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INTERACTION OF NANOPARTICLES WITH PLASMA MEMBRANE OF PLANTS

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Abstract. During the interaction of nanoparticles with the cell of plants, they can change both the structure and function of proton pumps of plasma membrane. The main purpose of these experiments was to study the effect of nanoparticles on redox and ATPase nature proton pumps present in the plasma membrane of higher aquatic plants *Elodea Canadensis* and *Vallisneria spiralis*. Membrane potential was studied using intracellular microelectrode technology. According to the results of these experiment, almost 21 nm ZrO_2 nanoparticles pass through the plasma membrane by a second mechanism.The second mechanism is the passage of nanoparticles through the formation of pores in the plasma membrane and through protein-containing channels. In this case, it may also damage the H^+-ATPase complex. The strong depolarization of the MP during the action of ferricyanide indicates that the redox system is not damages. When the leaves are exposed to light in a solution of iron nanoparticles, their metabolism is disrupted, the pigment content is broken down, and the leaves turn yellow quickly. In this case, it is assumed that iron nanoparticles can penetrate through the mechanism III - endocytosis and seriously damage the process of photosynthesis.

Keywords: *Nanoparticles, plasma membrane, membrane potential, redox proton pumps, ATPase proton pumps.*

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1. Introduction

At present, there is a great deal of research and extensive scientific information on the interaction of nanoparticles and nanomaterials with plants, their movement in plant organs, their entry into cells, the physiological and biochemical effects they create, and the mechanisms that regulate these processes. However, there are still many unresolved issues and questions that require new, more in-depth and molecular research. At the initial stage of application of nanotechnology in plant physiology and agriculture, the main purpose of research was the outline the toxic effects of nanoparticles (NPs) and nanomaterials (NMs) on plants (Dietz & Herth 2020). Therefore, a new field of science called nanotoxicology emerged, and research in this area began to study the toxic effects of NPs and NMs on plants, as well as their absorption, movement, accumulation, and elimination from plants.

The key issue in clarifying the effects of NPs on plants is how they enter plant cells, organs, and tissues. Until the answer to this question is found, we will not be able to clarify the exact mechanism of interaction of NPs with plants. The initial interaction of NPs with plants, apparently, occurs through their adsorption on the tissue surface

and, consequently, on the cell surface, the appearance of attraction and complementation between charged groups of corona proteins and peripheral and integral proteins that protrude from the electric double layer (EDL) as a dynamic structure on the surface of a charged cell wall or membrane of a living cell (Fleischer and Payne, 2014). The interaction of NPs with the cell surface is a case different from the interaction of ions (Bell *et al*., 2014). It is assumed that NPs are mobilized to the cell surface by diffusion, as with ions, but they do not seem to have specialized receptors. NPs have surface free energy, which is obtained by the action of electrons at the interface between the material and the environment. Comparing NPs with bulk material, due to their high surface / volume ratio, they have a much higher amount of surface free energy, which mainly explains the higher reactivity of materials in nanoscale sizes (Fischer *et al*., 2008). This high level of surface free energy suggests an imbalance of entropy, which tends to spontaneously decrease due to interaction with other molecules or the formation of NPs aggregates, which are deposited.

The interaction of nanoparticles with the cell wall and plasma membrane on the cell surface occurs through Van der Waals and electrostatic forces, hydrogen bonds, and chemical reactions. It has been found that during the integration of nanoparticles with biomolecules, biomolecules undergo conformational changes, and the surface of nanoparticles is modified by biomolecules and enzymes. When the size of the nanoparticles is close to the size of the lipid platforms of the plasma membrane, their interaction depends on the region where the nanoparticle sits on the surface. Thus, because the distribution of receptors on the surface of the membrane is irregular, it is difficult to analyze their interaction. On the other hand, due to the dynamic structure of the plasma membrane, the active transport of ions, the distribution of passive ion channels, endocytosis nanoparticles have a strong influence on the nature of the membrane surface interaction. Experiments with carbon nanoparticles in plant cells have shown that small carbon nanoparticles, due to their good solubility, easily diffuse into the cell wall under the influence of van der Waals and capillary forces due to their concentration gradient and initially distribute in the cell wall and form clusters. The size of these clusters is in the range of 50 - 400 nm. After a while, nanoparticles accumulate on the surface of the plasma membrane. The membrane electric field (zeta potential) on the surface of the plasma membrane regulates the interaction of nanoparticles with the membrane and their movement in apoplastic space, depending on the loads. Carbon nanoparticles accumulated on the surface of the plasma membrane are absorbed into the cytoplasm of the cell over time. It is likely that nanoparticles smaller than 4 nm pass directly through the membrane, while larger ones enter the cytoplasm through endocytosis. In the cytoplasm, nanoparticles regenerate clusters (Chen, 2012).

