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EFFECT OF Na-ASCORBATE IN THE PROTECTION OF PSII ACTIVITY UNDER CONDITIONS OF SIMULTANEOUS ACTION OF Co^{2+} AND PHOTOINHIBITION

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In nature, a plant organism is exposed to many stress factors that negatively affect the photosynthetic apparatus and especially PSII, which is most vulnerable to stress. Determination of the site of toxic action of stress factors in the electron transport chain (ETC) of PSII was the aim of this work. The functional state of the of PSII ETC in the leaves of wheat seedlings subjected to the complex toxic effect of Co^{2+} and photoinhibition was determined based on various characteristics of delayed chlorophyll *a* fluorescence (ms DF Chl *a*). The effect of Co^{2+} was expressed in a sharp decrease in the characteristic value of ms DF Chl *a* of the PSII reaction center (RC) and in a weaker blocking of the donor side characterizing the state of the Mn_4O_5Ca cluster and Y_z. Reactive oxygen species (ROS) generated in the process of photoinhibition also blocked to a greater extent the acceptor side of the PSII ETC. With an increase in the adaptation time, a significant decrease in activity on the donor side of the ETC of PSII was observed. The combined effect of both factors had little effect on the change in fluorescent characteristics, which remained almost at the level of Co^{2+} action. It was shown that the adaptive capabilities of photochemical reactions occurring in the PSII ETC under combined stress are stimulated by the low-molecular antioxidant Na-ascorbate. Restoration by Na-ascorbate of the processes suppressed by the simultaneous action of photoinhibition and Co^{2+} occurs during the induction period of the ms DF Chl *a*, and is apparently expressed as a result of effective neutralization of the formed ROS. This indicates that the mechanism leading to a change in the character of the induction pattern of the ms DF Chl *a* as a result of the action of both factors has a single nature. The stress resistance of the photosynthetic apparatus increases due to an increase in the activity of antioxidant enzymes or the effectiveness of low-molecular antioxidants. As a result, the photosynthetic apparatus switches to the adaptive program, which ensures an increase in its stress resistance. It is assumed that Na-ascorbate plays a decisive role in protecting chloroplasts from oxidative stress by quenching O_2^- and $^*OH$[1].

Key words: *Triticum aestivum* L., PSII, ETC, Co^{2+}, photoinhibition, ROS, Na-ascorbate.

To maintain the growth and development of a plant organism, natural programmed cell death occurs [1]. However, extreme abiotic factors negative-

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ly affect the plant organism, causing oxidative stress and suppressing physiological processes [2, 3]. Under these conditions, ROS are generated as by-products of most energy-producing processes, in particular, during photosynthesis. Chloroplasts are the main organ producing ROS [4, 5, 6]. The antioxidant system is not always able to maintain a balance between ROS formation and removal. In this situation, protection becomes ineffective [7, 8].

In nature, a plant organism is exposed to the simultaneous influence of many negative factors. The most vulnerable are PSII and its component, the oxygen-evolving complex [9]. Its destruction under stress conditions leads to denaturation, protein proteolysis and lipid peroxidation in the RC and suppression of electron transport in the ETC [10, 11, 12]. An important task is to determine the site of toxic action of stress factors in the PSII ETC.

It has been shown that heavy metals, being included in the photosynthetic pathways of electron transport in many areas, affect its photochemical activity [13, 14]. Photoinhibition reduces the rate of electron transfer at high light intensity and promotes the formation of photochemically inactive RC of PSII. Photoinhibition is determined by the rate of degradation and resynthesis of one of the key proteins of PSII — D1 protein [15, 16]. Inactivation of the PSII RC during oxidative stress can be restored only through degradation and synthesis of D1 protein *de novo* [16]. It is known that in nature, long-term exposure to stress factors leads to a non-specific increase in plant resistance called cross-adaptation. Perhaps, this phenomenon is associated with increased activity of high and low molecular weight protective antioxidant compounds, capable of neutralizing free radicals [18, 19].

The aim of this work was to determine the mechanism of effect of Na-ascorbate on the restoration of the PSII ETC function suppressed by dual stress — action of Co^{2+} and photoinhibition.

Materials and methods

We used 7-day wheat seedlings (*Triticum aestivum* L.) grown on an aqueous medium under controlled conditions 24 °C, humidity 80 %, lighting 250 μW/cm^2. The seedlings were exposed to $CoCl_2$ (10^{-3} M) for 48 h and to high-intensity light 4000 μmol photon/(m^2 · s) for 24 h. Seedlings treated with double stress were transferred to water (*1*) and to a $CoCl_2$ solution at the presence of Na-ascorbate $4 \cdot 10^{-4}$ M (*2*). The studies were carried out on leaves *in vivo*.

