BIOLOGIJA. 2018. Vol. 64. No. 3. P. 249–257

Genetic peculiarities of free radical oxidation of lipids and proteins in the semen of breeding boars

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Complex research into biochemical aspects of the functioning of the antioxidant system for the protection of sperm of the breeding boars has established that the intensity of the flow of peroxide oxidation of lipids in germ cells is much higher than in the extracellular space. Reactions of free radical peroxide oxidation of proteins and lipids in the semen of healthy breeding boars are characterized by a stable level of activity that is necessary for the normal course of implementation of processes of the reproductive function. All components of the antioxidant system stay in mutual compensatory ratios under physiological conditions. As a rule, reducing the concentration or activity of some antioxidant enzymes leads to corresponding changes in others. The main antioxidants of the germ cell genomes are superoxide dismutase and ceruloplasmin. Catalase is a key enzyme that neutralizes H_2O_2 in the semen fluid of breeding boars. The content of total proteins in the semen of the synthetic line SS23 animals is greater ($p < 0.05$) than in the breeding boars of the large white breed. The processes of the oxidative modification of proteins in the animals body of the synthetic line runs more intensely, as it is evidenced by the higher content of the aldehyde and ketodinitrophenyl hydrazones of the main and neutral character in the sperm cytoplasm.

Keywords: breeding boars, semen, sperm, peroxide oxidation of lipids, enzymes of antioxidant system, oxidation modification of proteins, medium mass molecules

INTRODUCTION

Today artificial insemination in pig breeding is the main technological means of reproduction of animals. However, the reproductive system of males is one of the most sensitive and vulnerable in the body. It is exposed to a number of adverse factors that can lead to a decrease in fertility capacity of the ejaculate, infertility, and the birth of non-viable young animals (Jung et al., 2015).

The main causes that lead to a dysfunction of the sexual glands include inferior and unbalanced feeding, and long-term adaptation of animals to technological conditions of exploitation. The indicated causes are accompanied by changes in metabolism, if particular oxidative stress occurs, which

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plays a key role in the development of male infertility (Rodriguez et al., 2017).

Sperm cells are extremely sensitive to free radical oxidation products. They reduce the survival and mobility of the germ cells (Moretti et al., 2017). The literature contains a considerable amount of data on studies into the content of lipoperoxidation products and the antioxidant system enzymes activity of animal sperm protection, but there is absolutely no information that would characterize the intensity of oxidative modification of proteins (OMP) in the plasma of sperm and germ cells.

In the state of oxidative stress, the reactive oxygen species (ROS) attack, primarily, not lipids, but proteins of the plasma membranes (Guedes et al., 2009; Polishchuk et al., 2014). OMP products have a longer decay period (oxidized proteins are destroyed for several hours or days) compared to lipoperoxidation products (neutralization of end metabolites), which makes them a promising marker for assessing the intensity of free radical oxidation.

The study of free radical oxidation of lipids and proteins intensity and the functioning of the antioxidant system of protection of the organism can have an important predictive value in the case of study into the etiology of infertility, it can also determine the use of antioxidants and membrane stabilizing drugs to protect cells and, in particular, the sperm from toxic effects of products of lipoperoxidation and ROS.

The purpose of the work was to examine antioxidant defence enzymes activity and the content of peroxide oxidation products of lipids and oxidative modification of proteins in sperm plasma and genital cells of purebred animals (large white line pigs) and hybrid animals (synthetic line SS23).

MATERIALS AND METHODS

The experimental part of the study was carried out in the conditions of production. Purebred fetal kennels of the large white breed and the specialized SS23 synthetic line at the age of two years were used in the study. They were kept in "Elita" LLC, Terezine village, Bila Tserkva district of the Kiev region. LLC "Elita" has the status of a breeding centre. To find out the peculiarities of free radical oxidation processes in the semen of the kennels on the principle of analogues, two groups of animals were formed, eight heads in each. Barns were kept in the same conditions using a complete feed (PC-57-2) and with free access to feed and water. These conditions corresponded to the general requirements specified for breeding farms. Sperm samples were taken once a week.

