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EFFECT OF PYRETHROIDS ON STRESS-INDUCED BIOSYNTHESIS OF SELECTED HAEMOPROTEINS IN *Saccharomyces cerevisiae* YEAST CELLS

WPŁYW PYRETROIDÓW NA INDUKOWANĄ WARUNKAMI STRESU BIOSYNTEZĘ WYBRANYCH BIAŁEK HEMOWYCH W KOMÓRKACH DROŻDŻY *Saccharomyces cerevisiae*

Abstract: The cellular response to stress is a basic protective mechanism enabling cells to adapt to changing environmental conditions. Logarithmic cultures of *Saccharomyces cerevisiae* yeast are a good model for research on this topic, because the stress response is accompanied by induction of biosynthesis of haemoproteins such as catalase and cytrochromes. In wild-type yeast cells growing on YPG medium containing 2 % glucose, catalase activity in the logarithmic culture is low. Cytochrome spectra under these conditions are flat, indicating low respiratory complex activity. Stress conditions induce expression of the gene CTT1, which codes for catalase T, and the enzyme is synthesized *de novo*. Within a short time catalase T activity increases sharply, attaining a value characteristic of the stationary phase of growth. Similarly, induced biosynthesis of cytochromes takes place under stress conditions. This study investigated the effect of pyrethroids on stress-induced biosynthesis of these haemoproteins in *S. cerevisiae* cells. The experiments were conducted on a standard wild-type strain of yeast. The yeast cultures were grown in liquid YPG medium. The effect of pyrethroids (deltamethrin, esfenvalerate and cypermethrin) on induced biosynthesis of haemoproteins was studied under conditions of alcohol stress or osmotic stress (induced by sodium chloride or sodium nitrate). Catalase activity was determined and low-temperature cytochrome spectra of the yeast cells were performed. Application of pyrethroids and stress conditions at the same time was found to inhibit synthesis of haemoproteins, ie catalase T and cytochromes.

Keywords: pyrethroids, stress, catalase, cytrochromes, yeast

Environmental stress is induced by a variety of factors, including changes in temperature, UV, ionizing radiation, changes in osmotic pressure, dehydration, metal ions, changes in environmental acidity, enzyme inhibitors, amino acid analogues,

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pesticides or lack of nutrients. Under stress conditions, a number of genes are expressed in cells, leading to induction of synthesis of a specific group of proteins and to temporary inhibition of the division cycle [1]. These proteins take part in various metabolic processes, including redox reactions, antioxidant protection, carbohydrate metabolism, DNA repair, and intercellular signal transmission. They are also involved in maintaining the pool of native cellular proteins and in cell wall modification [2]. The purpose of the cellular response to stress is to protect cell components from the dangerous effects of stress factors. The typical cellular response to changing environmental conditions is synthesis of a specific group of proteins called heat shock proteins (HSP). The action of various stress factors leads to an increase in the level of reactive forms of oxygen in cells as well as changes in the level of antioxidant enzyme activity [3]. The fact that various kinds of stress induce similar physiological effects has made it possible to attribute to ROS the role of second messengers, because during stress the concentration of free radicals in the cell increases. It has also been postulated that the effective concentration of reactive forms of oxygen as transmitters is very small, so that they can perform their function even when oxygen access is limited. Changes in the concentration of reactive forms of oxygen can be a factor triggering a stress response in a cell [4].

Nevertheless, attributing to ROS – highly reactive molecules characterized by low selectivity – the role of a second messenger raises many doubts. Opponents of this hypothesis argue that proteins characteristic for the stress response can be synthesized in anaerobic conditions after a stress factor has acted on them [5].

Pyrethroids are synthetic insecticides. They are esters of primary or secondary alcohols containing at least one double bond and chrysanthemic acid [2,2-dimethyl-3--(2-methylpropenyl)-cyclopropanecarboxylic acid), or halogen analogues of this acid [6]. Pyrethroids are neurotoxins that have a powerful effect on the nervous system of insects. Authors of numerous publications claim that the effects of pyrethroids on parts of an organism other than the nervous system may be associated with free radical generation [7]. In studies on the non-specific effects of pyrethroids on various organisms, oxidative stress markers are often determined, including lipid peroxidation level, activity of catalase, superoxide dismutase or glutathione peroxidase, and antioxidant concentration [8].