Vasir & Labhasetvar (2008) studied the penetration of nanoparticles into and out of the cell with an atomic force microscope (AFM) and a confocal microscope and found that the membrane adhesion of functional nanoparticles is 5 times greater than that of non-functional nanoparticles (Vasir & Labhasetwar, 2008). Wang et al (2012) studied the passive transport of nanoparticles in erythrocytes. With a fluorescent microscope, they observed that quantum dots could easily enter these cells and accumulate inside the cells. The structural changes created by nanoparticles as they pass through the membrane have been studied using the infrared spectroscopy method. In this way, it was determined that nanoparticles easily pass through the membrane of erythrocytes, forming a hole, while there is no significant change in the structure of the membrane (Wang *et al*., 2012).

Thus, three different mechanisms have been proposed for the process of nanoparticles entering the cell: Mechanism 1: Nanoparticles can diffuse and cross the membrane directly. Numerous factors - the size, shape, composition, hydrophobicity of nanoparticles, surface loads affect this process. Membrane dynamics, lipid / protein content, and membrane fluidity also play an important role in this process (Barua & Mitragotri, 2014). Mechanism 2: Nanoparticles enter the cell by "endocytosis". In this case, the nanoparticles falling on the surface of the membrane exert mechanical pressure on the membrane, the membrane collapses inwards, is surrounded by a layer of lipids, and after a while the membrane closes. The nanoparticle surrounded by a membrane breaks off from the membrane in the form of a vesicle and falls into the cell (Rejman *et al.*, 2004; Verma *et al*., 2008). Mechanism 3. There are a number of ion channels (K, Na, H, Cl, Ca) in the plasma membrane, and in these channels ions can move both passively (due to the concentration gradient) and active (due to metabolic energy) (Hedrich, 2012). The dimensions of these channels are in angstrom order. It has been found that nanoparticles of this size can pass through the membrane through ion channels (Navarro *et al*., 2008). Magnetic nanoparticles stimulate ion channels across the membrane (Hughes *et al*., 2005), patch-clamp electrophysiological experiments show that nanoparticles can damage ion channels (Shang *et al.*, 2014), single-layer carbon nanotubes of size ∼0.9 and 1.3 nm block dose-dependent K + channels (Park *et al*., 2003). The interaction of nanoparticles with ion channels depends primarily on their electrical charge. Because most ion channels are potential-dependent channels, nanoparticles approaching the channel can affect their opening and closing.

When nanoparticles are adsorbed on the surface of plant cells, it is assumed that they can change the structure and function of H^+-ATPase and redox-type proton pumps in the plasma membrane. The presence of H^+-ATPase-type proton pumps in the plasma membrane of plant cells and their function have been well studied (Fuglsang *et al.*, 2010; Sanders *et al.*, 1981). However, the availability of redox pumps is still controversial.

Since the 1980s, serious research has been conducted on the activity of the oxidoreductase (redox) proton pump in the plasma membrane of plant cells. The results of these experiments proved that the existence of a short electron chain in the plasma membrane of plants is not a fiction, but a reality. To date, a large number of experimental results have been obtained proving the existence of the redox system in the plasma membrane (Barr, 1988); Böttger *et al*., 1985; Novak. & Ivankina, 1983; Rubinstein & Stern, 1986; Foyer & Noctor, 2013; Lüthje *et al*., 2013; Bérczi, A., Møller, 2000). However, in all experiments with intact plants, the presence of the redox system in the plasma membrane could not be detected in the medium without the presence of an electron acceptor (mainly potassium or sodium ferricyanide - $K_3Fe(CN)_6$, $Na_3Fe(CN)_6$). This has always raised the right question, why do we need a redox system that removes protons from the plasma membrane of plants? Although there are many well-founded answers to this question today, there is no simple practical approach to proving which of them is correct. In our experiments with higher aquatic plants *Elodea canadensis, Vallisneria spiralis*, the existence of a redox system in the plasma membrane without electron acceptors in the environment was proved by UV lights. Using the UV light, first, we investigated the initial mechanism of UV action on plant cells and second, we found out that it is possible to study the functions of plasma membrane proton pumps separately (Ahmadov *et al.*, 2008; Khalilov *et al*., 2002). During the interaction of nanoparticles with the cell plasma membrane, they can change

both the structure and function of these proton pumps. The main purpose of these experiments was to study the effect of nanoparticles on redox and ATFase nature proton pumps present in the plasma membrane of higher aquatic plants elodea and valisneria.

