution of stress resistance and revealing the tendencies of formation of parasitic microorganisms with new properties.

Inorganic polyphosphates (polyP) are one of the factors involved in stress coping in microorganisms [3, 4]. In fungi they play an important role in overcoming the stresses caused by the toxic effects of heavy metal cations [5]. Understanding of polyP as antistress regulatory compounds promotes interest in the metabolic patterns of these compounds in fungi with different degrees of stress resistance.

As a result of influence of radioactive decay on living objects, the intracellular concentration of oxygen radicals increases [6]. Our previous works have shown that the stable growth rates of leading hyphae of the micromycetes *Alternaria alternata, Cladosporium cladosporioides*, and *Purpureocillium lilacinum* from the exclusion zone of the Chernobyl Nuclear Power Plant (ChNPP) under oxidative stress were maintained at higher H_2O_2 concentrations (up to 10^{-2}–10^{-1} M) compared to respective strains from the control habitats (10^{-4}–10^{-3} M). The growth strategy of Chernobyl isolates also differed from that of the control fungi [7, 8]. We have chosen the genus *Puipureocillium* out of three previously considered fungal genera for investigation of the mechanisms of resistance to oxidative stress.

The eurytopic species *P. lilacinum* (Thom) Luangsa-ard, Hou-braken, Hywel-Jones & Samson (2011) has been used in recent years as a bioindicator of the high level of Chernobyl soil contamination with

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Table 1. The strains of *Purpureocillium lilacinum* used in the work

Strain	Place and year of isolation	Radioactive contamination, Bq/kg	Tested characteristics
Smolensky SM	Umbric Albeluvisols soil, Smolensk oblast, rural settlement Gnezdovo, 2004	Background	Oxidative stress resistance, respiratory rate, polyP
CP-09	Umbric Albeluvisols soil, Moscow oblast, Voskresensk district, 2009	Background	Oxidative stress resistance
146	Farmstead Kartamysh, Lugansk oblast, 2002	Background; copper in soil >30 MPC	Oxidative stress resistance
804	Chernozem soil, Donetsk oblast, the outskirts of Konstantinovka	Background; heavy metals	Oxidative stress resistance
1941	Soil of the Red Forest, the ChNPP exclusion zone, 1994	5.9×10^5	Oxidative stress resistance, respiratory rate, polyP
1492	Soil of the Red Forest, the ChNPP exclusion zone, 1992	2.7×10^5	Oxidative stress resistance
744	Soil of the western trail of the 10-km zone of ChNPP, 1992	1.3×10^3	Oxidative stress resistance
1786	Soil of the Red Forest, the ChNPP exclusion zone, 1993	1.2×10^2	Oxidative stress resistance

The level of background radiation corresponds to the density of surface contamination for ^{137}Cs up to 1 Cu/km^2 (3.7 Bq/cm^2).
The strains were provided by the Department of Soil Biology (Faculty of Soil Science, Moscow State University) and by the Department of Mycology (Institute of Microbiology, National Academy of Sciences of Ukraine).

radionuclides (3.7×10^6–3.7×10^8 Bq/kg) [2]. Moreover, *P. lilacinum* is widespread under both oxic and anoxic conditions. The fungus can parasitize insects and fish, as well as humans, and is adapted to high copper concentration in a habitat.

In view of the above features of this species, the present work was aimed at studying the adaptation of *P. lilacinum* strains from the soils polluted and unpolluted with radionuclides and heavy metal ions to oxidative stress during cultivation in the media with different glucose concentrations (0.002, 0.2, and 2%). The quantity of carbonyl groups in proteins was determined as one of the frequently used criteria of oxidative stress [9, 10]. Other adaptive characteristics were compared, namely, the respiratory activity and the content of inorganic polyP in fungal cells under stress conditions.

MATERIALS AND METHODS

Subject of research. The subjects of research were 10 strains of *P. lilacinum* from different habitats: 6 strains were isolated from the soils with background radiation levels and 4 strains were obtained from the exclusion zone of ChNPP with different levels of radioactive contamination (Table 1). The strains from the soils unpolluted with radionuclides included two strains (146 and 804) isolated from soils with elevated content of copper ions.

P. lilacinum was grown in modified liquid or on solid Vogel medium [11]. Petri dishes with cellophane sheets inside them were used for the assay of carbonyl groups in the proteins and polyP content. The mycelium of *P. lilacinum* was grown for 40 h (the end of the exponential growth phase) at 26°C in the media with glucose concentrations of 0.002, 0.2, and 2%. For creating oxidative stress, 1 mL of 10 mM H_2O_2 was applied under a cellophane disc. After 1- to 2-h exposure, the mycelium was harvested and frozen in liquid nitrogen.