The aim of this study was to investigate the effect of selected pyrethroids on the stress response. Two types of haemoproteids were chosen as markers of stress response intensity: catalase and cytochromes, which are synthesized in cells of the yeast *S. cerevisiae* under stress conditions.

Material and methods

Yeast strains: SP-4α leu1 arg4, wild-type strain [5].

Media: The yeast were grown on liquid YPG medium – 1 % yeast extract, 1 % peptone, 2 % glucose.

Plotting of cytochrome spectra: Cytochrome spectra were determined in whole yeast cells frozen in liquid nitrogen. The yeast cells were centrifuged and dried on filter

paper. A few $Na_2S_2O_4$ crystals were added to the yeast. Cytochrome spectra were measured in a cuvette constructed by T. Biliński, in a wavelength range of 500–650 nm with a 1-mm layer of yeast cells frozen in liquid nitrogen. Absorption value was measured relative to a baseline connecting points representing absorption minima. The maximum absorption value was read at a wavelength of 551 nm for cytochrome c, 558 nm for cytochrome b and 605 nm for cytochrome a + a^3 [9].

Preparation of yeast cell extracts for enzyme determination: The collected yeast cells were washed with phosphate buffer (0.05 M, pH 6.8), centrifuged again, and then suspended in 1 cm^3 of this buffer, cooled in ice for 10 min and disrupted with glass beads (diameter 0.4–0.5 mm) in a Bosch homogenizer for 2 min. The glass beads, undisrupted cells and cell wall fragments were centrifuged for 5 minutes. The supernatant was transferred to clean test tubes, kept in ice and used for enzyme determination.

Protein determination: Protein in the yeast cell extracts was determined using the Lowry method [10].

Determination of catalase activity: Total catalase activity was determined spectrophotometrically using the method described by Beers and Sizer [11].

Incubation of yeast cells with pyrethroid was carried out in the logarithmic phase of growth for 2 h in standard aeration conditions. To assess the effect of the insecticide on yeast cells under stress conditions, stress conditions were applied simultaneously with various concentrations of the pesticide.

Stress conditions: Alcohol stress conditions were obtained by adding ethyl alcohol to the culture at a concentration of 6 % [12]. Osmotic stress conditions were obtained by adding 0.3 M sodium chloride or 0.5 M $NaNO_3$ to the logarithmic phase culture [13, 14].

The following pyrethroids were applied in the study:

– deltamethrin-(S)-alpha-cyano-3-phenoxybenzyl(1R)-cis-3-(2,2-dibromovinyl)-2,2--dimethylcyclopropane-carboxylate;

– cypermethrin-(R,S)-alpha-cyano-3-phenoxybenzyl(1RS)-cis,trans-3-(2,2-dichlorovinyl)-2,2-dimethylcyclopropane-carboxylate; and

– esfenvalerate-(S)-alpha-cyano-3-phenoxybenzyl (S)-2-(-4-chlorophenyl)-3-methylbutyrate.

Results

Catalase T activity in a wild-type yeast cell depends on growth conditions. In yeast cells in the logarithmic phase of growth catalase activity is very low, while in the stationary phase it is about 25 times higher (Table 1). It is in accordance with the results obtained by other authors.

After pyrethroids were added to the logarithmic phase of culture there was no increase in catalase activity, which would indicate induced biosynthesis of this enzyme (Table 1). When the stationary phase of yeast culture was incubated with pyrethroids for 2 h a decrease in catalase activity was noted.

Table 1

Catalase activity in SP4 yeast cells after incubation with various concentrations of pyrethroid, expressed as % of the logarithmic or stationary control

Culture conditions	Logarithmic phase of culture			Stationary phase of culture		
Control	Catalase activity					
	1.8 U · mg^{-1} protein · cm^{-3}			45.6 U · mg^{-1} protein · cm^{-3}		
	100 %			100 %		
Pyrethroid concentration [μg · cm^{-3}]	esfen-valerate	delta-methrin	cyper-methrin	esfen-valerate	delta-methrin	cyper-methrin
20	98	95	98	87	96	93
40	100	87	96	82	85	80
60	98	89	96	76	71	65
80	92	91	96	60	42	58

Activity of cytochromes of the respiratory chain has been studied on the basis on cytochrome spectra analysis. Yeast are facultative anaerobes. If glucose is available in the medium, they obtain energy from fermentation, that is why the absorbance values for individual cytochromes in the logarithmic phase are low (Table 2).