2. Materials and methods

In the experiments, we used photosynthetic leaf cells of higher aquatic plants - *Elodea canadensis Rich* and *Vallisneria spiralis L*. Large cells of these plants allow for a long time to carry out experiments with intracellular microelectrodes without disturbing their physiological state and the integrity of the membranes. Moreover, the electrogenesis of aquatic plant cells is well studied, and they are often used in electrophysiological experiments. Algae and wild celery were grown in tap water under laboratory conditions. The water was changed once a week. Before the experiment, the leaves were stored in a flow chamber in artificial pond water (APW) containing 1.0 mM NaCl, 0.1 mM KCl, and 0.1 mM CaCl2.

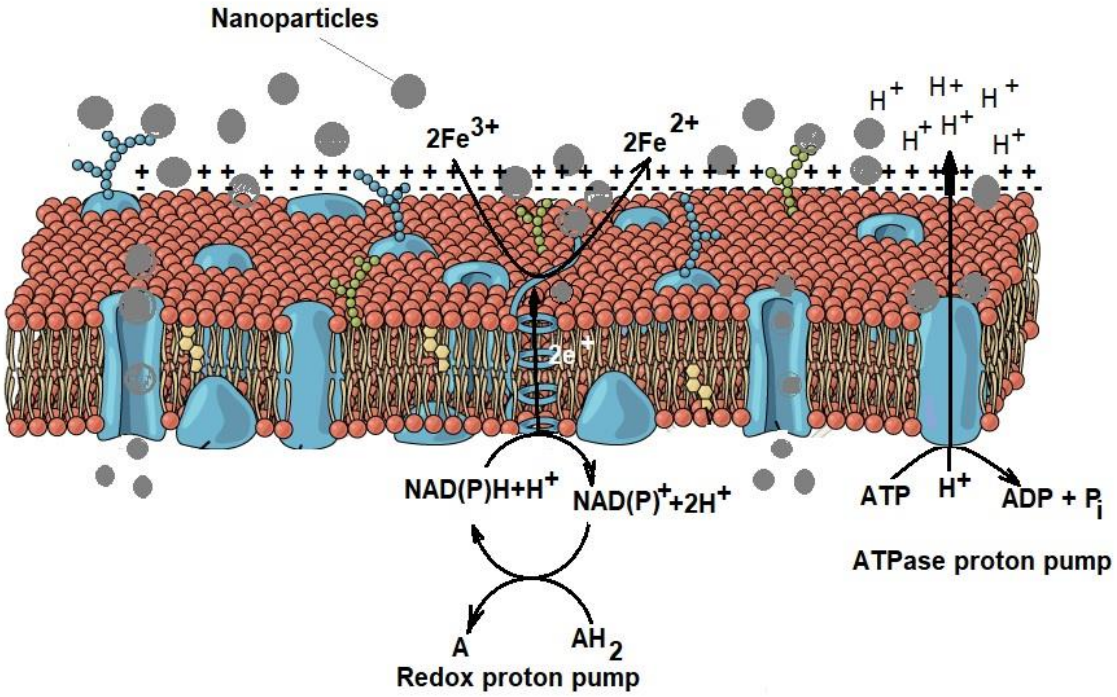

Fig 1. Possible effects of redox and ATPase proton pumps on the plasma membrane of plant cells of nanoparticles

The continuous flow of APW allowed the leaves to remain in a normal physiological state. Membrane potential and membrane impedance were studied using intracellular microelectrode technology, described in detail by Khalilov & Akhmedov (1992). Microelectrodes are special glass capillaries filled with 3 M KCl. The main source of UV radiation was a DRT-230 high-pressure mercury lamp with a linear radiation spectrum. The distance from the lamps to the exposed object was 0.25 m. The radiation intensity was 32 W m 2. Glass filters (UFS and BS) were used to study the action spectrum of membrane potential depolarization. UV transmissive filters (UFS and BS) were obtained from LOMO Russia. The transmission spectra of these filters are

the same as those of Toshiba Glass filters (UV-28, UV-29, UV-30, UV-31, UV-32). Each filter is referenced to the wavelength at which 50% transmission occurs [WL (T = 0.5)]. The exposure procedure allows recording the membrane parameters of the cell without interruption during typical recordings of the membrane potential, presented in the figures below.