To determine respiratory activity, the culture was grown in Erlenmeyer flasks (750 mL) on a shaker in a liquid Vogel medium (150 rpm) at 26°C for 42 h. The inoculum was a spore suspension (10^6 spores/flask).

Assay of carbonyl groups in proteins. The grown mycelium after treatment with H_2O_2 (experiment) or H_2O (control) was frozen, pounded with liquid nitrogen, resuspended in a 10-fold volume of buffer (50 mM potassium phosphate with 0.1% digitonin, 1 mM EDTA, 0.5 mM phenylmethanesulfonyl fluoride, pH 7.4) and, after 10-min incubation, centrifuged at 7500 *g* for 20 min. The concentration of carbonyl groups in the proteins was determined by spectrophotometry with dinitrophenyl hydrazine according to the known technique [12].

Experiments with 3,3'-diaminobenzidine (DAB). The colonies of *P. lilacinum* SM and 1941 were stab-inoculated and grown on the Vogel agar medium with 0.2 or 2% glucose for 10 days. Then they were treated with 10 mM potassium phosphate buffer solution, pH 6.9, containing DAB (1 mg/mL) and horseradish peroxidase (0.3 mg/mL) [13]. The incubation was car-

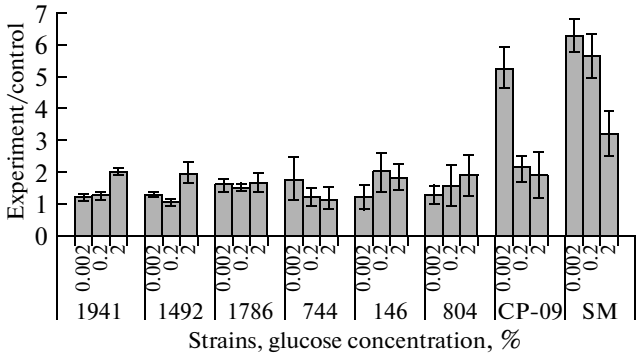

Fig. 1. Relative content of carbonyl groups in the proteins in *P. lilacinum* strains grown at different glucose concentrations in the medium under treatment with 10 mM H_2O_2.

ried out overnight. The amount of exogenous H_2O_2 was assessed by the intensity of brown color on the medium surface.

Respiratory activities of the strains were measured in protoplast preparations [14]. The pellets formed during cultivation on a shaker (26°C, 42 h, 150 rpm) were filtered through three gauze layers, washed with cold distilled water, dried with filter paper, and weighted. They were homogenized under mild conditions in a precooled Potter homogenizer containing cold buffer (1.2 M sorbitol, 10 mM HEPES, 0.5% BSA, pH 7.5) at a ratio of 1 : 5 (wt/vol) for 3 min in ice. The protoplasts were separated from the mycelium by filtering the homogenate through two layers of nylon in a glass funnel. The yield of protoplasts was controlled under a light microscope.

Oxygen consumption by the protoplasts was monitored in vitro in the isolation medium at 25°C in a polarographic cell with electrodes covered with a Teflon film. The constant potential difference of 660 mV was maintained. The level of KCN-sensitive and KCN-resistant respiration was assessed by analysis of the effects of inhibitors of the mitochondrial electron transport chain (1 mM KCN and 1 mM salicyl hydroxamate (SHAM)) on protoplast respiration.

Content of inorganic polyP in the *P. lilacinum* 1941 and SM cells was determined in biomass samples taken from the petri dishes. The biomass was weighted prior to analysis in order to calculate the content of polyphosphates per 1 g of wet biomass. PolyP was extracted from fungal material using a modification of the known method [15]. The biomass was treated with 0.5 N $HClO_4$ (10 mL per 1 g biomass) for 2 h under continuous stirring at 5°C. It was then separated by centrifugation at 5000 *g* for 15 min. The supernatant was an acid-soluble polyphosphate fraction. The content of orthophosphate and labile phosphorus in the latter was determined according to [15]. The content of polyphosphates in this fraction was assessed by labile phosphorus.

The biomass precipitate was treated with 0.5 N $HClO_4$ (10 mL per 1 g biomass) at 90°C for 1 h and centrifuged in the same mode; the content of orthophosphate in the supernatant was an indicator of the amount of acid-insoluble polyphosphates. The content of polyphosphates was recalculated per dry biomass.

