Inhibition of photosystem II in the presence of copper (Cu^{2+}) ions

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The study explores the inhibitory effects of copper ions (Cu^{2+}) on the photochemical activity of photosystem II (PSII), revealing a significant suppression of oxygen evolution in thylakoid membranes. A clear correlation was observed between increasing Cu^{2+} ($CuSO_4$) concentrations and a decline in PSII activity, emphasizing the metal's disruptive influence on photosynthetic function. Notably, the inhibition of O_2 evolution exhibited a time-dependent pattern, with an initial rapid decrease of 40-60% immediately after Cu^{2+} exposure, followed by a gradual and sustained decline. These findings suggest the presence of at least one high-affinity copper binding site within PSII, which may play a key role in mediating the complex inhibitory effects of Cu^{2+} on electron transport and overall photosynthetic efficiency.

Keywords: *Photosynthesis, photosystem II, copper, oxygen evolution, delayed light emission*

Abbreviations:
PSII – photosystem II
D_1, D_2 – reaction center proteins
P_{680} (P_{680}*, $P_{680}^{\bullet+}$) – photoactive chlorophyll, primary electron donor of PSII (its excited and oxidized forms)
Phe – pheophytin, electron carrier located in PSII reaction center
Q_A, Q_B – electron acceptors, plastoquinones
Y_Z, Y_D – tyrozines of the D_1 and D_2 proteins, electron donors to PSII
Mn_4CaO_5 – manganese cluster of PSII, the catalytic site of water oxidation
DCBQ – 2.6-dichloro-p-benzoquinone
MES – 2-(N-Morpholino)ethanesulfonic acid
HEPES – N-(2-Hydroxyethyl)piperazine-N′-(2-ethanesulfonic acid)
DE – Delayed emission

INTRODUCTION

Heavy metal contamination has emerged as a critical environmental issue due to its persistent nature and potential to disrupt biological processes. Among these metals, copper (Cu) holds a unique position as both an essential micronutrient and a potential stressor when present in excessive concentrations. While copper is required for various enzymatic and redox reactions in plants, its elevated levels can lead to significant physiological disturbances.

Photosynthesis which provides our life with food and energy is easily inhibited by different environmental factors, organic and inorganic pollutants, including heavy metals. One of the primary targets of heavy metal toxicity in photosynthesis is photosystem II (PSII) of oxygenic species. Photosystem II (PSII) is a functional unit in the photosynthesis process, linking the photochemical excitation of chlorophyll in thylakoid membranes of plants, algae, and cyanobacteria to water oxidation and electron transport to plastoquinone. In its reaction center (RC), photoactive chlorophyll P_{680} (primary electron donor), primary electron acceptor pheophytin (Phe), plastoquinones Q_A and Q_B (terminal electron acceptors), and electron donors Y_Z and Y_D (tyrosine residues) are located on a heterodimer composed of D_1 and D_2 proteins (Muh and Zouni, 2011; Shen, 2015; Shevela et al., 2023). When photoactive chlorophyll P_{680} is excited (P_{680}*) by absorbing light quanta, it gains high electronegativity (approx. –800 mV), and its electron within ~3 ps is transferred to pheophytin, which redox potential is more positive (approx. –600 mV), forming the radical pair $P_{680}^{\bullet+}Phe^{\bullet-}$ at the reaction center with high (~98%) efficiency (Klimov et al., 1977; Groot et al., 1997; Feyziyev, 2019; Shevela et al., 2023). The electron then transfers from the $Phe^{\bullet-}$ molecule to Q_A plastoquinone in 200-250 ps (De Wijn and van Gorkom, 2001; Feyziyev, 2019). The highly oxidizing photoactive chlorophyll $P_{680}^{\bullet+}$ (E_m ~1.2

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V) ultimately facilitates the oxidation of water molecules bound to the Mn_4O_5Ca cluster. Redox active tyrosine residues Y_Z and Y_D serve as intermediate redox mediators in this process (Feyziyev et al., 2003, 2013; Ishikita et al., 2006; Barry, 2011; Saitok et al., 2013). In the course of the photochemical reaction responsible for water oxidation, molecular oxygen (O_2) is released into the atmosphere, while four protons ($4H^+$) are transported into the thylakoid lumen (Shevela et al., 2023).