The material used for the study was manually obtained ejaculate. The native sperm was centrifuged (3000 rpm for 10 min), supernatant fluid (sperm plasma) was separated, the sperm precipitate was washed twice in physiological saline. The cytoplasm of germ cells was obtained by destroying cellular membranes of sperm, which was performed by differential centrifugation (14.000 g/min at 4°C for 10 min).

The biochemical part of the study was carried out in the interfacial research laboratory of biochemical and histochemical methods of research at the Bila Tserkva National Agrarian University. The content of common lipids (Kates, 1986) and proteins was determined in the study material (Lowry et al., 1951). The intensity of lipid peroxidation (LPO) in sperm plasma and germ cells was determined by the content of diene conjugates (DC) (Stalnaya, 1977), lipoprotein hydroperoxides (LHP) (Romanova, 1977), and TBA-active products (TBA-AP) (Andreeva et al., 1988). The state of the antioxidant system (AOS) was assessed by the activity of enzymes: superoxide dismutase (SOD, 1.15.1.1) (Chevari et al., 1985), catalase (CAT; 1.11.1.6) (Korolyuk et al., 1988), and the content of ceruloplasmin (CP) (Ravin, 1961).

The level of the oxidative modification of proteins was estimated by the number of formed 2.4-dinitrophenylhydrazones (aldehyde and keto-derivatives of neutral and basic character) (Meschyshen, 1998). Medium-mass molecules (MMM) in sperm plasma and germ cells were determined by the spectrophotometric method in the UV range of 254 nm (peptide fraction) and 280 nm (fraction with aromatic groups) (Kovalevsky, 1990), and expressed in conditional units quantifiable to the extinction index.

Statistical evaluation of the results was conducted using the arithmetic mean and the standard error (M ± m), and the adequate interval for assessing the degree of probability (*P*) using Student's criterion (t). Differences were statistically significant at $P < 0.05$. The results of the study were processed using the statistical package Statistica 6.0 (StatSoft Inc, USA). The normality of the distribution of the actual data was checked using the Shapiro-Wilka criterion.

RESULTS

Getting a complete vision of the fertilizing ability of sperm is possible only after complex research into its morpho-biochemical composition. A study into physiological and biochemical properties of ejaculate is a prerequisite for understanding the issues associated with the physiology and pathology of spermatogenesis (Tüttelmann et al., 2018).

As a result of the conducted researches, the content of common lipids (Fig. 1) in the semen plasma of purebred boars of the large white breed was found to be significantly higher (by 23.9; $P < 0.01$) compared with the boars of the synthetic line SS23. It is assumed that the heterosis effect causes such features in hybrid pigs. It should be noted that the concentration of lipids in the semen of the breeding boars of both experimental breeds was practically of the same level. It can be assumed that the chemical composition of the cytoplasm of the germ cells is more stable compared with the sperm plasma. Instead, the level of total lipids in the semen of the synthetic lineage was lower, compared to purebred animals. A similar pattern is confirmed by the data that is highlighted in literature (Bansal, Bilaspuri, 2008; Am-in et al., 2011).

Quantitative and qualitative composition of plasma lipids of sperm and cytoplasm of germ cells to a large extent depends on the intensity of the course of free radical oxidation processes and the functioning of the antioxidant system of protection in the organism of animals, which is confirmed by the established correlation bonds.

Plasma sperm of purebred boars of the large white breed is characterized by low activity of SOD (Table 1). Instead, the activity of the investigated enzyme in the sperm was the highest and exceeded the similar index in animals of the synthetic line SS23 by 16.1% ($P < 0.05$).