Table 2

Effect of pyrethroids on cytochromes of the respiratory chain in SP4 yeast cells in the logarithmic and stationary phase of cultures

Conditions applied			Relative cytochrome absorbance		
			b	c	a + a^3
Logarithmic phase of culture	control		0.09	0.11	0
	esfenvalerate	40 μg · cm^{-3}	0.09	0.11	0
	deltamethrin		0.085	0.1	0
	cypermethrin		0.09	0.11	0
Stationary phase of culture	control		0.31	0.35	0.25
	esfenvalerate	40 μg · cm^{-3}	0.31	0.34	0.25
	deltamethrin		0.3	0.34	0.25
	cypermethrin		0.31	0.33	0.24

Glucose depletion causes a change in the way yeast respire, from fermentation to oxidative phosphorylation, and on the cytochrome spectrum in the stationary phase one may observe absorbance maxima for cytochromes. Incubation of yeast cells with pyrethroids does not cause significant changes in cytochrome absorbance (Table 2).

In wild-type yeast cells growing on YPG medium containing 2 % glucose, cytochrome spectra are flat in the logarithmic phase, which indicates low activity of

respiratory complexes. When yeast cells from the logarithmic phase of culture are subjected to stress conditions, they alter their metabolism and begin a synthesis of many proteins, including cytochromes. Stress conditions were found to induce cytochrome biosynthesis within 2 h so that the number of cytochromes in the cells increased to high values characteristic of the stationary phase.

This study found that cytochrome biosynthesis is induced most strongly by NaCl osmotic stress, followed by alcohol stress. Pyrethroid alone added to the logarithmic phase of culture does not cause an increase in absorbance of the cytochrome spectrum. In the stationary phase of culture, 2 h incubation with pyrethroid does not significantly affect the absorbance value for individual cytochromes (Table 3). Simultaneous application of stress conditions and addition of pyrethroid to the yeast culture inhibits cytochrome biosyntesis.

Table 3

Effect of simultaneous application of stress and pyrethroid on catalase and cytochromes of the respiratory chain in SP4 yeast cells in the logarithmic phase of culture

Conditions applied			Catalase activity $U \cdot mg^{-1}$ protein $\cdot cm^{-3}$	Relative cytochrome absorbance		
				b	c	$a + a^3$
Control			1.8	0.09	0.1	0
Osmotic stress (NaCl)			28.4	0.43	0.65	0.03
+	esfenvalerate	40 $\mu g \cdot cm^{-3}$	1.71	0.04	0.05	0
+	deltamethrin		1.83	0.05	0.08	0
+	cypermethrin		1.8	0.06	0.06	0
Alcohol stress			22.2	0.37	0.44	0.03
+	esfenvalerate	40 $\mu g \cdot cm^{-3}$	1.65	0.05	0.06	0
+	deltamethrin		1.78	0.08	0.08	0
+	cypermethrin		1.75	0.08	0.07	0
Osmotic stress ($NaNO_3$)			24.5	0.18	0.22	0.02
+	esfenvalerate	40 $\mu g \cdot cm^{-3}$	1.63	0.01	0.01	0
+	deltamethrin		1.73	0.04	0.06	0
+	cypermethrin		1.8	0.03	0.05	0

The analysed yeast cells were capable to a stress response, which was manifested by increased catalase activity and higher cytochrome absorbance under conditions of osmotic stress, induced by adding 0.3 M NaCl or 0.5 M sodium nitrate, and 6 % alcohol stress (Table 3).

When osmotic stress was applied simultaneously with selected pyrethroids at a concentration of 40 $\mu g \cdot cm^{-3}$ to assess inhibition of induction of catalase T synthesis by the pyrethroids, no increase in catalase activity was noted. This observation was confirmed when other types of stress were applied together with pyrethroid. This suggests that pyrethroids inhibit induced biosynthesis of catalase T in *S. cerevisiae* yeast cells.

Discussion

In laboratory practice one way of determining the intensity and range of the cellular stress response is determination of the activity level of selected proteins induced by stress factors. *Saccharomyces cerevisiae* yeast are often used in research on the stress response. They have two types of catalase – cytoplasmatic catalase T and peroxysomal catalase A. Catalase T activity is a frequently used stress response marker [13–16].

In induced biosynthesis of catalase in yeast there is a frequently observed stress response induced by incubation of a logarithmic phase culture with certain pesticides, such as ammonium glyphosinate [15].