RESULTS AND DISCUSSION

The content of carbonyl groups in the proteins. Resistance of the strains to oxidative stress was assessed by comparing the changes in the level of carbonyl groups in their proteins in response to the effect of H_2O_2 (10 mM, 1 h). The content of carbonyl groups in the proteins of the control strains (CP, SM) increased 5- to 6-fold as a result of H_2O_2 treatment of the mycelium growing on a glucose-free medium (Fig. 1). When the level of glucose in the medium was increased to 2%, the content of carbonyl groups increased no more than 2- to 3-fold. This fact was indicative of enhanced resistance of these strains to oxidative stress at increasing glucose concentration in the medium (Fig. 1). On the contrary, peroxide stress in radiation-resistant strains increased the quantity of carbonyl groups in the proteins no more than 2-fold, and in strains 1941 and 1942 this increase was slightly more marked at higher glucose concentrations in the medium. Strains 146 and 804 resistant to copper ion pollution were similar to the radiation-resistant strains in the pattern of increase of the content of carbonyl groups in the proteins under the effect of H_2O_2. The similarity of the peroxide stress response in the strains from soils polluted with copper ions and radionuclides is probably associated with enhanced resistance to oxidative stress accompanying the action of radiation and heavy metals and confirms the absence of specific mechanisms of radiation protection [16]. It should be noted that the level of carbonyl groups in the strains from soils polluted with radionuclides and with copper ions is generally higher than in the isolates from the soils with background radiation (Table 2), which might reflect the properties of their glucose metabolism.

Thus, the strains of *P. lilacinum* from the soils polluted with radionuclides and heavy metal ions were resistant to oxidative stress, and their resistance did not depend on glucose concentration in the medium, in contrast to related strains from unpolluted soils.

Respiration rates of the protoplasts of strains 1941 and SM. The proposed method for isolation of intact protoplasts from *P. lilacinum* pellets by way of mild homogenization in the buffer without lytic enzymes makes it possible to obtain regular-shaped rounded protoplasts with the standard protein content, with no tendency to adhere or fuse. Analysis of the respiratory activity of strain 1941 growing in the media with 0.2 and 2% glucose showed that the rate of its endogenous respiration remained invariable (Table 3). The endog-

Table 2. The content of carbonyl groups in the proteins (nmol/mg protein) in *P. lilacinum* strains cultivated in the media with different glucose concentrations

Glucose in the medium, %	Content of carbonyl groups in the proteins, nmol/mg protein							
	1941	1492	1786	744	146	804	CP-09	SM
0.002	4.15 ± 0.25	1.70 ± 0.09	3.20 ± 0.33	1.20 ± 0.01	2.98 ± 0.28	3.60 ± 0.13	0.62 ± 0.13	2.10 ± 0.17
0.2	3.10 ± 0.20	1.76 ± 0.11	1.53 ± 0.08	1.79 ± 0.32	2.13 ± 0.38	2.51 ± 0.54	1.12 ± 0.17	1.66 ± 0.25
2	2.4 ± 0.25	1.57 ± 0.13	2.60 ± 0.31	1.84 ± 0.42	2.74 ± 0.36	2.64 ± 0.59	0.63 ± 0.19	1.21 ± 0.04

Table 3. Respiratory rates of the protoplasts of strains 1941 and SM grown on 0.2 and 2% glucose

Strain	Glucose concentration, %	Rate of endogenous respiration, ng-atom O/(min mg protein)	Respiration rate in the presence of 1% glucose, ng-atom O/(min mg protein)	Inhibition, %		
				KCN	SHAM	KCN + SHAM
1941	0.2	13.2 ± 1.3	11.6 ± 0.6	49.0	50.1	99.1
SM		9.4 ± 1.0	12.8 ± 0.6	43.8	54.8	98.6
1941	2	12.7 ± 1.1	16.2 ± 1.1	63.0	36.1	99.1
SM		12.9 ± 1.9	8.7 ± 1.0	24.3	74.7	99.0

enous respiration rate of strain SM was lower in the medium with 0.2% glucose and increased to the level of strain 1941 in the medium with 2% glucose. Addition of glucose to the incubation mixture did not have any noticeable effect on the respiration of the protoplasts of strain 1941 grown in the medium with 0.2% glucose, but enhanced the respiration of protoplasts of strain SM grown under the same conditions. At the same time, addition of glucose activated the respiration of protoplasts of strain 1941 and inhibited it by 33% in strain SM, when the strains were grown in the medium with 2% glucose.

Thus, the strains grown in the medium with 0.2% glucose had different rates of endogenous respiration. In the strains grown in the medium with 2% glucose, the rate of endogenous respiration was the same, but the oxygen consumption rates in the presence of glucose were cardinally different, reflecting different tolerance of the strains to glucose and being probably associated with the differences in glucose metabolism in these strains.