Photosystem II is highly vulnerable to various environmental stressors, such as herbicides, extreme temperatures, drought, and salinity. Consequently, the impacts of these stressors on PSII are commonly monitored as indicators of photosynthetic organism's health. Heavy metals, particularly copper, cadmium, zinc, mercury and lead ions, disrupt plant cell processes at different organelle levels, leading to complex, multi-faceted effects on roots, photosynthetic function, antioxidant systems, and signaling pathways. Simplified in vitro studies of these reactions and their phases allow for more detailed analysis of heavy metals including copper's impacts on PSII.

Understanding the specific impacts of copper ions on PSII oxygen evolution is crucial for assessing the broader implications of heavy metal pollution in aquatic and terrestrial ecosystems. By investigating the mechanisms through which copper modulates PSII activity, this study aims to contribute to a deeper comprehension of metal-induced stress responses in photosynthetic organisms and their potential consequences for environmental and agricultural sustainability.

This study provides a comprehensive analysis of the inhibitory effects of copper ions (Cu^{2+}) on the photochemical activity of photosystem II, emphasizing their detrimental impact on oxygen evolution in thylakoid membranes. Experimental results demonstrate a strong inverse correlation between increasing Cu^{2+} ($CuSO_4$) concentrations and photochemical activity of PSII, indicating that copper disrupts key biochemical processes involved in photosynthetic electron transport.

MATERIALS AND METHODS

Thylakoid membranes were obtained from chloroplasts isolated from spinach as follows: the leaves were ground homogenously in a chilled (~4°C) buffer solution containing 25 mM HEPES (pH 7.5), 300 mM NaCl, 2 mM $MgCl_2$, and 2 mg/ml sodium ascorbate for approximately 10 seconds. The homogenate was then filtered through a gauze-cotton sandwich to remove large leaf debris. The filtered suspension was centrifuged at 1000g to precipitate the chloroplasts. The pellet of chloroplasts was resuspended in a buffer solution composed of 25 mM HEPES (pH7.5), 10 mM NaCl, and 3 mM $MgCl_2$. To eliminate remaining cellular debris, the suspension was centrifuged briefly at 200g for 2 minutes. Chloroplasts were then collected from the supernatant through high-speed centrifugation at 1000g for 10 minutes and resuspended in a 25 mM MES-NaOH buffer (pH 6.3) containing 100 mM sucrose, 15 mM NaCl, and 3 mM $MgCl_2$. After incubation at 4°C for 30 minutes, centrifugation at 8000g for 30 minutes was performed, yielding the thylakoid membranes. The isolated thylakoid membranes were dissolved in a 25 mM MES-NaOH buffer (pH 6.3) containing 400 mM sucrose, 15 mM NaCl, and 3 mM $MgCl_2$. The chlorophyll concentration was standardized to 3 mg/ml, and small aliquots were stored in liquid nitrogen for subsequent experiments.

The oxygen evolution rate was determined with an amperometric method using a Clark-type oxygen electrode (Rank Brothers Ltd., USA). Measurements were conducted at an electrode potential of 0.6 V and a controlled temperature of 25°C. The reaction medium consisted of a buffer solution containing 25 mM MES (pH 6.5) or 25 mM HEPES (pH 7.0 or 7.5), along with 300 mM sucrose, 20 mM NaCl, and 2 mM $MgCl_2$. 2,5-dichloro-1,4-benzoquinone (DCBQ) was employed as the electron acceptor. The chlorophyll concentration was 15 μg/ml. The photochemical reaction was initiated by white light with an intensity of approximately 1000 μmol photons $m^{-2}s^{-1}$. Under these conditions, the oxygen evolution rate for the isolated thylakoid membranes measured in the presence of 0.5 mM DCBQ was approximately 330-350 μM O_2 $(mgChl \cdot hour)^{-1}$.

To investigate the effect of Cu^{2+} ions on photosystem II, thylakoid membranes were exposed to $CuSO_4$ in darkness at different values of pH (6.5, 7.0, and 7.5). The process was carried out at 25°C, and an electron acceptor was added before measuring oxygen evolution under identical conditions. The influence of copper ions was determined by analyzing changes in the oxygen evolution rate at varying Cu^{2+} concentrations.