The used nanoparticles Fe_3O_4, TiO_2 and ZnO were in the order of 10-30 nm, CuO particles in the range of 40 nm, and ZrO_2 nanoparticles in the size of 21 nm, 42 nm and 100 nm. The nanoparticles are from Skyspring Nanomaterials.Inc, USA, Houston TX.

3. Results and discussion

During study the membrane potential of water plant cells we identified in the plasmatic membrane of these plants two type of proton pumps - redox and ATPase proton pumps. We found this without the use of an external electronic acceptor.Where other authors have always used an external electron acceptor (eg, ferricyanide) to prove the existence of a redox pump. We observed this when the elodea and vallisneria leaves were irradiated with different wavelengths of UV-vis light. A complex change of membrane potential was detected when leaves of the water plants were exposed to UV. Fast and strong depolarization of the membrane potential occurred during the first minutes of exposure. Regardless of continuing exposure, the membrane potential returned to the starting level, after which a slow phase of depolarization set in (Fig. 2). Thus, UV can evoke two types of depolarization, rapid and reversible depolarization at first, and then slow depolarization. It was interesting to study the action spectrum of these two types of depolarization. To this end, we used different sources of UV and UFS and BS glass filters to investigate the kinetics of membrane potential changes during exposure to UV. Detailed study of this fast phase of membrane potential changes indicates that a fast and reversible depolarization occurred in cells during brief (15 –25 s) exposures to UV with 290 nm wavelength. Depending on the starting membrane potential level and the time of exposure, the depth of depolarization here attained more than half the value of the membrane potential. It is interesting to note that input impedance of the membrane and intercellular electrical couplings (conductance of plasmodesmata) did not change during depolarization development or after repolarization processes. We identified that the action spectrum of fast depolarization of membrane potential at the level of 300 – 330 nm means that, in this case, UV affects the component of a redox chain of the plasma membrane directly. The action spectrum of the slow phase of depolarization at the level 280 – 300 nm means that it affects a protein natural component of plasma membrane, which is H+-ATPase complex. Results of our experiments showed that redox and ATPase proton pumps at the same time, they work in parallel, complementing each other.

Adhering to the idea of parallel existence of the H^+ -ATPase and redox-active types of H^+-pump on the plant cell plasma membrane, we suggest the following explanation for the effect we obtained during the above-mentioned UV exposure. The action spectrum of the fast UV response at the level of 300 – 330 nm means that UV in this case directly affects to the nonprotein component of the plasmalemma. This may be a component of a redox chain. Evidently, UV with wavelength of 300– 330 nm alters the function or structure of a component of the redox system. This component is probably molecular quinone. By exciting and altering the form of quinone, UV brings about inactivation of the redox system. Inactivation of the redox system in turn leads to

membrane potential depolarization and acidification of the cytoplasm, which stimulates a pH_i-dependent H+-pump of the H^+-ATPase type. The initial strong membrane potential depolarization during the development of the fast UV response therefore undergoes repolarization and returns to the starting level irrespective of stoppage or continuation of the exposure. As for the slow depolarization phase at the wavelength level of 280 –300 nm, it coincides with the absorption spectrum of protein molecules. It may therefore be assumed that the H^+-pump of the H^+-ATPase type is inactivated at the same time as the redox system remains under UV exposure.