The functional activity of PSII was assessed based on the analysis of induction transitions of the kinetic curves of millisecond delayed fluorescence of chlorophyll *a* (ms DF Chl *a*) reflecting partial reactions of the PSII ETC in chloroplasts [20, 21]. The measurements were carried out by a fluorimeter including a phosphoroscope with a time interval between the moment of excitation and measurement of luminescence of 1.25 ms [22, 23]. Analysis of the induction pattern of millisecond chlorophyll fluorescence characterizing the state of the reaction center and its immediate environment, within PSII on the donor side — the fast phase, and the acceptor side — the slow phase, as well as those associated with oxidation-

reduction reactions of electron transfer — the stationary phase and their changes formed the basis for assessing the impact of stress factors (Fig. 1).

O-I state — reflects the restoration of the primary electron acceptor during the photochemical reaction in PSII and the transition of PSII RC to the closed state. I-D state — is associated with the transition stages of electron transfer in the ETC on the acceptor side when PSII RC are in the closed state. D-P state — reflects the electron transfer on the acceptor side in the photosynthetic reaction Q_A-Q_B to form an electrochemical gradient of protons (pH^+). P-S state — indicates the role of electrons released in the PSII reaction in the formation of oxidized products of PSI. S-O state — reflects the chlorophyll fluorescence, and arising as a result of interconnected oxidation-reduction reactions on the donor and acceptor sides of PSII RC.

Results and discussion

The activity of photochemical processes in the ETC of PSII after the action of Co^{2+} and photoinhibition on seedlings was estimated by the change in the induction transitions of the kinetic curves of ms DF of Chl *a*. The action of high-intensity light for 2 hours caused a decrease in the activity of the donor side of the ETC. The value of the ratio of fast fluorescence to steady-state fluorescence (f.ph/sl.ph), characterizing the donor side, decreased after 2 hours of the lag phase by 1.6 times, and after 24 hours of the lag phase, this value decreased by 3 times (Fig. 2).

The value of the ratio of slow fluorescence to steady-state fluorescence (sl.ph/st.ph), characterizing the activity of the acceptor side of the ETC, decreased after 2 hours of the lag phase by 1.3 times, and after 24 hours — by 2.3 times. When the seedlings were exposed to Co^{2+} for 48 hours, the f.ph/st.ph activity decreased after 2 hours of the lag phase by 1.3 times and, to a greater extent, the sl.ph/st.ph value by — 2 times, and after 24 hours the f.ph/st.ph value by 0.8 times, and the sl.ph/st.ph value remained almost

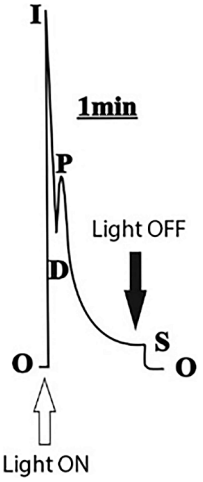

Fig. 1. Standart induction curves of delayed fluorescence of Chl *a* in millisecond range (ms DF Chl *a*) of plant leaves *in vivo* characterizing electron transport chain of photosystem II: O-I — fast phase (f.ph); D-P — slow phase (sl.ph); S-O — steady state (st.s)

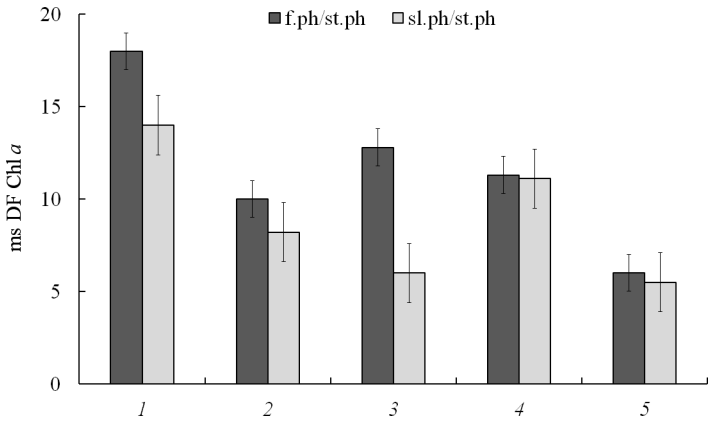

Fig. 2. Changes in the ratio of fast and slow fluorescence to steady-state fluorescence (f.ph/st.ph; sl.ph/st.ph) characterizing the work of the donor and acceptor sides of the PSII ETC under the conditions of $CoCl_2$ (10^{-3} M), and photoinhibition 4000 μmol photon/($m^2 \cdot s$):

1 — control; *2* — Co^{2+} (48 h); *3* — Co^{2+} (48 h) after 24 h; *4* — photoinhibition (2 h); *5* — photoinhibition (2 h) after 24 h

at the same level (see Fig. 2). After the simultaneous action of Co^{2+} and photoinhibition on the seedlings, no special deviations in the ETC activity were observed. The f.ph/st.ph and sl.ph/st.ph values remained almost at the level of the Co^{2+} effect.