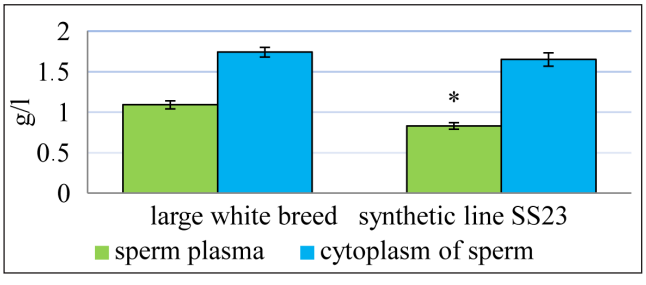

Fig. 1. Content of total lipids in the plasma of sperm and genital cells of boars breeding boars (M ± m; $n = 8$)

* The difference is probably relative to the purebred large white breed, $P < 0.05$

Table 1. **Antioxidant system enzyme activity and ceruloplasmin content in sperm plasma and sperm cells of boars fertilisers (M ± m; *n* = 8)**

Indexes	Large white breed		Synthetic line SS23	
	plasma	cytoplasm of sperm	plasma	cytoplasm of sperm
Superoxide dismutase, act/ml	0.99 ± 0.04	1.18 ± 0.06	1.06 ± 0.06	0.99 ± 0.05*
Catalase, mcat/ml	395.60 ± 16.31	189.14 ± 15.10	217.78 ± 15.77***	182.48 ± 7.91
Ceruloplasmin, μg/ml	72.63 ± 2.45	185.06 ± 9.71	73.50 ± 2.68	170.28 ± 11.89

Here and in tables 2–4, the difference is probably relative to purebred boars of the large white breed: * – $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

The activity of catalase in the sperm plasma of the synthetic line SS23 is significantly lower (by 45%, $P < 0.001$) compared to the index of purebred boars. The activity of the enzyme in the semen of both breeds of boars was practically at the same level. Effective antioxidant protection in tissues should maintain a certain proportion between the activity of SOD and CAT because they are involved in the regulation of two successive stages of the same chain of transformations. In the cytoplasm of the sperm of purebred boars, such consistency is manifested in the form of a negative correlation ($r = -0.71$).

The CP content in boars' semen was almost twice as high as in sperm plasma. A negative correlation was found between the content of ceruloplasmin and the catalase activity ($r = -0.64$). In semen plasma of the large white breed, the content of ceruloplasmin positively correlated with the activity of superoxide dismutase ($r = 0.54$).

The results of the study have shown that free radical oxidation processes in the body of a boar of the large white breed and the synthetic line SS23 proceeded with varying intensity (Table 2).

The concentration of primary LPO products, namely DC and LHP in the genital cells of the boars, was significantly higher in comparison with similar indicators in sperm plasma. No similar tendency was observed for TBA-AP content.

It is important to determine not only the absolute values of intermediate lipoperoxidation products, but also the ratio of their content to the level of the initial substrates of the LPO (Fig. 2) for the comprehensive evaluation of the state of oxidation-reducing homeostasis.

Table 2. **Content of lipid peroxidation products in sperm plasma and spermatozoa plasma of breeding boars (M ± m; *n* = 8)**

Indexes	Large white breed		Synthetic line SS23	
	plasma	cytoplasm of sperm	plasma	cytoplasm of sperm
Lipids hydroperoxides, unit. act/ml	3.29 ± 0.11	7.57 ± 0.29	2.94 ± 0.14	6.92 ± 0.30
Diene conjugates, unit. act/ml	0.19 ± 0.01	0.31 ± 0.02	0.22 ± 0.01	0.80 ± 0.04***
TBA-active products, nmol MDA/ml	3.54 ± 0.20	3.44 ± 0.23	3.79 ± 0.22	2.80 ± 0.13