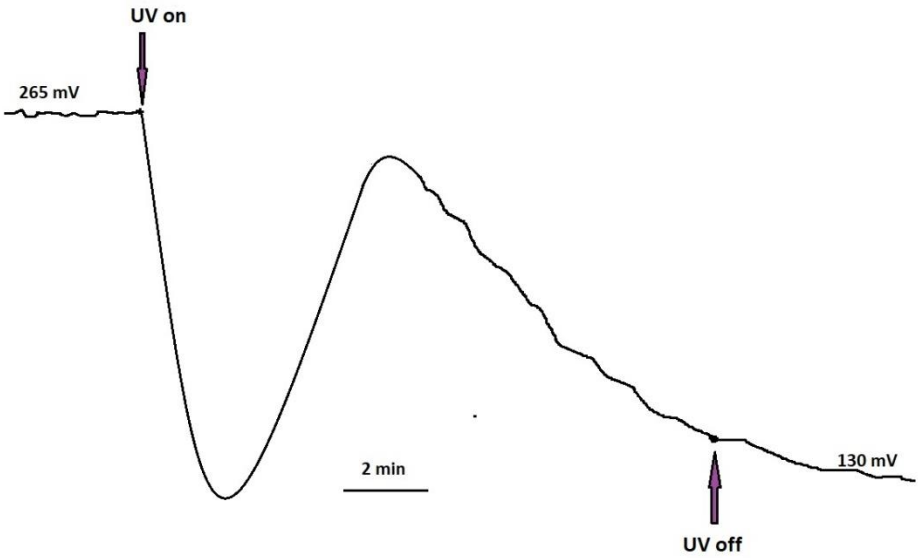

Fig. 2. Changes in membrane potential of elodea leaf cells

For a long time, a question that puzzled scientists remained unanswered. How can the redox system be functionally distinguished from the H + -ATPase complex? This is because, in all cases, MP depolarizes during the cessation of both the H-ATFase and the redox system, and it is not known by which system this depolarization occurs. Our experiments have shown that the redox system is present in the plasma membrane of elodea as well as other photosynthetic cells. When such a redox system is exposed to UV rays, the redox system first ceases to function, rapid depolarization occurs, the concentration of H + ions inside the cell increases, and the H + -ATPase is stimulated, resulting in MP repolarization. Then the H + -ATPase complex gradually breaks down and the MP slowly depolarizes. In principle, this kinetics should be observed in experiments with ferricyanide. After stopping the ferricyanide redox system, the MP must repolarize by stimulating the H + -ATPase. Researchers experimenting with ferricyanide ignored the second phase because they were only interested in the first phase of depolarization. In our experiments with ferricyanide, the depolarized MP then hyperpolarizes and returns to its previous level, although the ferricyanide remains in the environment.

Thus, we have confirmed that two types of complementary proton pumps operate in the plasma membrane of plant cells. These two proton pumps work together to provide ion transport, metabolism, intracellular status quo, and generate responses to external factors. Therefore, the effect of nanoparticle proton pumps on the plasma membrane, especially on the activity of the redox proton pump, is of great interest. It

has been determined that only nanoparticles smaller than 5 nm can pass directly through the membrane pores. Larger nanoparticles can enter the cell through endocytosis.

In view of this, we accept that the nanoparticles used in experiments pass into plant cells, and in our case they do not pass directly through ion channels, but through endocytosis. During the interaction of nanoparticles with the cell, they accumulate on the cell surface, participate in oxidation-reduction reactions, and many different free radicals, such as reactive oxygen superoxide, hydroxyl radical, etc. can form. In this case, nanoparticles can seriously affect the activity of proton pumps in the plasma membrane.

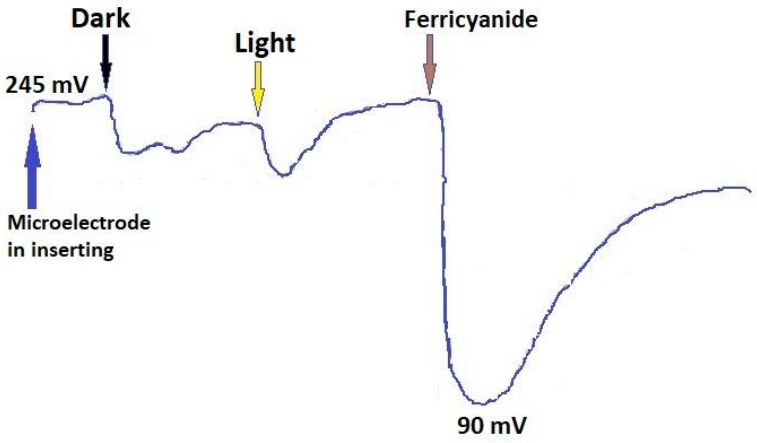

Fig. 3. MP-change kinetics during dark-light transitions and under the influence of ferricyanide in Elodea leaves stored in a solution of ZrO_2 nanoparticles üith size 21 nm for three days

In the first experiments, the instantaneous effect of nanoparticles was studied. The results of the experiments show that the nanoparticles do not affect the MP and membrane resistance during a few minutes of exposure. This indicates that nanoparticles cannot pass through the plasma membrane like ions. Because they are larger than the size of ion channels, they first accumulate in the space between the cell wall and the plasma membrane, and can then approach the surface of the plasma membrane. Nanoparticles that interact with the plasma membrane for a long time can finally enter the cell through endocytosis. Therefore, to study the effect of nanoparticles on the activity of proton pumps, the change kinetics of MP in elodea leaves kept in a dispersion solution of nanoparticles for 3,5,7 and 10 days was studied.