The treated seedlings after double stress were placed for 24 hours on a solution containing Co^{2+}, and on water. A sharp decline in the ETC activity was observed. The f.ph/st.ph value on water decreased by 2.2 times, and sl.ph/st.ph — by 2.3 times. Under the condition with Co^{2+}, the f.ph/st.ph value decreased by 2.4 times, and sl.ph/st.ph — by 3 times (Fig. 3). The action of Na-ascorbate restored the ETC activity suppressed by the simultaneous action of Co^{2+} and photoinhibition. After 5 hours of

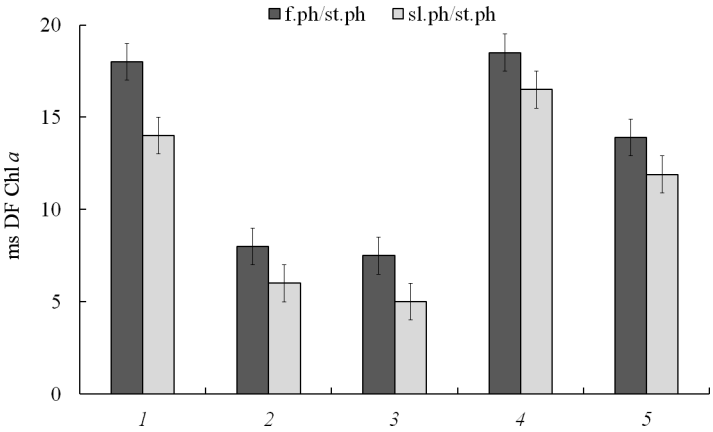

Fig. 3. Changes in the ratio of fast and slow fluorescence to steady-state fluorescence (f.ph/st.ph; sl.ph/st.ph) characterizing the work of the donor and acceptor sides of the PSII ETC under the conditions of the complex action of $CoCl_2$, photoinhibition, and at the presence of Na-ascorbate ($4 \cdot 10^{-4}$ M):

1 — control; *2* — Co^{2+}+photoinhibition after 24 h; *3* — Co^{2+}+photoinhibition → Co^{2+} after 24 h; *4* — Co^{2+}+photoinhibition → 5 h Na-ascorbate; *5* — Co^{2+}+photoinhibition → 24 h Na-ascorbate

exposure to Na-ascorbate, the f.ph/st.ph and sl.ph/st.ph values approached the control levels. After 24 hours of exposure to Na-ascorbate, these indices slightly decreased, but were 1.3 and 1.8 times higher than the indices under the complex action of stressors (see Fig. 3).

The changes in fluorescence upon reaching a steady state level depends on the action of stressors separately and on their combined action: control — 0.5±0.02; photoinhibition — 2.9±0.8; Co^{2+} — 2.6±0.08; Co^{2+}+ photoinhibition — 3.2±0.7; Co^{2+}+Na-ascorbate — 1.4±0.02; Co^{2+}+ photoinhibition → 24 h — 2.0±0.4; Co^{2+}+ photoinhibition → Na-ascorbate 5 h — 1.0±0.03. The blocking observed during electron transfer at the Q_B site explains the changes in the ratio of f.ph/st.ph and sl.ph/st.ph values, which is partially restored under the action of Na-ascorbate stress conditions.

The oxidative stress induced by the action of heavy metals, generating ROS, leads to the formation of long-lived $P680^{+*}$ and Tyr_Z radicals, which damaged their protein environment, thereby weakening the electron transport between P680 and Tyr_Z. In addition, ROS, disrupting the functions of Q_A-Q_B acceptors, leads to the formation of singlet oxygen and to the inactivation of the acceptor side in the PSII chain [22, 24]. The effect of photoinhibition leads to the inactivation of the donor side of the ETC as a result of the formation of a highly oxidized radical pair of $P680^*$ and Tyr_Z^+. Inactivation of the acceptor side is also observed. ROS involved in the process of photoinhibition leads to the destruction of protein D1, inhibit the synthesis of protein D1 *de novo* more slowly than the inactivation of PSII.

The toxic effect of Co^{2+} leads to a disruption of the equilibrium between the photosystems and a shift in the redox state of Q_A, increasing the electron outflow to PSI. This leads to an increase in steady-state fluorescence and a decrease in the ratio of fast and slow fluorescence to steady-state (see Fig. 2). It is possible that the decrease in fluorescent characteristics is associated with a disruption of membrane function and the destruction of chlorophyll in chlorophyll-protein complexes (CPC) in PSII [25].