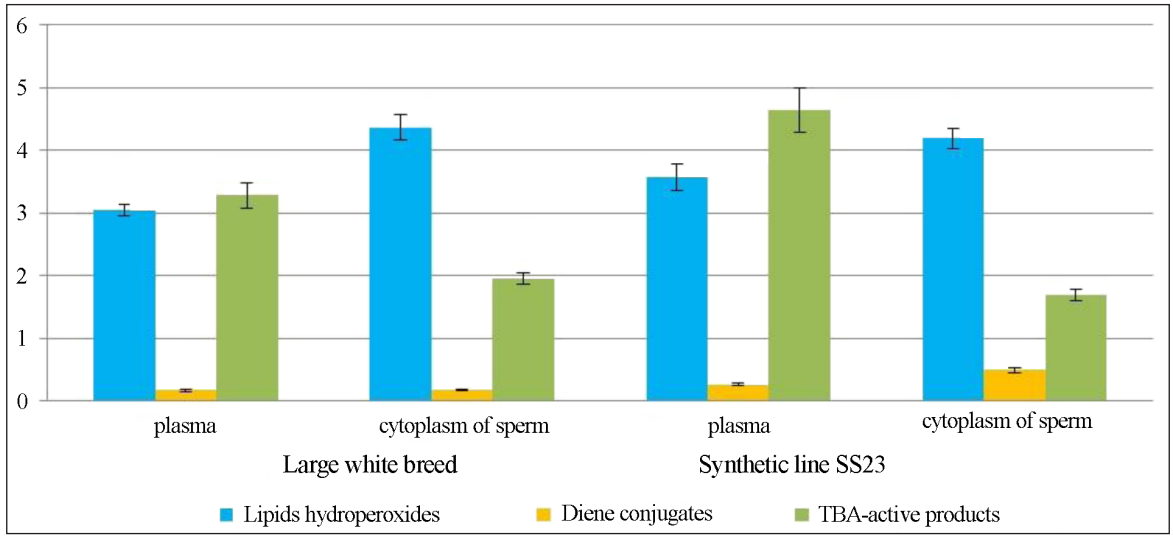

Fig. 2. The ratio of the content of peroxide lipid oxidation products to common lipids in the boar semen

The ratio of lipid hydroperoxides and diene conjugates to total lipids in the semen of the synthetic line was higher (17.2% and 40.6%, respectively) compared to the values of large white breed. In germ cells, this tendency is observed only in relation to the diene conjugates. The content of common lipids and hydroperoxides of lipids in the plasma of semen of large white breed of pigs have a high degree of linear correlation (r = +0.65).

It is known that the protein content of biological fluids is one of the main indicators that characterizes the level and direction of animal productivity. The amount of total protein correlates with the growth and productivity of animals. By its content it is possible to estimate the intensity of metabolic processes in the body.

The conducted research showed that the level of total protein in the semen of the boars of the synthetic line SS23 was higher than that of pure-bred animals (Fig. 3). Increased oxidoreductase activity and significant protein content in the semen of the boars of the synthetic line indicate an intensive metabolism associated with high growth energy and productive qualities of hybrid animals. It has been proved that biosynthesis of protein in tissues of pigs with better productive qualities is more intensive (Polishchuk et al., 2014).

The content of total protein in the spermatozoa of boars of the large white breed was 3.6 times higher compared with the same indicator in the plasma of the sperm. Probable changes in the total protein content in sperm plasma were not detected. At the same time, the concentration of total protein in the spermatozoa of the synthetic line was higher by 21.3% ($p < 0.05$) in relation to the boars of the large white breed.

It is known that destruction of proteins, as compared with the products of the LPO, is a reliable marker of oxidative tissue damage, since OMP derivatives are more stable (Guedes et al., 2009). In this regard, the next stage of our research was an analysis of aldehyde and ketone derivatives of OMP content in the sperm plasma and sperm cells.

Results of the research conducted in the semen of the kennel-breeders, show that products of oxidation of proteins that react with 2,4-dinitrophenylhydrazine were found (Table 3).