Fig. 3 shows the kinetics of MP change during dark-light transitions and under the influence of ferricyanide in elodea leaves kept in light for 3 days in a solution of ZrO_2 nanoparticles with dimensions of 21 nm. As can be seen from the figure, ZrO_2 nanoparticles did not significantly affect the MP value (245 mV) in elodea cells for 3 days. However, the depolarization and hyperpolarization observed in normal leaves during dark-light transitions have undergone significant changes. At a concentration of 5.10^{-4} M, the effect of ferricyanide was the same as in normal cells. Rapid depolarization has been observed since the introduction of ferricyanide into the ambient environment in light. After a while, depolarization was replaced by hyperpolarization, and the MP began to return to its previous value. This change in MP due to ferricyanide was similar to that in normal cells. Based on the results of these experiments, it can be said that ZrO2 nanoparticles do not affect the activity of the redox system in the plasma

membrane. However, ZrO2 nanoparticles has a significant effect on the activity of the H-ATFase proton pump.

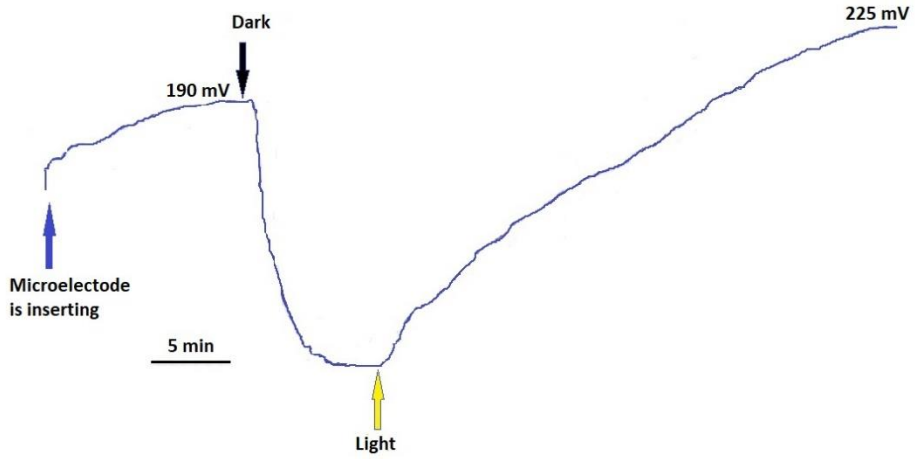

Fig. 4. MP change kinetics in *Elodea* leaves stored in a solution of Fe_3O_4 nanoparticles for 20 days at the dark environment

In other types experiments, the MP value was measured in leaves exposed to both light and darkness, the MP kinetics of MP variation in light-dark-light transitions were determined, and the MP effect of ferricyanide was examined. The results of these experiments showed that the value of MP in the leaves stored in a solution of Fe_3O_4 nanoparticles at the dark environment is in the range of 190-200 mV when the leaves are illuminated. The value of MP is not much different from normal leaves. During the light-dark transition, the MP is depolarized and its value is in the order of 100 mV, and after the leaves are illuminated, it is re-hyperpolarized and rises to 225 mV. These experiments were also performed with leaves kept in the light. It was found that the active part of the MP was completely lost in the elodea leaves, which remained in the solution of Fe_3O_4 nanoparticles in the light, leaving only the passive part. MP value was in the range of 80-110 mV. Slight depolarization of the MP was observed during the light-dark transition in most cells. In some cells, however, this reaction is completely lost. However, a ferricyanide reaction was observed. The results of these experiments are shown in Fig. 5. Thus, experiments have shown that the effect of MP Fe_3O_4 nanoparticles on elodea leaves depends on their storage in light or dark mode (Nasibova *et al*., 2017).