The observed greatest decrease in the sl.ph/st.ph value corresponds to the assumption that the site of the toxic effect of Co^{2+} is mainly determined by the acceptor side of the PSII ETC. Some recovery of fluorescent characteristics after 24 h lag phases is possible as a result of activation of protective antioxidant systems in the plant organism. The combined effect of both stressors led to insignificant changes in the fluorescent characteristics. Probably, the stress effect of high-intensity light and heavy metal led to an increase in the resistance of plants to additional stress or an increase in the activity of protective antioxidant systems important for the neutralization of radicals.

The restoration by Na-ascorbate of the processes suppressed by the simultaneous action of photoinhibition and Co^{2+} occurs in the induction period of ms DF Chl *a* and is expressed, apparently, as a result of the effective neutralization of the formed ROS [26, 27, 28]. This indicates that the mechanism leading to a change in the nature of the induction pattern of ms DF Chl *a* as a result of the action of both factors has a single nature. The mechanism of increasing the stress resistance of the photosynthetic

apparatus under the action of plant protective systems is an increase in the activity of antioxidant enzymes or the efficiency of low-molecular antioxidants. As a result, the photosynthetic apparatus switches to an adaptive program, which ensures an increase in its stress resistance. Being a strong antioxidant, Na-ascorbate is able to neutralize free radicals formed during stress and maintain oxidation-reduction reactions in the ETC of PSII.

Thus, the toxic effect of Co^{2+} ions and photoinhibition had a negative effect on the PSII functional state. It was found that under the combined effect of these factors, the activity of photochemical reactions in the PSII ETC remained at the level of the toxic effect of Co^{2+} ions. It was shown that the restoration of damage on both the donor and acceptor sides of the ETC was stimulated by Na-ascorbate through quenching O_2^- and $^*OH^1$ formed during oxidative stress.

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Conflict of interest

The authors declare that there is no conflict of interest.

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ВПЛИВ Na-АСКОРБАТУ НА ЗАХИСТ АКТИВНОСТІ ФС II ЗА УМОВ ОДНОЧАСНОЇ ДІЇ Co^{2+} ТА ФОТОІНГІБУВАННЯ

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У природі рослинний організм піддається дії багатьох стресових чинників, які негативно впливають на фотосинтетичний апарат і особливо на ФС II, яка найвразливіша до стресу. Метою досліджень було визначення місця токсичної дії стресових чинників у електронтранспортному ланцюзі (ЕТЛ) ФС II. Функціональний стан ЕТЛ ФС II у листках проростків пшениці, що зазнали комплексної токсичної дії Co^{2+} та фотоінгібування, визначали на основі різних характеристик затримки флуоресценції хлорофілу *a* (ms DF Chl *a*). Вплив Co^{2+} виражався в різкому зменшенні характерного значення ms DF Chl *a* реакційного центру ФС II та в слабшому блокуванні донорної сторони, що характеризує стан кластера Mn_4O_5Ca та Y_z. Активні форми кисню, які утворюються в процесі фотоінгібування, також більшою мірою блокували акцепторну сторону ЕТЛ ФСII. Зі збільшенням часу адаптації спостерігалося значне падіння активності на донорній стороні ЕТЛ ФСII. Сукупний вплив обох чинників мало вплинув на зміну флуоресцентних характеристик, які залишалися майже на рівні дії Co^{2+}. Було показано, що адаптивні можливості фотохімічних реакцій, що відбуваються в ЕТЛ ФС II за комбінованого стресу, стимулюються низькомолекулярним антиоксидантом Na-аскорбатом. Відновлення Na-аскорбатом процесів, пригнічених одночасною дією фотоінгібування та Co^{2+}, відбувається упродовж індукційного періоду ms DF Chl *a* та, очевидно, полягає в ефективній нейтралізації утворених АФК. Це свідчить, що механізм, який призводить до змін характеру індукційного патерну ms DF Chl *a* в результаті дії обох чинників, має єдину природу. Стресостійкість фотосинтетичного апарату зростає зі збільшенням активності антиоксидантних ферментів або ефективності низькомолекулярних антиоксидантів. В результаті фотосинтетичний апарат перемикається на адаптивну програму, що забезпечує підвищення його стресостійкості. Припускається, що Na-аскорбат відіграє вирішальну роль у захисті хлоропластів від окиснювального стресу шляхом гасіння O_2^- та $^*OH$[1].

Ключові слова: Triticum aestivum L., PSII, ETC, Co^{2+}, фотоінгібування, активні форми кисню, Na-аскорбат.

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