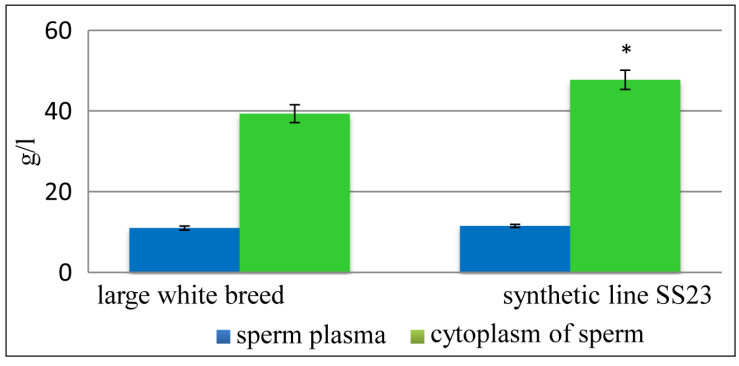

Fig. 3. Content of total protein in sperm plasma and semen cytoplasm

* The difference is probably relative to purebred large white breed, $P < 0.05$

Table 3. **Content of oxidative modification of proteins products in sperm plasma and boar semen cytoplasm, moles/g of protein (M ± m; n = 8)**

Group of animals		Neutral products		Alkaline products	
		KDNPH λ = 356	ADNPH λ = 370	KDNPH λ = 430	ADNPH λ = 530
Large white breed	Plasma	40.21 ± 2.44	31.29 ± 1.72	25.36 ± 1.80	3.50 ± 0.30
	Cytoplasm of sperm	4.55 ± 0.38	3.60 ± 0.27	2.08 ± 0.15	0.71 ± 0.06
Synthetic line SS23	Plasma	34.23 ± 2.29	32.72 ± 2.12	24.74 ± 1.49	4.3 ± 0.40
	Cytoplasm of sperm	5.23 ± 0.23	3.71 ± 0.18	2.17 ± 0.14	0.80 ± 0.07

The bulk of the formed dinitrophenyl hydrazones belongs to neutral aldehyde and ketod-initrophenyl hydrazones. The probable difference between these indices was not revealed in the conducted studies. The content of the KD-NPH of neutral and alkaline character in the semen plasma of the purebreds was slightly higher than that of synthetic animals. On the other hand, the amount of these products in the boar sperm cytoplasm was significantly lower compared to the animals of the synthetic line (Table 3). In sperm plasma and cytoplasm of the sperm of both studied species, a positive correlation between the content of carbonyl compounds of the main and neutral characters was found.

The study of ADNPH of alkaline and neutral nature showed a lower content of these products in the plasma and cytoplasm of purebred sperm. The concentration of OMP products in sperm plasma of purebred and synthetic animals was higher compared to sperm cytoplasm.

It is known that the content of medium-size molecular peptides correlates with the functional state of the organism. This could serve as a prognostic criterion for metabolic processes. As an additional indicator showing the degree of protein fragmentation in boar ejaculates, the content of medium mass molecules (MMM) was studied. A high content of medium-size molecular peptides in the tissues disrupts homeostasis of the cells and may cause development of endotoxicities (Matveev et al., 2013).

Table 4 shows the spectrum of maximal optical absorption of MMM at different wavelengths (λ = 280 and λ = 254). The aroma ratio is the ratio of the extinction of MMM containing aromatic amino acids (non-toxic fraction) to the excitations of MMM that do not contain aromatic amino acids and show toxic effects. The content of MMM in the reproductive cells of the large white breeding boars was significantly higher ($p < 0.05$) against the values of animals of the synthetic line SS23.

DISCUSSION

The problem of resistance of an organism and its adaptation to environmental conditions remains one of the key problems in physiology. The antioxidant system plays an important role in the processes of adaptation of the organism to the environment.

One of the main enzymes of antioxidant defence is superoxide dismutase. The low enzyme activity in sperm plasma of purebred animals is to some extent due to the high content of LPO (lipid hydroperoxides and TBA-active products). On the other hand, one should not forget that the sperm cell includes mitochondria (giant spiral mitochondria). It is known that the concentration of superoxide anion radicals in mitochondria is 5–10 times higher than that in cytosols and nuclei. With a high content of $O^{2\bullet-}$ in tissues, the activity of SOD compensatory increases (Bansal, Bilaspuri, 2009).