It was found, that the activity of catalase in logarythmic phase of yeast culture did not change after treatment with pyrethroids, while in the stationary phase it is decrease. In a previously published study there was also found that long-term yeast cell culture on a medium with various concentrations of deltamethrin decreased catalase activity [16]. Activity of this enzyme is a frequently used as oxidative stress marker in studies on the effects of pesticides on various organisms. Research on the effects of fenvalerate and its metabolite p-chlorophenylisovalerianic acid on the erythrocytes of rats has found that both fenvalerate and its metabolite can cause oxidative stress in erythrocytes, manifested as a significant decrease in activity of antioxidant enzymes, including catalase [17]. A single dose of only 0.001 % LD_{50} of cypermethrin or fenvalerate caused changes in catalase activity in the erythrocytes of rats [7]. In these studies catalase activity was found to increase maximally on the third day after application of cypermethrin or cypermethrin together with fenvalerate, while maximum catalase activity after application of fenvalerate was noted after 7 days. In the fish *Channa punctatus* (Bloch) exposure to deltamethrin caused catalase activity to decrease in the liver, kidneys and gills. Cypermethrin affects catalase activity in the liver and kidneys of the fish *Oreochromis niloticus* and *Cyprinus carpio* [18]. After exposure to a low concentration of cypermethrin – 1/20 LD_{50} – an increase in catalase activity was noted in the liver of both fish species, while in the kidneys catalase activity in *C. carpio* increased as much as 960 %, but in *O. niloticus* there was a 276 % decrease in comparison with the control.

Cytochromes are another haemoproteid that undergoes in induced biosynthesis in yeast. Induction of cytochromes of the respiratory chain caused by entering the stationary stage of growth or by reoxygenation stress has been well described [19]. The maximum absorption on the cytochrome spectrum is directly proportional to the concentration of respiratory chain cytochromes; there is even a method that makes it possible to quantitatively determine cytochrome concentration on the basis of absorbance values [20]. Yeast seem to be the most convenient eukaryotic organism for studying the role of the mitochondrial system in pesticide toxicity. Yeast can easily survive inhibition of almost all mitochondrial function, eg by anoxia, and tolerate respiratory inhibitors and genetic changes leading to respiratory deficiency [21].

Błaszczyński et al [21] found that the mitochondria are the site in yeast where paraquat is reduced to a toxic free-radical form. This hypothesis was supported by analysis of cytochrome spectra of yeast cells. After incubation by paraquat the

absorbance maxima for cytochromes b and c disappeared. According to Cochemé and Murphy [22], complex I is the site in the respiratory chain of yeast where superoxide anion radical is generated during incubation with paraquat. Other pesticides also cause damage to yeast cell mitochondria. Cadmium and thiuram applied together show synergistic toxicity and induce mitochondrial petite mutants in yeast [23].

Pesticides can also cause mitochondrial damage in the cells of higher eukaryotes. Paraquat induces cell death in dopaminergic neurons through a mechanism in which p53 and the mitochondrial apoptotic pathway are linked. Paraquat has been found to decrease activity of mitochondrial complex I and potential of mitochondrial transmembrane and to induce the release of cytochrome c from the mitochondria [24]. Chlorpyrifos-induced toxicity was characterized by the loss of mitochondrial potential, the appearance of nuclear condensation and fragmentation in placental cells [25]. Atrazine is a widely used triazine herbicide. A series of experiments with sperm and isolated mitochondria suggest that atrazine inhibits mitochondrial function, and mitochondrial F(1)F(0)-ATP synthase is a molecular target of atrazine [26].

A bioassay is a system for monitoring toxicity of chemicals in the environment via the biological responses of experimental organisms. In this study the stress response of yeast cells was used to test the toxicity of pyrethroids. The stress factors applied in the logarithmic phase of culture induce expression of the gene CTT1, which encodes catalase T [27]. Under these conditions catalase T is synthesized *de novo* and within a short time achieves a high level of activity.

Many compounds can inhibit the cellular stress response. Cycloheximide is known to prevent synthesis of stress proteins by inhibiting protein synthesis in cytoplasm. Some pesticides, such as paraquat, can destroy the internal membrane of mitochondria and cause cytochrome absorbance to decrease within a short incubation time.