The respiratory activity of protoplasts of the studied *P. lilacinum* strains was effectively blocked by KCN (1 mM), inhibitor of terminal oxidase of the mitochondrial respiratory chain. The value of KCN sensitivity of the strains was different, depending on glucose concentration in the cultivation medium (Table 2). Addition of SHAM in the presence of KCN resulted in the nearly 100% inhibition of respiration of both strains. The absence of complete inhibitory effect of the KCN + SHAM system could be explained by other, nonmitochondrial enzymes functioning in the cells, in particular, alcohol oxidase, lipoxygenase, peroxidase, and monooxygenase. The share of KCN-sensitive respiration of the protoplasts of strain 1941 was 49% during cultivation in the medium with 0.2% glucose and 63% during cultivation in the medium with 2% glucose. An increase in glucose concentration in the medium to 2% enhanced the share of KCN-sensitive respiration and decreased that of the alternative respiration. The share of KCN-sensitive respiration was 43.8 and 24.3% in the cells of strain SM grown in the medium with 0.2 and 2% glucose, respectively. The levels of alternative respiration were 54.8 and 74.7%, respectively.

Thus, the level of KCN sensitivity of the strains depended on glucose concentration in the cultivation medium. During cultivation in the medium with 0.2% glucose, the level of KCN-sensitive respiration in the strains under consideration was the same. During cultivation in the medium with 2% glucose, the share of alternative pathways decreased in strain 1941 and increased in strain SM. In some instances, alternative respiration in fungi is considered a way to decrease the formation of intracellular ROS [17]. The contribution of alternative respiration in the control strain, increas-

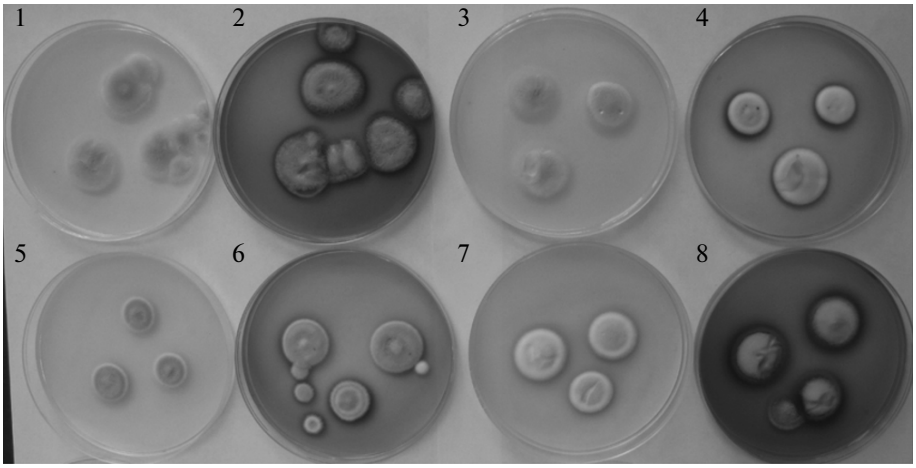

Fig. 2. H_2O_2 production by strains SM and 1941 during cultivation at different glucose concentrations in the medium (0.2 and 2%). Control (1, 3, 5, 7); staining for the presence of H_2O_2 (2, 4, 6, 8). Strain SM on 0.2% glucose (1, 2); strain 1941 on 0.2% glucose (3, 4); strain SM on 2% glucose (5, 6); strain 1941 on 2% glucose (7, 8).

ing together with glucose concentration in the medium, is in agreement with enhancement of its resistance to peroxide stress.

H_2O_2 production by the studied cultures. The ability to produce H_2O_2 depending on glucose concentration in the medium was compared in the radiation-resistant strain 1941 from the ChNPP exclusion zone and the strain SM from the zone with background radiation. DAB staining showed that the control strain in the medium with 0.2% glucose produced much more H_2O_2 compared to the radiation-resistant strain, while with 2% glucose the situation was the opposite: H_2O_2 production decreased in the background strain SM and enhanced in the Chernobyl strain 1941 (Fig. 2). Decreased H_2O_2 production in the background strain with increasing content of glucose in the medium is in good agreement with enhancement of its resistance to oxidative stress and considerable increase in the activity of the alternative respiratory pathway. Moreover, the cultivation of strain SM in the medium with 2% glucose was accompanied by decreased oxygen consumption by the protoplasts in the presence of additional glucose, which indicated the switching of the regulatory mechanisms that restrict the rate of mitochondrial respiration.