Against the background of reduction of superoxide dismutase activity, the increased catalase activity can be considered as an adaptive reaction of the organism. It should be noted that excessive amounts of H_2O_2 superoxide dismutase can form highly reactive hydroxyl radicals that lead to fragmentation of the protein part of the enzyme molecule and loss of its activity. Accumulation of hydrogen peroxide in

Table 4. **Content of medium mass molecules in sperm plasma and sperm cytoplasm of breeding boars, conditional units according to the method (M ± m; *n* = 8)**

Indexes	Large white breed		Synthetic line SS23	
	plasma	cytoplasm of sperm	plasma	cytoplasm of sperm
MMM containing aromatic amino acids, λ = 280	0.17 ± 0.01	0.21 ± 0.01	0.15 ± 0.01	0.16 ± 0.01**
MMM, that do not contain aromatic amino acids, λ = 254	0.82 ± 0.04	1.05 ± 0.05	0.73 ± 0.04	0.86 ± 0.05*
Aromaticity coefficient	0.21 ± 0.01	0.20 ± 0.01	0.21 ± 0.02	0.19 ± 0.02

semen adversely affects the functioning of germ cells and inhibits the acrosome response. For an effective SOD action, low molecular weight antioxidants or a coordinated work with peroxidases are required (Marchlewicz et al., 2016).

Elimination of superoxide anion radicals involves copper protein, ceruloplasmin. It is this compound that plays a key role in the transport and homeostasis of copper in humans and animals. Copper, which carries ceruloplasmin, affects the process of spermatogenesis, and the mobility and function of the germ cells (Ogórek et al., 2017).

The studied protein is important for the functioning of germ cells. The relatively stable content of ceruloplasmin in the ejaculates of the boars is due to the high resistance of the compound to the toxic effect of the ROS, which allows it to maintain biological activity in the conditions of intense generation of active forms of oxygen.

In the life of cells, a significant number of ROSs is formed in them, which negatively affects the structure of lipids, nucleic acids, and proteins. Moreover, the latter are most vulnerable to the ROS. Lipids of biological membranes are protected from a radical attack by fat-soluble antioxidants (tocopherol, retinol), but proteins that are found in aqueous environment do not have such protection. Due to the action of the ROS, fatty compounds collapse in the aquatic environment much earlier than hydrophobic compounds. Lipid radicals can also cause fragmentation of protein structures.

In the case of OMB, a non-enzymatic of the side radicals of the basic amino acids deamination occurs with the formation of carbonyl groups. In addition, fragmented protein molecules are capable of conglomerate formation by the type of prions. Available in cells, enzymes hydrolyze damaged protein molecules to amino acids and compounds of a low molecular weight in order to reuse or isolate them from the body. Thus, the determination of the content of modified proteins in cells, organs, and the body as a whole is a convenient way to assess the development of oxidative stress.

The intracellular level of oxidized proteins reflects the balance between the intensity of oxidation and the rate of degradation of oxidized proteins. It was found that the stems of the semen of the synthetic lineage boars are more susceptible to oxidative modification. Such changes can be linked to the morphological and functional characteristics of the semen of the breeding boars of the synthetic line SS23. On the other hand, the growth of the concentration of the products of oxidative modification of proteins can be considered a compensatory reaction of the organism, which is aimed at increasing the reserve of the antioxidant system (increase of glutamate, cysteine). Also, the intensification of OMP is one of the causes of inhibition of the enzymatic level of antioxidant defence of the organism.

A similar pattern in the distribution of oxidative forms of proteins in sperm plasma and sperm cytoplasm was noted. The total content of products of oxidation modification of a neutral nature exceeded the content of the alkaline products in the plasma of sperm by 2.5 times (purebred animals) and 2.3 times (synthetic line SS23); in the cytoplasm of sperm 2.9 and 3.0 times, respectively. The results of the conducted studies allowed us to reveal regularities and to follow the peculiarities of separation of oxidized forms of proteins in ejaculates of different breeds of breeding boars.