Delayed emission (DE) of chlorophyll was monitored using an optical spectrometer equipped with an electromechanical modulator (Safarova et al., 2021). This emission primarily originates from chlorophyll *a* molecule excited as a result of the recombination of the charge-separated states $P_{680}^+Q_A^-$. In this scenario, certain time-dependent redox reactions take place before chlorophyll re-excitation, causing a delay in light emission, a phenomenon known as delayed light emission. The

intensity of DE follows a polyphasic decay function over time after illumination, reflecting the kinetics of electron transport reactions occurring on both the donor and acceptor sides of PSII. The excitation of PSII was initiated using ~1000 μmol photon·m^{-2}·s^{-1} intensity λ> 650 nm actinic red light (the beam of actinic light was passed through a red glass filter KS-15, USSR). Delayed emission was monitored at wavelengths ≥ 680 nm. The time delay between sample excitation and signal detection was set at 2 ms. In assessing delayed emission, the amplitudes of the initial rapidly increasing phase of its millisecond component were taken into consideration. The reaction medium contained 25 mM MES (pH 6.5) or 25 mM HEPES (pH 7.0 or 7.5), 20 mM NaCl and 2 mM $MgCl_2$. When measured DE, samples were prepared similarly indicated for O_2 measurements, except DCBQ was added. The experimental data were analyzed using SigmaPlot software (version 10.0), and the results were presented with appropriate statistical indicators to ensure clarity and reliability in data interpretation.

RESULTS AND DISCUSSION

To investigate the inhibitory effects of Cu^{2+} on PSII function, experiments were performed using isolated thylakoid membranes under varying pH conditions. Samples were exposed to Cu^{2+} ions in darkness to evaluate their effect on oxygen evolution at pH 6.5, 7.0, and 7.5. The introduction of the components took 30 seconds at room temperature, after which DCBQ was added and the oxygen evolution rates were recorded.

Copper ions (Cu^{2+}), similar to other environmental stressors, have a profound impact on photosystem II, a key component of the photosynthetic machinery. The ability of Cu^{2+} to interact with specific binding sites in the PSII reaction center can lead to electron transport disruptions, ultimately reducing photosynthetic efficiency.

The data presented in Fig. 1 illustrate a progressive decline in oxygen evolution as Cu^{2+} concentration increased from 0 to 50 mM across all tested pH levels. A sharp reduction in oxygen evolution was observed at relatively low Cu^{2+} concentrations (≤1.0 mM), suggesting an immediate and potent inhibitory interaction between Cu^{2+} and photosystem II. Beyond 1.0 mM, additional increases in Cu^{2+} levels did not significantly enhance inhibition, implying the existence of both high- and low-affinity binding sites within PSII that interact differently with Cu^{2+} ions.

The least inhibition was observed at pH 6.5, where oxygen evolution exhibited a more gradual decline with increasing Cu^{2+} concentrations. At pH 7.0, Cu^{2+} exposure still led to substantial inhibition, though to a lesser extent than at pH 7.5. The inhibitory effect of Cu^{2+} was most pronounced at pH 7.5, where the reduction in oxygen evolution occurred more abruptly compared to pH 6.5 conditions.

These findings suggest that Cu^{2+} ions have a weaker inhibitory effect on PSII under acidic conditions (pH 6.5), possibly due to reduced metal ion availability or weaker interactions with metal binding sites. Conversely, at pH 7.5, the increased inhibition indicates that Cu^{2+} binding affinity is higher under alkaline conditions, resulting in a more pronounced impact on photosynthetic activity. These observations highlight the pH-dependent nature of Cu^{2+} toxicity and provide insight into the biochemical mechanisms by which heavy metals influence photosynthetic performance.