The mechanism for decreased H_2O_2 production or its more efficient decomposition in the radiation-resistant strain 1941 at a low content of glucose in the medium is still obscure. In spite of the high respiratory rate and rather high initial level of carbonyl groups in the proteins, strain 1941 demonstrated higher resistance to peroxide stress and maintained higher rate of growth of the leading hyphae compared to the background strain [7, 18]. Our previous study of the activity of antioxidant enzymes (SOD and catalase) showed that it was even higher in the background strain SM [8]. The higher level of H_2O_2 production in the radiation-resistant strain 1941 at glucose concentration in the medium increasing to 2%, may probably result from a considerable contribution of mitochondrial cyanide-sensitive respiration to glucose metabolism. In the strains 1941 and 1492, the increase in the content of glucose in the medium to 2% was even accompanied by a slight decrease of its resistance to peroxide stress (Fig. 1).

The content of polyphosphates and the effect of H_2O_2. The control SM and Chernobyl 1941 strains showed no difference in the total content of polyphosphates and their distribution between the two fractions (relatively short-chain acid-soluble and long-chain acid-insoluble), irrespective of glucose concentrations (Table 4). The content of polyphosphates was higher in the cells grown at higher glucose concentrations; this fact is explicable, because the synthesis of these polymers is an energy-intensive process [4]. At the high glucose concentration, the content of polyphosphates in both strains remained nearly constant 60 min after the addition of H_2O_2; after 120 min, increased content of polyphosphates was observed in both strains. At low glucose concentrations, the control strain SM demonstrated a decrease in polyphosphate content 60 min after the treatment with H_2O_2. It may be supposed that fungal cells consume polyphosphates as an energy source to maintain their activity under stress conditions. On the contrary, in the cells of the radiation-resistant strain 1941 tolerant to the H_2O_2 concentration used in the experiment, the content of polyphosphates increased at the low glucose concentration. Two hours after H_2O_2 treatment, both strains demonstrated the same increase in the content of polyphosphates at the low glucose concentration as in the medium with 2% glucose.

Thus, it was shown that polyP content increased during regeneration of the fungus after peroxide stress.

Table 4. Effect of H_2O_2 treatment on the content of polyphosphates (μmol/g dry weight) in the SM (background) and 1941 (Chernobyl) strains of the fungus *P. lilacinum*

Fraction	Content of polyphosphates, μmol/g dry biomass					
	glucose in the medium 0.2%			glucose in the medium 2%		
	control water 1 h	peroxide 1 h	after peroxide 2 h	control water 1 h	peroxide 1 h	after peroxide 2 h
SM (control strain)						
Acid-soluble polyP	36.1 ± 5.4	20.9 ± 13.3	116 ± 7.3	55.5 ± 5.9	45.9 ± 2.7	55.0 ± 1.4
Acid-insoluble polyP	84.8 ± 3.0	70.9 ± 1.2	106 ± 1.8	67.9 ± 0.9	82.6 ± 1.8	111 ± 5.0
Total polyP	121	92	222	123	129	166
1941 (chernobyl strain)						
Acid-soluble polyP	39.5 ± 7.2	51.8 ± 2.6	94.1 ± 9.8	45.8 ± 1.6	43.8 ± 8.3	74.9 ± 1.6
Acid-insoluble polyP	80.9 ± 1.3	129 ± 4.6	153 ± 7.9	80.6 ± 3.6	104 ± 5.2	113 ± 5.2
Total polyP	120	180	247	126	148	188

This phenomenon was observed for both strains, irrespective of glucose content in the medium.

The decrease in polyP content after H_2O_2 treatment was observed only for the background strain SM and at low glucose concentrations. It is probable that the fungus under these conditions consumes the energy of polyP to overcome the stress.

Thus, radiation-resistant strains were much more adapted to oxidative stress than the strains isolated from soils unpolluted with radionuclides and copper ions. Changing glucose concentrations in the medium had no effect on their resistance to peroxide stress. A similar mechanism of adaptation to oxidative stress has been shown for the *P. lilacinum* strains demonstrating enhanced resistance to copper ions. Resistance to oxidative stress in the strains from soils unpolluted with radionuclides and copper ions increased sharply when the content of glucose in the medium increased by 2%. The difference in the rates of oxygen consumption and in activities of the cyanide-resistant and cyanide-sensitive pathways of electron transfer at increasing glucose concentrations indicates adaptive rearrangement of glucose assimilation in the radiation-resistant strain. The data on the influence of peroxide stress conditions on the content of polyphosphates draw attention to the patterns of metabolism of these polymers under various unfavorable conditions. It is not improbable that extension of the set of these conditions will reveal the difference between the background and radionuclide-resistant strains, which will make it possible to establish the role of polyphosphates in the adaptive mechanisms of fungi.

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