Information on the state of metabolic homeostasis is more complete in the presence of data on the level of accumulation of endogenous intoxication substrates in the body. The content of median-molecular peptides in the germ cells of the studied boars was higher than in the semen fluid. The concentration of the non-toxic fraction of median-mass peptides (MMM280) and products of incomplete decomposition of proteins (MMM254) in the cytoplasm of spermatozoa of the synthetic lineage was significantly lower than in purebred animals. It is worth noting that a significant level of average mass molecules in ejaculates of purebred animals is recorded against the background of a high content of products of oxidative modification (carbonyl products of neutral and basic nature) and peroxide oxidation of lipids (lipid hydroperoxides and TBA-active products).

Accumulation of the average mass molecules in the semen of animals is associated with parallel processes of the LPO and OMP. It should be noted that purebred animals are more susceptible to the development of oxidative stress, since their bodies accumulates more products of free radical oxidation of proteins and lipids. High stress susceptibility of synthetic line boars may be due to the absence of halothane gene (stress gene) in their body (Suprun, 2014).

The obtained data indicate that the oxidative destruction of proteins in the ejaculate is a physiological process that occurs in cells and in the extracellular fluid. The total content of carbonyl compounds in the semen of synthetic lineage is higher than in that of purebred animals. This indicates that the OMP processes in their organism are somewhat more intense. Consequently, the accumulation of oxidized proteins can be regarded as one of the factors regulating their synthesis and degradation.

CONCLUSIONS

Complex researches of various indicators of free radical oxidation of lipids and proteins in the semen of breeding boars allowed an objective characterisation of the state of the protective antioxidant system in the studied animals. The oxidative modification of proteins is an early sign of tissue damage due to free radical pathology, so the indicators of OMP can be used in pathology as one of the indicators of the oxidative stress state. Certain regularity in the distribution and number of oxidized forms of proteins in the large white breed and in the synthetic line SS23 was noted. The level of OMP products in the semen of the animals under study is probably due to different rates of metabolic processes. According to the content of medium weight molecules, it was found that the level of endogenous intoxication in the organism of the breeding boars of the synthetic line was lower compared with purebred animals.

Received 29 April 2018
Accepted 18 September 2018

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GENETINĖS LAISVOJO RADIKALO OKSIDACIJOS YPATYBĖS KUILIO SPERMOS LIPIDUOSE IR BALTYMUOSE

Santrauka

Antioksidantų sistemos, apsaugančios kuilio spermos gyvybingumą, biocheminiai tyrimai rodo, kad lipidų peroksidacija gemalinėse ląstelėse yra kur kas intensyvesnė nei ląstelių išorėje. Baltymų ir lipidų laisvųjų radikalų peroksidacija sveiko kuilio sėkloje yra charakterizuojama pagal stabilų aktyvumo lygį, būtiną normalioms reprodukcinėms funkcijoms palaikyti. Visos antioksidantinės sistemos komponentai fiziologinėmis sąlygomis palaiko bendrus tarpusavio kompensacinius santykius. Kai kurių antioksidantinių fermentų koncentracijos ar aktyvumo mažėjimas gali lemti atsakomuosius pokyčius ir kituose fermentuose. Pagrindiniai gemalo ląstelių genomo antioksidantai yra superoksido dismutazė ir cerulopazminas. Katalazė yra pagrindinis fermentas, neutralizuojantis kuilio spermos H_2O_2. Bendras baltymų kiekis sintetinėje SS23 gyvūnų linijos sėkloje yra didesnis ($p < 0,05$) nei didžiųjų baltųjų veislių sėkloje. Intensyvesnį sintetinės linijos gyvūnų oksidacinį baltymų modifikavimą liudija didesnis aldehidų ir ketodinitrofenilhidrazono kiekis pagrindinėje ir neutralioje spermatozoidų citoplazmoje.

Raktažodžiai: kiaulių apvaisinimas, sėkla, sperma, lipidų peroksidacija, enzimų antioksidantinė sistema, baltymų oksidacijos modifikacijos, vidutinės masės molekulės