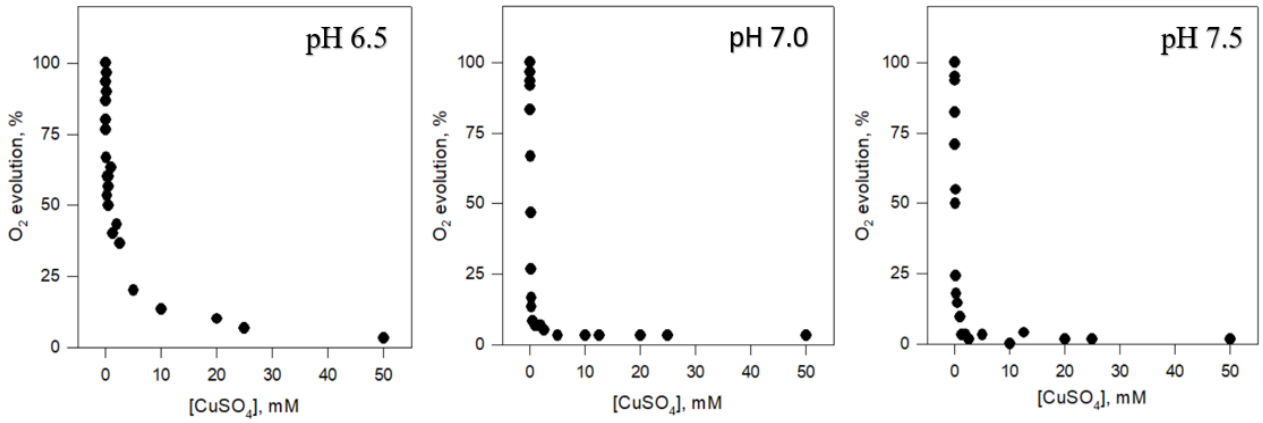

Fig. 1. Effect of copper ions on oxygen evolution in thylakoid membranes at different pH values. The concentration of chlorophyll was 15 μg/ml. The photochemical reaction was initiated by white light with an intensity of ~1000 μmol photon ·m^{-2}·s^{-1}. The rate of O_2 evolution 350 μM O_2 (mgChl·hour)$^{-1}$ of control samples was assumed to be 100%.

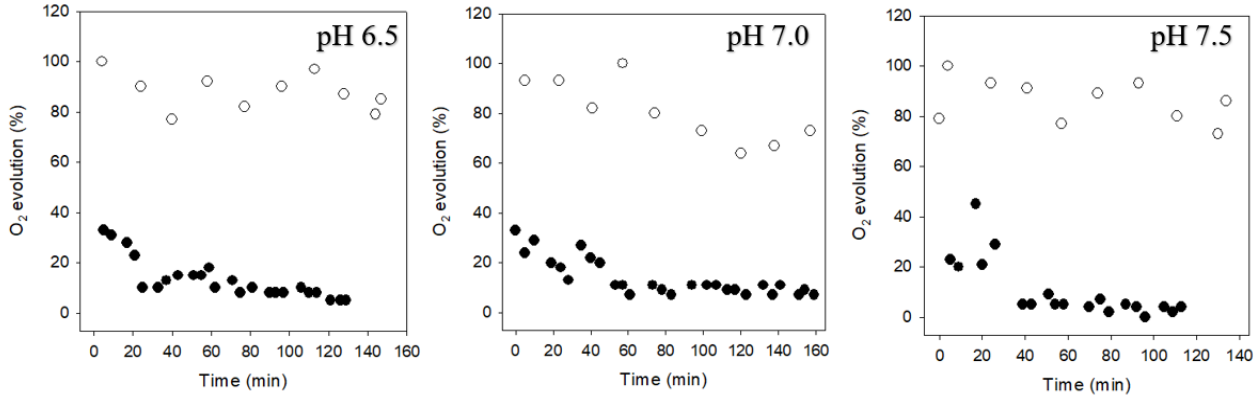

Fig. 2. Time-dependent inhibition of oxygen evolution in thylakoid membranes incubated with Cu^{2+} ions (1.0 mM) at different pH values. Incubation temperature – 4℃, chlorophyll concentration – 15 μg/ml. The photochemical reaction was initiated by white light with an intensity of ~1000 μmol photon m^{-2} s^{-1}. Open circles (○) – control, closed circles (●) – Cu^{2+} was added.