In this study inhibition by pyrethroids of induced biosynthesis of catalase and cytochromes was described. At this stage of research it is difficult to determine the stage at which biosynthesis of these proteins is inhibited. Both proteins are haemoproteids, so it may be postulated that pyrethroids affect the haeme biosynthesis pathway. Haeme and iron metabolism play a key role in maintaining integrated cellular metabolism. Haeme is necessary for activating the haeme-responsive transcriptional activator HAP1, involved in the expression of numerous genes [28]. Biosynthesis of haeme begins in the mitochondrion with synthesis of delta-aminolevulinic acid, and subsequent stages take place in the cytoplasm. The main product of the haeme biosynthesis pathway in yeast cells grown under aerobic conditions is haeme [9]. Yeast do not accumulate porphobilinogen and porphyrin [29]. Accumulation of haeme in any cellular compartment could be very dangerous, because this compound is a potential source of oxygen free radicals [28]. A previously published study found that pyrethroids can damage yeast cell membranes [30]. They may also damage mitochondrial membranes and prevent transport of coproporphyrynogen. After yeast cells were incubated with pyrethroids, a number of respiratory-incompetent rho^- mutants were found to increase [31]. One possible explanation for the inhibition of induced biosynthesis of the haemoproteids studied may be the free-radical effect of pyrethroids. On the haeme biosynthesis pathway there are several enzymes that are sensitive to the presence of free

radicals, such as ferrochelatase, which catalyzes insertion of iron into the protoporphyrin ring [9].

Conclusions

1. The effect of pyrethroid on catalase activity depends on phase of yeast culture growth.

2. Pyrethroid alone added to the yeast culture does not cause significant changes in cytochrome absorbance.

3. Stress conditions (NaCl, alcohol, $NaNO_3$) induce biosynthesis of catalase and cytochrome proteins in logarithmic yeast cells.

4. Application of pyrethroid and stress conditions at the same time was found to inhibit synthesis of haemoproteins, ie catalase T and cytochromes in logarithmic yeast cells.

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WPŁYW PYRETROIDÓW NA INDUKOWANĄ WARUNKAMI STRESU BIOSYNTEZĘ WYBRANYCH BIAŁEK HEMOWYCH W KOMÓRKACH DROŻDŻY *Saccharomyces cerevisiae*

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Abstrakt: Odpowiedź komórek na stres jest podstawowym mechanizmem ochronnym, pozwalającym dostosować się do zmieniających się warunków środowiska. Logarytmiczne hodowle drożdży *Saccharomyces cerevisiae* są dobrym modelem do tego typu badań, ponieważ reakcji na stres towarzyszy m.in. indukcja biosyntezy białek hemowych, takich jak katalaza i cytochromy. W komórkach drożdży szczepu dzikiego rosnących na pożywce YPG zawierającej 2 % glukozy w logarytmicznej fazie wzrostu hodowli poziom aktywności katalazy enzymu jest niski. Widma cytochromowe w tych warunkach są płaskie, co informuje o małej aktywności kompleksów oddechowych. Warunki stresu wywołują indukcję ekspresji genu CTT1 kodującego katalazę T i enzym ten jest syntetyzowany *de novo.* W ciągu krótkiego czasu poziom aktywności katalazy T gwałtownie wzrasta, osiągając wartość charakterystyczną dla stacjonarnej fazy wzrostu komórek drożdży. Podobnie pod wpływem stresu zachodzi indukowana biosynteza białek cytochromowych. Badano wpływ pyretroidów na przebieg indukowanej przez warunki stresu biosyntezę tych białek hemowych w komórkach drożdży *S. cerevisiae*. Doświadczenia przeprowadzono na standardowym szczepie dzikim drożdży. Hodowle drożdży prowadzono w pożywce płynnej YPG. Wpływ pyretroidów (esfenwalerat, deltametryna, cypermetryna) na indukowaną biosyntezę białek hemowych badano w warunkach stresu alkoholowego lub osmotycznego (wywoływanego przez chlorek sodu lub azotan(V) sodu). Oznaczano aktywność katalazy i wykonano niskotemperaturowe widma cytochromowe komórek drożdży. Stwierdzono, że równoczesne stosowanie pyretroidów i warunków stresu powoduje zahamowanie indukowanej syntezy białek hemowych, to jest katalazy T i cytochromów.

Słowa kluczowe: pyretroidy, stres, katalaza, cytochromy, drożdże