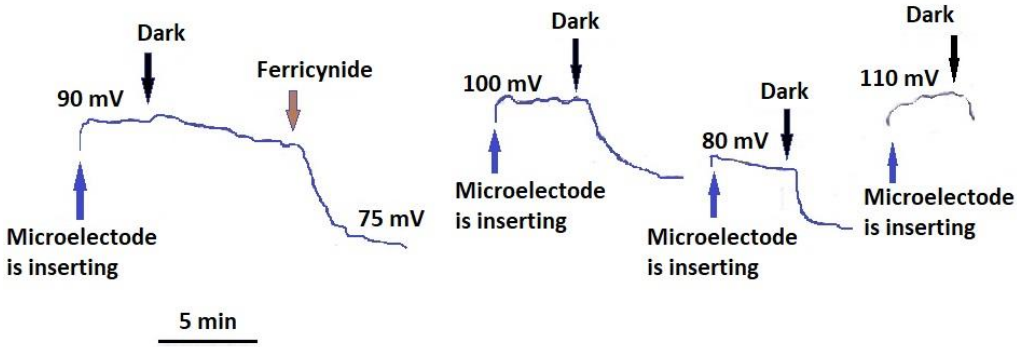

Fig. 5. MP change kinetics in Elodea leaves stored in a solution of Fe3O4 nanoparticles for 20 days under the light

4. Conclusion

Three mechanisms are proposed for the interaction of nanoparticles with plant plasma membranes during their entry into plant cells. Mechanism I: nanoparticles cannot cross the plasma membrane and accumulate on its surface. Nanoparticles accumulated on the surface of the plasma membrane can seriously affect its function, although they do not cause significant changes in its structure. The surface of nanoparticles is very active, they can exchange electrons, form free radicals, change the surface loads of the membrane. Therefore, nanoparticles, especially metal nanoparticles, can cause changes in the function of passive and active channels responsible for ion transport in the plasma membrane. From the study of the MP effect of nanoparticles, it is clear that some of the nanoparticles (Fe_3O_4, ZrO_2) can cross the membrane, while others cannot. According to mechanism I, when nanoparticles cannot cross the plasma membrane, they can sit on its surface and exchange electrons with the redox system. This feature of nanoparticles allows them to change the activity of the redox proton pump in the plasma membrane. The second mechanism is the passage of nanoparticles through the formation of pores in the plasma membrane and through protein-containing channels. In this case, the nanoparticles can break down the double lipid layer at once, or they can cross the double lipid layer by combining with protein molecules. Nanoparticles can change the function of active and passive ion channels as they pass through the membrane. In experiments with ZrO_2 nanoparticles, different results were obtained in the MP kinetics, depending on their size. The kinetics of MP change in the dark-light-dark transitions in leaves stored in 21 nm ZrO_2 nanoparticles undergo significant changes. Unlike normal cells, cells stored in ZrO_2 nanoparticles lose light-induced MP. However, the effect of ferricyanide remains the same as in normal cells (Fig. 3). According to the results of this experiment, almost 21 nm ZrO_2 nanoparticles pass through the plasma membrane by a second mechanism. In this case, the protein causes significant changes in ionic channels, especially in passive channels. It may also damage the H^+-ATPase complex. The strong depolarization of the MP during the action of ferricyanide indicates that the redox system is not damaged. In this case, 100-nm nanoparticles most likely accumulated on the surface of the plasma membrane and mechanically affected it. Thus, indefinite changes were observed during both light-dark and ferricyanide exposure (Fig. 4).

Significant physiological changes are observed when *Elodea* leaves are stored in a suspension solution of Fe_3O_4 nanoparticles for a long time. These changes depend on whether the leaves are kept in the light or in the dark. Thus, when the leaves are exposed to light in a solution of iron nanoparticles, their metabolism is disrupted, the pigment content is broken down, and the leaves turn yellow quickly. In this case, it is assumed that iron nanoparticles can penetrate through the mechanism III - endocytosis and seriously damage the process of photosynthesis. This may also be due to the intensification of the fenton reaction. The active part of the MP is completely lost in the leaves, which remain in the solution of iron nanoparticles in the light for a long time. The MP value ranges from 90 to 100 mV, but the effect of ferricyanide is still observed (Fig. 5). No significant physiological changes are observed in the leaves left in the iron nanoparticles in the dark. The value of the MP potential is in the range of 190-200 mV, the kinetics of PM change in dark-light transitions remain the same as in normal cells. In this case, the function of the redox system does not change. Interestingly, the redox system works more strongly when *Elodea* leaves remain in the nanoparticles in the dark

for a long time. It should be noted that additional experience is needed to confirm this idea.

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