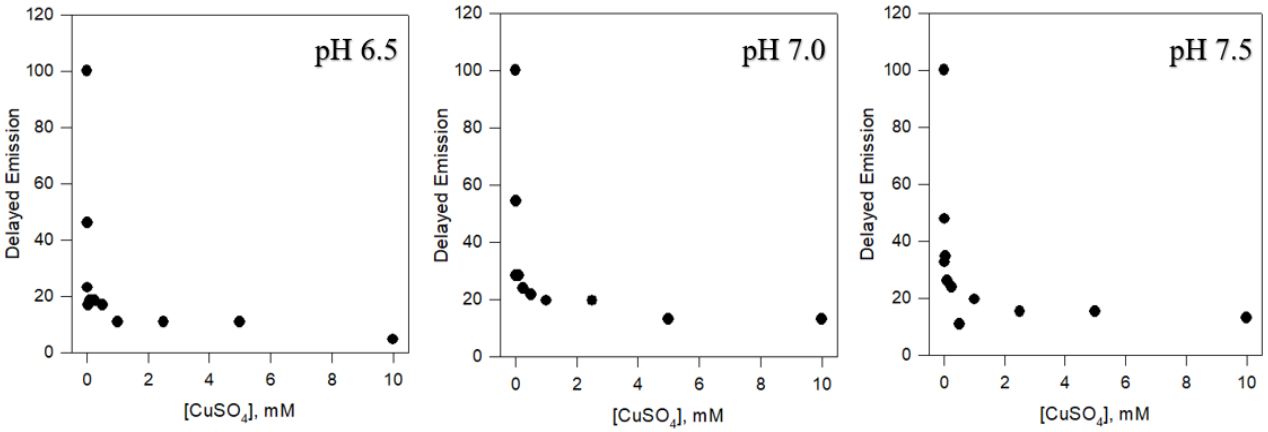

Fig. 3. Dependence of delayed emission of PSII on Cu^{2+} concentration at different pH levels. The wavelength and intensity of the excitation light were λ> 650 nm, ~1000 μmol photon□m^{-2}□s^{-1}, respectively. Delayed emission was detected at wavelengths ≥ 680 nm. The concentration of chlorophyll was 15 μg/ml.

The presence of Cu^{2+} ions has a significant time-dependent effect on oxygen evolution in photosystem II (PSII), as demonstrated in Fig. 2. The open circles represent control measurements, while the closed circles correspond to samples treated with Cu^{2+}. At pH 6.5, oxygen evolution drops sharply to approximately 40-60% within the first few minutes of exposure to Cu^{2+} and continues to decline gradually, stabilizing around 5-10%. A similar inhibitory pattern is observed at all tested pH levels (6.5, 7.0, and 7.5), with a rapid suppression of oxygen evolution followed by a plateau at lower values.

These findings suggest that Cu^{2+} ions interact with specific binding sites within PSII, leading to a disruption in electron transport and photochemical efficiency. The strong inhibition observed at higher pH levels implies the presence of at least one high-affinity Cu^{2+} binding site within the PSII complex. Previous studies have linked heavy metal toxicity in PSII to structural damage within the photosynthetic apparatus and electron transport components (Kalaji and Loboda, 2007; Wang et al., 2009). It is likely that Cu^{2+} interacts with key sites on either the electron acceptor side (Q_A-Fe-Q_B complex) or the donor side (Mn_4CaO_5 cluster and tyrosine residues Y_Z and Y_D) of PSII (Huang et al., 2017). The observed decline in photochemical activity may result from Cu^{2+}-induced alterations in PSII reaction center proteins and its interference with essential cofactors such as Mn^{2+}, Ca^{2+}, and Cl^- ions within the water-oxidizing complex (Faller et al., 2005).

During the electron transfer in the PSII reaction center the delayed emission of chlorophyll (DE) ranging from a few hundred microseconds to hours, and referred also as delayed luminescence or afterglow, formed as the result of the recombination of charges in $P_{680}^+Q_A^-$ pair (Xu et al., 2000; Rappaport, 2005; Goltsev et al., 2009).

Delayed emission is characteristic of green plants, algae, and photosynthetic bacteria, and it occurs in the red-infrared region of the spectrum for a short period after the cessation of illumination, once prompt fluorescence of chlorophyll has already decayed. The effect was first discovered by Strehler and Arnold (Strehler and Arnold, 1951)

during their experiments on the green alga *Chlorella* which is widely used in studies of photosynthesis.

Fig. 3 illustrates the effect of Cu^{2+} ions on the delayed emission of PSII at three different pH values: 6.5, 7.0 and 7.5.

These results suggest that Cu^{2+} ions effectively quench delayed emission in a concentration-dependent manner. At all pH levels, similar to O_2 yield, a sharp decline in DE is observed as Cu^{2+} concentration increases. The most significant reduction of DE amplitude occurs within the 0-2 mM Cu^{2+} range, after which the amplitude of DE stabilizes at minimal levels: at a concentration of Cu^{2+} ≥2 mM DE intensity remains relatively stable, suggesting a weak inhibitory effect of Cu^{2+}.

The inhibition of DE in the presence of copper could be attributed to a higher affinity of Cu^{2+} for PSII components leading to disruptions in electron transport and charge recombination processes. In photosystem II, DE results from the state $P_{680}{}^{*}Q_A$ formed due to recombination charges at the state $P_{680}{}^{+}Q_A{}^{-}$. Given this, the inhibition induced by Cu^{2+} may be related to the formation of non-active $P_{680}Q_A{}^{-}$ or $P_{680}{}^{+}Q_A$ states, which do not contribute to DE generation. The first scenario is likely associated with the blocking of the $Q_A{}^{-}$ acceptor, while the second may result from disruptions in electron transfer involving photoactive chlorophyll $P_{680}{}^{+}$.

The observed inhibitory effects suggest that Cu^{2+} ions interfere with the structural and functional integrity of PSII, potentially by targeting specific protein-cofactor interactions essential for oxygen evolution. Moreover, the extent of inhibition may be influenced by environmental factors such as pH, ionic strength, and the redox state of PSII components, suggesting a complex regulatory mechanism governing Cu^{2+} toxicity. Understanding these mechanisms is crucial for assessing the broader implications of heavy metal stress on photosynthetic organisms and for developing potential strategies to mitigate Cu^{2+}-induced damage in aquatic and terrestrial ecosystems.

CONCLUSION

Environmental pollution by heavy metals poses a significant threat to ecosystems, particularly to photosynthetic organisms that play a crucial role in sustaining life. Although copper is an essential micronutrient, its elevated concentrations can severely disrupt physiological and biochemical processes in plants. By competing with other essential elements such as iron, zinc, and calcium, copper can interfere with enzymatic activities, disrupt electron transport chains, and induce oxidative stress, leading to cellular damage.

The detrimental effects of Cu^{2+} on photosynthetic organisms are particularly evident in photosystem II, where these ions can interfere with electron flow, alter protein structures, and compromise photochemical efficiency. The inhibition of PSII activity observed in this study suggests that copper ions may target specific binding sites within the complex, affecting both its donor and acceptor sides. Additionally, variations in pH influence the extent of Cu^{2+} toxicity, highlighting the importance of environmental conditions in determining the severity of metal-induced stress.

Understanding the mechanisms by which heavy metals impact PSII provides valuable insights into plant stress responses and adaptation strategies. This knowledge is essential not only for assessing environmental risks but also for developing approaches to mitigate the harmful effects of heavy metal pollution in aquatic and terrestrial ecosystems. Further studies on plant resilience mechanisms may contribute to advancing bioremediation strategies and improving crop tolerance to metal toxicity.

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Mis (Cu^{2+}) ionlarının təsiri ilə fotosistem II-nin inhibirləşməsi

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Tədqiqatda mis ionlarının (Cu^{2+}) fotosistem II-nin (FSII) fotokimyəvi fəallığına inhibitor təsirlərini araşdıraraq, tilakoid membranlarında oksigenin ayrılmasının əhəmiyyətli dərəcədə zəiflədiyi aşkar edilmişdir. Cu^{2+} ($CuSO_4$) ionlarının qatılığının artması ilə FSII fəallığının azalması arasında aydın əlaqə müşahidə edilmiş və bu, metalın fotosintetik funksiyaya zədələyici təsirini vurğulamışdır. Xüsusilə, O_2 ayrılmasının inhibirləşməsi zaman asılılığı nümayiş etdirmişdir: Cu^{2+} ionlarının təsirindən dərhal sonra oksigen ayrılmasının sürətlə 40-60%, daha sonra isə tədricən və davamlı zəifləməsi müşahidə edilmişdir. Bu nəticələr FSII daxilində ən azı bir yüksək affinlikli mis birləşmə saytının mövcud olduğunu və bunun Cu^{2+} ionlarının elektron daşınması və ümumilikdə fotosintez prosesinin səmərəliliyinə mürəkkəb inhibiirləşdirici təsirində iştirak edə biləcəyini göstərir.

Açar sözlər: *Fotosintez, fotosistem II, mis, oksigen ayrılması, gecikən işıq şüalanması*

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